





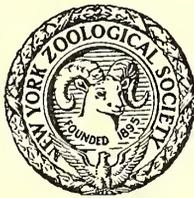




# ZOOLOGICA

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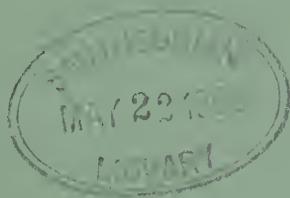
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# Social Behavior of the American Buffalo (*Bison bison bison*)

TOM MCHUGH<sup>1</sup>

*Jackson Hole Biological Research Station, Moran, Wyoming*

(Plates I-III; Text-figure 1)

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## I. INTRODUCTION

THE American buffalo (*Bison bison bison*) not only shaped the life of the Plains Indians but also figured more prominently in American history than any other animal. A vast literature has grown up around the

buffalo, but there is still no adequate scientific study of its social behavior. This paper aims to add to the present limited knowledge in that field and to compare its contents with historical literature.

In the gathering of data on which this paper is based, I observed both free-ranging and confined herds of buffalo through the seasons. Mannerisms and basic behavioral patterns of the animals themselves were noted as well as interactions with other buffalo in the coordination, integration and movement of the herds. Interactions between various herd members were also recorded to determine the type of social organization. The herds were further studied to determine their composition. Reproductive behavior was observed during the rut and the subsequent calving season.

Due to the limitations of space, large sections of data had to be condensed into a few sentences. These conclusions, abrupt as they may seem at times, nevertheless rest on a substantial foundation of repeated observations recorded in field notes.

I have used "buffalo" throughout in preference to "bison" because of common usage. The term "herd" refers to all the buffalo in any one geographic area. Each herd is in turn composed of smaller units called "groups."

## SOURCES OF INFORMATION

*Observations.* Most of the observations reported here were made on three buffalo herds, with additional data gathered from six other herds. The various herds are listed in approximate order of their importance as contributions to this paper in the following discussions of their size, origin, and range:

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Yellowstone National Park: The Yellowstone Park Herd contained approximately 1,360 animals when a census was made by air in 1951. These buffalo inhabit grassland areas which are divided into four main sections by natural barriers of forests and mountains. The four herds remain fairly distinct with only occasional intermingling:

Hayden Valley Herd	440
Lamar Valley Herd	380
Pelican Valley Herd	340
Lower Firehole River Herd	200

The present Yellowstone Park Herd developed from the intermingling of introduced animals with the "native herd." The introduced group was started in 1902 with 18 cows from the Pablo-Allard Herd of Montana and three bulls from the Goodnight Herd of Texas. These increased to 764 by 1925. In the meantime, a decrease in poaching permitted the native herd to grow from a remnant of 22 in 1902 to an estimated 100 to 125 animals by about 1925. Natural intermingling between the native and introduced (Lamar Valley) herds began in the early 1920s and was well developed by 1929.

Remnants of the native herd plus an introduction of 36 animals from the Lamar Herd led to the start of the Hayden Valley Herd in 1936. The Hayden Herd was particularly valuable in this study because it furnished the greatest number of observations and because it was the only "undisturbed" herd studied. It had never been managed by reduction or artificial feeding since its start in 1936. Hayden Valley (Text-fig. 1) is a triangular-shaped, sagebrush-grassland valley of about 36 square miles located with its broad base along the Yellowstone River between Lake and Canyon.

Yellowstone Park herds were observed during periods from March through November, 1951; in January and August, 1952; and in March, July, August and November, 1953.

Systematic observations in Hayden Valley were possible only from May through October or November. Inaccessibility at other times was due to snow cover and the closing of all park roads. One trip was nevertheless made into Hayden Valley in March, 1953, in two snowplanes. The Lamar Herd was followed during the winter months from November to May. Access to this herd is possible by a road which is kept open throughout the year.

Jackson Hole Wildlife Park: The herd in the Jackson Hole Wildlife Park at Moran, Wyoming, was composed of 22 animals in 1951. About the same number was maintained in later years by

removal of surplus buffalo. The herd was kept in the fenced "Display Area" of 133 acres from June to September. Tourists drove through this area to observe and at times disturbed the animals. The buffalo were moved into a fenced "Winter Area" of 380 acres from approximately September to June. Hay and prepared concentrated stock feed were provided from September or October through part of May—a period when available natural forage was scarce or buried under as much as four feet of snow. This Wildlife Park Herd was established in 1948 with 20 animals brought in from the Lamar Herd of Yellowstone Park. Observations were made during periods from February through November, 1951; in February and May, 1952; and in March and November, 1953.

Wind Cave National Park: The Wind Cave Herd of approximately 500 animals was enclosed in a fenced area of 28,056 acres near Hot Springs, South Dakota. U. S. Route 85A passes through part of the park. The original 14 animals were shipped from the New York Zoological Park. Observations on this herd were made during periods from May through August, 1952, and from June through October, 1953.

Approximately 350 buffalo were observed in the Wichita Mountains Wildlife Refuge near Cache, Oklahoma, during July and August, 1953. The herd was kept in a fenced area of 54 square miles. It developed from 15 animals originally shipped from the New York Zoological Park.

The 700 buffalo in the Crow Indian Reservation live on 34,000 acres of grassland at an elevation of 6,000-7,000 feet in the foothills of the Big Horn Mountains of Montana. They are enclosed by one mile of heavy log fence and the precipitous cliffs adjoining the canyon of the Big Horn River. The Forest and Range Division of the Indian Service manages the herd for the benefit of the Crow tribe. The herd originated from buffalo shipped from Yellowstone National Park (Lamar) and the National Bison Range. It was observed during periods in August and September, 1953.

Additional incidental observations were made on herds in the following four areas: National Bison Range at Moiese, Montana; Custer State Park at Hermosa, South Dakota; R. B. Marquiss' Little Buffalo Ranch near Gillette, Wyoming; and Fort Niobrara National Wildlife Refuge near Valentine, Nebraska.

*Literature.* The amount of historical literature on buffalo exceeds that of scientific treatises. This is because the pioneers in the West were virtually the only observers before the millions of buffalo on the Great Plains were slaughtered.

Such historical material contains many casual observations on behavior and can at times be very useful but can also be most misleading if not carefully evaluated. I have cited pertinent historical evidence in this paper, regarding it as supplementary to actual observations and not necessarily of great scientific value.

#### METHODS

*Observations.* Stalking under cover was used most often in approaching the herds in Hayden Valley and occasionally in other areas. Several devices aided observations. An automobile was used either as a blind or as a convenient and maneuverable base in Wind Cave, the Wichita Refuge, the Wildlife Park, the National Bison Range and the Crow Reservation. In winter in the Wildlife Park a canvas blind was used for warmth and concealment. Two platforms in trees about 15 feet from the ground facilitated viewing aggressions of buffalo feeding on hay.

Most observations were made with the aid of  $7 \times 50$  binoculars or a 27 to 60 power spotting scope. Telephoto lenses up to a focal length of 16 inches were used to record various activities on 16 mm. motion picture film. Later analysis of the film in a viewer supplemented the original observations.

Movements of herds were noted on mimeographed maps of Hayden Valley, the Wildlife Park, Wind Cave and the Wichita Refuge. A hand counter was used at times to make a census of herds.

*Identification of individual buffalo.* Natural differences in the physical features of the various animals in a herd served to distinguish them as individuals. All of the 16 animals of the Wildlife Park Herd were identified by sight in this fashion. Identification of individuals in other herds was more difficult because more animals were involved. Individuals were often followed during a continuous daily observation but were seldom traced from day to day.

Damaged or misshapen horns were the surest features for identifying individuals in large herds over long periods of time. Even the slight natural variations in horns served to identify individuals in the small, confined Wildlife Park; the main characters of horn structure in six mature cows were still obvious after a two-year lapse in observations. The different positions of ear tags on these animals served as a further absolute check on identity.

Natural distinctions between young animals of the Wildlife Park Herd were occasionally inadequate for individual recognition, making supplementary marking with white paint necessary.

Two methods were used to mark six calves, two yearling heifers and a pair of two-year-old heifers.

In the first, arrows were fitted with rubber balls covered with layers of absorbent cloth. The ball was dipped in paint and fired at the buffalo from distances of 50 to 100 feet. The herd became irritable after one or two animals were marked and soon stampeded away.

In the second technique, hay was used to lure the buffalo close to the slatted doors of a shed. A stick was tipped with absorbent cloth which was dipped in paint and thrust between the slats to daub different patterns on their heads. This method was simpler and quicker than the bow and arrow but could be used only during periods when no natural food was available.

*Aging of buffalo.* Ages of buffalo were estimated by techniques considered adequate for the purposes of this paper. These were largely an expansion of the methods described by Hornaday (1889). Further refinement of technique would be desirable for detailed population studies. Much additional research could well be done on herds where ages are accurately known and easily determined from brands on all animals. This condition applies in the National Bison Range and the Wichita Mountains Wildlife Refuge. Such brands are difficult or impossible to read in winter because of concealment by thicker fur. Variations in the location and scarring of these brands are also helpful in identifying individuals.

As with cattle (Pope, 1919), the age of buffalo may be estimated by the development and subsequent wear of the permanent incisor teeth on the lower jaw. Age up to and including five years is estimated by the appearance of each pair of incisors. Beyond five years the age is approximated by the levelling or wear on the incisors. The correlation with cattle is similar but was not determined exactly.

Age may also be estimated by counting the number of growth rings on the horns, but any determination based on the number of rings should be increased by approximately three years to allow for the juvenile period when no obvious rings are formed. An alternate method is to estimate the amount of horn growth in this period by comparison with the horn of a known three-year-old. Aging by such rings can be only an estimate.

Most determinations of age for the purposes of this paper were reached by a visual examination of the physical features of the buffalo, chiefly the size and shape of the horns. Bulls were aged accurately up to five or six years and

approximately up to about fourteen years. Cows were aged accurately up to three years.

Plate I, Figures 1 & 2, demonstrate the technique of aging by size and shape of horns more completely than any written description. Aging was most easily accomplished when the horns were viewed head-on and was more difficult in profile views. Complementing the horns as indicators of age were several other physical features of the buffalo. These included relative size, profile of the body and head, size of the hump and the amount of hair on the crown, forehead and forelegs. The size of the chin "bell" was a helpful indicator that was sometimes indefinite since some animals wore it off in grazing.

#### ACKNOWLEDGMENTS

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## II. FUNDAMENTALS OF BEHAVIOR

### STANCES

Loafing positions of the buffalo included standing, lying flat on the side with legs and head outstretched on the ground and lying on the belly with legs tucked under or alongside. In the latter pose the head was sometimes rested on the ground. The eyes were partially or completely closed at times in all of these positions.

Attitudes of "fear" were reactions to disturbance by strange objects, usually human beings. The buffalo stopped and stared for several seconds with ears brought forward and head directed toward the disturbance. This happened before running away or midway in the retreat. In a more accentuated *alarm position*, the head was raised above the level of the hump.

Another stance involved the positions of the tail. Switching of the tail back and forth flushed insects from the rear of the buffalo. Yet frequent tail-switching also occurred in a variety of situations when there was no apparent function of insect removal. It was prominent during playful battles and other types of play such as chasing and bounding. Elevation and switching of the tail also occurred during the violent battles of the rut. Tail-switching was general during nursing, more frequently by the calf than by the cow. It was seen among calves during herd movements when they were hesitating between staying with the calf subgroup or moving on with the cows. It was observed in a cow as she resisted each approach of a tending bull. Tail-switching may have been a "displacement activity" (Tinbergen, 1952:24-6), particularly in the latter two cases.

The tail was raised and stiffly held 0° to 90° above the horizontal—most frequently at least 45°—during the following circumstances: (1) In some trotting, running or bounding, such as during playful chases, stampedes and short charges; (2) While moving toward or investigating unfamiliar objects, such as the vulva of a cow, a new bull or bull group, a new calf, human beings and a dead buffalo; (3) During moments of tenseness or excitement, such as moving through the herd in rut, before each attempted mount, "mock battles" (Section VI), disturbance from human beings, pauses in or before battles, play, anger and irritation.

In the stance of *bucking*, the buffalo kicked its legs up or out to the side. Bucking usually involved the hind legs, singly or together. It occurred frequently during play.

*Arched back* involved the humping of the back up into an arc. Bulls arched their backs during vicious battles, during some "mock battles" (Section VI) and while walking among the rutting herd or, more typically, in a bull subgroup during the rut. Arched backs during the last two occasions were usually accompanied by tail lifting and bellowing.

#### GROOMING BEHAVIOR

Buffalo commonly rubbed their heads, necks and sometimes their sides on stumps, large low branches and trunks of trees. They also occasionally used smaller bushy pine trees, pine branches, boulders, sage-brush bushes, earth and earthen banks and snow banks. On trees, rubbing smoothed but did not remove the bark, although persistent rubbing could conceivably wear through the bark. Rubbing trees removed tufts of shed winter fur, yet this was not the sole purpose of rubbing since it occurred during all seasons.

In addition to rubbing against trees, buffalo often *horned* lodgepole pine by stripping bark with the ends of their horns. The *horning* was sometimes accompanied by eating of bark and rubbing. Buffalo preferred *horning* the bark or branches of previously *horned* trees rather than starting on fresh material. Most *horning* occurred during the rut (Section VI).

Buffalo *wallowing* usually consisted of one to three actions: a sniffing of the ground, a preliminary pawing, followed by rolling on the ground. Although the first two actions were sometimes omitted, rolling never was. In rolling, the buffalo lay down on one side and then kicked the legs so as to roll onto the back. Buffalo were never seen to roll completely over. The action of the legs, particularly the forelegs, and the rolling of the body stirred up much dust. Wallowing was preceded or followed by *horning* or rubbing the head in the earth, and a type of "neck-crooking" where the neck was stretched and flexed and the horns occasionally scratched against the back. Some buffalo wallowed once on one side, stood, then wallowed on the other side. One or two rolls as an incomplete wallow sometimes preceded the arising of a lying buffalo. Most wallowing was done in places where previous wallowing had broken the sod. Such wallows were scattered thickly over the entire range, as noted by aerial survey. Buffalo also wallowed in eroded or other natural bare areas, on prairie dog mounds, in wet mud holes, occasionally on snow and during the rut on any area. Wallowing among calves, first seen at the age of 13 days, lacked the skill of adult wallowing for at least the first month. The calves lay down and stretched or raised their

legs slightly but did not roll thoroughly. Although both sexes wallowed during all seasons, wallowing was most noticeable among bulls during the rut (Section VI).

I was not able to correlate rubbing or wallowing with the peak of concentration of mosquitos or black flies in Hayden Valley. The correlation of other authors (Garretson, 1938: 34; Goodwin, 1939: 367; Hornaday, 1889: 413; Roe, 1951: 100; Soper, 1941: 385-6, 394) may have been genuine or may have been confused with the increase in wallowing among bulls during the rut.

#### FEEDING BEHAVIOR

Buffalo grazed most commonly in meadows but also in open lodgepole pine and aspen to some extent. Browsing was infrequent.

The Wildlife Park Herd fed on aspen bark only rarely. Buffalo in the Crow Reservation barked aspen extensively only during one severe winter when the range was depleted. Both cows and bulls in the Wildlife Park and Hayden Valley infrequently stripped and ate bark from lodgepole pine at all seasons.

When there was a thin snow cover of only a few inches, buffalo clipped off the exposed forage within one inch of the snow. In deeper snow, the buffalo pushed their noses into the snow and then cleared a trench down to the forage by swinging the head. The side of the head and even the neck were used to clear very deep snow. Pawing with either front hoof aided this nosing only infrequently. Considerable feeding by nosing snow resulted in shortened hair around the mouth and crusted snow conditions produced raw noses. Buffalo fed by these techniques in snow up to four feet deep, leaving large pits as evidence of their work.

Buffalo went to water at least once each day in all herds observed. Water in these areas was always rather accessible in springs, streams, lakes or rain-flooded puddles. The Wind Cave Herd sometimes stayed near water for one or more days when watering holes were scarce. The Superintendent of the National Bison Range found that the most heavily grazed areas were near water holes and the most lightly used areas away from water. He established new water holes to effect more even use of the range.

When water holes froze in the winter, buffalo ate snow. If both snow and open water were available, however, they preferred water. When ice covered small puddles, they broke through with their noses or front hooves. They had no aversion to drinking the very brackish water found in stagnant pools.

Both the Wind Cave and Wildlife Park Herds regularly visited the salt blocks that were put out for them. Other herds occasionally ate the mud from natural salt licks.

#### VOCALIZATIONS

Observations on several herds showed that vocal expression consisted mostly of grunting and some snorting and sneezing sounds. The variation in grunts was extensive, difficult to describe, and was correlated with a variety of responses from other buffalo. The frequency of grunting increased during group movements, such as stampedes or direct movements, and was noticeable when the Wildlife Park Herd was temporarily split by a fence.

During feeding on hay, the dominant cow in the Wildlife Park frequently uttered *threat grunts* as she advanced on nearby buffalo. These subordinate animals yielded to her. She also gave the threat grunt when other buffalo or human beings approached within a few feet of her new calf. This threat grunt was quite similar to the usual buffalo grunt, such as the one she used to call her calf. Threat grunts were also heard from one bull in the Wildlife Park and two others in Yellowstone Park. They would be noticed in wild herds only under ideal conditions of close observation.

During periods of intense play, buffalo infrequently uttered a loud short sneeze, a loud belching snort, or a bellow-like grunt. Calves or juveniles who were hit by the full force of a charge from another buffalo uttered a loud screaming or bellowing grunt. Buffalo ground their teeth together to produce a squeaking noise. Waving of hands stimulated this from cows enclosed in a small corral in the Lamar Valley. Bellowing and snorting will be discussed later (Section VI).

#### RECEPTION

Buffalo apparently relied most on an acute sense of smell for detecting danger, raising their heads to test the air when new odors drifted in. Whenever scenting human beings, the Hayden Herd stampeded without hesitation even though the source of scent was not visible. They reacted to scent carried at least one mile, but Inman (1899: 246) stretched this distance to four miles. Two authors stated that buffalo scented water when it was "five miles or more" away (Garretson, 1938: 46) or "miles distant" (Inman, 1899: 247).

Vision was evidently not as acute nor relied upon as much as scent. It should not be underestimated, however. Buffalo in the Crow Reserva-

tion spotted our moving jeeps when they were more than a mile distant. Buffalo in the National Bison Range paid no attention to horses yet became restless as soon as they spotted a horse and rider. One herd immediately became restless when a horse and rider appeared on the skyline 0.8 mile distant (oral comment from Supt. John Schwartz). The Hayden Herd paid little attention to people walking more than 0.5 to 0.8 mile from them if neither noise nor scent were detected. They would become alarmed by a closer approach. Closer approach often went undetected, however, if there was no movement or slight camouflage from sagebrush or tree shadows. Sometimes the buffalo would momentarily stare, only to start grazing again. Small groups of buffalo were stalked in open view by moving only when all were grazing or facing away and by "freezing" whenever any animal looked up.

#### PLAY

Play among buffalo consisted of battling, mounting, *frolicking*, or, more generally, a combination of these. Bucking was quite typical of all play. From an anthropomorphic viewpoint, these activities were assumed to be pleasurable and non-utilitarian, two features discussed by Beach (1945: 524) as characteristics of playful behavior. This play also fitted the description given by other authors. Schein & Fohrman (1955) stated that playing in cattle "is an activity engaged in solely for the sake of the activity itself and not for the normal end result of the activity." Thus, battles among buffalo would occur for the sake of the battle itself and without the emotion of competition over a specific object. Mountings occurred without the specific emotion of a sexual drive. Racing occurred without the specific emotion of fleeing from an enemy or reaching a goal. Such reasoning makes a satisfactory hypothesis for play, yet the actual recognition of these activities in the wild is often virtually impossible without relying on a subjective interpretation.

Numerous observations revealed that play was most frequent among calves, frequent among yearlings, common among two-year-olds, and occasional in older buffalo. There was more play—chiefly battling—among bulls than among cows in the group two to three or more years old. Most play occurred during the period of evening dusk. Play was also common during direct and semi-direct group movements (including stampedes) and just after feeding, particularly in the Wildlife Park. (Play occurring during dusk may have followed feeding, but the weaker light was adjudged to be a more important stimulus than

removal of hunger since the period of evening play was more intense than that after any diurnal feeding period.)

Buffalo battled in play by butting and twisting their crowns together or by hooking horns with some pushing back and forth or circling. Calves butted their small horns against the opponent's shoulder, neck or head (Plate II, Figure 3). Many battles were started when one opponent approached another, shaking its head or bucking up and down on its front legs. Pairs of yearlings and calves "shadow-butted" by facing each other with heads low and then quickly shifting sideways so that each "butted" the space his opponent had just vacated. Since battles occurred between a variety of sexes and ages, many opponents were unevenly matched, yet viciousness or severe routs were rare. The latter two qualities characterized battles that were not considered play (Section VI). Occasional battles involved just one buffalo who butted a trunk of a tree or a springy sapling that "fought back."

Mounting as play occurred without regard to sex, age or dominance. It consisted either of attempted mounting where the chin was placed on the partner's rump or of complete mounting where the buffalo clasped its forelegs around the flanks of its partner and rode for several seconds (Plate II, Figure 4). Attempted mounting was sometimes a complete act with no intention shown of proceeding further. Unsheathing of the penis or thrusting actions were very rare. Mounting among calves was first noted when a 15-day-old calf made three feeble and unsuccessful attempts. A 20-day-old calf mounted another for four seconds. Such mounting during play was probably not based specifically on sexual motivation (Carpenter, 1942: 198; Nissen, 1951: 439).

Mounting and battling were often coupled in play as one frequently initiated or followed the other.

Frolicking included the aimless racing of one or several animals, playful stampedes and "race-and-hide." Most aimless racing was done in the bounding or galloping gaits as one animal or small groups dashed back and forth, in circles, among the group, or in short charges. The bounding of one animal away from the group usually resulted in the quick following of another and then the aimless racing of the pair. Some juveniles raced in these games for so many minutes that they finished with tongues hanging out and panting heavily. Calves as young as one day trotted, ran or bounded in 15-50 foot circles from their mothers. Some racing took the form of playful stampedes as the entire group or

subgroup dashed aimlessly about. In still another form of racing, *race-and-hide*, single animals galloped for some distance and then abruptly lay down. The pattern sometimes repeated, and there were indications that some animals lay down near certain other individuals.

Grooming behavior—mainly wallowing with occasional rubbing—occurred so commonly with play that it should be considered an accessory to play or sometimes a form of play itself.

#### INVESTIGATIVE BEHAVIOR PATTERNS

Curiosity was well developed in buffalo. They thoroughly investigated new or strange objects such as an observation platform, recently shed elk antlers, a skeleton, horses, a porcupine, prairie dogs, and a human being lying or sitting after the buffalo were used to seeing him standing. Juveniles were more curious than adults. Herd members moved in to investigate, sniff and lick new calves. Older calves were particularly curious about new calves.

*Exploring* further manifested the development of curiosity. It was uncommon and restricted mainly to the Wildlife Park Herd. Subgroups moved several hundred feet away from the main herd to investigate various objects and then returned. Entire herds also explored. This exploring may have been a type of play since it was often accompanied by activities discussed previously as play.

In earlier times, investigative behavior may have played a part in the creation of what hunters called a *stand* at which entire herds were slaughtered by methodical shooting from under cover. There are numerous historical references to this (Allen, 1876: 212; Dodge, 1877: 135-7; Garretson, 1938: 44, 116-7; Hornaday, 1889: 466-9, 1922: 143; Inman, 1899: 261-2; Mayer, 1934, II: 36-7; *et al.*).

Three instances of shooting in present day herds are of interest in this connection. Rangers in Yellowstone Park successively shot all seven members of a cow group and another bull group by approaching so the buffalo could neither see nor smell them. The groups did not stampede away when their members started to drop. Some cows in the cow group started to walk gradually away, but the motion was slow and without panic. When a hunter in the Crow Reservation shot from cover, the buffalo did not run away but milled around and sniffed the first slaughtered animal. Mr. Q. Marquiss killed 20 animals each year in his herd of 150 by driving up to it and shooting the desired animals one by one. The herd was not afraid of cars or human beings and did not run away during the shooting, remaining instead to mill about the dead buffalo.

In discussing stands such as these, several authors mentioned the attraction of buffalo to dead animals or blood. Mayer (1934, II: 36) stated, "... they would begin what we call 'milling.' They would nervously smell the wounded animal, then hook her with their horns, then smell her again, bewildered . . ." Hornaday (1889: 476) noted that "They cluster around the fallen ones, sniff at the warm blood . . ." Allen (1876: 212) told how "The hunter must drive away the stupid creatures to prevent the living from playfully goring the dead!" Dodge (1877: 135-6) mentioned how "Attracted by the blood they collect about the wounded buffalo."

Similar incidents in present-day herds are interesting. Buffalo milled around and sniffed the spot where an elk calf was born. Another herd milled about, looked at and sniffed the carcass of an old bull killed in battle. Butchering of buffalo in the Wildlife Park was twice impeded by the herd, which pressed close to sniff and lick the viscera and carcass. During one of these butchering, the two older bulls pawed the snow and engaged in a vicious battle. Buffalo in the Lamar Herd mauled and gored a dead mature elk. If Mr. Q. Marquiss' slaughterers did not immediately move in to each killed buffalo, the herd milled about and horned it. When buffalo were killed from cover in the Crow Reservation, the group remained about and sniffed the carcasses. The grass in the National Bison Range surrounding a buffalo carcass was very well trampled. All buffalo sniffed another area where blood was spilled on the ground. Bulls pawed, rolled in and horned this spot.

#### CHARGING

Buffalo are potentially dangerous animals and should always be approached with caution. On six occasions I was faced with situations in which danger was latent, and was charged at five other times. Each charge was a bluff, ending with the buffalo stopping a few feet distant. There is no reason to believe that this would be a constant pattern, however.

### III. HERD COORDINATION, INTEGRATION AND MOVEMENT

#### LOCOMOTION

*Gaits.* Buffalo progress by means of four different gaits, *walking*, *trotting*, *galloping* and *bounding*. The detailed description of gaits in various animals was pioneered by Muybridge (1907), who analyzed them with a series of photographs. I have relied heavily on his work, using his definitions combined with my own observa-

tion and analysis of motion picture film of moving buffalo.

The descriptions of the four gaits are dependent upon a few definitions: The *step* of a moving buffalo is an act of raising, thrusting and returning one hoof to the ground so that it can reassume the complete or partial support of the body. The normal *stride* of a buffalo consists of a sequence of four steps as each hoof is lifted and again placed on the ground. For brevity, the sequence of steps is listed by the number of each hoof, according to the following system:

1. Left anterior
2. Right anterior
3. Left posterior
4. Right posterior

In walking, the sequence of hoof movements is 3, 1, 4, 2. This was a standard sequence for all quadrupeds investigated by Muybridge. The support during each stride of an average walk falls on two or three hooves. The slowest walk, such as the "hesitant gait" of bulls during the rut, involves the movement of only one hoof at a time so that the support during each stride falls on three or four hooves. In the fastest walk, an *amble*, the buffalo supports its weight alternately on one hoof and then two hooves.

Trotting is the next faster gait in buffalo. The sequence for limb movements is 1-4, 2-3 with each diagonal pair of limbs moved more or less simultaneously. During each stride, the buffalo advances twice with all four feet off the ground.

Gallop or *running* is the most rapid gait. The sequence here is 1, 2, 3, 4, making the type of gallop of buffalo a "transverse gallop." Other animals showing this same type are horse, goat, cat, bear, raccoon and hog (Muybridge, 1907: 156), in contrast to a lesser number of animals showing the "rotary gallop" (1, 2, 4, 3). Some slower speeds of galloping in buffalo show a forward-backward rocking motion.

Bounding is a less commonly seen gait in which the buffalo springs ahead by the more or less simultaneous flexing of all four legs. It is similar to bounding in mule deer. This bounding type of gait was observed mainly under two conditions. It was frequent during periods of play, accompanying such actions as battling, butting, mounting, frolicking and bucking (Section II). Buffalo often bounded in their playful chases or races and it was first seen among calves at an age of two months. Buffalo also bounded when frightened or suddenly surprised. The approach of a human being, especially if abrupt, resulted in the fleeing buffalo using this gait. The animal characteristically stopped at a distance of 20 to 100 feet, looked back, and then continued in a walk, trot or gallop.

*Speed.* Herds of buffalo chased by a jeep in the Crow Reservation maintained a steady speed of 30 miles an hour. The jeep could not go faster over the uneven ground of these meadows, and on one occasion a group spurred from behind and passed jeep, travelling at about 35 miles an hour.

Cottam & Williams (1943) measured the speed of a three-year-old bull on level ground as 30 miles an hour and stated that older and younger animals were slower. Howell (1944) timed the top speed of a two- or three-year-old buffalo at 32 miles an hour.

Buffalo generally increased their speed on downhill sections of a path when proceeding steadily and directly toward some goal, such as water or food, or when stampeding. If the group was walking at the time, they trotted or galloped downhill and for a short distance out onto the level. If galloping, they increased their pace still more.

Buffalo moving toward a goal sometimes increased their speed as they neared their destination. This happened with animals returning to a herd after being temporarily separated and with those joining new herds. It also occurred in groups moving toward water or food.

*Trails.* The trails of buffalo have been described in a glowing and often exaggerated fashion. Garretson (1938: 57) states that "The buffalo was the best natural engineer the world has ever known . . ." Hornaday (1889: 417) believes that "The trail of a herd . . . is usually as good a piece of engineering as could be executed by the best railway surveyor . . ."

The more reserved opinions of Allen and Dodge better describe the extensive system of trails which I saw in Hayden Valley. Allen (1876: 63) says: ". . . a buffalo trail can be depended upon as affording the most feasible road possible through the region it traverses." Dodge points out that ". . . though a well-defined buffalo trail may not be a good wagon road, one may rest well assured that it is the best route to be had."

The extensive network of trails in Hayden Valley included good routes from any one section of the valley to any other. The trails were almost invariably the most practical routes available, but they were not necessarily the best engineered routes. Main trails traversed rolling country with a minimum of wasted climbing. They cut through corners of timber for a more direct path. They veered around the edge of marshy areas containing quicksand. Fords of streams and creeks had gradual approaches and

shallow water. Direct approaches were made to the only feasible crossings of an almost impassable canyon. Trails cut about one-half mile through large areas of timber in a fairly direct line from one meadow to another.

The buffalo took a gradual route up hills if such a route was essentially direct, but they had no aversion to steep climbs. If there was a choice between a longer, more gradual incline and a shorter route through a steep-walled ravine, the buffalo took the latter. The route over the Mary Lake Divide was so steep that a horse with rider could negotiate it only by following a series of switchbacks superposed on the buffalo trail.

The only impractical choice of route by the buffalo that I observed occurred on the trail over the southern divide in Hayden Valley. An 1,800-foot section of this was very difficult to traverse because of fallen timber. Another side trail, seldom used by the buffalo, was 700 feet longer but completely avoided the tangle of fallen timber.

Trails through timber had many shunts and were occasionally hard to detect. Trails through meadows were usually more clear-cut and easily followed, although seldom-used trails sometimes disappeared in large meadows.

Buffalo sometimes started new trails from eight inches to several feet to the side of the old ones. These were started under the following conditions: (1) Trails on hills became trampled and eroded to considerable depth. Erosion in particular produced a trail that was deep yet very narrow, and thus difficult to walk in. Similar narrow trails also occurred in soft, marshy areas. When these trails became deeper than about one foot, the buffalo started new parallel paths. (2) Trails pushed through areas with thin topsoil over a rocky subsoil soon eroded down to the rocks. Such rocky trails were abandoned for new parallel routes.

Buffalo can at times wear down trails with surprising speed. On one occasion when the soil was muddy, 265 buffalo passed over one trail and thereby cut it one-half to two inches deeper and from 12 to 15 inches wide on this single trip. Buffalo soon trampled a path through rotten logs lying across trails, yet large, recently fallen logs were either crossed or bypassed.

*Maneuvering in snow.* Snow accumulated in Hayden Valley to a depth up to four feet in the ravines, level meadows and forests but was largely blown or melted from the ridges and some south-facing hills. The buffalo spent most of their time on such bare or near-bare areas and also on thermal areas, where the snow was melted by the heat of the ground.

They showed a distinct aversion to travelling through deep snow. A group of five bulls chased by a snow plane refused to go into the deeper snow of a ravine; a bull dashed six feet in front of the plane to take the shortest route to a bare spot. In summer the buffalo in Hayden Valley characteristically took flight when the observer was 1,000 feet distant, yet they were not this way in winter. In one case a group of 26 cows rushed through snow six inches deep within 30 to 50 feet of the author rather than move through snow farther away that was one to two feet deep. One bull galloped through the cold, shallow water of a stream rather than plunge through snow two or more feet deep on the surrounding ground.

A complex system of well-packed trails through deep snow connected the ridge tops so that the buffalo could move almost anywhere in the valley without plunging into deep snow. The warm water of Alum Creek melted snow for one to two feet along the bank and this bare area was used as a trail. In making new trails, the buffalo tended to follow in the hoofprints of the leader, but older trails lost most of this pitted pattern. Buffalo headed directly toward the proper trail when leaving a bare area, suggesting that they were well aware of the system of trails.

Although the buffalo avoided plunging into unbroken snow whenever possible, they were still able to negotiate deep snow. When an airplane frightened a group of 25 in Hayden Valley, they blindly ran off a bare spot over a cornice twenty feet deep. The group floundered badly, and one buffalo even clambered over the back of another. They still plodded through. In another case, two bulls struggled through snow four feet deep. The lead bull broke trail by climbing up on the snow with his front feet and then plunging down. Travel was very slow and was interrupted with frequent periods of rest of a minute or so. On another occasion, a cow group of 30 moved single file or occasionally two abreast for 4,000 feet across unbroken snow 40 inches deep in a large meadow. The extremely slow speed of the cows under such conditions would allow Indians to approach closely and slaughter them, as recorded by Catlin (1876, I: 253) and Seton (1929, I: 271). In March, 1945, rangers trailed a group of 54 buffalo that moved six miles through snow 42 inches deep from the Nez Perce meadows to Violet Springs in Hayden Valley (recorded by Chief Park Naturalist David Condon).

*Swimming.* Buffalo seldom hesitated to enter water yet were usually hesitant about crossing swift, deep streams. When the Wind Cave or Wichita Herds waded out to drink in a lake,

occasional animals swam out into deeper water. Buffalo in the Wichita Refuge also swam across ponds in their movements even though wading or walking around them would have added little extra travel. Buffalo in Yellowstone Park regularly waded and swam the flood-swollen Lamar River in spring.

#### COORDINATION DURING MOVEMENTS

*Leadership.* Leadership during travels of a herd was apparent when one or a small group of animals initiated or directed the movement, usually from in front of the herd. Leadership during movements of the confined Wildlife Park Herd of 16 buffalo is tabulated in Table 1. Three cows accounted for 66% of the leadership, with no cow acting as the exclusive leader. All individuals led the herd at least once, and leadership sometimes varied during each movement. Frequent changes in leaders also occurred in free-ranging herds.

TABLE 1. LEADERSHIP DURING 43 MOVEMENTS OF THE HERD OF 16 BUFFALO IN THE WILDLIFE PARK

Cow	% of trips in lead in herd	Age	Position of dominance in hierarchy among cows (from Table 4)
F3	27%	7	Third
F1	23%	5	First
F6	16%	4	Sixth

Highest percentage for any remaining herd member was 7%.

Leadership depended upon cooperation. The lead buffalo characteristically looked back to see if the rest of the group was following and usually advanced alone no more than about 100 feet. In the occasional cases where the group balked and did not follow, the leader either turned back to become a follower or waited several minutes until some individuals began to follow.

During situations of disturbance by human beings, one animal was able to initiate movement in the entire group by moving in one direction in a steady walk. Leadership under such conditions was not balked.

Leadership was not readily detectable in many group movements, particularly during grazing. This mass-action type of travel, where the group moved as one unit without any obvious leader, seemed to be based on several factors. Contagious behavior was important and especially noticeable when all animals were facing in the same direction and moving at the same rate.

Dominant animals in the center or rear of the group seemed to direct the procession by moving all subordinates ahead of them. The leader or leaders were not conspicuous because of the close coordination of their actions with the mass of the group. Movement was also based on a high degree of cohesiveness within the group. The advance of a group of buffalo from the main herd was more apt to result in the remainder following and joining than in separation into two or more groups or the return of the first group. Large groups of 100 or more sometimes moved by the successive and repeated closing of gaps between subgroups. Some movements were so random that leadership probably never existed.

*Stampedes.* Stampedes involved the sudden and usually simultaneous trotting or, more typically, galloping of a group of buffalo. Clouds of dust rose up around and sometimes completely enveloped the stampeding group. The noise of a stampede resembled a continuous rumble, the rush of wind, or the rain-like patter of hooves. Stampedes through timber were characterized by the very clamorous breaking of branches and hitting of hooves against fallen trees.

The following notes on stampedes are based on numerous observations in all herds studied. In addition, I spent thirteen days in the Crow Reservation in Montana with the express purpose of starting and filming as many buffalo stampedes as possible. During the latter part of this period stampedes were started by parties of hunters who chased the buffalo in jeeps to carry out the annual program of herd reduction.

Stampedes were started by the sudden trotting or galloping of one or a group of buffalo, with the herd usually taking the direction of the first group. Some stampedes started so abruptly that the initiating group was not evident.

Stampedes were often caused by the disturbance of a wary group. They also occurred in all herds for reasons of seemingly insignificant importance.

For example, stampedes were started by the sudden running of one animal which voluntarily decided to join the group from the outskirts or which was scared by a sudden snap of a twig. Subgroups stampeded to rejoin the main group when there was no apparent reason for such a burst of speed. The sudden flight of elk, deer or a pair of mallards near the herd caused the buffalo to stampede in the same direction, even though they may never have seen the reason for the flight. Such stampedes as these, covering only a few hundred feet, were shorter than those result-

ing from the approach of human beings toward a wary herd.

At the start of a stampede, all the buffalo in the area usually massed together quickly and then galloped away. After this initial burst, the herd either stopped and looked or continued moving. The continuation of the stampede was made at a gallop, a trot or a fast walk. The same massed pattern was held, or, more commonly, the herd strung out as a column of groups, a long continuous column or single file.

Stampedes initiated by the presence of human beings, were not a blind fleeing from the disturbance. Rather, the path of these stampedes was regulated mainly by the end-point, which was usually a small timber-secluded meadow or timber itself.

One stampede observed in the National Bison Range was, however, quite directionless. A severe hailstorm in August, 1954, completely covered the ground with stones up to half an inch in diameter. A group of 150 buffalo was loosely spread out into many smaller subgroups when the storm arrived. They quickly massed and then galloped at intervals in an aimless fashion. Despite rather frequent stampeding, they circled in no more than a quarter square mile. Playful stampedes observed in the Wildlife Park were also rather directionless.

Three incidents were observed where animals fell under the herd during a stampede. The first occurrence was observed by Gordon Powers when a motion picture company was attempting to film a stampede in the Crow Reservation. Stationary lines of vehicles and of men were supposed to funnel the herd past the camera. As a group of jeeps started to drive the herd of 400, the buffalo headed directly for the line of men. When they were only 50 feet away, the four lead animals suddenly turned back. They were trampled under the rest of the herd, which could not turn so abruptly. None was killed, but one animal walked away stiffly as though badly bruised. A similar incident occurred when a stampeding herd suddenly caught sight of a group of hunters in the Crow Reservation. Three lead animals were trampled as they turned abruptly. In another case, a buffalo fell in front of a stampeding herd. Other animals jumped over or passed by this buffalo as it made one complete roll and got up again.

*Wariness.* Wariness varied greatly in different herds. The Wildlife Park herd was in constant contact with people and would allow approach within three to five feet. The Wind Cave animals allowed approach of cars or people within 25

feet. The Wichita herd tolerated the approach of cars within five feet or less but persons could approach only to within 30 feet. Disturbance by cars or people caused the herds to move no more than a few feet. Buffalo in the National Bison Range permitted the gradual approach of cars to within five feet or less, yet would usually stampede away if the occupants got out.

Further discussion of wariness hinges on a definition of *flight distance*. It is here defined as the distance between an approaching disturbance and the herd, measured at the time when the herd takes flight.

The Crow and Hayden Herds had little contact with human beings. Either herd stampeded several miles when disturbed by cars or people. The flight distance for the Crow Herd was one mile or more on some occasions. It lessened, however, after the fifth day of chasing and hunting. This herd used to be relatively tame and allowed approach of people to within 15 to 50 feet. Gordon Powers of the Bureau of Indian Affairs noted that the herd grew progressively wilder in the past seven years as jeeps were used to chase and hunt it. Flight distance varied seasonally in the Hayden Herd. In the summer it was 1,000 to 1,500 feet, and the herd would also move away upon catching human scent. In November, when there was no snow, the flight distance was 300 to 600 feet and the retreat of the herd was slower and covered less distance than in summer. It was still less in winter, sometimes as low as 200 feet. The herd was slower in starting to move away, particularly if on a bare spot surrounded by deeper snow.

Other herds in Yellowstone Park were less wary than the Hayden Herd. Both the Lamar and Firehole River Herds had more contact with cars or people and also had shorter flight distances than the Hayden Herd.

Historical literature shows instances of wild or wary herds (Audubon & Bachman, 1849: 47; Catlin, 1876, I: 254-5; Parkman, 1903: 91-2, 404-5; Long, 1905, XV: 255-6, XVI: 140, 288; Hornaday, 1889: 536; Inman, 1899: 57; and Roe, 1951: 131-8). There are also records of relatively tame or unwary herds (Dodge, 1877: 120-1 and 1885: 283; Hornaday, 1889: 389, 404-5, 465, 471; Long, 1905, XVI: 153; Parkman, 1903: 423-5; and Roe, 1951: 131-8). The herds became notably wilder as their numbers decreased near the end of the period of slaughter (Hornaday, 1889: 430; Roe, 1951: 139-140). This survey of historical literature on wariness shows that probably none of the original free-ranging herds were as tame as those in the Wildlife Park, Wind Cave or the Wichita Refuge.

There are records of wariness comparable to the wilder Crow or Hayden Herds.

#### THE DAILY ROUND

The *daily round*, consisting of behavior during an entire day, was divided into two main types of activity: (1) *Feeding behavior* which included short periods of walking to select and eat natural forage or hay, and (2) *non-feeding behavior* which included much loafing behavior such as lying and standing, and also ruminating, traveling, watering, licking salt, playing and grooming.

Feeding usually commenced sometime after dawn, but the exact time varied. Throughout the day, cycles of feeding alternated with those of non-feeding. This is quite similar to grazing behavior in cattle (Hancock, 1953: 3). Feeding activity sometimes declined during periods of high temperature around noon. Groups continued feeding into complete darkness at times. A period of feeding and traveling occasionally occurred at any time during the night in all herds. These periods of nocturnal activity were relatively short when compared with the greater amount of time spent loafing. Nocturnal periods of feeding were usually singular and there was no evidence of any cyclic rhythm. It should be realized, however, that nocturnal observations were too meagre to support any general conclusion.

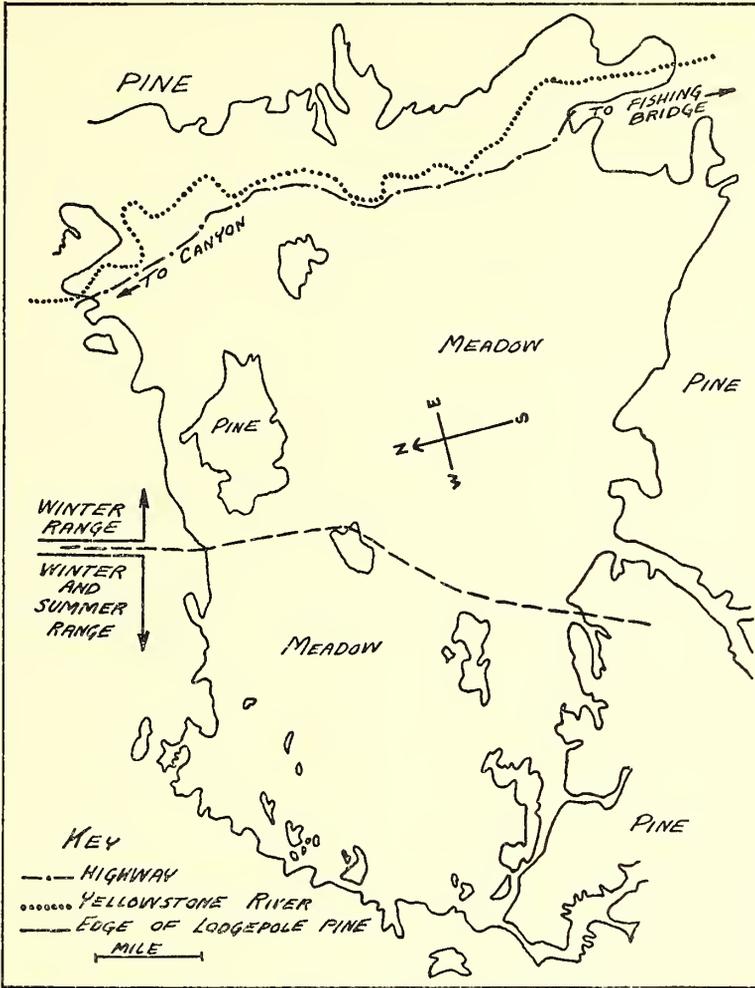
The *daily radius* (Leopold, 1947) was that distance traveled by a group of buffalo in one 24-hour period. The average daily radius during the rut for five group-days of travel in Hayden Valley was two miles, with a range from 1.5 to 2.4 miles. The maximum daily radius was recorded during a stampede over the southern divide, when the group traveled at least nine miles.

The average daily radius for 20 group-days of travel during the rut in the Wichita Refuge was 2.1 miles, with a range from 0.5 to 5.8 miles per day.

The average daily radius during the rut in the Wildlife Park was 1.7 miles, but the 133 acres of this park probably reduced the radius to less than that for wild herds.

The daily radius for herds in areas where water holes were scarce would be expected to be considerably greater than any of the above averages. In late summer, the Wind Cave Herd sometimes made daily round trips to water of at least six miles.

Hancock (1953: 8) surveyed the literature for daily radius in cattle. A free-ranging herd



TEXT-FIG. 1. Range of Buffalo in Hayden Valley.

traveled 3.0 miles per day, while herds enclosed in 1.0 to 5.5 acres moved from 1.4 to 1.7 miles per day.

#### HOME RANGE OF FREE-RANGING HERDS

Text-figure 1 pictures the home range of the Hayden Herd. It was approximately 12 square miles in summer and extended to 36 square miles in winter (October-November through April-May). This extension in winter coincided with a cover of snow and an absence of tourist traffic on the main highway. The Hayden range was largely confined by lodgepole pine forests on all sides. The herd nevertheless often penetrated part way into this border. It moved into all small meadows that jutted out into the timber from the main meadow, and also went through the timber to reach isolated meadows. The timbered

border on the north and south of the valley still proved to be an effective barrier against egress to new range. The highway on the east stopped most egress or ingress in summer, yet there may have been some interchange between the Hayden Herd and the Pelican and Lamar Herds toward the east in winter. The only known interchange of any extent occurred to the west across a 3.6 mile trail through the timber over the Mary Lake Divide. Interchange over this trail took place between the Hayden Herd and the Nez Perce Herd, which was part of the Lower Firehole River Herd.

The Lamar Herd moved each year about 10-25 miles from meadows at 8,000-9,000 feet to the lower Lamar Valley at 6,500 feet with the advent of fall snows. It returned to the higher meadows again with the disappearance of snow in May or June.

#### INTEGRATION OF THE HERD

The high degree of cohesiveness of the Wildlife Park Herd was demonstrated when the herd was artificially split. A fence divided the herd into a group of five cows, one yearling and one bull, and another group of five cows, three yearlings and one bull. The two groups regularly lay down as one herd in spite of the fence. There was much exchange grunting between them. They also paced back and forth along the fence, a type of behavior which was not seen at other times. Their daily schedule of activity was almost identical. Other groups of buffalo also lay together as one on each side of the fence separating Wind Cave from Custer State Park.

This high degree of cohesiveness in the Wildlife Park was remarkable in view of the great amount of aggression between members of the herd, particularly during feeding on hay (Section V). Mutual toleration must have overbalanced aggressive behavior in this group, as shown objectively by its tendency to aggregate (Collias, 1944: 89).

A high degree of cohesiveness was shown by individuals who became temporarily separated from the main group through differential movements. When they discovered their isolation, they abruptly ran back to join the group.

Herds also displayed a high degree of cohesiveness during drives and stampedes. If one animal broke through a line of men driving them, the rest of the herd would quickly follow. During direct movements or stampedes, the path chosen by the first member of each subgroup or by the first member of the herd was followed closely by every succeeding buffalo, even though men shouted from a short distance away. Interesting in this respect are Dodge's (1877: 121-2) references to the derailing or the stopping of trains by the insistent passage of herds.

Different degrees of cohesiveness were observed during movements of herds. Herds were most compactly bunched during direct movements and stampedes. Either of these movements was also characterized at times by a herd strung out for more than a mile in small groups or a column of several animals abreast. Direct movements were frequently single file. Single file was the usual pattern on trails through snow and through timber, and was also common on trails through broad meadows, yet it did not depend on the presence of a trail.

The cohesiveness of a herd depended on a balance of centrifugal (dispersive) and centripetal (gregarious) forces. Grazing was a centrifugal factor, since the distance between mem-

bers of a herd characteristically increased when the herd arose to graze. Centripetal factors included the occurrence of localized shade or bare areas that brought herd members closer together when lying in them. Other factors were moderately dense or loosely spaced timber, and rain or falling snow. Herds were usually more closely grouped when loafing while standing or lying. Disturbance from foreign objects such as man caused a massing of the herd. Stampedes and some direct movements were also centripetal factors.

#### IV. HERD COMPOSITION

##### BULL GROUPS AND COW GROUPS

I classified groups of buffalo into two types according to their composition: (1) *Bull groups* contained males with an infrequent female. (2) *Cow groups* contained a majority of females and a smaller number of males. During the rut, the increase in group size and the fusion of some bull groups into the cow groups did not create a third classification. Such groups were still classed as cow groups since their nature was essentially matriarchal. The bulls here were largely followers and had little effect on group coordination.

*Composition.* Table 2 analyzes the size of bull groups. They were small groups of one to 12 members. The average size in Yellowstone Park increased slightly from 3.3 to 4.7 during the calving season (May) and decreased greatly to 1.2 during the rut when most bulls entered the cow groups. Most members of bull groups were four years old or older and the groups included some three-year-olds and occasional two-year-olds. Two- to four-year-old bulls were more commonly distributed in the groups of three or more members than in smaller groups. Solitary bulls were sometimes several miles from any other buffalo. The only cows attached to bull groups were rare cases of one to four old, barren cows.

Table 3 analyzes the size and composition of cow groups. Group size (average about 23) remained rather constant during the non-breeding season but varied more during the calving season. There was a great increase in size during the rut as many groups in Hayden Valley coalesced and were joined by bull groups. Cow groups during the non-breeding season were composed of cows, yearlings, calves, two-year-old bulls, some three-year-old bulls, and rare bulls four or more years old.

Cow groups virtually never had an equal socionomic sex ratio (that ratio within groups—Carpenter, 1952: 236). The mean of males in these groups was 24% in the Lamar in January-

TABLE 2. SIZE OF BULL GROUPS

Area and period observed	No. of groups observed	Percentage of each group size								Mean Size
		1	2	3	4	5	6	7	8 to 12	
Lamar, Jan.-Mar.	33	18.2	30.3	18.2	6.1	18.2	3.0	0	6.1	3.3
Lamar, May	24	16.7	16.7	16.7	4.2	8.3	8.3	4.2	25.0	4.7
Wind Cave, May	21	28.6	14.3	9.5	19.0	14.3	4.8	9.5	0	2.4
Hayden, rut	42	81.0	19.0	0	0	0	0	0	0	1.2

March and 31% in May, 17% in Wind Cave in May, and 44% in Hayden Valley during the rut. All of these percentages were calculated using data for animals two or more years old. Much of the inequality in sex ratios is accounted for by bull groups living outside these cow groups.

Numerous observations on cow and bull groups in several areas were examined to formulate the following trends; behavior in the two types of groups is contrasted in each category:

**Leadership.** Older bulls tended to lead bull groups more often than younger ones, but there was great variation. Cow groups were led principally by older cows and seldom by younger cows or bulls. Leadership changed among these cows.

**Irritability.** Cow groups were more wary, more watchful and showed a greater flight distance than bull groups. Flight distances in Yellowstone Park were usually under 300 feet for bull groups

and 200 to 1,000 feet or more for cow groups. Some bull groups were so obstinate that approach within ten feet and tossing of stones did not move them.

**Winter range.** The winter range of bull groups from all four Yellowstone Park Herds extended into areas in which cows were not seen. This included the Mary Bay thermal area for the Pelican Herd, the area around Mud Volcano and the Yellowstone River for the Hayden Herd, meadows along the Madison River for the Firehole River Herd, and the Hellroaring Drainage, lower Lamar Valley and upper Lamar Valley above Soda Butte for the Lamar Herd.

**Daily round.** Cow groups showed greater uniformity of activity during any one time interval than bull groups; that is, almost all of the members were more or less simultaneously engaged in grazing, loafing or the activity of the moment.

**Intermingling.** Cow and bull groups occa-

TABLE 3. SIZE AND COMPOSITION OF COW GROUPS

Group and period observed	Group size				Group composition							
	Number of groups observed	Mean	Standard deviation	Range	Number of groups censused	Mean size	Mean grouping tendency					% bulls <4 years old
							Cows two or more years old	Yearlings	Calves	Bulls two-three years old	Bulls four or more years old	
Lamar, Jan. to Mar.	18	23.0	11.4	10-50	12	20.3	12.1*	4.4	0	3.8	0	0
Lamar May (calving)	15	23.6	18.4	4-63	10	17.3	8.6†	4.8	3.9	3.7	0.2	1.0
Wind Cave (calving)	17	21.9	21.2	3-76	14	16.8	7.4	4.0	3.9	1.1	0.4	2.1
Hayden during rut	36	175.3	108	19-480	3	115.2	39.3	20.0	25.3	16.3	14.3	9.2‡

\*19.3% two-year-olds. †19.5% two-year-olds. ‡Computed from census of 8 groups.

sionally intermingled during the non-breeding season for a few hours or less. Intermingling during the rut was, of course, frequent.

*Integration.* At times during the entire season, various groups joined together into larger units, and separated into smaller ones either by differential drifting or by direct withdrawal. This splitting and joining occurred in both cow and bull groups and even involved solitary bulls. There were indications that the stability of bull groups with one or two members was greater than in groups of larger bulls and cows. One pair of bulls remained together from December 10 to March 15 in the Lamar Valley.

*Cohesion.* Bull groups (with the exception of some pairs) showed a low degree of cohesiveness, and cow groups a high degree. The average distance separating members of bull groups was greater and more variable than that for cow groups. Cow groups moved as more compact units while bull groups sometimes strung apart for 100 to as much as 2,000 feet, the lead animal disappearing from sight before the last buffalo started to move.

*Closed groups.* There were a few indications that some bull groups and possibly some cow groups were closed groups. Such observations were unusual compared with the frequent observations of random coalescing and splitting of cow or bull groups.

Among bull groups there were three cases where they approached closely yet did not join and two cases where newcomers were challenged. Included in these cases was a pair of two-member bull groups in the Lamar Valley which remained within a few hundred feet of each other for three months, occasionally grazed within sight of each other, yet did not join.

Cow groups showed fewer indications of being closed, yet the following three incidents are of interest: A group of 33 cows moved single file through a scattered group of 48, and a group of 27 trotted through a group of 16, both without any loss or gain in members (Hayden Valley, March, 1953). One group of six cows in the Lamar Herd picked up three new members while wandering through a group of 14.

#### SUBGROUPS

Wild groups of all sizes and types readily broke into smaller subgroups that were spatially distinct from other clusters in the group. Some subgroups contained a random cross-section of ages and sexes. Others, particularly in larger cow groups, showed tendencies toward bulls, barren cows, cows-with-calves, calves and yearlings, with some two-year-olds. The bull sub-

groups tended to be on the edges of the herds, and the last animals in herd movements were regularly bulls. The presence of bulls on the flanks and in the rear of herds was noted by several authors (Allen, 1876: 55; Aubrey, 1908: 216; Audubon, 1849: 41; Bradbury, 1904: 147; Inman, 1899: 231; Parkman, 1903: 423). There was no evidence that these peripheral bulls were sentinels, as proposed by Inman (1899: 231).

The more distinct subgroups in the Wildlife Park Herd were delineated by repeated observations of such close groupings over a period of time. Maps of the patterns of lying in the herd aided this study. There were three main subgroups: juveniles, mature cows and the older bulls. The subgroup of cows-with-calves was much more distinct than that of pre-partum mature cows. The subgroup of older bulls (two animals) commonly stayed aloof from the cow group, yet joined them during the rut. When these two bulls were divided temporarily by a fence, the five-year-old repeatedly returned to the fence in search of the six-year-old. The attachment between two yearling heifers was the closest in the herd. Subgroups of new calves were first noted at an age of two to four weeks. Calves alternated between calf subgroups, their cows, or a cow-with-calf subgroup. There was no evidence of closed groups in the Wildlife Park Herd.

#### CLANS

The preceding description of subgroups and closed groups contains no more conclusions than my observations permitted. Four authors went farther, however, and stated that subgroups were blood relations, family groups, or clans (Grinnell, 1904: 129; Inman, 1899: 234; Seton, 1929: 693; Soper, 1941: 391-2), while Mayer (1934, II: 36) thought that small groups remained "separate and apart" in spite of coalescing and splitting. All of these authors failed to give conclusive evidence. I have noted several cases where yearlings and two-year-olds, particularly heifers, followed cows, but such groupings could not be construed as clans.

Garretson (1938: 59) did not believe the clan theory and Dodge (1877: 123) called the formation of subgroups "entirely accidental." From the present study of group composition these last two authors would appear to be correct. I believe, as merely a personal conclusion, that subgroup or group formation was flexible and depended little on blood relations beyond the age of one year.

## V. THE DOMINANCE HIERARCHY

### DISPLAY OF DOMINANCE

The herd in the Jackson Hole Wildlife Park was studied intensively for information on social organization. The outcome of interactions between individuals delineated the social structure of this herd. It was a linear type of dominance hierarchy with dominant individuals exercising a virtual constancy of success in interactions. Subordinates recognized dominants quickly and avoided them.

I distinguished the herd members as individuals by physical differences or painted markings. Their interactions were divided into *passive dominances* and *aggressions*. Out of 1,027 interactions recorded, 72.8% were passive dominances and 27.2% were aggressions.

Passive dominances were the more gentle of the two types of interactions. They were characterized by a lack of any obvious show of force or threat. Typically, the dominant individual walked toward and displaced the subordinate with no aggressive action. The most subtle passive dominance took place when one animal avoided another while moving through the herd.

Aggressions occurred when the dominant individual displaced a subordinate by force or by threat. Threat usually involved an intention movement (Tinbergen, 1951: 79) of an aggressive act. The most gentle form of threat involved a mere look toward the subordinate, causing it to move away. The most common form was horn swinging, where the horns were swung up and down or sideways toward the subordinate with occasional contact. Partial or complete charges were also used to displace subordinates. The dominant animal appeared to be trying to impale or gore the subordinate, but actual contact was uncommon. Occasional violent charges threw the victim for several feet or tossed it as much as twenty feet. One mature bull hooked a cow on his horns and tossed her over his back, where she fell to the ground (in a corral at the Lamar Buffalo Ranch). She was able to walk away, but subsequent autopsy revealed two broken ribs and a punctured, collapsed lung.

Battles were tabulated as aggressions. They consisted of hooking of horns and pushing back and forth that lasted a few seconds or several minutes. The loser usually either moved away or was pushed back a few feet, yet many battles were indecisive. They were started by dominant or subordinate individuals and occurred between younger bulls and between calves, yearlings and two-year-olds. Most battles in the Wildlife Park occurred between one-year-old bulls and two-

year-old cows. This may have been correlated with a later change in rank between these two groups. Battles between cows were rare.

Another indication of dominance was the intention movement of mounting, seeming to occur without any sexual motivation. This was tallied as an aggression if the subordinate moved out when the dominant placed its chin on the rump of the subordinate. Both the intention movement for mounting and genuine mounting also occurred as play, apparently with no regard for dominance. Attempts by a subordinate to mount a dominant resulted in a prompt reversal of the same behavior, playful battles, or other forms of play. This mounting during play produced no withdrawal by the subordinate and was not tallied as an aggression.

### SITUATIONS IN WHICH DOMINANCE WAS DISPLAYED

More than 90 per cent. of the interactions in the Wildlife Park were recorded during displacements on the feeding grounds. These buffalo were fed on hay from November to May, approximately. Practically no natural food was available during most of this period. Since the hay was spread in piles over at least 100 feet of ground, there was a surplus of piles at all times except in the first few minutes of distribution. Most buffalo fed from separate piles of hay. They continually shifted every few minutes, even though there was little difference between various piles. A shift of one dominant animal might eventually cause a shift in more than half the herd as the move was passed down the line.

Dominance was also recorded during interactions over special objects as follows: (1) an item of curiosity, (2) a spot for lying, (3) a wallow, (4) a water hole or puddle, (5) a tree for rubbing or horning, (6) choice grass, (7) a salt lick, (8) shade under a small group of trees (dominants clustered in the shade and subordinates were in the sun), (9) sniffing the vulva of a cow, (10) a cow in heat.

Dominance was evident during group movements as well. Most commonly, a dominant animal in the rear or middle of the group pushed subordinates in front or stopped those directly behind. When two dominants stopped on a packed snow trail, subordinate animals wishing to press ahead had to flounder around through deep snow (March, 1951, Wildlife Park). Dominance was also occasionally recorded during grazing.

The preceding paragraphs discuss dominance that was usually traceable to interaction over a certain object, yet much aggressive dominance

also occurred apparently independent of any inciting situation. In these cases, one member of a herd suddenly and inexplicably interrupted its feeding to charge another member. This happened most frequently between a cow and juvenile, occasionally between two cows.

#### STRUCTURE AND DYNAMICS OF THE DOMINANCE HIERARCHY IN THE WILDLIFE PARK

*Factors influencing dominance.* Table 4 illustrates some factors that determine dominance. Distinct differences in size and weight insured dominance. Seniority in age usually insured dominance, yet one seven-year-old cow was subordinate to two five-year-olds. Within groups of similar size, bulls were dominant over cows; aggressiveness or certain undetermined factors were more important than slight differences in size.

*Reversals.* Out of 726 interactions in the spring of 1951, there was only one temporary reversal when F4\* displaced F3 by a swing of the horns. Occasional reversals were attempted by cows which horned either M1 or M2, yet these bulls did not yield. The two-year-old heifers did this most frequently. It was classed as play. Schein & Fohrman (1955) recorded 248 reversals in 4,935 interactions among 163 dairy cows.

Permanent changes in the dominance hierarchy resulted from the differential growth of bulls and cows. Previous to July and August, 1951, M3 and M4 were slightly smaller than F8, F9 and F10. During those two months, M3

\*Nomenclature of individuals refers to sex and position in hierarchy. Thus, M2 was the second in position in the hierarchy of males and F4 was fourth among the females.

TABLE 4. DOMINANCE HIERARCHY IN THE WILDLIFE PARK, MARCH 14 THROUGH MAY 4, 1951 (Buffalo listed in order of decreasing dominance; M = male and F = female)

Individual	Total number of interactions	% of total that were victorious	% of total that were aggressions	% of victorious interactions that were aggressions	Age in spring '51	Individual differences within each group
M1	29	100%	28%	28%	6	M1 larger in size and weight than M2. M1 stronger than M2 in battles.
M2	36	94%	25%	26%	5	
F1	112	94%	22%	23%	5	All in this cow group smaller in size and weight than M1 and M2. No distinct difference in size and weight among these cows with the exception of F7, which was slightly thinner and shorter in height than all others.
F2	100	75%	10%	11%	5	
F3	142	70%	8%	11%	7	
F4	133	76%	23%	29%	5	
F5	112	38%	18%	7%	5	
F6	126	54%	12%	9%	4	
F7	84	40%	26%	44%	4	
F8	84	37%	30%	45%	2	Smaller in size and weight than F1-7.
F9	77	40%	51%	68%	2	No noticeable differences in size or weight within this group. F8 stronger than F9-10 and F9 stronger than F10 in battles. All stronger than following subordinates in battle. (The progeny of F1-7 born in Wildlife Park.)
F10	56	18%	32%	60%	2	
M3	98	32%	43%	68%	1	Smaller in size and weight than F8-10.
M4	78	12%	44%	78%	1	No noticeable differences in size within this group. M3 stronger than M4 in battles. (The progeny of F1-7 born in Wildlife Park.)
F11	65	5%	45%	67%	1	Smaller in size and weight than M3-4.
F12	54	0	52%	—	1	No noticeable difference in size and weight between these two, although F12 was at least two weeks older than F11. F11 stronger than F12 in battles. (The progeny of F1-7 born in Wildlife Park.)

TABLE 5. DOMINANCE HIERARCHY IN THE WILDLIFE PARK, FEBRUARY 4 TO 9, 1952

F1 dominates 13:	F12	F11	F10	F9	F8	F7	F6	F5	F3	M4	M3	F4	F2
F2 dominates 10:	F12	F11	F10	F9	F8	F7	F6	F5	F3			F4	
F4 dominates 10:	F12	F11	F10	F9	F8	F7	F6	F5		M4	M3		
M3 dominates 10:	F12	F11	F10	F9	F8	F7	F6		F3	M4			F2
M4 dominates 9:	F12	F11	F10	F9	F8	F7	F6		F3				F2
F3 dominates 9:	F12	F11	F10	F9	F8	F7	F6	F5				F4	
F5 dominates 9:	F12	F11	F10	F9	F8	F7	F6			M4	M3		
F6 dominates 6:	F12	F11	F10	F9	F8	F7							
F7 dominates 5:	F12	F11	F10	F9	F8								
F8 dominates 4:	F12	F11	F10	F9									
F9 dominates 3:	F12	F11	F10										
F10 dominates 2:	F12	F11											
F11 dominates 1:	F12												
F12 dominates 0:													

and M4 grew to be approximately the same size as these two-year-old heifers. The exact time schedule for the advance in dominance of M3 and M4 is not available, since it occurred during the summer and fall when interactions were uncommon. By September 12, both M3 and M4 had advanced above F8, F9 and F10. By October 9, both had moved above F6 and F7.

By February 4, 1952, M3 and M4 had advanced still farther up the hierarchy, as shown in Table 5. Both M3 and M4 were dominant over all cows except F1, F4 and F5. The irregular gain in dominance of M3 and M4 produced eight triangles (Table 6). By the following summer the advance of M3 and M4 over all cows eliminated these triangles.

The dominance hierarchy was checked during November, 1953, to finish a survey of almost three years. During that period there was no permanent reversal among the two bulls or the top seven cows. There was a dominance hierarchy in the remaining five mature cows, all progeny of the first seven. None had moved ahead of their parents.

*Dominance hierarchy among calves.* Dominance among calves developed slowly. Although they were alert to advances from adults within three weeks after birth, no dominance hierarchy among calves was detected during the first two months. The first definite signs of dominance were noted at an age of four months. At that time, the only male calf in a group of six was dominant over others and there were interactions among female calves.

I was not able to determine the complete dominance hierarchy among calves until February, 1952. Even during this period of feeding on hay, when there were numerous interactions

among other adult herd members, interactions between calves were infrequent. Table 7 shows the hierarchy among calves.

The male calf was dominant over all females and accounted for 41.4% of the interactions in the entire calf group. There was no correlation between the position of dominance of the calf and its seniority in the calf group, small yet noticeable size differences, or the position of dominance of its mother. There was one reversal out of 70 calf interactions when D displaced B with an aggression.

TABLE 6. TRIANGLE SITUATIONS IN THE DOMINANCE HIERARCHY OF TABLE 5.

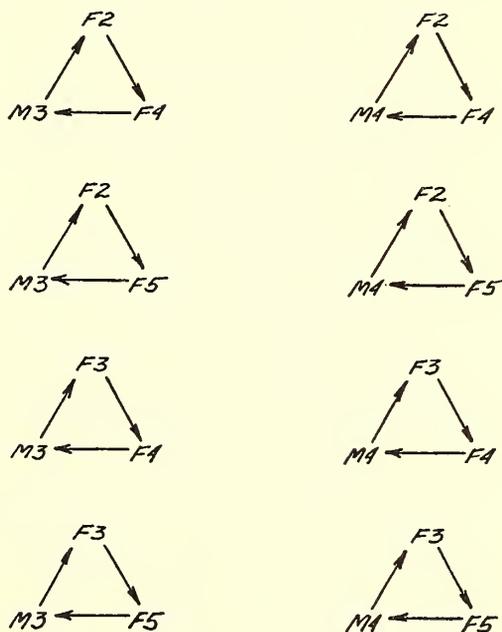
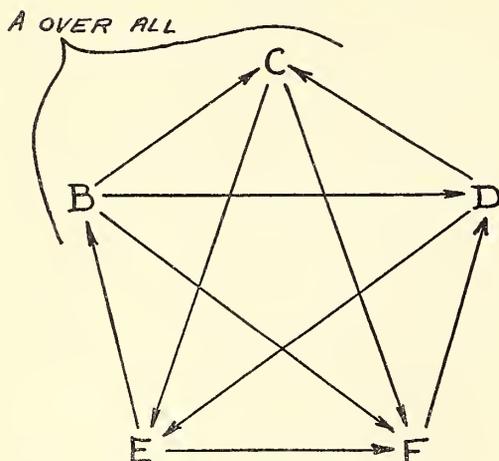


TABLE 7. DOMINANCE AMONG SIX CALVES IN THE WILDLIFE PARK HERD, FEBRUARY 4 TO 9, 1952 (Computed from 70 interactions)



Calf	Dominant over	Relative age (date of birth)	Sex	Dominance of mother
A	BCDEF	Sixth (5/16)	M	Second
B	CDF	Second (4/29)	F	Fifth
C	EF	Fourth (5/5)	F	Third
D	CE	First (4/21)	F	First
E	BF	Fifth (5/15)	F	Fourth
F	D	Third (5/1)	F	Sixth

There were no triangles among the four calves in the herd one year previous on March 15, 1951. On this basis, one would expect the five triangles in the 1952 calf group to straighten out in a few weeks.

*Factors affecting frequency of interactions.* The number of interactions among certain animals or during certain time intervals varied with the factors discussed in the following paragraphs.

Table 8 shows the tendency for dominant cows to have more interactions with the cows immediately below them than with the less dominant cows. "Probability" indicates the probability of getting such a skewed distribution if a column of values was picked at random. It was computed by chi-square. The distribution of interactions for F1 and F2 are statistically significant. While the remaining columns are not, they still show the same distributional trend. Schein & Fohrman (1955) statistically analyzed similar interactions in a herd of dairy cows. They found that "fight contests involved cows closer together on the social rank scale than do threat or butt contests."

The total number of interactions and the per-

centage of aggressive interactions for each individual are listed in Table 4. Bulls M1 and M2 had fewer interactions than any other herd member. With this exception, the more dominant animals tended to have more interactions. This is in line with findings on pigeons (Masare & Allee, 1934: 327), chickens (Allee, 1951: 135) and canaries (Shoemaker, 1939: 404). An analysis of the percentage of aggressions shows just the reverse tendency. The percentages increased distinctly among the less dominant juveniles.

Hunger and palatability of food caused variations in the frequency of interactions. Table 9 shows the pattern for a typical day of feeding on hay. There was a high peak of interactions and aggressions during the first 20 minutes of feeding. Fewer interactions and no high peak occurred during the afternoon feeding period, when the herd was not as hungry. This positive correlation between hunger and number of interactions was further verified on days when a surplus of hay remained from the previous day's feeding. When fresh hay was put out under such conditions, there were fewer interactions than usual. In addition to hay, the herd was also fed concentrate on some days. The buffalo preferred the concentrate, as evidenced by their quick withdrawal from the hay to feed on it. Even though the concentrate was fed about one hour after the hay, the initial peak of interactions sometimes doubled the initial peak for hay on the same day. The interactions over concentrate were also more aggressive.

Various disturbances also increased the number of interactions in a herd. They increased greatly in any group enclosed in a corral or pen. Interactions were increased by disturbance from the presence of a strange object, such as a car, a recently shed elk antler, a human being or a person concealed under a buffalo hide. One cow in the Wildlife Park Herd increased the fre-

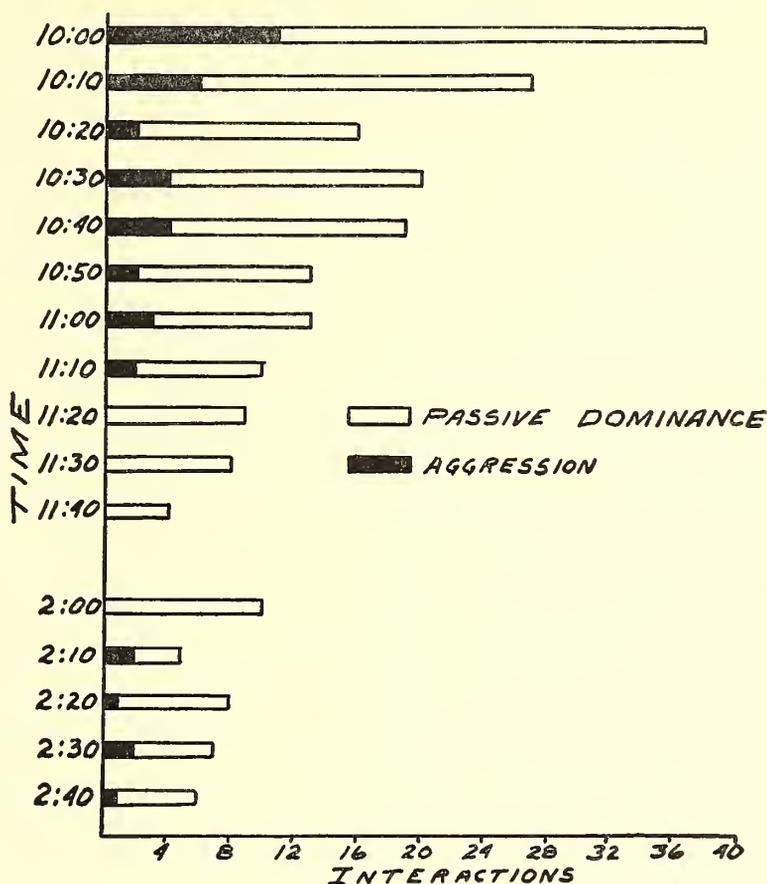
TABLE 8. INTERACTIONS BETWEEN MATURE COWS IN WILDLIFE PARK, MARCH 14 TO MAY 4, 1951

Cow	F1	F2	F3	F4	F5
F2	20 +				
F3	25 +	22 +			
F4	9 -	5 -	17 +		
F5	9 -	14 +	21 +	17 +	
F6	13 -	3 -	15 +	12 +	9 +
F7	5 -	6 -	6 -	8 -	6 -
Mean	13.5	10.0	14.8	12.3	7.5
Probability	.005 *	.005 *	.04	.18	.62

+ = Above the mean for column.

- = Below the mean for column.

TABLE 9. INTERACTIONS PER TEN-MINUTE INTERVAL WHILE WILDLIFE PARK HERD WAS FEEDING ON HAY (FEEDING TIME: 10 A.M.)



quency of interactions by her numerous aggressions which resulted in a chain reaction of interactions. The herd was noticeably more calm after the cow was removed.

*Quality of dominance.* Rough or gentle displays of dominance varied with age and sex. Comparatively gentle displacements were made by bulls over cows, by a mother over her calf, among juveniles, among calves, and occasionally among bulls outside the rut. The dominant buffalo used moderate force, and the subordinate moved away slowly for no more than a few feet. The subordinate sometimes returned to feed with the dominant. More forceful displacements were made by cows over yearlings, by a cow to a strange calf, among cows, and among bulls during the rut. The dominant was more aggressive and the subordinate moved faster, farther, and did not return.

There were no obvious behavior characteristics correlated with rank in the hierarchy. Subordinates showed no unusual amount of fear. All

buffalo showed a keen awareness of the identity of the animals near them. The approach of a dominant from almost directly behind the subordinate resulted in a passive submission with hardly a glance at the dominant.

*Derived dominance.* Some buffalo derived a higher status in the dominance hierarchy by associating with a more dominant buffalo. Calves thus benefited from the positions of their mothers. The calf was elevated to her status when close to her and if tolerated by her. The mother sometimes pushed close subordinates away from her calf. Most of these instances of derived dominance occurred during hay feeding. Derived dominance was also recorded once during the rut in Hayden Valley: A seven-year-old bull stopped chasing a cow when she started to follow an older bull closely.

#### DOMINANCE IN WILD HERDS

The extent of development of dominance hierarchies in wild herds could not be determined

because enough individuals could not be recognized. Animals in wild groups frequently exhibited passive dominances and aggressions. The frequency of these interactions never exceeded half those recorded for the Wildlife Park Herd during hay feeding. It was usually considerably less. The highest frequency occurred in a cow group of 15 that was feeding in deep snow (Lamar Valley, January 24, 1952). Displacements were frequent as each buffalo moved into an area recently cleared of snow by a subordinate. The more dominant buffalo would be expected to have a particular advantage in a severe winter.

A dominance hierarchy was noted in the above cow group and in a bull group of eight (Madison River, March, 1953) and of five (Hayden Valley, March, 1953). A wild group of 55 that was fed on hay in a Yellowstone Park corral showed numerous passive interactions. But the fact that groups of two to four cows were regularly observed feeding from the same hay pile would seem to indicate a lack of a completely developed hierarchy.

#### INTERSPECIFIC DOMINANCE

Free-living buffalo sometimes interacted with other species on the same range. These species included elk, antelope, mule deer, bighorn sheep and coyotes. In the Wildlife Park, buffalo fed during the winter in the area with a herd of 29 elk and some pronghorn, mule deer, whitetail deer, moose and horses. In free-living or enclosed herds the number of interspecific interactions greatly exceeded the number of intraspecific ones. The buffalo were dominant over all these species with only occasional reversals among elk and horses.

*Elk.* In the Wildlife Park, month-old buffalo calves were always successful in observed attempts to displace six-point elk bulls. Interactions involving younger calves were not observed. The buffalo herd completely dominated the hay feeding circuit and could push the elk from any section. They occasionally stampeded back and forth on the hay feeding circuit in order to force the elk into deeper snow. They also chased the elk in a steady, rapid walk during grazing in summer. Buffalo and elk sometimes fed within three feet of each other, but the elk soon became wary of the buffalo and moved farther away. Although elk nervously watched buffalo and usually dodged all charges, the violent charge of a cow buffalo threw one yearling elk three feet into the side of the hay shed.

Five- or six-point elk bulls were dominant

over a buffalo cow or yearling in rare cases. The displacement always occurred on the edge of the buffalo herd. Such reversals were considered temporary since the aggression of any buffalo never failed to move the largest elk.

The buffalo herd chased the elk herd on three occasions when a new elk calf was present. The speed of the chase was so fast that the elk calf dropped behind within a few hundred feet. The buffalo then milled about the calf. In the first incident the calf was bruised, cut behind the ear, and bleeding at the mouth, yet still able to walk back to its herd. The buffalo herd bruised the calf again on the next day. It had no broken bones yet was so badly mauled it could not stand. It died in spite of careful nursing by the attendants of the Park. A second calf was rescued just before the buffalo herd reached it. They milled about and smelled the spot where the calf was born. When this calf moved out with the elk herd a few days later, the buffalo followed and slowly chased the elk.

Groups of elk and buffalo in Yellowstone Park moved within 30 feet of each other and even intermingled. The buffalo occasionally charged the elk, but the wary elk withdrew quickly. Buffalo disrupted the elk trapping program since elk would not enter a trapping corral if buffalo were inside or nearby. One incident was observed in the Lamar Valley where the buffalo killed an elk calf they found in hiding. Rush (1942: 225) and Chapman (1937: 148) mention deaths of elk in Yellowstone Park due to buffalo.

Superintendent John Schwartz noted a few cases of dominance of elk over buffalo in the National Bison Range. One elk raised on a bottle showed an attachment for two buffalo bulls at an age of eighteen months despite the presence of other elk. When two and a half years old, he rounded up a group of 15 buffalo cows and bugled. Another bull elk assembled a harem of cow elk during the rut and belligerently chased any buffalo that wandered near. This same elk rammed a tine of his antler through the palate of a yearling buffalo. The buffalo bled profusely and died from this injury within an hour.

*Pronghorn.* Buffalo in the Wildlife Park occasionally charged pronghorns (antelope) which wandered near the herd. They killed one eight-month-old pronghorn buck. Pronghorns in Wind Cave passed near or through buffalo groups, and the latter occasionally charged them, but the alert and agile pronghorns easily out-manuevered these attacks. A two-month-old buffalo calf chased one pronghorn buck for almost a hundred feet. The walking of a buffalo group within 150 feet of resting pronghorns caused the pronghorns

to rise and watch the group. Bryant (1885: 132) observed in Wyoming that "The deer and antelope are compelled to frequently shelter themselves from the attack of wolves under the strong protection of buffalos and you sometimes see herds of buffalos and antelopes mingle in grazing together."

*Mule deer.* One charge of a buffalo cow in the Wildlife Park tossed a mule deer ten feet. The attack left the deer lying on the ground, but it arose and rapidly moved away when the cow charged a second time. Another charge by a cow knocked a mule deer to the ground.

*Moose.* When a moose calf was placed in the Wildlife Park in August, the buffalo sometimes chased it. The buffalo killed the calf when it was seven months old. One rib was broken and the chest was pierced with a hole two inches in diameter (oral comment from James R. Simon).

*Horses.* Two draft horses were dominant over all cow and yearling buffalo during interactions at a salt lick in the Wildlife Park in October, 1951. The horse made no passes toward the buffalo, which moved slowly away as the horses came in to the salt. In March, 1953, the draft horses had lost some rank with the buffalo and were dominant over only a minority of cows and all yearlings. All buffalo were dominant over one saddle horse.

Head Animal Keeper David Pierson recorded one death of a horse in the Lamar Valley in 23 years of observation. This horse was ranging free in the valley at the time. He also noted three other horses and one mule that were gored by buffalo.

*Bighorn sheep.* Cy Young observed three cases in the National Bison Range where an older bighorn ram associated with a buffalo bull during the summer.

*Dominance hierarchies.* The interspecific dominance hierarchy among the big game species in the Wildlife Park was determined for the period February-May, 1951. With the exception of reversals noted below, the order was as follows: adult human beings, buffalo, elk, mule deer, pronghorn, moose and whitetail deer. The exact order of the last two species was not known.

The man who fed these animals maintained his dominant position by the use of a pitchfork. Tame elk, mule deer and pronghorns enjoyed derived dominance over the buffalo when they followed this man closely.

The elk exercised dominance by charges, by swinging antlers or by rapid downward strikes of the forelegs.

The mule deer involved in this hierarchy included two tame bucks and a tame and a wild doe. They used short charges or rapid downward strikes with the forelegs to display dominance. Bucks were dominant over does. The mule deer bucks dropped below the pronghorn buck in dominance when they shed their antlers. The horns of the pronghorn were becoming larger and harder at the same time. The reversal was not absolute; both deer occasionally resisted the horning of the pronghorn buck and drove him away. The pronghorn buck later gained dominance over the tame mule deer doe.

All pronghorns were tame. Pronghorn bucks dominated pronghorn does and other species by horning them. One buck was dominant over a castrated buck of the same age.

## VI. THE RUT AND SEXUAL BEHAVIOR

### DEVELOPMENT OF THE RUT

A marked increase in or the onset of certain behavior patterns in bulls marked the beginning of the rut or rutting season. These activities included sniffing of vulvas, tending of cows, bellowing, wallowing, horning, vicious and non-vicious battles and incomplete and fertile mountings. Section IV discussed the changes in group composition during the rut—the great increase in average group size, the union of groups in Hayden Valley and the almost complete dissolution of the bull groups as they mingled with the cow groups. This pattern of aggregation during the rut was not as well marked in Wind Cave or the Wichita Refuge. Groups here were larger than at other seasons but combined into one gigantic group only rarely. The fusion of smaller groups on the Great Plains and elsewhere into larger masses during the rut was mentioned by several authors (Bradbury, 1904; Branch, 1929: 7; Catlin, 1876–I: 249, II: 13; Hornaday, 1889: 415-6; Long, 1905–XV: 246; Soper, 1941: 390).

The rutting season in Hayden Valley ran from about June 15 to September 30, with less activity during the first and last two weeks. The rut in Wind Cave ran from about June 23 to September 14. The sporadic birth of calves outside the main calving season (see Section VII) would depend on occasional rutting activity at any time of the year.

There was more general activity in the herd during the rut than during other seasons. This was most obvious among bulls tending cows but was also typical to a lesser degree of other bulls and the rest of the herd. Peaks in rutting activity occurred just after dawn and at dusk. Any disturbance that altered the organization of the herd

also increased the rutting activity. This included traveling and the approach of a car into the center of a herd. During periods when the herd lay down, bulls tending cows often remained standing. Bulls bellowed at times during the entire night.

#### SNIFFING AND EXTENDING NECK WITH UPCURLLED LIP

Sniffing of cows' vulvas by bulls was observed during all months but increased greatly during the rut. Extending of neck with upcurled lip commonly but not always followed the sniffing (Plate III, Figure 5). There were indications that this was omitted after sniffing cows which showed no sign of heat. Some bulls remained with and tended one cow after sniffing several. In other cases, a bull displaced a subordinate which was tending a cow, sniffed the cow, and then moved on through the group to inspect others.

Bulls made methodical checks by sniffing all cows of a group in their paths. New bulls sniffed cows after first entering the group. Lying cows were prodded into standing so that the bull could sniff them. Urination by the cow was a stimulus for sniffing by nearby bulls, and sometimes the extended neck and upcurled lip of one bull after sniffing was a stimulus for another close one to move in and sniff. Interactions resulted when as many as three bulls sniffed the same cow consecutively. The subordinate bull or bulls moved back only a few feet and still kept the neck extended and lip upcurled.

In sniffing, the bull often moistened his nose from the liquids exuding from the vulva or licked this organ. If the cow was urinating, he wet his nose or licked his tongue in the stream of urine and then sometimes continued to lick the vulva after the stream stopped. When separated from cows, some bulls even wet their noses with or sniffed cow's urine on grass and then extended their necks with upcurled lips.

This sniffing activity was not restricted to bulls or the stimuli of vulvas. Cows extended their necks with upcurled lips at times after sniffing or licking the vulva or stream of urine from another cow, a rotted skeleton, the bloody urine on snow from a cow about to calve, human urine on a tree, a new calf—either her own or a strange one—the vulva and stream of urine from her own calf, her own urine on grass or the torn scrotum of a bull. Both male and female calves (45 days or older) and yearlings also extended their necks with upcurled lips after sniffing urine or the vulva of another buffalo. A two-year-old bull extended his neck with upcurled lips after sniffing a new calf.

#### THE TENDING BOND

*Technique.* The bond between the bull and cow during the rut is here called the *tending bond*. The bull kept alongside or behind a particular cow at a close distance—usually from one to five feet but sometimes touching the cow. When more than one tending pair was operating in a group, each pair was generally on the edge of the group with the bull maneuvering so as to keep the cow peripheral. The tending pair also occurred in the center. Only two instances were observed in which the tending pair completely separated from the group.

Bulls took either a passive or an aggressive part in the tending bond. Some followed the cows closely, turning around or moving forward with each move of the cow. Others guided the movements of the cows at times by swinging their heads or by moving back and forth in front of the cows. The only two observed cases of extreme control by the tending bull involved young bulls three or four years old. They isolated or completely restrained selected cows by running alongside or ahead and cutting back in front of them whenever they started to run back toward the herd.

In spite of the efforts of the bull, the tending bond was still essentially matriarchal. The cows usually moved anywhere by momentarily dodging from under the pressure of the bulls. For example, during stampedes the cows moved off and the tending bulls followed close alongside. Of regular occurrence were cases where one cow dashed several hundred feet from the group, followed by at least one bull. As many as eight bulls chased after a cow in this fashion. One chase in the National Bison Range continued intermittently for three hours, at the end of which time the cow appeared completely exhausted, with tongue hanging out. Other cows regularly resisted the advances of the bulls by threatening with motions of their horns, by horning the bulls or by kicking out with one hind leg. The bulls either ignored these attacks or moved one or two feet farther away.

Exceptions to the customary tending bond of one bull and one cow were rare. Cows were sometimes shared consecutively yet exclusively by more than one bull as a more dominant bull displaced the current bull by threat or battle. This tending bond lasted for no more than a few days—usually much less. Among buffalo it can be said that there is, therefore, a *temporary monogamous mateship*. Some bulls were promiscuous because they successively served several cows in any one season.

While tending cows, many bulls showed in-

tolerance toward surrounding group members of either sex which ventured close. Most intolerance was displayed toward nearby bulls, which were repelled by threat, aggressive charges or battle. The tending bull also kept away even the calf or yearling of the cow he was tending. Other behavior accessory to the tending bond is discussed later (attempted mountings, bellowing, wallowing, horning and sniffing the vulva of the tended cow or other nearby cows).

*Age of tending bulls.* Almost all of the tending in Hayden Valley was done by bulls ranging in age from six to at least fourteen years, with bulls eight or more years old being most active. Bulls one to five years old usually were not successful at tending due to pressure from other bulls. Two-year-old bulls often failed because many were subordinate to cows, and this was even more true of one-year-olds.

Yet tending bonds among younger buffalo still occurred. There were various combinations among yearling or two-year-old bulls and heifers and those between three-year-old bulls and females two or more years old. Such yearling heifers probably were not in heat. It was also doubtful whether the other females were in heat, since older bulls paid no attention to them. These tending bonds among younger animals were comparatively short-lived and were often characterized by more resistance than usual on the part of the female.

In the Wichita Refuge, most tending was done by bulls six to eleven years of age with some done by five-year-olds. (There was only one bull older than eleven years in this refuge.)

Tending in the National Bison Range was done mostly by bulls four or more years old, slightly by three-year-olds, and rarely by two-year-olds. (Observations of John Schwartz and Hugh Wilmar). Yearlings tended momentarily when they got a chance, as older bulls left temporarily or were absent. The composition of this herd was unbalanced since there were very few bulls five or more years old. Interesting in this area was the pattern of tending in the exhibition herd of about seven cows and two bulls. In 1952, a bull 13 or 14 years old dominated the nineteen-year-old bull and did all the tending. In 1953, the twenty-year-old white bull dominated a five-year-old bull and did all the tending.

The despot six-year-old bull in the Wildlife Park tended any cow that was in heat. The five-year-old bull was able to tend or mate only when more than one cow was in heat.

The preceding notes on ages of tending bulls are interesting when compared with data on sexual maturity and physical growth. At least

one bull was sexually mature at an age of 14 months, since a domestic cow bred by this bull aborted midway during pregnancy. The testis of a twenty-one-month-old bull killed in January in Yellowstone Park showed no spermatogenesis, but this does not necessarily mean that the bull could not breed with the advent of the rut. The testis from an eighteen-month-old bull killed in the Crow Reservation in September also showed no spermatogenesis. A three-year-old and possibly a two-year-old sired eight calves conceived in the Wildlife Park in 1948. Both two-year-olds and three-year-olds have successfully bred cows in or near the National Bison Range (oral comment from George Mushbach, John Schwartz and Cy Young).

Although bulls attained near maximum growth in size by the fifth or sixth year, small yearly increments in growth continued for a few years afterward.

*Atypical tending bonds.* Loose tending bonds were discussed previously in connection with tending among younger buffalo. Other loose bonds occurred at all times during the rut and included all ages of bulls. Loose bonds were marked by close tending that lasted for only a few minutes, by intermittent tending where the bull tended for a few minutes and then moved off to graze nearby for a while, and by lax tending where the bull did not follow closely nor try to control the movements of the cow. Many of these loose bonds involved cows which were not in heat, as determined by the non-swollen condition of the vulva.

Three unnatural tending bonds were observed: On September 20 in Hayden Valley a three-year-old bull closely tended a five-month-old calf for at least 25 minutes. On October 12 near Old Faithful a two-year-old bull closely tended a five-month-old calf for at least 15 minutes. In both of these cases the bulls attempted many mountings. On July 16 a two-year-old bull closely tended a yearling bull for at least four hours in the Wichita Refuge and attempted mounting with penis unsheathed. This was not classed as play, due to the duration and intensity of the tending.

*Heat in cows.* Heat in cows was determined by the condition of the vulva and the tail. The swelling of the vulva in cattle is slight during proestrus, becomes more pronounced during heat, and subsides rapidly after heat has passed (Asdell, 1946: 346; Dukes, 1937: 647-651). The vulvas of buffalo cows swelled into a globular mass that protruded an inch to an inch and a half. The switching of the tail sometimes brushed the lips to expose the red mucosa,

although during heat it was held slightly out from the vulva and seldom switched. Cows with swollen vulvas were vigorously tended by bulls and those with little or no swelling were usually tended loosely or not at all.

A further symptom of heat in cattle is a tendency to mount other cows (Dukes, 1937; Schein & Fohrman, 1955). One two-year-old buffalo heifer in heat in the National Bison Range disrupted the mounting attempts of her tending bull by almost continuously attempting to mount him. She kept this up for at least 30 minutes. In two other cases, a buffalo cow in heat mounted a nearby cow, and another in heat mounted her tending bull.

#### BELLOWING AND SNORTING

*Nature of bellowing.* Bellowing, produced only by bulls, was an extreme variation of the grunt. It sounded like a guttural, growling roar and was unlike bellowing of a domestic bull. The simultaneous bellowing of more than three or four buffalo resolved into a continuous roar. The bellowing bull opened his mouth, stuck out his tongue for a few inches, and contracted his abdominal muscles so that his belly rose slightly.

The sound of bellowing was audible for at least three miles in still air and for lesser distances under windy conditions. Audubon & Bachman (1849: 38) reported this distance as at least ten miles and Hornaday (1889: 416), five miles. I located some groups by the sound of bellowing rather than by sight and assumed that straggling bulls or herds did likewise.

Bellows varied in length from a third of a second to more than five seconds (single breath), in intensity from a very soft purring noise to a loud roar, and in quality. Some of this variation was correlated with the emotional state of the moment. For example, a rapid interchange of loud bellows frequently preceded vicious battles. Exchange bellows were longer and louder between bulls or from a tending bull than those from lone bulls, grazing bulls or those which did not elicit competitive bellowing from others.

Bulls often continued to bellow even while engaged in activities such as running or trotting in a stampede, ruminating, grazing and wallowing.

*Circumstances of bellowing.* Bellowing was frequent during the rut and sporadic or rare at all other times, with a gradation of activity between those two periods. Bulls bellowed under the following circumstances: (1) while tending a cow—loose tending bonds were sometimes characterized by weak bellowing or a lack of it;

(2) while approaching another bull previous to meeting or battle; (3) while moving through a bull subgroup or the herd, accompanied at times by sniffing of vulvas; (4) while following the trail of the herd or moving toward it; (5) in answer to the bellow of another bull, resulting commonly in a constant interchange of bellowing (one tending bull answered distant rumbles of thunder, and another bull answered my crude imitation of a bellow); (7) while another bull was approaching. Some bellowing occurred during other situations, such as standing or lying, that did not fit the above categories. Bellowing subsided partially or completely during periods of lying in the group.

Bellowing was induced among bulls in the Wichita Refuge and once in the Wildlife Park by the observer's approach in an automobile to 25 to 35 feet of a bull tending a cow. The bull looked directly at the car and increased the length and loudness of his bellows for the next 30 to 45 seconds. A few bulls which were not tending cows responded similarly.

Analysis of this incident seems to indicate that the bellow was threat behavior. This was corroborated by instances in which one or more bulls stood and listened to the increase of bellowing of another bull and then retreated from him.

Bellows were never heard from two-year-old bulls and were uncommon from three-year-olds; those from four-year-old bulls were shorter than those from older bulls. Older bulls had lower pitched bellows than younger bulls. Bellowing was comparatively rare among the five- and six-year-old bulls in the Wildlife Park. This may have been correlated with the fact that dominance was well established between the two, and the younger seldom challenged the older during the rut.

*Snorting.* Snorting was produced by the slight, quick contraction of the abdominal muscles to force blasts of air through the nostrils. This sound carried at least 4,000 feet in still air but was difficult to hear under windy conditions unless at close range. Snorting sometimes alternated with, followed or preceded bellowing. It was heard infrequently, and was given most commonly by one bull approaching another previous to meeting but also occurred under the same circumstances listed previously for bellowing. It was quite typical from a lone bull heading toward and entering a cow group. Tending bulls in such a group usually looked toward the snorting bull. This bull often took over another cow by threat alone. One old bull in Hayden Valley shortened the interval between snorts from three seconds to one second as he moved

closer to another bull during the rut. Neither was tending a cow at the time.

#### WALLOWING AND HORNING

*Nature of wallowing.* The great increase in wallowing by bulls during the rut was attributed more to conflict occurring as a result of the rut than to irritation from insects. Wallowing most typically consisted of one to three acts: (1) sniffing of the ground; (2) vigorous pawing with the forehooves; (3) rolling. Rolling and particularly pawing also occurred independently. The bull customarily moved a short distance backward with each pawing. He often unsheathed his penis and urinated a thin stream during the pawing and during and after the rolling. Such urination was quite typical of any hostile situation during the rut. The bull also dug his horns into the ground at times and rubbed his head in the earth after pawing.

Cows showed no noticeable increase in wallowing during the rut. They were observed to urinate pulsatingly and weakly on only three occasions previous to wallowing. In one instance, the act appeared to be a direct reaction to my crawling into the herd under a buffalo hide.

*Circumstances of wallowing.* Bulls wallowed under the following circumstances: (1) as two or more bulls approached each other previous to meeting or battle—lone bulls which wandered within sight of each other often wallowed immediately and simultaneously after catching sight of each other; (2) while tending a cow; (3) while following the trail of a herd, moving toward and entering a herd, or walking through the herd; (4) during "mock battles" (discussed later); (5) previous to a possible meeting with human beings (three occasions); (6) in a wallow in which a cow had been lying, had urinated, or had wallowed a few minutes previously (several bulls sometimes wallowed successively in such a spot); (7) just previous to getting up after lying. These were the usual occasions; a few others were rare.

Bulls used established wallows most of the time but tore up the sod to form new or temporary wallows when a regular wallow was not immediately available. For example, a tending bull wallowed close to his cow, and one bull approaching another wallowed wherever he was.

Bulls pawed vigorously without rolling during the first six circumstances listed above. Pawing was also done by bulls or cows during the following circumstances: (1) by either opponent during a pause in battle; (2) by a mature cow enclosed in a corral when I motioned toward her from a distance of ten feet; (3) by a cow

with a one-hour-old calf when I started to approach her; (4) by a lone cow three hours and five minutes previous to the birth of her calf; (5) by a cow with a two-hour-old calf as a larger cow moved in and licked the calf; (6) by a four-year-old bull as I imitated a bellow from under a buffalo hide; (7) by bulls previous to charging as a result of the approach of human beings (Allen, 1876: 64; Chapman, 1937: 145; Dodge, 1877; Garretson, 1938: 51; Inman, 1899: 249).

A survey of these occasions for wallowing or pawing shows that most of this behavior occurred previous to, during or in anticipation of hostile situations. Such situations presumably involved the simultaneous activation of the drives of attack and escape. The resulting behavior may thus be considered "displacement activities" (Tinbergen, 1952: 24-6), which here will be called "displacement wallowing" and "displacement pawing." Both were a part of grooming behavior and thus were "irrelevant" during hostile situations.

Displacement wallowing differed at times from its genuine "example" of grooming behavior (Section II). It was incomplete since it consisted of pawing alone or was done in areas other than regular buffalo wallows, such as on unbroken, grassy meadows. It was also more vigorous, particularly the pawing. As such it may have been recognizable as threat by other buffalo.

*Horning.* Horning of lodgepole pine trees by bulls increased during the rut. The bulls debarked the trees (Plate III, Figure 6), gouged their horns into them to make gashes as deep as three-fourths of an inch, uprooted smaller trees and thrashed their horns in the branches. Some also butted against or rubbed on the trees.

#### BATTLES

*Preliminaries.* Preliminary to battle, a bull usually indulged in bellowing, snorting, wallowing (pawing and/or rolling) and the *hesitant gait*. Bulls approaching each other at close range used this gait, a modification of walking where but one foot was slowly advanced at a time. All of these preliminaries functioned at times as threat, as evidenced by the fact that one bull yielded to another without battle. If these displays of threat were given by a bull tending a cow, they functioned to warn invading bulls, which in turn were announced by giving such displays. Bulls also threatened others away by using aggressions such as short charges or shaking of the head. Since the response to aggression was often active retreat or passive avoidance, *vicious battles* were uncommon.

*Vicious battles.* Vicious battles differed from

most fighting in their brisk and violent movements, so much so that chunks of sod flew into the air or clouds of dust cloaked the action. These battles started as one bull slowly approached another, as one shook his head toward a close opponent, as one charged toward another and attempted to horn his flanks or crash head-on, or as both bulls were slowly butting and pushing back and forth. Vicious battles consisted of quick horn jabs with thrusts to the side or upward after contact, forceful head-on butting, violent charging back and forth with heads together, and swift routs where one bull was driven backward for several feet (Plate III, Figure 7). There were two instances in which a bull momentarily fell under the powerful charge of the victor. Battles ended as both bulls stopped and remained close together, as both bulls separated, or as the loser backed away from the constant jabs of the victor. Contestants were usually at least four years old. Battles commonly lasted from one to 35 seconds with most ranging from five to ten seconds. A few lasted several minutes with repetition of fighting at intervals. Most battles occurred during daylight hours, yet some took place at night, as shown by the fact that George Mushbach noted new injuries on certain bulls early in the morning. Catlin (1876-II: 13) observed "desperate battle" while a herd was swimming a river.

The shock of these encounters was partially absorbed by the cushion of long hair on the crown. These hairs measured eight to ten inches long on bulls three to eight years old, while Hornaday (1889: 404, 414) measured some up to 22.5 inches. A .30/06 bullet fired into the head of a bull in the Crow Reservation from a distance of 30 feet bounced back from the matted hair and was recovered as a twisted piece of lead.

*Casualties.* Several casualties of battle were recorded. A fourteen-year-old bull was discovered within two hours after death that probably resulted from battle, since he was found in the middle of a small group that was battling viciously and frequently. The only apparent injuries were a bloody wound just below the eye that did not penetrate the skull and a hernia just to one side of the penis. This hernia was seven inches in diameter, protruded 2.5 inches, and had a bloody cut from a horn jab.

Three other bulls found dead in Hayden Valley may have been killed in battle. Rangers Kittams and Coleman discovered two dead mature bulls lying about 20 feet apart in early August, 1939. I found a dead bull at least 16 years old that was killed or died about August 23, 1951.

George Mushbach found three successive casualties of rutting battles in the National Bison Range. All were lying when discovered, yet could rise and walk short distances with great difficulty. The viscera of one were hanging out. All died within a few hours or were so seriously injured that they were shot. In the same range, John Schwartz found a dead bull during the rut. The bull probably died after battle, since he was badly wounded, with the hide torn open in several places and a puncture in one rear leg.

David Pierson saw one bull with a crippled rear leg being killed during a rutting battle in August in the Lamar. The victorious bull lunged for 40 feet with the crippled bull on his horns. He also reported that during the hay-feeding period in the Lamar, two mature bulls first successively and then collectively battled and killed another old bull. Two other deaths in the Lamar were recorded in winter by Baggle (1933). Both of the bulls, "rather old and not in good shape," came to the feed grounds after being absent for a long time. Both were killed by a mass attack of younger bulls ("seven or eight" in one case). Baggle further states that "such occurrences are not uncommon in the buffalo herd even on the summer range."

A mature cow battled a two-and-one-half-year-old bull in January in the Wildlife Park. The bull was not cornered, yet chose to remain and fight back in several battles. He died later from numerous bruises and a punctured lung resulting from a horn jab.

Seton (1929: 689) reports one bull that killed another in a battle in an enclosure in the Philadelphia Zoo in July. Fremont (1845: 26) saved one old bull from certain death in July by dispersing 18 or 20 bulls which were attacking him and which had already knocked him down several times. Hornaday (1922: 296-7) observed one bull kill another in an enclosure in a zoo by puncturing the lungs with horn jabs. He also reports that fatal fights sometimes occurred in the large 27,000-acre reserve of the Corbin Blue Mountain Forest Association. Plate 105 from Catlin (1876, I) depicts a rutting scene with three battles in progress and one dead bull. Several authors believed, however, that death from battle in the wild was non-existent or rare (Allen, 1876: 46; Audubon & Bachman, 1849: 38; Bradbury, 1904; Garretson, 1938: 36; Goodwin, 1939: 366; Hornaday, 1922: 282-3; Inman, 1899: 12; Soper, 1941: 390).

Injuries yield further evidence concerning the violence of vicious battles. Such injuries were noted in bulls butchered during the annual herd reduction in the Lamar. I counted from one to

three healed fractures of the ribs in 23 per cent. of the bulls over four years of age. Other observers noted a similar proportion of healed fractures in bulls and occasionally cows (David Pierson, John Schwartz, Cy Young). Examination during this butchering also revealed that most older bulls had scars on their sides from horn jabs. A few had abscessed sores resulting from horn jabs.

Injuries were also observed in the wild. David Condon discovered one injury probably from battle in the Nez Perce area (Yellowstone Park) on August 22, 1953. A lone, large, mature bull had one horn broken off next to the skull with much blood in this region. Cy Young observed a similar injury during the rut in the National Bison Range. In the same area during the rut, George Mushbach saw occasional lame bulls. They walked with difficulty and had fresh bloody scars.

*Occurrence.* Vicious battles took place under a variety of circumstances. Some involved a bull tending a cow in heat. The victor moved to tend the cow but was occasionally displaced by still a third bull as a result of battle or threat. Other battles occurred without the presence of a cow in heat. "Battle subgroups" formed infrequently. Such a subgroup of several bulls four or more years of age was characterized by numerous battles. One battle subgroup collected immediately after two bulls battled viciously 100 feet from the edge of the herd.

Vicious battles were limited mostly to the rutting period, while less violent, non-vicious battles occurred during all seasons among bulls. These latter battles increased in frequency during the rut and were prevalent among bulls younger than four years. There was no obvious distinction between these battles and those discussed previously as play (Section II).

*Mock battles.* These were so called because they contained many of the preliminaries to genuine battles. Mock battles were seen on five occasions during all seasons between the two older bulls in the Wildlife Park. They were also observed four times in the National Bison Range, once in Hayden Valley and once in Wind Cave. They consisted of bellowing and tail-lifting but usually no fighting. Such battles also exhibited one or more of the following activities: bounding, aimless charges, frolicking, bucking, hesitant gait, arched back, pawing or wallowing, horning and butting a tree.

#### PRECOPULATORY AND MOUNTING BEHAVIOR

*Amatory behavior.* Licking of the cow's fur by the bull was classed as amatory behavior.

This was rare, however. In the most extreme case of such behavior (August 4, 1953, Wichita Refuge), both bull and cow licked each other for at least 90 minutes previous to copulation. This same pair also butted each other head-on gently, and on five occasions the cow mounted the bull for a few seconds with no thrusting. Another case involved the same cow which was discussed previously as mounting her tending bull almost continuously (National Bison Range). She also licked the sexual organs of this bull.

*Incompleted mountings.* Attempted mountings by bulls tending cows were of regular occurrence. These showed three degrees of completeness:

1. The bull merely swung his head toward the cow, usually without being in a position for proper mounting. The cow turned away.
2. The bull put his chin on the cow's rump and the cow moved out from underneath. His penis was sometimes unsheathed.
3. The bull mounted the cow with his forelegs around her rump, but she dodged out. Unsheathing was typical here.

Some bulls made short panting sounds just before attempting to mount, lasting at times until the bull put his chin on the cow's back. The sounds were so soft that they would not be heard more than 20 to 100 feet from the bull. They seemed to forewarn the cow, which sometimes prematurely dashed away from the bull as a result.

*Completed mountings.* The following data on completed mountings were compiled from six observations (mountings lasted for so few seconds that many were probably missed because another section of the herd was being watched). The bull swung up onto the cow by using his chin as a lever on her rump. He then pressed his forelegs together in front of her hips and his head against her side. He remained mounted for four to ten seconds and thrust steadily. The mounting ended either when the bull voluntarily dropped off or when the cow walked out as the bull released his grip.

After copulation, the cow characteristically moved a few feet ahead and voided a pulsating stream of milky urine. She also kept her tail lifted up in the air, lowering it gradually during the next few hours.

Cows suffered occasional injuries from the rough treatment of the bulls during mounting. Close observation in the National Bison Range (Hugh Wilmar) revealed fresh, bloody wounds on several cows. The injuries were always on the

same area on the flanks, where the front hooves of the bull would strike in the mounting position.

As soon as one bull mounted his cow, other bulls in the herd converged on the pair and followed them for some time afterward. All of these investigating bulls were not tending cows at the time and were generally younger than six years. As many as nine bulls followed one tending pair as it left one group and wandered toward another. The tending bull remained with the cow in all observed cases and sometimes repelled nearby bulls with threat, short charges or vicious battles.

Masturbation was observed on four occasions when a bull unsheathed his penis, moved his hind quarters as though thrusting in copulation, and ejaculated.

#### BULL GROUPS DURING THE RUT

Even though most groups of older bulls joined the cow groups during the rut, a few parties of one or two older members still remained apart. Some of these bulls stayed in approximately the same area for several days and probably never joined the cow groups. Others circulated more freely between cow groups and bull groups. Stray bulls lay down or grazed from 100 feet to a mile distant from the main herd and also straggled after the traveling herd. They followed the trail of the herd several hours later by sight, sound or scent, and often joined the herd. Some bulls passed near the herd, looked or listened momentarily, and then passed on by. Bulls also voluntarily left the herd, and some returned again within a few hours.

There were four observations where a bull voluntarily left the herd after a battle and two observations where a bull which was not tending a cow kept another bull outside the herd by threat. There was no indication that such "outcast" bulls could not enter the same group a few hours later or enter any other group. The unsubstantiated convictions of several authors (Goodwin, 1939: 366; Inman, 1899: 231, 235; Seton, 1929: 690-1; Soper, 1941: 389, 392-3) that lone bulls are outcasts driven from the herd is further refuted by the evidence that bulls circulated freely during the rut. The view of Dodge (1877) is more logical: "The old bulls do undoubtedly leave the herd . . . but I am disposed to believe this to be due to a misanthropic abnegation of society on the part of these old fellows, to whom female companionship no longer possesses its charm, rather than to their being driven out by the younger bulls, as is generally believed." Allen (1876: 55) and Garretson (1938: 37) also corroborated this interpretation. It is

my opinion that such isolated bulls remained temporarily or permanently separate from the cow groups as a result of choice or physiological reasons rather than aggression of other bulls. (Permanent isolation of a few such bulls was suspected yet never adequately proved).

Many of these isolated bulls during the rut were quite tolerant of human intrusion. Some ran 50 to 100 feet after first catching sight of human beings but then paid little attention. A few were extremely stubborn and could not be moved from their location with considerable noise or disturbance, such as shouting or rock throwing.

### VII. REPRODUCTION AND FAMILY RELATIONS

#### PARTURITION

*Calving season.* The main calving season in the Lamar Valley ran from April 15 to May 31 with a greater concentration of births in the central two weeks of this period. The season was similar in the Wildlife Park and Wind Cave. A scattering of calves nevertheless arrived outside of this main season in most of the herds studied.

A few calves were born from June through October in all Yellowstone Herds, the Crow Reservation, Wind Cave and the National Bison Range. Audubon & Bachman (1849: 47) reported that one cow found ready for calving in August "was an extraordinary circumstance at that season of the year." Rush (1932) autopsied 185 cows in the Lamar in December, 1931, and noted a "great variance in the size of the fetuses," indicating an extensive calving season.

Birth of calves during the winter season of November to March occurred at least five times in the Yellowstone Herds and once in the Niobrara National Refuge. Both Roe (1951: 94, 98) and Aubrey (1908:133) mentioned rare instances of winter calving. Seton (1929: 672) described one calf that was born and survived during January, 1884, when the temperature was  $-38^{\circ}\text{F}$ .

*Reproductive data on cows.* Cows were sexually mature at two years and calved at three years, according to data in Table 10 and observations in all herds. Cy Young and George Mushbach, however, noted rare cases in the National Bison Range and on neighboring ranches where two-year-old cows gave birth to calves. Negus (1950) states that cows do not bear young until they are four years old, but his findings are inaccurate, since they were based on inconclusive evidence from the Wildlife Park Herd.

Table 10 also shows that incidence of preg-

TABLE 10. RECORDS OF PREGNANCY IN 125 COWS  
AUTOPSIED IN OCTOBER 1950-1953  
(National Bison Range 1950-1953)

Age of cow	Size of sample	Per cent. pregnant
2	12	92%
3	5	80%
4	2	100%
5	6	100%
6	7	86%
7	2	100%
8	9	78%
9	5	80%
10	14	85%
11	1	100%
12	7	85%
2-12	70	87%
15-18	22	77%
19-24	19	58%
25-35	14	21%

nancy declined gradually after an age of 12 years and markedly after 24 years. Two cows, however, were lactating and one was pregnant in a group of five cows more than 30 years of age killed in the National Bison Range in 1951. Burns (1953: 128) reports that slaughter of the herd in Wainwright Park, Alberta, showed that several of the cows earmarked 40 years earlier were accompanied by calves.

Most cows bore one calf every year, although David Pierson observed one set of twins within about five days after birth in the Lamar Valley in 1953.

Barrenness in cows was not necessarily an individual trait that appeared yearly. Evidence for this lies in an analysis of both pregnancy and lactation during slaughtering. Eighteen per cent. of 61 cows (National Bison Range, 1941-1953) and 24 per cent. of 206 cows in the Lamar Herd (Rush, 1932) were lactating and yet not pregnant when autopsied on October-December. The few out-of-season pregnancies discussed previously might account for a very minor part of these percentages.

The gestation period is reported as nine months (Brown, 1936), 270 to 300 days (Burns, 1953: 199), and 9½ months (Seton, 1929: 695).

*Ratios for calves.* Calf ratios are defined as that percentage of a group of buffalo bearing calves. They are recorded in Table 11.

Sexing of 1,465 calves during the fall and early winter of twelve years (National Bison Range, 1941-1953) yielded a male:female ratio of 50.4: 49.6. The same ratio for cattle is listed as 52:48 (Crew, 1925:255). In spite of this

almost equal sex ratio for buffalo, three of the more divergent years yielded distinctly unequal ratios: 132 calves in 1950 had a ratio of 57:43, 100 in 1949 had 55:45, and 109 in 1942 had 42:58.

*Preliminaries to parturition.* The pregnant cow was restless and wandered in short trips away from the herd for one to sometimes several days previous to calving. Physical changes previous to parturition included a viscous, mucous discharge from the vagina, swelling of the vulva into a heart-shaped, flaccid mass, and filling of the udder.

One pregnant cow was observed at close quarters in the Wildlife Park (field notes from James R. Simon). Three hours and 24 minutes previous to parturition she humped her back in a strained fashion while standing. There was a leakage of about three ounces of a thin, almost clear fluid from the vagina following this labor and again after 20 minutes. Five minutes later she pawed and rolled and then horned a small pine tree quite viciously.

One pregnant cow was harassed for five hours previous to calving by a three-year-old bull which licked and nosed her vulva. Other herd members occasionally sniffed the vulva of cows soon to calve.

*Parturition.* Cows gave birth to calves either when separated completely from cow groups or when in them. In the latter case, the groups were usually smaller and composed of several cows which either were pregnant or possessed young calves. Some authors similarly concluded that cows gave birth in or out of the herd (Aududon & Bachman, 1849: 37, Hornaday, 1889: 425; Roe, 1951: 98) while others maintained that cows regularly separated from the herd to give birth (Aubrey, 1908: 133; Grinnell, 1904: 132; Seton, 1929: 695; Soper, 1941: 391; Stone & Cram, 1902: 69).

The following data on the birth of calves were compiled from notes on two calves observed in parturition (field notes of James R. Simon).

The two calves were born when the cow was flattened on her side with legs and neck outstretched. The neck was strained dorsally and the upper hind leg was kicked violently upward and forward a few times. One calf was born in 20 minutes and the other in 27 minutes. Each cow broke the umbilical cord as she rose from the ground after parturition. The amnion ruptured about the head of one calf but tightly enclosed that of the other. Both cows immediately devoured these membranes and a part of the umbilical cord to within a few inches of the calf. The umbilical cord shriveled and dried several hours after birth.

TABLE 11. CALF RATIOS IN VARIOUS HERDS

Locality	Date	Calf ratio	No. adults sampled	Source of data
Percentage of Entire Herd with Calves				
Hayden Valley	Sept. 4, 1951	25%	384	Ground observ. (McHugh)
Hayden Valley	Mar. 1, 1950	22%	301	Aerial survey (YNP)
Hayden Valley	Mar. 7, 1949	18%	312	Aerial survey (YNP)
Lamar Valley	May 29, 1945	20%	495	Aerial survey (YNP)
Wood Buffalo Park	Feb. 1948	8%		Fuller 1950
Wood Buffalo Park	Nov. 1932-33	15%	605	Soper 1941
Percentage of Cows Two or More Years Old with Calves				
Hayden Valley	Jun. 15, 1951	63%	70	Ground observ. (McHugh)
Hayden Valley	July 11, 1951	65%	92	Ground observ. (McHugh)
National Bison Range	Fall 1952	78%	119	Census (NBR 1952)
National Bison Range	Fall 1951	64%	128	Census (NBR 1951)
National Bison Range	Fall 1950	75%	177	Census (NBR 1950)
National Bison Range	Fall 1949	64%	229	Census (NBR 1949)
National Bison Range	Fall 1948	63%	250	Census (NBR 1948)
National Bison Range	Fall 1947	72%	233	Census (NBR 1947)
National Bison Range	Fall 1943	68%	204	Census (NBR 1943)
National Bison Range	Fall 1942	55%	199	Census (NBR 1942)
National Bison Range	Fall 1941	61%	183	Census (NBR 1941)
Lamar Valley	Winter 1932	69%	250	Tunnickliff Marsh 1935
Lamar Valley	Winter 1931	55%	469	Tunnickliff Marsh 1935
Percentage of Cows Three or More Years Old with Calves				
National Bison Range	Oct. 1953	95%	87*	Census (NBR 1953)

\*Only seven cows older than nine years in this group.

Expelling of the afterbirth was observed in only one cow, which expelled these tissues about one hour after birth and devoured them.

*Early life of the calf.* The cows licked their calves almost constantly for at least the first 10 to 25 minutes after birth. The wet hair on the calf dried within an hour.

One calf first stood up after 18 minutes and another after 28 minutes following birth. The first attempts at standing by new calves usually soon resulted in collapse again, mainly due to the weak, bowed legs. One calf tottered over on its chin and another somersaulted back on its rump. Not only did the calves have difficulty rising, but some also showed a lack of coordination in lying for the first time. The first attempts at walking involved small, spider-like steps and a wavering gait.

The earliest attempts at bucking occurred 70 minutes after birth. Within 180 minutes one calf playfully ran in circles and bucked around its mother. Another calf kicked its hind legs in the air at an age of about 100 minutes.

All calves tried to nurse soon after standing

but most failed at first, since they pushed their mouth up between the front legs. A close observation showed that one calf continually moved its tongue in and out while trying to nurse in front and in back. Another failed in an early attempt between the hind legs because it probed too low. No cow made an effort to direct the nursing attempts of her calf.

As each calf grew older, various transformations were evident. At an age of about four to six days the calves started to graze. At about nine to ten weeks the reddish-orange pelage started to darken. The moult to a dark brown color was largely complete five weeks later. At two to three months the grunting started to lose its nasal quality and become more mature-sounding.

#### RELATIONSHIPS BETWEEN COWS AND CALVES

*Cohesion.* For the first few days the calves remained particularly close to their mothers, often running to keep just ahead of the moving cows. The calves were closer to the cows during direct movements than at other times. Calves younger

than two or three weeks generally lay down within a few feet of their cows, while older calves often lay down farther away, sometimes in calf subgroups. Up to an age of eight to twelve months cohesion between cow and calf was sufficiently evident to identify each pair during most periods of the day.

After this age the attachment between the two weakened considerably, particularly with bull calves. Aggressive displays by a cow toward her calf-yearling were rare before the birth of the new calf but became frequent and firm within a few days after the new calf arrived. Mild aggression toward other nearby yearlings and two-year-olds also became more frequent. A few calves—more heifers than bulls—followed their cows for more than a year and infrequently for more than two years.

Recognition between calf and mother depended upon scent, sight or sound. Cows on seven occasions identified their own calves mainly by scent when they sniffed closely one or two strange calves and then sniffed and stayed with the last calf, their own. Cows also commonly sniffed their calves when returning to them after grazing. Instances of recognition by scent were rare for calves older than one month. Cows also identified their calves by sight or sound when they proceeded directly to their own calf or chased away a strange calf. Recognition by grunts without aid of sight showed that some grunts were distinctive. This was observed on four occasions between a cow and her calf and on one occasion between two calves.

Calves identified their mothers largely by sight. They searched for and then moved directly toward their mother, avoiding strange cows after one glance. Scent and sound also appeared to play a part in some recognitions, but my observations here are incomplete.

The cohesion between mother and calf sometimes resulted in the calf's controlling the mother's movements. Cows moved faster or farther at times due to the sudden advances of their calves. At other times, the calf detained its mother by failing to get up.

Cohesion between mother and calf was further demonstrated by the start or intensification of grunting between the two under the following circumstances: (1) by a mother when her calf strayed away; (2) by a mother during moments of danger, such as the approach of a foreign animal; (3) by a calf when its mother strayed away; (4) by either calf or mother when one was separated artificially from the other; (5) by mothers or calves during herd movements, with a distinct increase in grunting synchronized with

the movement; (6) by mothers when a wide river was to be crossed (Aubrey, 1908: 133); (7) by either in answer to the other, with the possibility of an interchange of grunts; (8) by either prior to nursing (discussed below). The customary result of grunting under these conditions was a closer grouping between mother and calf.

*Defense of the calf.* Mothers never abandoned their calves or hesitated to defend them against approaching animals or human beings by quick charges or slow advances. Mothers were seen to make twelve attacks against human beings, five against horses, two against ravens, one against a pronghorn and one against a porcupine.

Many authors have noted this characteristic of the buffalo cow to defend her calf against marauding animals and human beings (Aubrey, 1908: 133; Audubon & Bachman, 1849: 37; Allen, 1876: 58; Garretson, 1938: 39; Grinnell, 1904: 133; Hornaday, 1889: 432; Inman, 1899: 58, 135, 154, 205; Seton, 1929; and Stone & Cram, 1902). The picture is not complete, however, without note of the numerous records where the cow abandoned her calf when the calf either fell behind on a long chase or was roped from the herd (Bradbury, 1904: 84; Dodge, 1877: 124; Garretson, 1938: 61; Grinnell, 1904: 133; Hornaday, 1889: 396, 400; Inman, 1899: 62, 67, 76-80). Coues (1897: 177) and Inman (1899: 141) recorded one instance each where a cow later returned to look for her calf, which had dropped behind the herd on a long chase.

I observed no cases in wild herds where a bull defended a cow or calf. In fact, such defense would have been quite unlikely since older bulls did not join the cow herds until most calves were at least five weeks old (discussed further in Section IV). This lack of defensive behavior by bulls is surprising in view of the numerous records of it in the literature (Branch, 1929: 7; Catlin, 1876: I: 255; Dodge, 1877: 124-126; Garretson, 1938: 39; Hornaday, 1889: 433; Inman, 1899: 248; Seton, 1929: 695; Soper, 1941: 391).

Interesting in this connection is one case in the Wildlife Park where a lone calf was trapped inside a corral. The entire herd, including two older bulls, clustered about the calf and could not be chased away. This incident and the lack of personal observations on defense of calves by bulls accords well with Grinnell's (1904: 134) comment: ". . . it is true that a group of buffalo, if one of their number is attacked or threatened by wolves while they are close together, will all rally to the general de-

fense, and will stand by each other. But that bulls make it their business to defend calves . . . I do not believe."

Calves aided their own defense in three ways: (1) they often quickly moved close to their cows when approached by a strange animal or human being; (2) they occasionally counter-attacked; (3) they uncommonly hid themselves.

A two- to four-day-old calf that was captured and placed in a corral charged and butted whenever pursued by a human being. The butting was so gentle that no injuries resulted. Hornaday (1889: 396) described one captured calf that firmly butted horses and any person who approached it. Four other calves that were tied by the neck charged any approaching persons and butted hard enough to knock a man off his feet (Inman, 1899: 134, 138).

One calf hid in foliage in much the same manner as an elk calf (James R. Simon). This calf was missing when the herd in the Wildlife Park was driven by several men from the winter area to the display area on June 7. The cow was allowed to return into the area 28 hours later. She went directly to her calf, which was lying close to a log. A thorough search had failed to reveal the calf, and it did not stir in spite of the fact that one person had stepped ten feet from it. Similar reports of calves hiding are uncommon (Allen, 1876: 67; Catlin, 1876, II: 50, 255; Coues, 1897: 177; Grinnell, 1904: 132, 146).

*Nursing.* In the customary position for nursing, calves faced to the rear while alongside the cows, but some calves also infrequently suckled from between the hind legs. Calves after six days of age occasionally roughly jabbed the udder.

Up to an age of three months, calves suckled for eight to ten minutes at a time. This period dropped gradually to about four minutes at five months and slightly more than three minutes at six months. An examination of cows slaughtered in the Lamar (David W. Pierson; Rush, 1932: 372), coupled with field observations, indicated that most cows suckled their young for seven to eight months. Hornaday (1889: 426) mentioned nine or more months, but Roe's (1951: 98) figure of three or four months is incredible.

Eight instances in which a yearling nursed a mature cow were observed in Yellowstone Park and Wind Cave between May 7 and July 14. Duration of the suckling was two to eight minutes with a mean of four minutes. These yearlings were allowed to suckle unmolested until the end of these periods. None of the cows had calves, although at least two of them were pregnant and would calve soon.

*The cow-with-calf subgroup.* Cows with their calves often came together to form one or several subgroups within the groups. They moved either within or at a short distance from the edge of the group. Sometimes calves initiated these smaller units, acting as a nucleus to which all mothers returned after grazing. Cow-with-calf subgroups were most obvious through July but continued at least into September.

With the arrival of the first calf in each cow group, the flight distance of the group became greater than at any other time. The group moved away more quickly and for a greater distance when disturbed. Withdrawals were usually initiated by cows with calves, but sometimes by animals in advanced pregnancy. The increase in wariness was most noticeable in the Wildlife Park, where the herd that normally tolerated approach within a few feet stampeded whenever it caught sight of human beings at distances up to 500 feet. This wariness subsided greatly by the end of May.

During the entire summer, however, stampedes away from human beings in Hayden Valley were often led by a cow with a calf. Stampedes away from people in the Crow Reservation were led in about 85 per cent. of 34 cases by mature cows, most of which possessed calves.

#### RELATIONSHIPS BETWEEN CALF AND GROUP

During the first few hours after the birth of a calf, several group members characteristically came over to investigate. They looked at the calf, sniffed it and licked its fur. These curious buffalo were of all ages and both sexes, and included cows which already had calves. They seldom investigated the calf in this manner after its first day. The mother generally tolerated these buffalo, yet sometimes chased them away if they were subordinate to her in the group hierarchy.

At two or three weeks the calf's cohesion for other calves began to compete with that for its mother. This was shown by the frequent occurrence of calf subgroups, an increase in communication between calves, and instances in which a calf voluntarily returned to the calf subgroup when both mother and calf were temporarily separated from the herd. Grunting by calves and occasionally by older animals in juvenile subgroups increased when one or a small group was detached or was separating from another. The grunting often resulted in one section rejoining the other. Of interest in this regard is Allen's (1876: 207) description of how an Indian, disguised under a buffalo hide, "bleated like a calf" to decoy a herd of buffalo into a

pen. Other Indians on foot and on horse helped drive the herd.

Calves also had interactions with strange buffalo. Four instances were observed where calves of ages of 30 minutes, one day, two days, and 20 days, started to nurse the wrong cow. On three occasions a very young calf was seen to follow an animal other than its mother for a few minutes. One thirty-minute-old calf followed a strange cow that was sniffing it. Its mother tried to retrieve the calf by driving off other cows but did not succeed until the strange cow lost interest in the calf. Again, when a yearling bull sniffed and then started to walk away from a calf about 5½ hours old, the calf followed. The bull trotted away and then butted the calf, which persisted in following. The cow also followed, but the calf did not return to her until the group stopped after trotting about 100 feet. Still another calf about one day old started to follow David Pierson when he was riding a horse through a Lamar group. The calf followed so persistently that it had to be roped and taken back for release near its cow.

These three incidents are interesting when compared with historical accounts of capturing young calves by separating them from the herd and then letting them voluntarily follow the horse and rider into camp (Audubon & Bachman, 1849: 47; Catlin, 1876: 255-6; Coues, 1897: 176; Garretson, 1938: 40, 61; Hornaday, 1889: 398). Hornaday and Audubon thought that following was induced by letting the calf suck on one's finger, while Catlin recommended breathing into the nostrils of the calf.

## VIII. ECOLOGICAL RELATIONS OF BUFFALO

### RELATIONSHIPS WITH OTHER ANIMALS

An animal as large and, under some conditions, as numerous as the buffalo inevitably affects the lives of birds and other mammals sharing the habitat. Such an influence works both ways, and we here examine the relationships between the buffalo and other animals.

*Buffalo birds.* "Buffalo birds" is the term loosely but generally applied to the various birds that gathered about buffalo. Listed in order of decreasing abundance, they included cowbirds (*Molothrus ater*), Brewer's blackbirds (*Euphagus cyanocephalus*), starlings (*Sturnus v. vulgaris*), redwings (*Agelaius phoeniceus*) and magpies (*Pica pica hudsonia*).

Friedmann (1929: 289) mentions that motions of the buffalo flush grass-inhabiting insects

and thus render them far more available to the birds. Birds were frequently seen feeding on flushed insects within a few inches of the heads or feet of grazing or walking buffalo.

The birds frequently lit on and rode the backs of moving buffalo, sometimes crouching low and firmly grasping the fur to keep from being jostled off. They readily clung to the backs of walking buffalo but flew off when the gait became faster. Buffalo sometimes swung their heads around toward the birds to dislodge them. Older bulls were most tolerant—five cowbirds were seen roosting on the back of one old bull. Three Brewer's blackbirds roosted on the backs of buffalo during a severe rain storm. In winter birds sank low into the fur on the buffalo's back and fluffed out their feathers. Seton (1929: 685) recorded a cowbird that slept at night in a hollow in the fur behind the horn of an old bull.

The buffalo birds also fed on invertebrates that were attracted to the buffalo. One cowbird walked all over the head, horns and body of a sleeping bull to feed for 35 minutes on swarms of flies. Other birds occasionally picked in the fur, presumably taking insects, and fed in the grass around resting buffalo. Magpies sometimes tried to pick open sores, but the buffalo prevented this by rolling the body or swinging the head. Audubon & Bachman (1849: 46) described magpies picking the scabs or sores of buffalo emaciated by a hard winter.

The relationship between buffalo and buffalo birds is thus a mutualism. The bird benefits from an increased food supply and a roost, while the buffalo benefits to a much lesser degree by the removal of flies or external parasites. In no case did the birds warn the buffalo of danger, so far as could be seen.

Ravens (*Corvus corax*) followed buffalo at times, particularly during the calving season. They closely approached newborn calves, possibly in search of the eyes, a fondness for which they have often demonstrated (Aldous, 1942). They also scavenged on the remnants of the afterbirth.

*Prairiedogs.* Buffalo in Wind Cave frequented the towns of prairiedogs (*Cynomys ludovicianus*) more than the surrounding grassland. They may have preferred the numerous bare areas around the mounds for lying and wallowing or the greater variety of forbs in the town. The prairiedogs disappeared into their burrows during moments of great activity in the herd, such as during battles, wallowing or rapid herd movements, but came out again and fed without showing any fear when the buffalo were grazing or lying quietly. Resting buffalo sometimes covered

and thus sealed off a prairiedog burrow for as long as two hours.

Wallowing caused the most disturbance in prairiedog towns, since the buffalo often selected the bare areas around the burrows. Their pawing, horning and wallowing tore up the craters and sometimes filled in the burrows. Prairiedogs rebuilt the craters but could not keep repairs ahead of the constant destruction in some of the more heavily-used wallowing areas. As the width of the wallow increased it was used even more frequently. The prairiedogs usually abandoned burrows in such areas (King, 1955).

*Predators.* Grizzly bears commonly hunted over meadows in Hayden Valley. They usually came out of the timber at dusk and returned within a few hours after dawn, yet were seen during all hours of the day, particularly in spring or fall. When a female grizzly and three cubs hunted and captured a hidden elk calf within 700 feet of a buffalo herd of 78, the herd paid no attention to the bears. Catlin (1876-I: 254), Goodwin (1939: 369) and Soper (1941: 403) noted a similar indifference to wolves close to the herd. No definite grizzly kills were ever discovered in Hayden Valley, although the bears obviously had devoured one old bull, the cause of whose death was unknown, and another bull killed in battle. Approximately one per cent. of the buffalo in Hayden Valley had one shriveled rear leg, an injury that could have been caused by bears. Four buffalo were seen with claw-mark scars on their flanks or legs, probably from grizzlies.

Way (1951) presented circumstantial evidence for the killing of a grizzly by a buffalo in the Lamar Valley of Yellowstone Park on about June 7. The badly mutilated carcass of a mature female grizzly bear was discovered three or four days after death.

Coyotes occasionally lay within a few feet of buffalo herds, closer in winter than in summer. It is conjectured that they caught mice that were trapped in pits in the snow left by the feeding herd, but there is no observational evidence to support this theory. Joffe (1931) discovered the remains of a calf in the Lamar Valley that had been devoured by 10 or 12 coyotes. Whether it had been killed by the coyotes or died from natural causes was not determined. Buffalo killed a coyote on two occasions in the National Bison Range, according to Cy Young. As the coyote tried to move through the middle of the herd, the buffalo closed in and trampled and horned it.

*Miscellaneous associates.* Piles of buffalo dung increased the invertebrate population, for they

were the only droppings in the area that remained moist inside and underneath for several months. They were frequented most by numbers of Coleoptera and Diptera. Unusually large droppings, some of them ten inches tall, were used as singing perches by Western meadowlarks and possibly other prairie birds. Buffalo chips, as the dry dung is called, were an important source of fuel for pioneers on the treeless prairie.

Tufts of shed buffalo hair commonly clung to low-hanging pine branches. Buffalo fur was found in a red squirrel nest and was probably used in the nests of many other birds and mammals.

#### INTERRELATION WITH VEGETATION AND SOIL

Buffalo wrought their most conspicuous change on the vegetation of Hayden Valley by horning the lodgepole pine (Plate III, Figure 6).

In a 12 by 150-foot sample strip of 68 lodgepole pine, 51.4 per cent. of the trees was horned. The proportion of the circumference horned ranged from two per cent. to 100 per cent. with a mean of 49 per cent. The vertical range of the horning was from 0 to 62 inches with a mean of 11.4 to 42 inches. Of those trees horned, 14.3 per cent. died and another 8.6 per cent. were completely debarked within the past few months and probably would die shortly. Trees not horned in this sample area were usually in closely-spaced clusters of two or more, a pattern of grouping that made access by the buffalo difficult. The converse of this is also true—solitary trees were most apt to be horned. Numerous low branches did not hinder the horning.

This sample strip of horned trees was located at the edge of a much-frequented meadow near the junction with a main trail. There was an above-average amount of horning. In localized strips such as this, the reproduction of lodgepole pine was completely stopped and the tree line in rare cases was moved back. But a survey of the extensive border of pine in the entire valley showed that the over-all effect on the reproduction of pine was minor. Moss (1932: 405-6) reported that the buffalo was doubtless an important factor in checking the invasion of prairie by aspen.

Buffalo also helped to disseminate seeds. The fur, particularly the long hair on the head and legs, of several buffalo in Wind Cave was thickly clotted with cockleburrs. The seeds of St. Johnswort (*Hypericum perforatum*) were also found clinging to buffalo fur. Superintendent John E. Schwartz of the National Bison Range believes that this weed was spread through that area by buffalo.

Buffalo affected the soil with their droppings, trails, wallows, and feeding patterns.

Droppings served as fertilizer and were of greater importance in areas of heavy concentration, such as on tops of ridges.

Trails were cut deeply into the sod by the constant trampling, as deep as 28 inches below the sod for one trail in Hayden Valley. Such trails then started other disturbances in the soil; they eroded still more deeply, particularly on steep slopes. They occasionally acted as drainage canals to lower the water table in uphill areas and thus eventually produce a change in vegetation. Trails cut near the top of steep, sandy hills initiated washing and slippage of sand to create barren areas.

Buffalo also caused erosion in other ways. Wallows on hillsides sometimes started eroding gullies. Concentration of buffalo on south-facing, wind-blown ridges in winter produced almost complete denudation of vegetative cover. Such areas then eroded badly.

#### SUMMARY

- A. Behavior of buffalo was studied in free-ranging and fenced herds in Yellowstone National Park, the Jackson Hole Wildlife Park, Wind Cave National Park, and other areas.
- B. Some general characteristics of buffalo were noted: They most typically grazed all their forage, browsing only infrequently. Forage in winter was reached by clearing the snow with a swinging motion of the head, only uncommonly by pawing with the forehoof. Vocal expression consisted of grunting, belching and occasionally some snorting and sneezing sounds. Buffalo relied most on acute sense of smell for detecting danger. Play among buffalo involved battling, mounting, frolicking, bucking, or a combination of these.
- C. In locomotion, buffalo use four principal gaits—walking, trotting, galloping and bounding. In bounding, they spring ahead by the more or less simultaneous flexing of all four legs. Their trails were considered to be the most practical routes for cross-country travel by human beings, though not necessarily the most precisely engineered routes. For example, such trails customarily took a gradual climb up most hills yet cut steeply up and down others in order to achieve a more direct route.
- D. The leader of a moving herd was usually a cow, but several individual cows changed in this position so that there was no exclusive leader. No leader was apparent in some mass-action types of travel.
- E. Groups of buffalo were classified into two types according to composition.
  1. Bull groups contained mature males with an infrequent female. They were small clusters of one to 12 members, most of whom were four or more years old.
  2. Cow groups contained a majority of females and a smaller number of males, mostly younger bulls. They averaged 23 members during the non-breeding season but increased in size during the rut, when many cow groups coalesced and were joined by bull groups. Cow groups during the non-breeding season were composed of cows, yearlings, calves, two-year-old bulls, some three-year-old bulls, and rarely bulls four or more years old.
  3. Cow and bull groups broke into smaller subgroups of similar or random age and sex classes. These were spatially distinct from other subgroups in the area.
- F. Observation of interactions between individuals of the Jackson Hole Wildlife Park Herd revealed a linear type of dominance hierarchy with dominant individuals exercising a virtual constancy of success.
  1. Such interactions were classified into passive dominances (72.8%) and aggressions (27.2%). Aggressions included at times, as an indication of dominance, the intention movement for mounting.
  2. Permanent changes in the hierarchy resulted from the differential growth of bulls and cows. Two yearling bulls grew to about the same size as three two-year-old heifers during the summer of 1951. Previously subordinate to all older cows, these two bulls then advanced above all cows in the next few months. Their irregular gain in dominance produced eight triangles, which finally straightened out.
  3. Dominance among calves developed slowly, with the first definite signs noted at an age of four months. At about nine months, five calves demonstrated a pentagonal hierarchy.
  4. The interspecific dominance hierarchy in the Wildlife Park showed the following order: adult human beings > buffalo > elk > mule deer > pronghorn > moose or whitetail deer.

- G. The rut was delineated by a marked increase or the onset of the following activities among bulls: sniffing of vulvas, tending of cows, bellowing, wallowing, horning, vicious and non-vicious battles and incomplete or fertile mountings.
1. Bulls customarily extended the neck with upcurled lip after sniffing a vulva.
  2. The rutting bond between bull and cow was called a tending bond and resulted in a temporary monogamous mateship. Heat in cows was detected by swelling of the vulva and a slight elevation of the tail.
  3. Bulls bellowed frequently during the rut, typically as a display of threat.
  4. Wallowing by bulls was attributed to tension between bulls rather than to irritation from insects. It was thus considered a "displacement activity" occurring during situations involving the simultaneous activation of the drives of attack and escape.
  5. The vicious battles of the rut differed from other fighting in their brisk and violent movements. Injuries were of regular occurrence and occasional deaths were recorded.
  6. Bulls circulated freely among herds. Lone bulls were apparently not outcasts but voluntary isolates.
- H. Most cows were sexually mature at two years and calved at three, although a very few calved at two. Incidence of pregnancy declined gradually after an age of 12 years. Cows gave birth to calves when isolated from cow groups or when with them. Mothers defended their calves vigorously.
- I. Relations with the environment.
1. Buffalo influenced various birds and mammals living near them, and these animals sometimes affected buffalo in return. "Buffalo birds," the species gathering about buffalo, included cowbirds, Brewer's blackbirds, starlings, redwings and magpies. Buffalo damaged prairiedog mounds by repeated wallowing on them.
  2. Buffalo wrought their most conspicuous change in the vegetation of Hayden Valley by horning the bark of lodgepole pine. They also influenced the soil with their droppings, trails, wallows and concentration of grazing in certain areas.
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## EXPLANATION OF THE PLATES

## PLATE I

- FIG. 1. A series of heads from cows slaughtered in the Lamar in January, 1952. Each age indicated on the photograph is represented as that at the approaching calving season (April-May).
- FIG. 2. A series of heads from bulls slaughtered in the Lamar in January, 1952. Each age indicated on the photograph is represented as that at the approaching calving season (April-May).

## PLATE II

- FIG. 3. Two calves butting head-on in play in

Yellowstone Park. (Photograph by courtesy of Yellowstone National Park).

- FIG. 4. One young bull mounting another in play. (Photograph by courtesy of Yellowstone National Park).

## PLATE III

- FIG. 5. A bull extending neck with upcurled lip after sniffing a stream of urine from the adjacent cow.
- FIG. 6. A bull debarked this lodgepole pine by horning it during the rut in Hayden Valley.
- FIG. 7. Two bulls engaged in a vicious battle in the National Bison Range. (Photograph copyright by Walt Disney Productions).

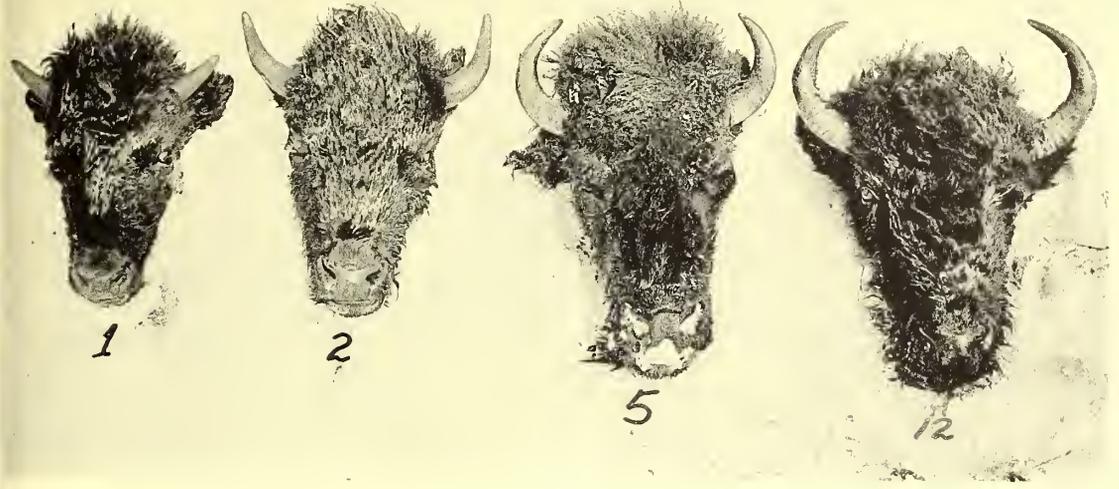


FIG. 1



FIG. 2

SOCIAL BEHAVIOR OF THE AMERICAN BUFFALO (BISON BISON BISON)





FIG. 3



FIG. 4

SOCIAL BEHAVIOR OF THE AMERICAN BUFFALO (BISON BISON BISON)





FIG. 5



FIG. 6



FIG. 7

SOCIAL BEHAVIOR OF THE AMERICAN BUFFALO (*BISON BISON BISON*)



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## 2

# The Iguanid Lizard Genera *Urosaurus* and *Uta*, with Remarks on Related Groups

JAY M. SAVAGE

Department of Biology, University of Southern California, Los Angeles 7, California

(Text-figures 1-6)

IN the course of studies leading toward a re-evaluation of the supraspecific units within the lizard family Iguanidae it seems expedient to pause from time to time and make available portions of the completed work. It is hoped that these progress reports can eventually be correlated with additional material to form a comprehensive revision of the family. This paper is the second of a series pertaining to the systematics of the Iguanidae.

### STATEMENT OF THE PROBLEM

Until recently all North American iguanids with a well-developed gular fold, a large rostral scale, non-imbricate supralabials, imbricate superciliaries, large and regularly arranged upper head shields, a large interparietal scale, a well-defined ear-opening, sternal fontanels and with the parietal organ consistently piercing the parietal bone posterior to the suture between the frontal and parietal bones, have been placed in the genus *Uta* Baird & Girard, 1852. Mittleman (1942) suggested that this assemblage was artificial and purported to demonstrate that the group was actually comprised of four distinct genera, *Petrosaurus* Boulenger, 1885; *Streptosaurus* Mittleman, 1942; *Urosaurus* Hallowell, 1854; and *Uta* Baird & Girard, 1852. Although the differences used by Mittleman to separate these groups were of questionable significance, support for the division of *Uta* was provided by his ideas of the phylogeny of the North American iguanids. This supposed natural subdivision of the Iguanidae traditionally has included the following genera: *Callisaurus* Blainville, 1835; *Crotaphytus* Holbrook, 1842; *Ctenosaura* Wiegmann, 1828; *Dipsosaurus* Hallowell, 1854; *Enyaliosaurus* Gray, 1845; *Holbrookia* Girard, 1851; *Iguana* Laurenti, 1768; *Phrynosoma*

Wiegmann, 1828; *Sator* Dickerson, 1919; *Sauromalus* Duméril, 1856; *Sceloporus* Wiegmann, 1828; *Uma* Baird, 1858; *Uta* Baird & Girard, 1852. According to Mittleman's system there were two main evolutionary lines represented in this group, both stocks being derived from the genus *Ctenosaura*. One line was composed of the relatively primitive genera *Dipsosaurus* and *Sauromalus* (and presumably *Enyaliosaurus* and *Iguana*) and the more highly specialized *Callisaurus*, *Holbrookia*, *Uma* and *Crotaphytus*. Also placed in this section were two of the component genera, *Petrosaurus* and *Streptosaurus*, removed from *Uta* by Mittleman. These two genera were supposed to be derived from *Crotaphytus*. The second major stock included *Phrynosoma*, *Sceloporus*, *Sator*, *Urosaurus* and *Uta*. The last three genera were considered by Mittleman to be independent derivatives of *Sceloporus*.

Stejneger & Barbour (1943) and Smith & Taylor (1950), in their checklists of the lizards of the United States and Mexico, adopted Mittleman's arrangement of the "utas," while Smith (1946, p. 92) presented a somewhat modified phylogeny of North American iguanids that is nevertheless in basic agreement with Mittleman's work. Many herpetologists, some perhaps influenced by the above acceptance of Mittleman's nomenclature, have followed his conclusions. On the other hand, other workers have been inclined to follow Oliver (1943, p. 106), who was loathe to recognize Mittleman's genera because so few characters separate them, and have retained all the species within a single genus. Schmidt (1953) and Stebbins (1954), among others, adhered to the latter view.

It is obvious from the above discussion that Mittleman's classification hinges more upon his

interpretation of the phylogeny of the North American iguanids than upon marked structural differences between the several species groups. If his conception of the evolution of these lizards is correct, it would appear that recognition of four genera of "utas" is necessary. If, however, his interpretation of the group's phylogeny is erroneous and no additional morphologic features can be discovered to support his divisions, Oliver's conclusion that but one generic unit is involved must be accepted. The problem, therefore, is: (1) to determine if any characteristics will separate the groups included in the genus *Uta* prior to Mittleman's study and (2) to evaluate the relationships between these groups and other iguanid genera.

#### PLAN OF ANALYSIS

My interest in this problem was originally aroused during preliminary examination of skeletal material being assembled for studies on the Iguanidae. At that time it was noted that there were remarkable differences between several species of *Uta* (*sensu lato*) in the nature of the sternum and associated structures. If these differences proved to be constant for each species group, it was thought that they might validate generic segregation. Consequently, since the external features used to distinguish between the several groups of "utas" were of doubtful significance, the present analysis has centered around a review of their comparative osteologies. A survey of external differences has also been undertaken in order to determine if these substantiate differences in internal characteristics.

It became apparent early in the study that the principal difficulties of the problem lay in the allocation of the genera *Urosaurus* and *Uta*. Once these genera had been properly placed, the position of *Petrosaurus* and *Streptosaurus* can be readily understood. For this reason, a comparison of *Urosaurus* and *Uta* forms the first part of this report. The second section deals with the status of *Petrosaurus* and *Streptosaurus*. A third section considers a recent attempt to classify these lizards on the basis of ecologic characteristics. The final portion of the paper is concerned with the general relationships between the "utas" and other iguanid lizards.

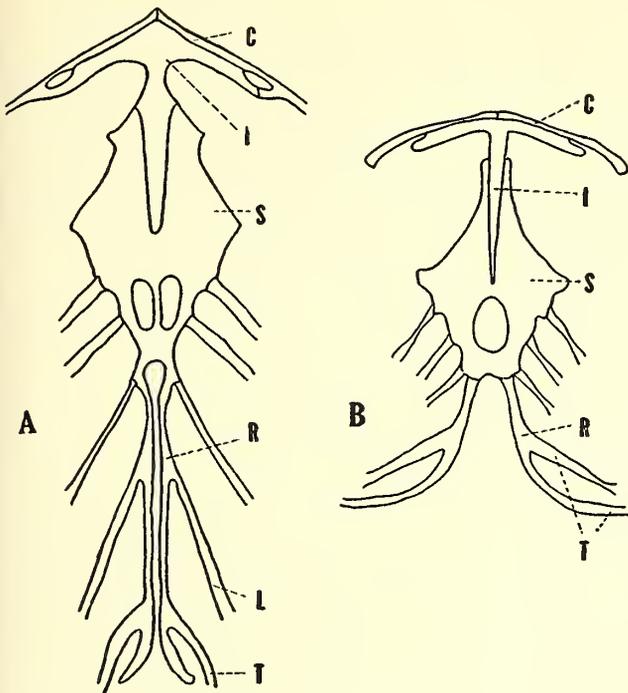
Information for this report has been derived from preserved material of all genera and species mentioned. In addition skeletons of the following species, prepared by the Bolin Method (Bolin, 1936), have been examined: *Callisaurus draconoides* (4), *Crotaphytus collaris* (1), *Crotaphytus wislizeni* (2), *Ctenosaura hemilopha* (1),

*Dipsosaurus dorsalis* (3), *Phrynosoma coronatum* (4), *Phrynosoma platyrhinos* (1), *Sator angustus* (2), *Sator grandaevus* (2), *Sauromalus ater* (1), *Sauromalus obesus* (1), *Sceloporus magister* (5), *Sceloporus occidentalis* (10), *Sceloporus orcutti* (1), *Uma notata* (1), *Urosaurus graciosus* (2), *Uta mearnsi* (1), *Uta slevini* (1), *Uta stansburiana* (5). Also available was additional skeletal material or cleared and stained specimens of: *Amblyrhynchus cristatus* (5), *Anolis garmani* (2), *Anolis leucophaeus* (1), *Brachylophus fasciatus* (1), *Conolophus pallidus* (1), *Conolophus subcristatus* (10), *Ctenosaura acanthura* (1), *Ctenosaura pectinata* (2), *Ctenosaura similis* (3), *Cyclura carinata* (1), *Cyclura cornuta* (3), *Cyclura stejnegeri* (1), *Holbrookia maculata* (1), *Holbrookia texana* (1), *Iguana iguana* (15), *Leiocephalus psammodomus* (2), *Sauromalus hispidus* (1), *Sauromalus varius* (1), *Uma inornata* (1), *Uta scoparia* (1), *Urosaurus auriculatus* (1), *Urosaurus bicarinatus* (1), *Urosaurus nigricaudus* (1), *Urosaurus ornatus* (1) and *Uta thalassina* (2). The pertinent morphological points have been uncovered by dissection on specimens of *Enyaliosaurus quinquecarinatus*, *Urosaurus microscutatus* and representatives of most of the major subpopulations of *Uta stansburiana* and its insular allies.

#### COMPARISON OF *Urosaurus* AND *Uta*

Mittleman (1942, pp. 109-112) presented what purport to be extensive differential diagnoses of *Petrosaurus*, *Streptosaurus*, *Urosaurus* and *Uta*. Oliver (1943, p. 106) pointed out that few of the listed features satisfactorily distinguished between these groups and that none of them clearly indicated the existence of more than one genus. Mittleman (1942, p. 106) stated that there were no differences in the bony structures of these lizards that would separate them from one another or from *Sator* and *Sceloporus*. Preliminary examination of skeletal material tended to dispute this latter assertion and my study has been aimed at discerning whether osteological features distinguished the nominal groups of "utas."

The lizards placed in the genera *Urosaurus* and *Uta* resemble one another rather closely in the structure of the skull, vertebral column, girdles and limbs. The two groups are profoundly divergent, however, in the condition of the sternal plate and associated structures. These differences, supported to some extent by external structures, convince me that two genera can be recognized. The differences between *Urosaurus* and *Uta* in sternal anatomy are summarized as follows:



TEXT-FIG. 1. Sternal plates and associated structures in iguanid lizards from ventral view. **A.** Diagram of urosaurine sternum from specimen of *Urosaurus graciosus*. **B.** Diagram of utiform sternum from example of *Uta stansburiana*. Abbreviations denote the following structures: **C.** clavicle; **I.** interclavicle; **S.** sternal plate; **R.** xiphisternal rod; **L.** lateral xiphisternal rib; **T.** terminal xiphisternal rib.

*Urosaurus*.—Sternal plate rather long and relatively narrow, with the posterior margin tapering almost to a point; xiphisternal rods originating near center line of sternal plate, long, being much longer, when measured from the sternal plate to origin of terminal xiphisternal ribs, than sternal plate is wide; lateral xiphisternal ribs present.

*Uta*.—Sternal plate relatively short and broad, with the posterior margin truncate and forming a wide base; xiphisternal rods originating at lateral edges of posterior margin of sternal plate, short, being much shorter, when measured from sternal plate to origin of terminal xiphisternal ribs, than sternal plate is wide; no lateral xiphisternal ribs, only terminal ones.

These sternal characteristics have been observed in osteological material of the generic types, *Urosaurus graciosus* Hallowell, 1854, and *Uta stansburiana* Baird & Girard, 1852, and verified in examples of all major groups within these nominal genera. Text-fig. 1 illustrates the sternum in these groups. The apparent differences in the nature of the interclavicle-clavicle relationships shown in these figures are not constant throughout the two groups. Elsewhere in the family Iguanidae the shape and relative position of these elements are frequently of value in generic determination.

The condition of the sternum has not previ-

ously been employed to characterize genera of the Iguanidae and some question may arise as to the validity of a distinction made upon this feature. Conceivably, the observed differences could be due to modifications of a single sternal type within a single genus. To confirm the generic significance of the sternal condition, an examination of this structure was made on examples of the majority of North American iguanids, exclusive of the myriad forms within the genus *Sceloporus*. This examination revealed that not only is the type of sternum consistent within every genus but that the condition of the structure appears to have considerable phylogenetic significance. Although the sternal plates and associated structures of some other American iguanids superficially resemble the condition found in *Uta*, within the section of the family closely allied to *Urosaurus* and *Uta* the sternum seems indicative of two evolutionary lines. In this regard, the distribution of the two sternal types in this section of the Iguanidae is informative:

Urosaurine	Utiform
<i>Sator</i>	<i>Callisaurus</i>
<i>Sceloporus</i>	<i>Holbrookia</i>
<i>Urosaurus</i>	<i>Phrynosoma</i>
	<i>Uma</i>
	<i>Uta</i>

In the material examined, the typical uro-

saurine sternum is found only in the three genera listed above, although some *Sceloporus* tend to have rather short xiphisternal rods. These groups have usually been held by previous workers to be closely allied on the basis of external features, and the sternal arrangement fully supports this view. It seems likely that *Urosaurus* is best understood as a specialized off-shoot of *Sceloporus* from which it differs primarily in the presence of a fully developed gular fold and the absence of a scapular foramen, no gular fold but a scapular foramen being present in *Sceloporus*. *Uta* appears to be a specialized genus related to the highly adapted, but apparently more primitive, *Callisaurus-Holbrookia-Uma* series. *Uta* is probably best considered as a recent derivative of this stock and as such can only be distantly allied to *Urosaurus*, which it resembles in several external features. In view of the evidence of complete morphological separation and the probability of different origins it would seem that *Urosaurus* and *Uta* ought to be retained as distinct genera.

Because the principal characteristics diagnostic of the genera *Urosaurus* and *Uta* are internal ones, it seemed worthwhile to attempt to determine if there were any external features that distinguish them. Such characters might be useful for rapid identification or in artificial keys. Careful examination of examples of all the species groups within the two genera reveals that a single scutellational character can be used for generic recognition. This feature involves the arrangement of the scales in the nasal region and makes it necessary to digress at this point from the major problem of the paper to treat a matter of terminology.

Unfortunately herpetologists have seldom attempted to standardize the nomenclature of the head scales in lizards. General agreement has been reached in dealing with the comparatively simple arrangement of snakes, but since the size, shape and position of the scales vary from lizard group to lizard group, the subject has become surprisingly complex. In the case in point, for example, Smith (1946, p. 276) and Mittleman (1942, p. 123), in naming the head scales of *Urosaurus* and *Uta*, use entirely different terms for what appear to be positionally homologous units. It is understandable under these circumstances why previous workers have overlooked scale characters that readily separate these two genera. Because of the great diversity in the number and disposition of head scales in different lizard families, it does not seem possible or desirable to instigate a universally applicable nomenclature. Nevertheless, it does seem worthwhile to employ a standard

set of terms within familial or subfamilial limits. While this cannot be accomplished as yet with the iguanids because of our lack of understanding of the suprageneric groupings within the family, I have attempted to standardize the scale nomenclature for the nasal region in the genera allied to *Urosaurus* and *Uta*. Subsequent work will probably find that this system can be applied without too much difficulty to more distantly related and less specialized genera.

#### TERMINOLOGY FOR SCALES IN NASAL REGION

*Rostral*.—Scale at tip of snout, bordering upper lip.

*Internasals*.—Usually a double pair (anterior and posterior) of scales lying between the nasals on top of the snout.

*Nasals*.—Scales in which the nostrils are pierced.

*Postrostrals*.—These are the subnasals of *Urosaurus* as defined by Mittleman (1942) and the postrostrals of *Uta* and *Sceloporus* according to Smith (1946); the two series are homologous in position, bordering the nasal along its anterior and lower margins and on occasion separating the rostral from the anterior internasals.

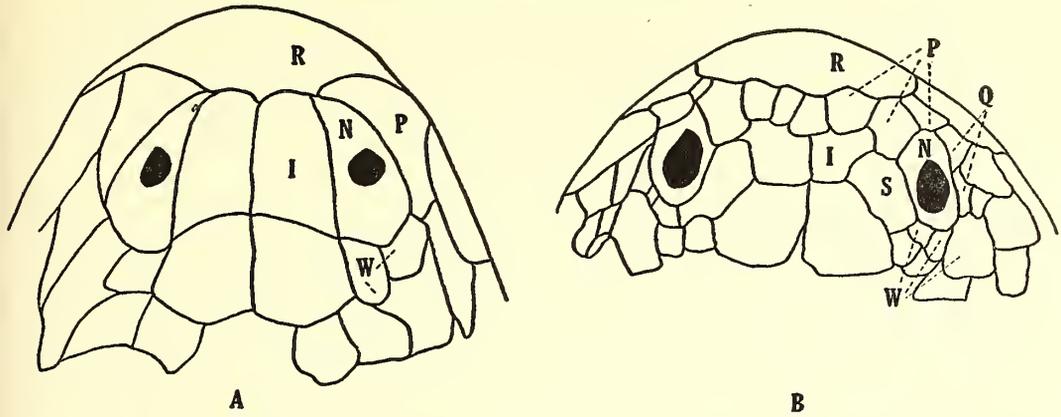
*Supranasals*.—Scales bordering the upper margins of the nasals and separating the nasals from the internasals.

*Subnasals*.—Scales bordering the lower edge of the nasals and lying posterior to the postrostrals; they separate the nasals from the supralabials.

*Postnasals*.—Scales bordering the posterior margin of the nasals and separating them from the loreals or canthals.

The set of terms here defined and figured (Text-fig. 2) can be applied to the scales in the nasal region of the following genera (names as listed by Mittleman): *Petrosaurus*, *Sator*, *Sceloporus*, *Streptosaurus*, *Urosaurus* and *Uta*. The system is not satisfactory when working with genera with a more or less homogenous complement of head scales as in *Crotaphytus*, *Ctenosaura*, *Dipsosaurus*, *Enyaliosaurus*, *Iguana* and *Sauromalus*. *Callisaurus*, *Holbrookia*, *Phrynosoma* and *Uma* have the head scales somewhat intermediate between the *Urosaurus-Uta* group and the *Iguana*-like lizards. There is probably little need to distinguish between the scales in the nasal region at such a fine level as is profitable in *Urosaurus* and *Uta* in this *Phrynosoma-Holbrookia* line.

The genera *Urosaurus* and *Uta* are distinguished by: *Urosaurus* having the nasals and internasals in contact and lacking supranasals



TEXT-FIG. 2. Scutellation of nasal region in iguanid lizards. A. Dorsal view of snout of *Urosaurus*. B. Dorsal view of snout of *Uta*. The following symbols indicate the pertinent scales: I. internasal; N. nasal; P. postrostral; Q. subnasal; R. rostral; S. supranasal; W. postnasal.

(Text-fig. 2,A); *Uta* has the anterior internasals separated from the nasals by definite supranasal scales (Text-fig. 2,B). Although *Urosaurus* is distinct from members of the *Uta stansburiana* group in having two distinct abdominal patches in the adult males and sometimes in the female and never any axillary or shoulder dark spots (in *Uta stansburiana* and its allies no well-defined abdominal patches of color are present in either sex, although the belly may be suffused with blue, gray or black in adult males and there is usually a dark blue or black axillary spot and frequently a dark spot anterior to the shoulder insertion), these differences break down when other members of the genus *Uta* are considered.

In *Urosaurus* and *Uta* the rostral scale may or may not be in contact with the internasals. If the rostral and internasals are separated the postrostrals lie between them. This arrangement appears to be quite variable in populations of *Uta* but it is more consistent within specific limits in *Urosaurus*. In my material usually 90 per cent. or more of the specimens of a single form have the same internasal-rostral relationship. In *Urosaurus bicarinatus* (A. Duméril, 1856), not all subspecies seen, *Urosaurus nigricaudus* (Cope, 1864) and *Urosaurus microscutatus* (Van Denburgh, 1894), the rostral usually meets the anterior internasals. *Urosaurus auriculatus* (Cope, 1871), *Urosaurus graciosus* Hallowell, 1854, and *Urosaurus ornatus* (Baird & Girard, 1852), not all subspecies seen, usually have the postrostrals preventing a contact between the rostral and internasals.

In related genera these external features are variable. *Sator* has supranasals and definite abdominal color patches in adult males. Supranasals may be present or absent in *Sceloporus*

although apparently consistently present or absent within species limits, and the abdominal color patches are regularly present in many species in adult males and sometimes in females. In several species these color patches are totally absent. As previously indicated, the scales in the nasal region of *Callisaurus*, *Holbrookia*, *Phrynosoma* and *Uma* are relatively small and cannot be recognized as definite postrostrals, supranasals or internasals. Definite abdominal color patches are present in males (and sometimes in females) of all these genera except *Phrynosoma*.

#### THE STATUS OF *Petrosaurus* AND *Streptosaurus*

Since *Urosaurus* and *Uta* have been shown to be distinct, the position of *Petrosaurus* and *Streptosaurus*, two nominal genera formerly included in *Uta*, can now be analyzed. According to Mittleman, *Petrosaurus* was derived from *Crotaphytus* and *Streptosaurus* from *Petrosaurus*. There can be no question regarding the close relationship of *Petrosaurus* and *Streptosaurus* but their supposed affinity to *Crotaphytus* is, on the basis of data accumulated in the preparation of this report, subject to considerable doubt. Evidence showing why *Petrosaurus* and *Streptosaurus* cannot be closely related to *Crotaphytus* will be presented later in this paper.

The first problem at hand is to determine the generic status and differences between *Petrosaurus thalassinus* (Cope, 1863) and the doubtfully valid form *Petrosaurus reprens* (Van Denburgh, 1895) on the one hand and the two nominal species of *Streptosaurus*, *mearnsi* (Stejneger, 1894) and *slevini* (Van Denburgh, 1922) on the other. Mittleman (1942, pp. 110-111) attempted to segregate these two species-groups

on the basis of numerous characters. Many of the features listed by him were given under both genera, however, and an analysis of the others indicates that few of the differences hold. The features employed by Mittleman are given below:

<i>Petrosaurus</i>	<i>Streptosaurus</i>
1. Larger ventrals	1. Smaller ventrals
2. Enlarged, strongly keeled caudal scales	2. Caudals weakly keeled
3. Three rows of enlarged supraoculars	3. Two rows of enlarged supraoculars
4. Anterior gular fold (pregular) well-developed	4. Anterior gular fold poorly developed
5. Lateral fold poorly developed	5. Lateral fold well-developed
6. Dorsal pattern of bands, no neck ring	6. Dorsal pattern without bands, a neck ring
7. No abdominal color patches	7. Abdominal color patches in males
8. No palatine bones	8. Palatine bones present

These features are considered in the order given above. (1) There appears to be a definite difference in the size of the ventral scales in the two groups but this character is of questionable generic significance. (2) The differences in the degree of keeling of the caudal scales are evident but hardly generic in character. (3) The number of rows of enlarged supraoculars is a consistent feature. (4) The condition of the preular fold in life is variable and the degree to which it appears to be developed in preserved material is not consistent within any available sample. This character is therefore useless for distinguishing between the two groups. (5) The same remarks given for the preular fold apply to the condition of the lateral fold. (6) The dorsal bands and nuchal collar are present in both *Petrosaurus* and *Streptosaurus* but differ in degree of intensity. The dark nuchal collar of *Streptosaurus* appears to be the same pattern element as the anterior dorsal band in *Petrosaurus*. The posterior bands are prominent in the latter genus but, although present in the former group, they are obscured to some extent by the darker body coloration. (7) Both groups have the same type of abdominal coloration in adult males although the predominant color in both living and preserved material is blue in *Streptosaurus* and blackish in *Petrosaurus*. These colored areas appear to constitute definite abdominal patches although the color tends to suffuse over the entire ventral surface. Laterally the suffusion of darker color is similar to the condition found in adult male *Uta stansburiana*; however, this latter group does not have ex-

tensive coloration superimposed on the ventral abdominal surfaces. (8) A palatine bone is present on both sides of the skull in all specimens of either group seen by me, although the bone is somewhat thinner than in less specialized iguanids.

It is obvious that the two presumed genera are distinct from one another in a few minor details of scutellation and coloration and that none of the observed differences seem indicative of two distinct generic groups. Examination of skeletal material of the several species shows that they are essentially similar. The only points of difference between them are in the relative proportions of a few elements. Because of the absence of trenchant distinguishing features and the fact that all workers, including Mittleman, have considered these taxa to be closely related, inclusion of these lizards in a single genus seems appropriate. Fully supporting this conclusion are the facts of morphology and the distributional pattern of the several species. The form *mearnsi* has a range from Riverside County, California, south in Baja California, Mexico, to the region of Santa Rosalia. *Thalassina* occupies the southern portion of the peninsula from Comundú (about 75 miles south of Santa Rosalia) southward. If the form *reprens* is recognized, it would occupy the northern portion of the range given for *thalassina*. Although additional evidence is needed to verify this point, it is likely that *thalassina* is more primitive than *mearnsi*. The insular form, *slevini*, is obviously of close affinity with *mearnsi*. It is restricted to Isla Angel de la Guarda and adjacent islets in the Gulf of California.

The question now arises as to the generic placement of these three species. Since the pectoral apparatus as well as the scutellation and general morphology of these forms are of the uniform type, the genera allied to *Sceloporus* need not be considered. The condition of the vertebrae, the nasal structure, the scapulocoracoid foramina (Text-fig. 5) and the sternum of these three forms are totally different from these features in *Crotaphytus* and its relatives. Consequently these genera also need not be discussed. (See the section on classification at the end of this paper for additional information on the affinity between these species and *Crotaphytus* postulated by Mittleman). These eliminations leave only the genera associated with *Uta* as possible congenitors of *mearnsi*, *slevini* and *thalassina*. Within this series, only *Uta* approaches the three in osteological and other morphological features and it is here that the relationship apparently lies. The following summary of characteristics

will separate *Uta stansburiana* and its allies from the giant Baja California forms:

*Uta*: enlarged supraoculars in a single series; well-defined median and lateral frontonasal scales; scales along gular fold much larger than gulars; no definite dorsal bands, no nuchal collar; neural spines well-developed, higher than long; usually three sternal ribs (rarely four).

*Petrosaurus*: enlarged supraoculars in two or three series; no definite median and lateral frontonasals; scales along gular fold same size as gulars; back with definite dark bands, a nuchal dark collar; neural spines low, longer than high; four sternal ribs.

The differences between *Uta* and *Petrosaurus* are slight and no single feature in itself is particularly significant. However, the total character-complements of the two groups are rather divergent and a decision as to the most propitious allocation of the species involved is difficult. Although there is considerable merit in recognizing *Petrosaurus* as a phylogenetic line distinct from *Uta*, the obvious close relationship between the two and the kind of differences separating them lead me to conclude that the evolutionary picture can best be explained by placing them in a single genus. Recognition of two subgeneric categories within the genus *Uta*, one for *stansburiana* and its immediate allies and a second (*Petrosaurus*) for the *mearnsi* group, may be a useful way to emphasize the differences between the two evolutionary lines in the genus.

In this regard it should be noted that the shoulder spot of *Uta stansburiana* and related forms appears to represent the remnant of the nuchal collar of *Uta mearnsi*, *Uta slevini* and *Uta thalassina*. In these latter forms, the dark blue or black lateral and abdominal suffusions of the male are most intensive in the axillary region, and the axillary spot in the *Uta stansburiana* section is probably a retention of the anterior portion of this densely pigmented area.

#### THE ECOLOGIC GENUS AND THE PRESENT PROBLEM

The concept of the genus adopted in the present report agrees in principle with that given by Mayr (1942, pp. 282-286). Because of the nature of the material studied, the degrees of relationship and difference between the several groups are based upon morphologic characteristics, although it is clearly understood that other kinds of characters may be used, and ought to be used when available, in generic definition. The genera accepted in this account

are therefore convenient but natural groupings of species separated from other such units by discontinuities in morphologic variation.

A radical conception of the genus in terms of ecology has recently been adopted by one herpetologist (Lowe, 1955a; 1955b) and applied to the problem of the generic status of *Uta* and its allies. Lowe holds the extreme position that genera can be recognized on the basis of ecologic divergence alone, without support from any other kind of characteristics. The difficulties arising from the rigid application of this idea are too numerous to consider at this time, but may be summed up as follows: (1) any two species, if different from each other in ecology, regardless of similarities in morphology, physiology or other features, may be recognized as distinct genera; (2) all species having the same or very similar ecologies, regardless of genetic relationships or differences in other features, may be placed in the same genus.

Lowe and Norris (in Lowe, 1955a) utilized this concept as the basis for a classification of the lizards formerly placed in the genus *Uta*. They maintained Mittleman's arrangement of these species because of supposed differences between and similarities within the groups involved. According to these authors the species can be arranged as follows:

- Genus *Petrosaurus*
- Subgenus *Petrosaurus*
- Subgenus *Streptosaurus*
- Genus *Urosaurus*
- Genus *Uta*

*Petrosaurus* and *Streptosaurus* were placed together because of their cliff-dwelling propensities. *Urosaurus* was retained as a distinct genus because the species within the group are, according to Lowe and Norris, plant-dwellers and plant-climbers. *Uta* is supposedly distinguished from the other two genera by living on the ground. The genera are thus recognized because they occupy different ecologic niches.

The primary reason why Mittleman's classification of these lizards has not been generally accepted lies in his failure to present convincing evidence that the several groups were morphologically different from one another. The most striking morphologic feature listed by him as separating *Uta* and *Urosaurus*, for example, was the homogeneous dorsal scutellation of the former and the differentiation of the paravertebral scales in the latter. This character fails to hold for *Urosaurus microscutatus* and some examples of *Urosaurus nigricaudus* which have a homogeneous complement of dorsal scales.

The system adopted by Lowe and Norris can only have merit if it is based upon consistent ecologic features that do not vary within the several groups established by Mittleman.

Unfortunately this is not the case. Firstly, several species placed within the nominal genera do not have the ecologic mode of life attributed to them by Lowe and Norris. *Urosaurus microscutatus* and *Urosaurus nigricaudus* are typically found on rocks and boulders, often in association with *Uta* (*Petrosaurus*) *mearnsi* or *Uta* (*Petrosaurus*) *thalassina* and only rarely in bushes or other plants. Secondly, there is considerable variation in the habitats occupied by different individuals or populations within many species. The supposedly ground-living *Uta stansburiana* is frequently found in low bushes or on rocks or boulders. Many of the insular forms of *Uta* are more or less restricted to this latter habitat. It may be assumed that the species in the other generic groups also exhibit some variation in habitat selection. Finally, it ought to be pointed out that members of the related genera *Sator* and *Sceloporus* are found in all three habitats attributed to *Petrosaurus*, *Urosaurus* and *Uta*. Within the limits of *Sceloporus*, various species tend to be inhabitants of trees and bushes, or are typically found on the ground or in rocky and boulder regions. Other members of this genus may occur in two or three of these habitats. The two species of *Sator* are unselective in habit, individuals of the same form being commonly found in all three situations. If ecologic characteristics alone were used in setting up the genera in this section of the Iguanidae, all of the taxa mentioned above would have to be placed in a single genus since no clear-cut distinction can be made between them. If all other characters were disregarded, it would be possible to re-align the species into several genera on the basis of habitat preference, but genera erected on this criterion would be extremely artificial. Either of these alternatives, particularly in the light of the morphologic data presented in this report, illustrates the tangles that ensue from application of a strictly ecologic concept of the genus.

The statement by Lowe and Norris (apparently based upon their evaluation of ecologic features) that *Petrosaurus* is not closely related to either *Crotaphytus* (as postulated by Mittleman) or to *Uta*, needs no further comment here.

#### REMARKS ON THE CLASSIFICATION OF NORTH AMERICAN IGUANIDS

The principal argument advanced by Mittleman (1942) for the division of the genus *Uta*

into four genera was his idea of the phylogeny of the several species groups. His system of classification was based upon the assumption that the North American iguanids form a natural group of genera and that this stock includes two related but divergent evolutionary lines. Mittleman suggested that the genus *Ctenosaura* represents the primitive ancestor from which both lines evolved. One of these stocks contained the genera (in approximate order from primitive to advanced) *Dipsosaurus*, *Sauromalus*, *Callisaurus*, *Holbrookia*, *Uma*, *Crotaphytus* and the nominal genera *Petrosaurus* and *Streptosaurus*. The other group included *Phrynosoma*, *Sceloporus*, *Sator*, *Urosaurus* and *Uta*. Smith (1946, p. 92) retained Mittleman's basic arrangement but added *Leiocephalus* Gray, 1827, to the *Phrynosoma-Uta* line.

In the preceding sections of this report, information is presented to substantiate Mittleman's concept of *Urosaurus* and *Sator* as allies of *Sceloporus*. However, all other data accumulated during an investigation of this problem are in strong contradiction to Mittleman's and Smith's basic classification of northern iguanids. Evidence at hand clearly indicates that the consideration of the North American iguanids as a natural inter-related group is without factual foundation. Because my views are in sharp contrast to those of Mittleman it has been necessary to present a summary of tentative conclusions regarding the relationships of these lizards. Conclusions are based upon available information in the literature (especially Boulenger, 1885; Cope, 1900; Camp, 1923) and on a preliminary evaluation of skeletal and other morphological features. The classification outlined is therefore a tentative one to be modified in its details by later work. The main lines of evolution, however, appear to be clearly recognizable, and it is hoped that my arrangement will stand scrutiny better than that proposed by Mittleman.

Insofar as can be determined at this time, the so-called Nearctic iguanids form two diverse groups that can be only distantly related. These two sections are distinguished by marked differences in vertebral and nasal structures and include several genera not usually recognized as being allied to Nearctic forms. No species intermediate in significant characters has been found to bridge the gap between the two lines. Since a thorough revision of the entire family would be necessary to establish the exact status of the suprageneric groups, no attempt has been made to place them in a definite classificatory category.

One of the primary divisions in the Iguanidae, represented by a number of genera in North America, is a stock characterized as follows:

*Vertebrae*: each dorsal vertebra provided with zygosphenes and zygantra in addition to the zygapophyses.

*Nasal structure*: nasal organ of the relatively simple S-shaped type, concha present (*Dipsosaurus*-type of Stebbins, 1948, p. 209).

This section, hereafter referred to as the iguanine group, includes the following genera:

*Amblyrhynchus* Bell, 1825

*Brachylophus* Cuvier, 1829

*Conolophus* Fitzinger, 1843

*Crotaphytus* Holbrook, 1842

*Ctenosaura* Wiegmann, 1828

*Cyclura* Harlan, 1824

*Dipsosaurus* Hallowell, 1854

*Enyaliosaurus* Gray, 1845

*Iguana* Laurenti, 1768

*Sauromalus* Duméril, 1856

Although I have not been able to examine the nasal structure of *Amblyrhynchus*, *Brachylophus*, *Conolophus* and *Cyclura*, these genera have the typical iguanine vertebrae with zygosphenes and zygantra. Their agreement with other members of the group in this regard and their close similarity in basic features make it probable that they possess S-shaped nasal organs. Additional genera may be added to this section when their skeletons and nasal structures have been studied.

The second group, essentially North American in distribution, is characterized by:

*Vertebrae*: dorsal vertebrae without zygosphenes and zygantra.

*Nasal structure*: nasal organs of the sink-trap type, no concha (*Uma*-type of Stebbins, 1948, p. 205).

This section, hereafter called the sceloporine line, contains:

*Callisaurus* Blainville, 1835

*Holbrookia* Girard, 1851

*Phrynosoma* Wiegmann, 1828

*Sator* Dickerson, 1919

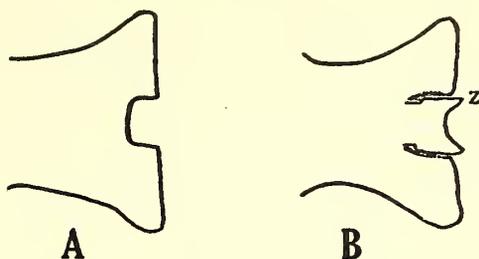
*Sceloporus* Wiegmann, 1828

*Uma* Baird, 1858

*Urosaurus* Hallowell, 1854

*Uta* Baird & Girard, 1852

Illustrations of the differences in vertebral and nasal structure are given in Text-figs. 3 & 4. It should be noted that in some species of *Phrynosoma* and *Sceloporus*, a vertical facet is present on each side of the neural lamina at the anterior end of the vertebrae in the same position where



TEXT-FIG. 3. Anterior portion of dorsal region of vertebrae in iguanid lizards. **A.** Diagram of sceloporine vertebra of *Uta mearnsi*. **B.** Diagram of iguanine vertebra of *Crotaphytus wislizeni*. The letter **Z** lies adjacent to one of the zygosphenes.

zygosphenes are developed in iguanine lizards. There are no zygantra in species with these facets, and the latter structures do not appear to be morphologically similar to true zygosphenes, which are horizontally flattened and markedly projected anteriorly from the base of the neural spine.

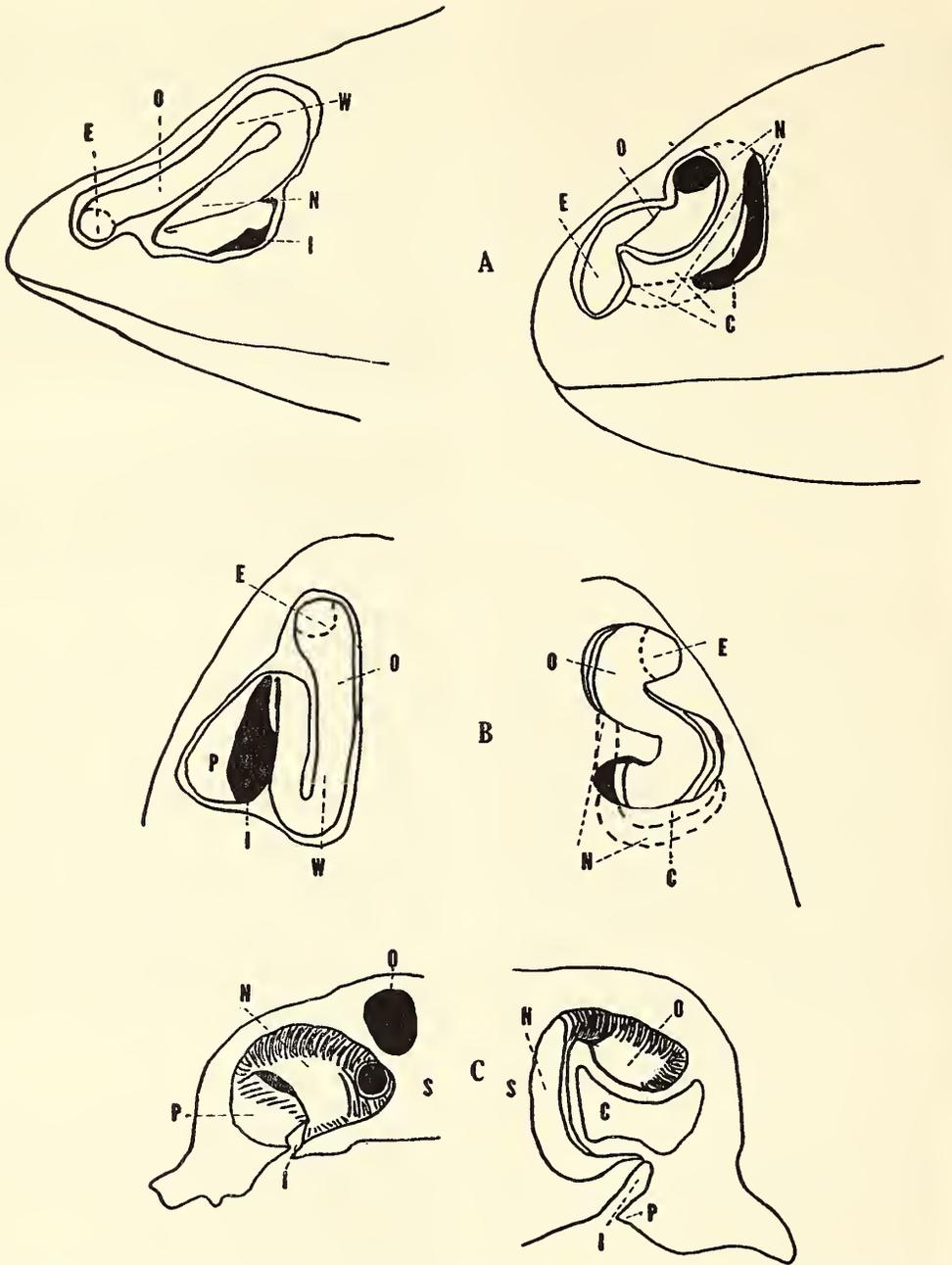
In addition to the primary differences listed above, the two groups differ from one another in several general tendencies that hold for a majority of genera.

*Iguanine line.*—Teeth usually on pterygoid (usually on palatine as well in *Crotaphytus wislizeni*); the small parietal foramen usually pierced in frontal or in suture between frontal and parietal bones; parietal bone thick; pectoral girdle usually with primary and secondary coracoid foramina, scapular and scapulocoracoid foramina also present (Text-fig. 5); head scutellation essentially a homogenous group of small scales not arranged into definite series; interparietal scale small, not markedly larger than adjacent head scales; usually a mid-dorsal crest of enlarged scales.

*Sceloporine line.*—Never any palatal teeth; usually a large parietal foramen pierced in a thin membranous parietal bone; never any secondary coracoid foramen in pectoral girdle, scapular foramen often absent (Text-fig. 5); head scutellation usually a heterogeneous mixture of enlarged and smaller scales arranged in definite series; interparietal scale usually enlarged, much larger than adjacent scales; never a mid-dorsal crest of enlarged scales, although paravertebral scales may form an enlarged series.

Table 1 indicates the distribution of these features in the individual genera.

The evolutionary significance of the development of the specialized vertebrae with zygosphenes and zygantra and the divergent types of nasal structure are not certainly known. The



TEXT-FIG. 4. Structure of nasal organs in iguanid lizards. **A.** Lateral view. **B.** Dorsal view. **C.** Cross-sectional view. Figures on the left of the sink-trap nasal organization of *Callisaurus draconoides* typical of the sceloporine line. Figures on right of the S-shaped nasal organization of *Dipsosaurus dorsalis* typical of the iguanine line. Abbreviations indicate the most important parts as follows: **C.** concha; **E.** external naris; **I.** internal naris; **N.** nasal cavity; **O.** vestibule; **P.** palatine fold; **S.** nasal septum; **W.** nasal passage. All figures after Stebbins (1948).

vertebral modification which provides for two additional points of contact and support between vertebrae probably has something to do with the large size attained by most iguanine lizards. The

zygantra are significantly reduced in size in *Crotaphytus*, the genus including the species having the smallest adult size within the section. Stebbins (1948, p. 213), the original discoverer

of the differences in nasal structure, has considered at length the possible functional significance of the sink-trap nasal arrangement. He concludes that this feature is an evolutionary adaptation to intensification of the problem of cleansing inspired air in arid environments and under circumstances where the lizard buries itself in the soil. The S-shaped nasal structure of the iguane line is interpreted by Stebbins to represent a somewhat specialized stage intermediate in its adaptation for an arid environment between the relatively unmodified structures of other lizards and the complex condition in the sceloporines.

The genus *Leiocephalus* suggested by Smith

(1946, p. 92) as a possible ally of *Sceloporus* has an unmodified nasal organization totally unlike that found in either the iguanines or sceloporines. *Leiocephalus* does not appear to be particularly closely related to any of the genera considered in this report.

It does not seem advisable at present to speculate on the relationships of the iguane lizards, due to lack of adequate material. Final decisions on the phylogeny of the sceloporine section must also await additional research. However, a tentative scheme of relationships within the latter group has been drawn up and is presented in Text-fig. 6.

TABLE 1. CHARACTERISTICS OF IGUANINE AND SCELOPORINE LIZARDS<sup>1</sup>

Group	Pterygoid Teeth	Parietal	Parietal Foramen	Pectoral Foramina				Head Scales	Inter-Parietal Scale	Mid-Dorsal Crest
				S	S-C	C	C'			
Iguanines:										
<i>Amblyrhynchus</i>	+ (B)	T	sm. F or F-P	X	X	X	X	H	sm.	+
<i>Brachylophus</i>	+	T	sm. F or F-P	-	-	-	-	H	sm.	+
<i>Conolophus</i>	+ (B)	T	sm. F or F-P	X	X	X	X	H	sm.	+
<i>Crotaphytus</i>	+	T	sm. F or F-P	X	X	X	X	H	sm.	-
<i>Ctenosaura</i>	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
<i>Cyclura</i>	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
<i>Dipsosaurus</i>	+ (B)	T	sm. F	X	X	X	O	H	sm.	+
<i>Enyaliosaurus</i>	+	T	.....	-	-	-	-	H	sm.	+
<i>Iguana</i>	+	T	sm. F or F-P	X	X	X	X	H	sm.	+
<i>Sauromalus</i>	+	T	sm. F or F-P	X	X	X	X	H	sm.	-
Sceloporines:										
<i>Callisaurus</i>	-	t	l. P	X	X	X	O	h	l.	-
<i>Holbrookia</i>	-	t	l. P	X	X	X	O	h	l.	-
<i>Phrynosoma</i>	-	T	sm. F-P	X	X	X	O	H	l.-sm.	-
<i>Sator</i>	-	t	l. P	O	X	X	O	h	l.	-
<i>Sceloporus</i>	-	t	l. P	X	X	X	O	h	l.	-
<i>Uma</i>	-	t	l. P	X	X	X	O	h	l.	-
<i>Urosaurus</i>	-	t	l. P	O	X	X	O	h	l.	-
<i>Uta</i>	-	t	l. P	O	X	X	O	h	l.	-

<sup>1</sup>The following list indicates the meaning of the symbols utilized in the table:

+ = present

- = absent

(B) = according to Boulenger (1883)

T = thickened

t = thinned

sm. = small

l. = large

F = frontal bone

P = parietal bone

F-P = suture between frontal and parietal bones

S = scapular

S-C = scapulocoracoid

C = coracoid (primary)

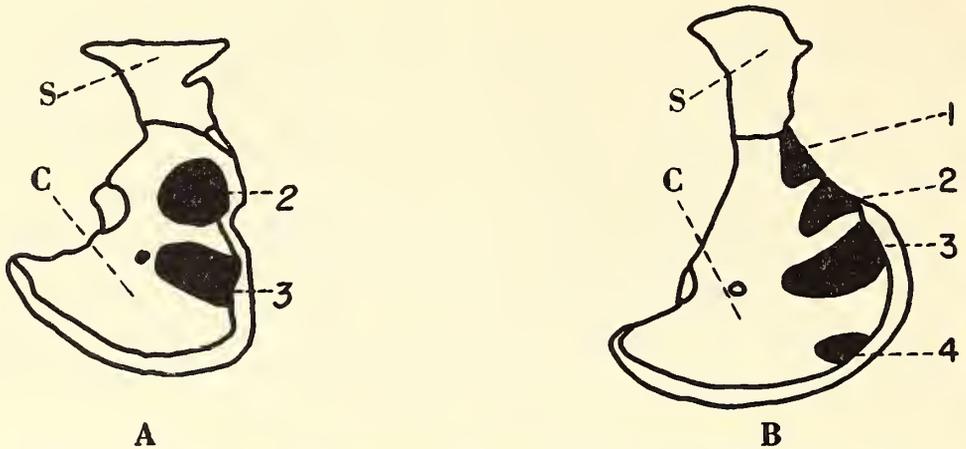
C' = coracoid (secondary)

X = present

O = absent

H = homogeneous

h = heterogeneous



TEXT-FIG. 5. Pectoral girdles of iguanid lizards in lateral view. **A.** *Uta mearnsi*. **B.** *Crotophytus wislizeni*. The letters **S** and **C** indicate the suprascapula and scapulocoracoid respectively. The numbered structures are: 1. scapular foramen, 2. scapulocoracoid foramen, 3. primary coracoid foramen, 4. secondary coracoid foramen.

Two major subdivisions are recognized within this group, based upon the type of sternal arrangement. Within the line having a utiform sternum, two distinct stocks are indicated. One of these is represented by the highly specialized genus *Phrynosoma*, which lacks xiphisternal ribs, has bony spines projecting from the skull and exhibits a very peculiar hyoid apparatus. The other group contains the highly specialized genera *Callisaurus*, *Holbrookia* and *Uma* and the less specialized but probably more recently evolved genus *Uta*. Within *Uta*, the subgenus *Petrosaurus* appears to be most primitive although highly adapted for a rock habitat. The genera *Urosaurus*, *Sator* and *Sceloporus* are closely allied and differ from other sceloporines in having a urosaurine type of sternum. *Sceloporus* presumably is the most primitive genus, with the other two groups apparently derived from it.

#### GENERIC DESCRIPTIONS

The genera *Urosaurus* and *Uta* have never been adequately characterized. To rectify this situation these groups are briefly described below:

Both genera share the following features in common: skull not produced posteriorly into a projection or spines; premaxillary teeth conical; anterior maxillary teeth simple, posterior maxillary teeth weakly triconodont; mandibular teeth simple anteriorly, weakly triconodont posteriorly; no teeth on palatine or pterygoid; parietal organ piercing the parietal bone posterior to frontoparietal suture; parietal very thin in region about parietal foramen; vertebrae

without zygosphenes and zygantra; no scapular foramen, a scapulocoracoid foramen, a primary coracoid foramen, no secondary coracoid foramen; one or two sternal fontanels; three or four sternal ribs; xiphisternal ribs present; no parasternal ribs.

Nasal organ of the sink-trap type; no concha.

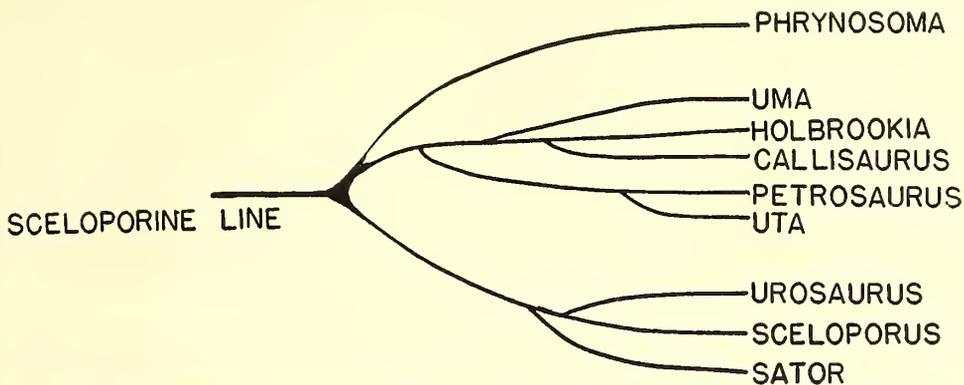
Rostral a well-developed scale; supralabials not imbricate, supercilliaris imbricate; interparietal scale large; tympanum present; auricular scales enlarged; a distinct gular fold but no gular pouch or pocket; digital lamellae not expanded to form pads, strongly keeled; toes without lateral fringes of small scales; no mid-dorsal crest of enlarged scales; some scales in paravertebral region are usually enlarged in *Urosaurus*.

#### Genus *Urosaurus* Hallowell, 1854

*Type of genus.*—*Urosaurus graciosus* Hallowell, 1854, by monotypy.

Distinctly different from all other iguanids in the characters mentioned above and in: (1) pectoral girdle of urosaurine type; lateral xiphisternal ribs present; (2) no supranasal scales.

*Included species.*—*Urosaurus auriculatus* (Cope, 1871); *Urosaurus bicarinatus* (Duméril, 1856); *Urosaurus clarionensis* (Townsend, 1890); *Urosaurus gadovi* (Schmidt, 1921); *Urosaurus graciosus* Hallowell, 1854; *Urosaurus irregularis* (Fischer, 1882); *Urosaurus microscutatus* (Van Denburgh, 1894); *Urosaurus nigricaudus* (Cope, 1864); *Urosaurus ornatus* (Baird & Girard, 1852); *Urosaurus unicus* (Mittleman, 1941).



TEXT-FIG. 6. Phylogenetic diagram indicating the suggested relationships between the genera of sceloporine line.

#### Genus *Uta* Baird & Girard, 1852

*Type of genus.*—*Uta stansburiana* Baird & Girard, 1852, logotype by subsequent designation of A. E. Brown, 1908, p. 117.

Distinct from groups with which it might be confused as indicated above and in having: (1) pectoral girdle of uniform type; no lateral xiphisternal ribs; (2) supranasal scales separating nasals from internasals.

*Included species.*—Subgenus *Petrosaurus* Boulenger, 1885: *Uta mearnsi* Stejneger, 1894; *Uta slevini* Van Denburgh, 1922; *Uta thalassina* Cope, 1863 (type of subgenus by monotypy).

Subgenus *Uta* Baird & Girard, 1852: *Uta concinna* Dickerson, 1919; *Uta martinensis* Van Denburgh, 1905; *Uta nolascensis* Van Denburgh & Slevin, 1921; *Uta palmeri* Stejneger, 1890; *Uta squamata* Dickerson, 1919; *Uta stansburiana* Baird & Girard, 1852 (type of subgenus); *Uta stellata* Van Denburgh, 1905.

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### 3

## Feeding Habits of the Northern Water Snake, *Natrix sipedon sipedon* Linnaeus<sup>1, 2</sup>

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#### INTRODUCTION

THE present paper summarizes the food content of 207 stomachs of the northern water snake, *Natrix sipedon sipedon* Linnaeus, from central New York and northern Michigan, and presents additional material on the feeding habits of this species.

These stomachs became available to me between 1933 and 1938. Most of the New York stomachs are from the general vicinity of Ithaca, in the central part of the state. In Michigan, work centered at the University of Michigan Biological Station at Douglas Lake and was confined mostly to the two northernmost counties of the Lower Peninsula and adjacent islands.

We now have a fair amount of information on the food of the northern water snake. Surface (1906) reported upon an unstated number (apparently about 30) of Pennsylvania stomachs. Uhler, Cottam & Clarke (1939), reporting upon 30 stomachs from the George Washington National Forest in western Virginia and adjacent West Virginia, found that fishes made up 61 per cent. and amphibians 35 per cent. of the total food volume. King (1939), with 48 stomachs from the Great Smoky Mountains National Park, found fish remains in 29 stomachs and amphibian remains in 17. Raney & Roecker (1947), examining 59 stomachs from western New York streams, found fishes to comprise 96 per cent. of total volume and amphibians 4 per cent. Lagler & Salyer (1947) provided from Michigan a valuable report on 106 stomachs from trout streams, with 7 per cent. con-

taining trout (19 per cent. of volume) and 73 per cent. containing forage fishes (59 per cent. of volume). They also reported 18 stomachs from inland lakes and 64 from fish hatchery situations. Hamilton (1951b) examined 23 stomachs of *Natrix sipedon insularum* and reported the food to be equally fish and amphibians. Additional observations from more limited numbers of stomachs have been recorded by Evermann & Clark (1920), Boyer & Heinze (1934), Conant (1938), McCauley (1945), Barbour (1950) and Neill (1951). Minor notes on food items are scattered widely through the literature.

#### METHODS

Food was secured from specimens by dissection, by voluntary regurgitation and by manually-induced regurgitation. Used carelessly, the latter method might lead to gross inaccuracies, but a high degree of proficiency in its use may be attained, especially with less "muscular" forms such as water snakes and garter snakes. By this method, in several instances, food items smaller than 0.2 cc. in volume were removed from snakes that were needed alive. Sampling checks by x-ray and by dissection suggested that in the majority of cases material that could not be detected and removed by manually-induced regurgitation was too far liquefied to be of value in any event.

Findings are presented in the form of (1) percentage frequency of a given item in the total number of food items taken, (2) percentage of stomachs in which a given item was found, and (3) the percentage of total food volume (both actual and estimated) attributed to a given type of food item. The first two frequencies were usually found to give somewhat comparable, but not similar, results.

*Actual* volume means just what it says. *Esti-*

<sup>1</sup>Extracted in part from a doctoral thesis at Cornell University.

<sup>2</sup>Contribution from the University of Michigan Biological Station and the Zoological Laboratories, Cornell University.

ated volume, however, means that if an item were 80 per cent. digested, the lost 80 per cent. of volume was restored in the record. In one sense, this procedure would seem to give a much greater degree of accuracy than if the item were credited only with the *actual* 20 per cent. of its original volume. In practice, the two methods of recording volume were found to give comparable, but again not similar, results.

Workers in food studies do not agree as to the relative importance of the various *frequencies* versus *volume*. Each factor is obviously important, and each obviously does not tell the whole story (for snakes of all sizes). Percentage frequency of a given item appears to tell more regarding the food preference, or food availability, for the average snake of the study sample. Volume appears to emphasize the predation impact of the study sample on the total available food mass. It may at times over-emphasize the unusual.

The two points of view may sometimes give vastly different pictures of the food habits of an animal. In the present study, 23 per cent. of the food items taken consisted of minnows, but minnows comprise only 7 per cent. of the volume of food taken. Lake lampreys were taken less than 1 per cent. of the time, yet they make up 13 per cent. of total volume. This study involves contents of 207 stomachs with a total volume of 1,372 cc. However, if only 10 selected stomachs were missing from the study material, total volume would be reduced to 653 cc.

In some food habit studies there appears to be a real need for a formula that will adequately evaluate both frequency of occurrence and volume, and perhaps other factors as well—if, indeed, such evaluation is practicable.

#### HABITATS REPRESENTED

Typical small, rocky streams of south-central

New York are represented by 120 stomachs (Table 1). Minnows, darters, suckers and sculpin comprise 72 per cent. of the food items taken, although they make up slightly less than half of the total volume of food. Lake lampreys are important in volume (23 per cent.) but are represented by only two food captures. Game fishes were taken only twice (one fingerling each of brown trout and small-mouth bass). Amphibians are represented by 15 per cent. of the food captures. These were mostly frogs, toads and small salamanders (*Eurycea*).

Small New York lakes are represented by only 15 stomachs containing 23 food items (Table 2). Slightly more than half the items taken were amphibians (mostly frogs, toads and tadpoles). The fish most frequently taken was a catfish (*Ameiurus*). However, game fishes (*Perca* and *Lepomis*), representing 9 per cent. of the food captures, made up 30 per cent. of the food by volume.

Michigan lakes of the Cheboygan region are reasonably well represented by 48 stomachs containing 60 food items (Table 3). Minnows and darters together made up 52 per cent. of the items taken, although their volume was only 10.5 per cent. of the total. Game fish (*Perca*) represent 15 per cent. of the food captures. Although the burbot (*Lota*) was taken only twice and *Necturus* four times, their volumes (17 and 45 per cent. respectively) were impressive.

Great Lakes beaches of the Cheboygan region, and of Bois Blanc Island, Hog Island and Garden Island, are represented by 19 stomachs (Table 4). These stomachs contain only sculpin (89 per cent. of food captures) and frogs (11 per cent.).

Michigan bog ponds are represented by only 4 stomachs with 11 food items (Table 5). These few suggest a considerable dependence upon amphibian food in this type of habitat.

TABLE 1. FOOD OF 120 SPECIMENS FROM STREAMS OF CENTRAL NEW YORK

	No. of food items taken (% of 129)	No. of stomachs in which the food occurred (% of 120)	Volume of food taken (%)	
			Actual (777 cc.)	Estimated (886 cc.)
Minnows	27.9	27.5	7.7	8.3
Darters	21.0	19.1	3.1	3.0
Suckers ( <i>Catostomus</i> )	15.5	16.7	35.4	36.0
Sculpin ( <i>Cottus</i> )	7.8	8.3	1.4	1.8
Catfish	2.3	2.5	9.3	9.0
Lamprey	1.5	1.7	23.0	20.2
Game Fishes	1.5	1.7	1.2	1.1
Unidentified Fish	7.0	7.5	1.6	3.3
Amphibians	15.5	16.7	17.3	17.3

TABLE 2. FOOD OF 15 SPECIMENS FROM NEW YORK LAKES

	No. of food items taken (% of 23)	No. of stomachs in which the food occurred (% of 15)	Volume of food taken (%)	
			Actual (122 cc.)	Estimated (141 cc.)
Catfish ( <i>Ameiurus</i> )	21.7	26.7	18.6	16.9
Game Fishes ( <i>Perca, Lepomis</i> )	8.8	13.3	30.4	28.5
Sculpin ( <i>Cottus</i> )	4.4	6.7	0.9	1.0
Unidentified Fish	13.0	20.0	0.2	0.4
Amphibians	52.0	60.0	50.0	53.6

TABLE 3. FOOD OF 48 SPECIMENS FROM MICHIGAN LAKES

	No. of food items taken (% of 60)	No. of stomachs in which the food occurred (% of 48)	Volume of food taken (%)	
			Actual (407 cc.)	Estimated (491 cc.)
Minnows	36.7	35.4	9.1	9.4
Darters	15.0	18.7	1.4	1.6
Sculpin ( <i>Cottus</i> )	5.0	6.25	2.2	2.0
Catfish	6.7	6.25	0.3	0.4
Troutperch ( <i>Percopsis</i> )	5.0	6.25	2.8	2.7
Burbot ( <i>Lota</i> )	3.3	4.2	17.4	20.3
Game Fishes ( <i>Perca</i> )	15.0	8.3	14.1	12.7
Amphibians	13.3	16.7	52.8	50.8

TABLE 4. FOOD OF 19 SPECIMENS FROM MICHIGAN GREAT LAKES BEACHES

	No. of food items taken (% of 28)	No. of stomachs in which the food occurred (% of 19)	Volume of food taken (%)	
			Actual (50 cc.)	Estimated (60 cc.)
Sculpin ( <i>Cottus</i> )	89.3	89.0	78.0	81.0
Frogs	10.7	15.8	22.0	19.0

TABLE 5. FOOD OF 5 SPECIMENS FROM MICHIGAN BOG PONDS

	No. of food items taken (% of 11)	No. of stomachs in which the food occurred (% of 5)	Volume of food taken (%)	
			Actual (17 cc.)	Estimated (20 cc.)
Frogs & Tadpoles	91.0	80.0	90.3	89.0
Mudminnow ( <i>Umbra</i> )	9.0	20.0	9.7	11.0

## SUMMARY OF FOOD ITEMS

A broad picture of water snake food is obtained by combining the 207 stomachs from all the above habitats (Table 6). Seventy-nine per cent. of the total 251 food captures (68 per cent. of volume) are seen to involve fish forms; 21 per cent. (32 per cent. by volume) involve amphibians. Minnows, darters, suckers or sculpin were taken in 61 per cent. of the captures.

Catfish and game fishes were each taken in 5 per cent. of the captures.

## DISCUSSION OF FOOD FINDINGS

*Fish.*—All evidence presently available testifies to the prominence of fish in the food of the northern water snake—50 to 96 per cent. It is likely that virtually every species occurring in favorable habitats with the snake may at times fall prey. Minnows, darters, suckers and sculpin

TABLE 6. FOOD OF ALL 207 SPECIMENS COMBINED

	No. of food items taken (% of 251)	No. of stomachs in which the food occurred (% of 207)	Volume of food taken (%)	
			Actual (1,372 cc.)	Estimated (1,598 cc.)
Minnows	23.1	24.1	7.1	7.5
Darters	14.3	15.4	2.2	2.2
Suckers ( <i>Catostomus</i> )	8.0	9.7	20.0	19.9
Sculpin ( <i>Cottus</i> )	15.5	15.0	4.3	4.7
Catfish	4.8	4.8	7.1	6.7
Troutperch ( <i>Percopsis</i> )	1.2	1.5	.8	.8
Burbot ( <i>Lota</i> )	.8	.96	5.1	6.2
Lamprey ( <i>Petromyzon</i> )	.8	.96	13.0	11.2
Mudminnow ( <i>Umbra</i> )	.4	.48	.12	.2
Game Fishes	5.2	3.9	7.6	7.0
Unidentified Fish	4.8	5.8	.9	1.9
Amphibians	21.1	21.2	31.7	31.7

(doubtless reflecting the availability of these forms) appear to be the fishes most frequently captured, especially in stream habitats, although they do not loom so large in total bulk. It is of considerable interest that, even in the stomachs from Michigan trout streams reported by Lagler & Salyer (1947), 72 per cent. of the food captures involved forage fishes (56 per cent. of volume), while only 6 per cent. involved trout (19 per cent. of volume).

In studies involving habitats of the large lake lamprey, this animal may be expected to rank well from the standpoint of total volume. However, it is likely to be an important food item only for large snakes and then only during the limited period of spawning. How large a snake must be to capture or swallow a lake lamprey has not been determined. Only 7 per cent. of the snakes of this study were as large (900 mm.) as the two that had taken lampreys.

It has sometimes been asserted that dead fishes make up a large part of the water snake's diet, but there is little evidence to support this belief. Several of the fish which I recovered from stomachs apparently had been picked up dead. Dead fish are readily eaten, although some of my captive specimens seemed to prefer fresh or only slightly decayed fish. Alexander's (1943) and Lagler's (1943) observations concerning the preference of snapping turtles for fresh meat may be of interest here. However, the water snake can, and does, readily capture live fish, and the taking of large numbers of dead fish is probably exceptional and fortuitous in the average habitat. (See page 60).

Trembley (1948), ably seconded by Conant, has done the cause of reptilian conservation and common sense a real service in raising a voice from the heart of the Pennsylvania "bounty

country," pointing out the possible utility of water snakes in the ecology of ponds and lakes.

*Amphibians.*—In a general way, the food of the water snake may be said to consist of fishes and amphibians, with the latter occupying a substantial second place. In the present series of 207 stomachs, amphibian material was represented in 21 per cent. of the food captures, in 21 per cent. of the stomachs and in 32 per cent. of total food volume. Frogs and toads together seemed to play a more important part than did salamanders (especially in some lakes), with the latter becoming more important in the food of very young snakes in stream habitats. Tadpoles were taken sparingly in all habitats.

The taking of very large salamanders has now been reported a number of times for *Necturus* (Gentry, 1941; Creaser, 1944; Lagler & Salyer, 1947) and *Cryptobranchus* (Welter & Carr, 1939; Anon., Penn. Angler, May, 1935), in addition to the instances cited in this paper. Because of the large average size of these animals, they are more likely to be taken by sizeable snakes and to be more conspicuous in the volumetric results of food studies than their infrequent capture might warrant.

Conant (1938) mentions specimens of *Natrix sipedon insularum* that would not eat frogs. I have had specimens of *N. s. sipedon* that seemed unaccustomed to frogs, although it was found that an amphibian meal, even though forced, would often convert these specimens to a diet of either type available.

Dunn (1935) was not successful in inducing garter snakes to eat the pickerel frog (*Rana palustris*). This frog was not found in the snake stomachs of the present study, although some snakes were collected from pickerel frog habitats. However, Gentry (1944) found 8 young

pickerel frogs in a specimen of *N. s. sipedon* and Hamilton (1951a) recorded it from *Thamnophis*. Among captive snakes that were good feeders, I have had some specimens of both the northern water snake and the eastern garter snake that would, and some that would not, take the pickerel frog experimentally. Pickerel frogs were accepted by several different snakes on about a dozen occasions. One water snake captured and swallowed a small pickerel frog, then took another away from a garter snake that was attempting to swallow it. The frogs were retained and digested in all cases. However, these frogs were usually accepted less eagerly than were other species, and they seemed to be mouthed with a noticeable degree of gentleness and caution during the process of swallowing. After such a frog had been swallowed, the snake usually went through the motions of rubbing the sides of its head against nearby objects.

Newts are not a popular water snake food, although snakes and newts are at times abundant in the same habitat. Fitch (1941) and Fox (1952) reported larvae of *Taricha* from Pacific coast garter snakes. Hubbard (1903) was unable to induce *Thamnophis elegans* to take adult *Taricha*, and Fox (1951, 1952) reported it only from the race *atratus* and from two specimens of *Thamnophis sirtalis* of the San Francisco area. Hamilton (1951b) reported a specimen of *Diemictylus* from *Natrix s. insularum*, but did not find it (1951a) in eastern *Thamnophis*. My own best water snake feeders in captivity could not be induced to take this salamander. One old specimen, accustomed to accepting instantly anything shaken in her direction, grabbed a newt, quickly gulped it down several inches, then suddenly changed her mind and ejected the salamander with such violence that it was flung to a distance of about four feet. The back of the newt was covered with the milky-looking secretion from skin glands.

*Crayfish*.—It is likely that the importance of crayfish as water snake food has been unintentionally exaggerated. Some of the generalizations about crayfish in the literature seem to be indirectly traceable to Ortmann (1906) and to Atkinson (1901). Unfortunately, the statements in these sources refer to more than one snake species, and seem to be incapable of definite interpretation with regard to the northern water snake.

Ditmars (1912) recorded a definite instance of crayfish as northern water snake food. Conant (1938) reported crayfish from Ohio snakes but did not say how often he had found them. The major studies of the food habits of this snake have not included crayfish in the findings. I

myself found none, although many stomachs were examined from habitats in which crayfish were abundant. The best feeders among my captive snakes could not be induced to take this type of food. The fact that Barbour (1950) and Neill (1951) report crayfish from *sipedon* in the mountain region farther south suggests that there may be some regional differences in the importance of this animal as water snake food.

*Other Vertebrates*.—That small mammals may very occasionally be taken by the water snake is indicated by Surface's (1906) record of meadow mouse and shrew. Uhler, Cottam & Clarke (1939) reported mammal hairs from two stomachs, and Lagler & Salyer (1947) reported a rodent trace. Gloyd (1928) did not succeed in interesting captive specimens in warm-blooded prey. I also was unsuccessful here.

Conant (1938) found a small northern water snake in a stomach of a snake of the same species. Uhler, Cottam & Clarke (1939) found a few snake scales in one specimen, and Lagler & Salyer (1947) recognized a fragment of shed skin. Conant & Bailey (1936) reported a fence lizard taken by a captive snake. I have noted only indirect tendencies toward "cannibalism"—when two snakes were attempting to swallow the same food, or when one snake had crawled over fish and therefore carried the odor of the food.

I know of no records of the taking of birds by the northern water snake. However, it would not be surprising if this does occur in rare circumstances.

*Other Invertebrates*.—Minor amounts of material representing various other invertebrates have been reported from this snake, to the extent of 2.4 per cent. of the volume of the 30 stomachs of Uhler, Cottam & Clarke (1939) and 1.6 per cent. in the 106 trout stream stomachs of Lagler & Salyer (1947). These items have included young or adults of various insects (Coleoptera, Odonata, Plecoptera, Orthoptera, Diptera, Lepidoptera), earthworms, leech and millipede. Breckenridge (1944) reported a spider. Arthropod material should always be examined critically, since some of it may be traceable to the stomachs of vertebrates that have themselves been preyed upon.

King (1939) reported a slug from one stomach, and Lagler & Salyer (1947) an aquatic snail. Mr. William C. Wise, of Quentin, Lebanon County, Pennsylvania, informed me (letter) of finding a water snake "captured" by a large aquatic snail. The snail, in retracting its operculum, caught the fore part of the snake's head between shell and operculum. The snake apparently could not free itself and smothered. A

photograph of this specimen appeared in the June, 1939, issue of *Pennsylvania Game News*. Mr. Frederick Tresselt of Hunting Creek Fisheries, Thurmont, Maryland, told me (conversation) in 1938 that at least a dozen times he had observed water snakes "caught" by large "Japanese snails" in his goldfish ponds. It appears likely that in such cases the water snake has actually attempted to feed upon the snail. This snake-snail relationship has not been checked experimentally.

#### FOOD OF YOUNG SNAKES

It is desirable to know how the food of very young snakes compares with the broad findings. Of the 207 stomachs, 73 were from snakes known, or estimated, to be in their first year of life (207-380 mm. in length). The findings from these are listed in Table 7. According to these data, fishes are still the most important type of food. Minnows, darters and amphibians together comprise 4 of every 5 food items taken. The amphibians included very small frogs and the slender northern two-lined salamander. Most of the animals captured were quite small, and 90 per cent. of these young snakes contained only a single food item.

It was interesting that even these young snakes did not hesitate to take catfish. This practice occasionally results disastrously for a water snake, but it is frequently managed safely.

The food of young snakes is important but it should not be over-emphasized. It appears important because, if the snakes of the present study are a representative sample, about 40 per cent. of all water snakes would be members of this first-year class. However, on the basis of the same sample, I estimate at present that snakes of this size would consume only about 8 per cent. of all the food taken by water snakes.

#### FOOD VARIATION UNDER SPECIAL CONDITIONS

Fish hatcheries often offer situations where access may be had to dense populations of few species and where fish may be captured with greater ease than elsewhere. Under such circumstances one might expect to find snakes gorged with the species at hand, and stomach contents would not yield a completely natural picture of food habits. Lagler & Salyer (1947) examined many stomachs of snakes taken at trout rearing stations in Michigan. Slightly more than half of these (56 per cent.) contained the fish being propagated.

The occasional practice of planting large numbers of hatchery-reared fish without sufficient scattering may also offer excellent opportunity for predation by water snakes. According to A.

S. Hawkins, a party of local sportsmen planted trout along the Stein Kill near Chatham, New York, in early August, 1934. Little more than an hour later Harry Carr, a member of the party, returned to one of the points of planting. He found a water snake containing 5 two-inch fingerlings.

Conant (1938) mentions a number of instances of the eating of dead fish by *Natrix sipedon insularum*. Around Lake Ontario and in the Finger Lakes region of New York water snakes would be expected to take advantage of the extensive dying off of the alewife (*Pomolobus pseudo-harengus*), during such seasons as this occurs. G. F. MacLeod told me of seeing a number of snakes on a cove at the north end of Seneca Lake gorging themselves on these fish as the latter drifted in to shore.

Isolated pools during drought conditions, pools from which metamorphosing frogs are emerging, the presence of spawning lampreys in the spring, assemblages of breeding frogs and toads, are examples of other local conditions that might temporarily influence water snake diet.

#### CAPTURE OF FOOD

Wilde (1938) found that chemical sense, operative through the tongue, lips and organs of Jacobson, is extremely important in feeding reactions of *Thamnophis s. sirtalis*. Fox (1952) considered odor particularly and also sight to be used in food recognition by his garter snakes of the *Thamnophis elegans* group. Methods used by water snakes in capturing prey will not be fully understood until a thorough study has been made of the relative importance of the various senses employed. Present information seems to indicate:

1. That the sense of touch may be extremely important in a large proportion of under-water hunting.

2. That sight may be of some importance in daylight under-water hunting with reference to the detection of near moving objects.

3. That a submerged snake, especially if it is moving, apparently does not see objects above the surface.

4. That near moving objects are readily detected in terrestrial operations.

5. That the extent of the role of chemical sense in under-water hunting is problematical. This sense is efficient on land, at least with respect to some odors, but its degree of utility under natural conditions is uncertain. Many observers have noted the confusion into which a group of hungry water snakes may be thrown when dead fish is placed in their cage. I have

TABLE 7. FOOD OF 73 YOUNG SPECIMENS (ALL HABITATS)

	No. of food items taken (% of 86)	No. of stomachs in which the food occurred (% of 73)	Volume of food taken (%)	
			Actual (72 cc.)	Estimated (91 cc.)
Minnows	{25.6	27.4	{26.0	28.0
Darters	80}{30.2	31.5	71}{27.0	25.0
Amphibians	{24.4	24.6	{18.0	19.7
Sculpin ( <i>Cottus</i> )	7.0	6.8	10.0	9.8
Suckers ( <i>Catostomus</i> )	4.6	5.5	7.0	6.0
Catfish	3.5	4.1	1.7	1.6
Troutperch ( <i>Percopsis</i> )	1.2	1.4	5.6	5.0
Game Fish ( <i>Micropterus</i> )	1.2	1.4	5.0	3.9
Unidentified Fish	2.3	2.7	0.3	1.0

had captive specimens which would tear to bits paper that had been wrapped around fish; ones which, after I had handled fish, would greedily swallow a finger as far as anatomy would permit.

It is difficult to describe anything that might be called typical procedure in the taking of fish, and I am aware that it may be neither advisable nor possible to classify hunting methods. However, for organizational convenience, this subject is dealt with under several headings.

*Groping or Exploratory Method of Hunting.*—Abbot (1884) early called attention to this method. He remarked about the haphazard way in which the snake hunted, not seeming to single out any particular fish in a group. It "opened its mouth and left the rest to luck."

Evans (1942) carefully described a number of instances of hunting by water snakes of several species. In most cases the snake swam or drifted in the water near the surface. "The head was submerged and the mouth kept open wide as it swept through the water from one side to the other in a continuous series of figure eights, the entire body following the path of the head." Although this exploratory method would seem particularly suitable to night fishing, Evans' account points out that it may also be used by day.

Stoner (1941) made an observation that may apply to this method, but it appears incapable of exact interpretation.

Kellogg & Pomeroy (1936), in their maze experiment, gained the impression that a snake "felt" its way through the maze by pushing against the sides with its nose. In 1937 and 1938 I made many observations on water snakes actively fishing in tanks and aquaria. Motion picture films of some of these operations were also studied, and the actions of the snake gave a strong impression that it was "groping" for the prey. Often it did not move toward nearby fish easily within reach (even though the water

was clear and visibility presumably good). The mouth might or might not be open but it frequently was. With rather deliberate movements, the snake "felt" around in an almost aimless manner, first in one direction then in another. However, the instant any part of the head or neck touched a fish, a wild grab was made in that direction. The efficiency of the method is surprising. If a fish was grasped, the snake often bent its head around at a sharp angle and pressed the prey against its body till it secured a firmer grip.

An apparent modification of the groping method of hunting is that of exploring under rocks and other objects on the bottom. Many observers have encountered evidence of this activity. The large proportion of sculpin, darters and two-lined salamanders found in snake stomachs seems to support the idea that this type of hunting may be very important in suitable habitats. Uhler, Cottam & Clarke (1939) reported a case in which a brook trout was caught beneath a rock.

*Direct Attack Method.*—Here the sense of sight seems to play a dominant part. Fishing tactics may at times be a mixture of this and the exploratory method, and probably some of the following examples might be interpreted as illustrating either type of procedure.

DeKay (1842) mentioned a water snake that was seen to fall from a bush into a stream and seize one of a number of chubs that were swimming by.

In describing the capture of a *Notropis procerus* by a snake, Cope (1869) said, "approaching cautiously, he struck right and left below the surface, as the minnows passed him, but often fell short."

On the Cayuga Lake inlet about 1916, A. H. Wright saw a water snake swim out from shore, seize a 14-15-inch lamprey on its nest and drag it back to shore.

In the summer of 1926 on a small tributary of Wolf Creek, Wyoming County, New York, P. W. Claassen and others were watching a brook trout about six inches long. Suddenly, from the bordering vegetation a few inches away, a water snake lunged, grasped the trout amidships and swam off with it.

S. C. Vanderbilt, of Clyde, New York, for several minutes watched a water snake in the edge of aquatic vegetation as it seized tadpoles that swam by. The snake was killed and found to contain 16 tadpoles.

While observing spawning minnows near Ithaca, New York, in May, 1936, W. J. Koster saw three small snakes fishing among the minnows "without success, although they made quite a few lunges at the fish."

C. W. Creaser observed a snake 15 feet out from shore on Burt Lake, Michigan, striking among members of a school of minnows. The snake was neither touching bottom nor anchored to any object in the water.

W. J. Koster, sitting motionless on the bank of Danby Creek, near Ithaca, in May, 1936, watched a water snake crawl ashore nearby. "It was just about settled, apparently to bask in the sun, when two *Notropis cornutus* began splashing in very shallow water. The snake immediately lifted its head, which had been about an inch from the ground, and turned in the direction of the disturbance. After watching for several minutes it crawled into the water and attempted to catch a fish."

Raney & Roecker (1947) observed the banded water snake "actively chasing and capturing fishes" in Erie County, New York.

In Delaware County, New York, on the inlet of Silver Lake, I watched a two-foot snake attempting to capture fish at midday in August, 1935. The snake was in a pool eight or ten inches deep. The caudal end of the body extended under a log, perhaps for anchorage. The rest of the body was moving around in the water in a manner that appeared to be partly exploratory, partly directed. Of the dozen or so small suckers, horned dace and mad toms in the pool, one or more were almost continually approaching the snake, apparently in a state of curiosity. When one came within range the snake would make a lunge for it. Although this occurred a number of times during the two or three minutes before the snake became alarmed, the fish were a little too quick each time. The procedure clearly demonstrated, however, how an unwary fish might easily fall victim. The fish never exhibited wild excitement or dashed about in the pool. They gave the impression of mild curiosity

toward the snake. When it lunged, they would simply dart a short distance out of reach, often "gathering around" again within a few moments.

The interesting feature of this incident is not the behavior of the snake but rather that of the fish. It suggests that, if *game fish* behave in the same manner in the presence of a snake, their speed might be of little advantage to them. There is no present indication that water snakes actually pursue fish. Swimming speeds of the snake are far too slow, as compared with that of almost any fish. Under the circumstances here indicated, the competing characteristics of the two animals probably are the *speed of lunge* of the snake and the *alertness* and *speed of take-off* of the fish.

*Deep Water Hunting.*—While most hunting by water snakes is probably done in relatively shallow water, they are capable of working at greater depths. The finding of *Lota maculosa* in stomachs suggests, but by no means proves, this. At Hook Point on Douglas Lake, Michigan, in 1932, Sol R. Baker and a group of students saw a water snake emerge some distance from shore with a struggling *Necturus* and swim to land. At the point where the snake appeared, the depth was somewhere between 10 and 25 feet. From the same lake I have another account of a snake that was seen to swim straight out from a rockpile at the water's edge (near the Biological Station boathouse). In about ten minutes it came ashore again with a *Necturus*. The water in which the prey was secured could scarcely have been less than 8 to 10 feet in depth. Again at Douglas Lake (1933), F. C. Gates saw a snake swim to shore from beyond the rim of the beach shelf carrying a live fish. The increase in depth beyond the rim of the shelf is extremely rapid. But whether the fish was secured at the surface or near the bottom is not known.

*Is Prey Brought Ashore For Swallowing?*—The prey may, or may not, be brought ashore to be swallowed. If its size, compared with that of the snake, is large enough to require considerable time and effort for overpowering and swallowing, it is almost certain to be dragged ashore. A small snake would probably find this necessary with almost any prey. So also would a large snake with a good-sized fish, lamprey or *Necturus*. However, the swallowing of a minnow by a large snake may be a matter of only a few seconds, and I have seen a snake swallow a good-sized green frog under water in a large outdoor tank. On dozens of occasions I have observed this with minnows or other small fish in aquaria or tanks.

*Capture of Prey on Land.*—This probably involves a relatively small proportion of the food

of the average water snake. Sight seems to be the sense of prime importance here, with chemical senses playing a secondary role at times. The feeding of frogs to water snakes or garter snakes in large enclosures is likely to illustrate well the comparative safety of the prey, just so long as it remains motionless. But the moment it leaps, the snake may take notice and be in hot, though at times clumsy, pursuit. If the frog is a powerful and persistent jumper, it may outdistance, or "lose," the snake, but if it hesitates between jumps, it is likely to be overtaken. G. J. Leversee told me that he once observed a water snake on the bank of a stream in Greenbrier County, West Virginia. A frog, which apparently had been sitting very near the snake, leaped for the water. So instantaneous was the snake's reaction, that the frog was grasped in mid-air. He thought that the snake had been aware of the frog's presence.

*Method of Swallowing Food.*—Observation of water snakes in captivity is likely to give the impression that the method of swallowing is altogether haphazard and that the prey is as likely to go down tailfirst as headfirst, and at times even sidewise. However, of 200 swallowings of fish, frogs, toads and salamanders in nature—checked by examination of stomach contents—the prey went down headfirst in 80 per cent. (160) of the cases, tailfirst in 18.5 per cent. and otherwise in 1.5 per cent. Fish seem most likely to go down headfirst, salamanders least likely to do so. For details see Table 8.

TABLE 8. HEAD-TAIL ORIENTATION OF FOOD IN 200 SWALLOWINGS BY WATER SNAKES IN NATURE

Food Type	Headfirst	Tailfirst	Otherwise
Fish	140	27	2
Salamanders	9	24	0
Frogs and toads	11	8	1
Totals	160	37	3
Percentages	(80%)	(18.5%)	(1.5%)

Since a fish is a form of food that would pass down more easily headfirst than tailfirst, I once supposed that it might be possible to check on the learning ability of the water snake by comparing the proportion of food swallowed headfirst with the age of the snakes involved. However, the actual condition seems to be about the opposite of what might at first be expected. A snake swallowing food is usually dealing with a more or less elongated object. It has of necessity to work the object around in its mouth and begin swallowing from an end. If one end

does not seem to go down readily, the other is often tried. A small snake in its first year of life may find any minnow that it attempts to swallow such a tight fit that it will go down only headfirst. On the other hand, a larger snake may have a relatively easier time with the swallowing process, and is more likely to be able to pass the food down oriented in whatever way it is first tried. This explanation is supported by actual findings. Of 73 young snakes less than 400 mm. in length, 90 per cent. (66) had swallowed the prey headfirst. Of the 127 older specimens, 74 per cent. (94) had taken the prey headfirst.

#### DIURNALITY VERSUS NOCTURNALITY

According to Walls (1931 and 1942) *Natrix* possesses a reasonably typical diurnal colubrid type of eye. However, the highly efficient "groping" method of fishing fits this snake admirably for nocturnal activity as well, apparently without the aid of sight. That the activity of *Natrix s. sipedon* may be to a high degree both diurnal and nocturnal is now well established by records in the literature and by the experience of many observers.

Variations in the degree of diurnality or nocturnality in a given region are probably largely a matter of weather conditions, season and temperature factors in the available habitat. Swanson (1952) noted in Venango County, Pennsylvania, that the cooler streams were seldom frequented by this snake. He noted further that along moderately cool Big Sandy Creek, water snakes were common by day but almost never seen at night. Along Carp Creek, a cool woodland trout stream (water temperatures 52°-56° F. at times of observation) near the University of Michigan Biological Station, I found no water snakes except at the stream's mouth where it enters Burt Lake. The late Dr. George E. Nichols, who fished the stream for many years, said that he had seen *Natrix* only at a small stagnant pool adjacent to the creek at one point. These observations merely agree with those of Lagler & Salyer (1947) for cold, shaded streams. After hot (90° F.) mid-summer days at Ithaca, New York, I found water snakes active at night in water temperatures of 72°-73° F. In my experience this snake is most active at temperatures between 70° and 80° F., tending to seek shelter at air temperatures much above 80° F., and with activity ceasing altogether at temperatures in the low fifties.

It will no doubt be found that this snake is more diurnal in the northern portions of its range and during spring and fall, more nocturnal farther south and during mid-summer months.

#### MAXIMUM SIZE OF A MEAL

Here we are not dealing with the average size of meals in nature, but with the maximum size under the most favorable circumstances possible. The size of the meal is expressed in terms of percentage of the weight of the snake, previous to the meal. The question is, what percentage of its own weight in food may a snake take (voluntarily accept) at one time?

Uhler, Cottam & Clarke (1939) reported a water snake swallowing a bullhead whose weight was 40 per cent. of that of the snake. In 7 snakes collected in nature that appeared to contain unusually large amounts of food, I found that the food varied from 11 to 37 per cent. of the weight of the snake, with a mean of 20 per cent.

Nineteen empty snakes that were good feeders in captivity<sup>3</sup> were gorged until they refused to take more food. The food taken ranged from 11 to 43 per cent. of the weight of the snake, with a mean of 26 per cent.  $\pm$  2.35 and a standard deviation for the distribution of 10.2.

It is interesting to note that a snake may at one meal take food amounting to 40 per cent. of its own weight. It seems reasonably certain that this is a near maximum figure for this water snake—a figure which may occasionally be reached but which is probably seldom exceeded. The individual in this series that took a meal amounting to 43 per cent. of its weight later disgorged part of the food, apparently because it had taken too much for comfort. This same individual on three other occasions took maximum meals amounting to 32, 34 and 35 per cent. of its weight. Another snake on two occasions took meals of 36 and 39 per cent. Most of the other specimens took somewhat smaller meals.

It was noted that following these maximum feedings the forward region of the alimentary canal was always left unobstructed. When a snake had fed until it refused further food, its stomach and esophagus were usually gorged to a point 1 to 1½ inches (25 to 44 mm.) caudad of the heart. This meant that the heart and at least part of the highly vascular and functional anterior end of the lung were permitted freedom of movement. In eight cases the length of the unencumbered anterior end of the body equalled 15 to 23 per cent. of the total length of the snake.

<sup>3</sup>All "captive" snakes referred to in this paper in connection with various feeding observations were kept out of doors on the ground. Some were in a roofless wire enclosure, others were in a roofed enclosure that had all sides open. All snakes were exposed to natural conditions of temperature, sunshine and moisture. The enclosures contained logs and boards under which specimens could seek shelter.

#### AVERAGE SIZE OF A MEAL

There is no doubt that under unusually favorable conditions water snakes will gorge themselves. Most hatchery men have seen examples of this. Lamson (1935), without stating the source of the record, says, "as many as sixty fingerling trout have been taken from the digestive tract of a single snake." Blatchley (1891) found seven *Rana pipiens* in one. I have fed as many as 42 black-nosed dace at one time to a large specimen before the snake finally refused to take more.

However, there is much doubt that the average water snake meal in nature consists of such proportions. This doubt is based upon the contents of the 207 northern water snake stomachs from nature. Of this number, 183 (88 per cent.) contained only one food organism. The contents of the remaining 24 stomachs (12 per cent.) varied from 2 to 7 food organisms, averaging 2.8 per stomach. The mean for the entire group of 207 was 1.2 organisms per stomach. It was relatively unusual for a single food organism to be of maximum meal size.

In my experience, after a captive snake had been fed a "maximum" meal, it refused to take additional food for three to five days. In other words, it would take no more until *gastric* digestion, at least, was apparently complete. On the other hand, snakes that were fed small or moderately sized meals (i.e., a medium sized frog for a large snake) would continue to feed every day, or at least every other day, almost indefinitely.

It is not desired to give the impression that snakes will not feed if they already contain some food. Snakes containing food are not always found lying quietly away under cover. I have collected individuals that were active and apparently hunting, although they contained food. Individuals have also been collected containing two or more food organisms that had been captured many hours apart. However, these findings merely further suggest that the average snake probably takes moderate meals at fairly frequent intervals, rather than gorging itself to capacity when it feeds.

#### MAXIMUM AMOUNT EATEN DURING A GIVEN PERIOD

The time demanded by this type of work made it impossible for me to make observations on large numbers of individuals. Nevertheless, records are available for 11 of the best feeders on hand during the summer of 1938. These specimens were so accustomed to human beings and to being fed that they practically never refused to eat unless they were already gorged.

Four of the 11 were young approaching the end of their first year of life, 2 were second-year individuals, 1 was in its third year, and the remaining 4 were adults in their fifth or sixth year. The feeding was carried on during July and August, which months had the highest mean temperatures (73° F.) for the summer. All food taken by the snakes was weighed. All of the specimens were fed fish, except for number 11 which was fed entirely on frogs. In order to make food consumption the maximum possible, each snake was offered all that it would take at each feeding. During 2 of the 9 feeding periods for specimen number 10, it refused to take food, apparently because of shedding complications. The period of experimental feeding lasted from 25 to 55 days in various cases. Final weighing of the specimens was done 4 to 6 days after the last feeding. Feeding data on these specimens are summarized in Tables 9 and 10.

The gross amount of food consumed is of interest. For the first-year specimens this averaged 61 per cent. of the original weight of the snake per week, or 247 per cent. per month (of four weeks). For the four adult specimens food consumption averaged 43 per cent. of the original weight of the snake per week or 174 per cent. per four-week month, with the frog-eater (number 11) consuming a slightly higher percentage than the three fish-eaters. The few specimens of intermediate age exhibited lower, but rather consistent, consumption of 30 per cent. per week and 121 per cent. per month.

Specimen number 9 may be considered a con-

servative example among the adult fish-eaters. This snake consumed 360 grams (12.7 ounces or 153 per cent. of the original weight of the snake) of fish in 28 days. This weight of fish is the approximate equivalent of any one of the following: 164 medium black-nosed dace, or 89 three-inch common shiners, or 34 four-inch horned dace, or 24 three and one-half inch carp, or 18 five-inch brook trout, or 6 seven-inch common suckers.

Snake number 11 was actually fed 15 frogs of varying sizes during the 25 days. These weighed 507 grams and would be the approximate equivalent of either 14.5 fair-sized *Rana pipiens* or 6.8 large *Rana clamitans*.

There is certainly much variation among captive snakes in their inclination to feed. Evidence suggests that snakes in the wild state also vary in proportionate amounts of food consumed. This is reflected in varying growth rates among snakes of the same age in the same wild habitat. Nevertheless, the feeding habits of the best captive feeders may provide a rough optimum index to conditions in the wild state.

The statement is occasionally made that captive snakes are probably much better fed than are those in the wild state. If winter feeding is disregarded there is reason to doubt this. Snakes in poor physical condition are often seen in captivity. But in my experience the more usual occurrence is for wild specimens to be in excellent condition (aside from occasional heavily parasitized individuals) and to contain extensive visceral fat deposits, even immediately following hibernation.

TABLE 9. BASIC DATA ON EXPERIMENTALLY-FED SNAKES

	Sex	Original Length (mm.)	Original Weight (gm.)	Times Fed	Duration of Feeding Period (wks.)
(Young Ending First Year)					
1:	F	256	5.3	11	7
2:	M	278	5.7	10	7
3:	F	288	6.7	11	8
4:	F	320	10.4	13	8
(Ending Second Year)					
5:	F	516	32.7	10	7
6:	M	475	25.2	6	3½
(Ending Third Year)					
7:	M	607	53.2	8	3½
(Adults Ending Fifth or Sixth Year)					
8:	F	870	237.	9	4
9:	F	887	235.	9	4
10:	M	770	114.	7	4
11:	F	945	255.	10	3½

TABLE 10. FEEDING RECORD OF EXPERIMENTALLY-FED SNAKES

	Food Eaten				
	Gross (gm.)			In % of Orig. Wt. of Snake	
	Total	Per Wk.	Per Mo.	Per Wk.	Per Mo.
	(Young Ending First Year)				
1:	26.6	3.8	15.2	71	286
2:	23.1	3.3	13.2	58	232
3:	30.4	3.8	15.2	57	227
4:	50.1	6.3	25.2	60	242
(Avs.:	32.5	4.3	17.2	61	247
	(Ending Second Year)				
5:	62.8	9.	36.	27	110
6:	31.2	8.4	33.6	33	133
(Avs.:		8.7	34.8	30	121
	(Ending Third Year)				
7:	58.5	16.1	64.4	30	121
	(Adults Ending Fifth or Sixth Year)				
8:	403.	101.	403.	42	170
9:	360.	90.	360.	38	153
10:	197.	49.	197.	43	173
11:	507.	127.	507.	50	199
(Avs.:	366.	92.	366.	43	174

#### GROWTH DURING PERIOD OF EXPERIMENTAL FEEDING

Growth data for the same 11 snakes during the period of experimental feeding are summarized in Table 11.

Although the number of specimens is still small, the data exhibit sufficient consistency to suggest that they have some value.

Increases in gross length averaged about the same for the first-year specimens as for the adults: 7 mm. per week or 28 mm. per month (of four weeks). (This, of course, means that young would double in length much more rapidly than would adults). Although the rate of gross length increase is about the same for young and adults in this series, other data indicate that in still older snakes (from 7th or 8th year on) the rate would be somewhat slower.

On the other hand, increase in gross weight is seen to be much more rapid in adults than in young. However, increase in weight, in terms of percentage increase over the original weight of the snake, was approximately twice as rapid in the first-year specimens as in the adults.

Young individuals of the first three groups consumed about 3 grams of food for each gram of gain in weight. Among the adults, the three

fish-eaters averaged about 50 per cent. greater consumption (4.5 grams) of food for each gram of gain in weight, while the highest consumption (6.9 grams) per gram of gain was registered for the single frog-eater in this particular series. It is impossible to say whether this last item has any significance.

Lacking more extensive data on food consumption, on ages of specimens and on the effect of hibernation upon weight, I do not consider it advisable to attempt to calculate, from the weight of specific snakes, the bulk of fish that may have gone into the make-up of those snakes. Also, it should be noted that the specimens recorded here were given maximum feeding. Parallel observations might well have been made on specimens subjected to more moderate feeding.

#### RATE OF GASTRIC DIGESTION

When we think of "digestion" in a snake we usually have in mind gastric digestion. When food material leaves the stomach, it usually has become liquefied and its presence is no longer evident from the exterior.

The time required for gastric digestion will depend upon at least three important factors: environmental temperature, size of meal and

TABLE 11. GROWTH RECORD OF EXPERIMENTALLY-FED SNAKES

Gain in Wt. (gm.)		% Increase over Original Wt.			Food Eaten per Gm. of Gain (gm.)	Gain in Length (mm.)			
Total	Per Wk.	Total	Per Wk.	Per Mo.		Total	Per Wk.	Per Mo.	
(Young Ending First Year)									
1:	6.7	.96	126	18	72	3.97	60	8.75	35.0
2:	6.3	.9	111	16	64	3.66	24	3.5	14.0
3:	9.3	1.16	139	17	68	3.27	46	5.85	23.4
4:	15.6	1.9	150	19	76	3.21	82	10.4	41.6
(Avs.:.)		1.23		17.5	70	3.53		7.1	28.5
(Ending Second Year)									
5:	19.8	2.8	61	9	36	3.17	38	5.43	21.7
6:	11.7	3.15	46	12	48	2.67	20	5.38	21.5
(Avs.:.)		2.97		10.5	42	2.92		5.4	21.6
(Ending Third Year)									
7:	20.2	5.6	41	11	44	2.9	11	2.96	11.8
(Adults Ending Fifth or Sixth Year)									
8:	75.	18.7	32	8	32	5.3	24	6.	24.
9:	85.	21.2	36	9	36	4.2	39	10.	40.
10:	49.	12.2	43	11	44	4.0	20	5.	20.
11:	73.	20.4	29	7	28	6.9	23	7.	28.
(Avs.:.)		18.1		9	35	5.1		7.	28.

size of snake. Both of the last two are important because the actual stomach of a snake is a relatively short portion of the alimentary tract. When a large meal is taken, some food may occupy the esophageal region anterior to this. But the food remains apparently unchanged until space is available for it in the stomach proper.

Although investigations of the rate of digestion at various controlled temperatures were not carried out, some observations were made under "normal" mid-summer temperatures at Ithaca, New York. One important difficulty was the determination of the end-point of gastric digestion, i.e., the point at which all solid material in the stomach had become liquefied. It was found that this could be determined approximately for most foods by careful manual examination of the gastric region<sup>4</sup> at intervals throughout the period of digestion. In a number of cases the observer's findings were checked by X-ray examination to determine his degree of accuracy. It was noted that about two days might be suggested as an average length of time required for gastric digestion of a moderately large

summer meal. W. A. Kenyon informed me (letter) that garter snakes on which he made observations (1925) seemed to require 2 to 3 days for gastric digestion of a frog.

In ten cases water snakes were fed one frog each, the weight of the frog varying from 16 to 38 per cent. of the weight of the snake (mean: 28 per cent.). The time required for gastric digestion ranged from 42 to 66 hours (mean: 50.4 hours) at mean temperatures<sup>5</sup> of 75° to 76° F.

In three cases snakes were fed large meals of fish. The weights of the meals were equal to 30 to 43 per cent. (mean: 36 per cent.) of the weight of the snake. The time required for gastric digestion ranged from 42 to 60 hours (mean: 49 hours) at mean temperatures of 74° to 75° F.

In other miscellaneous observations the rate of gastric digestion tended to be slower at lower temperatures, more rapid at higher temperatures (e.g., 73 to 80 hours in four instances at 63° to 64° F.; 29 to 50 hours in four at 79° to 82° F.).

<sup>4</sup>Very careful palpation will usually disclose the position of the gall bladder and pancreas. This is, of course, a useful landmark as it marks the level of the caudal end of the stomach.

<sup>5</sup>Mean temperature, as here used, is the average of readings taken at six-hour intervals throughout the 24 hours of a day.

It was pointed out by Benedict (1932) that probably little, if any, digestion in snakes proceeds at temperatures below 50° to 60° F. This was nicely illustrated for the observer by a large water snake that swallowed a lamprey just at the beginning of an unusually cool period during late May, 1936. After five days the lamprey was removed from the snake's stomach. It was still only about half digested. The mean temperature for this period had been 55° F.

At these lower temperatures snakes also show less inclination to feed with, however, considerable variation in different specimens. Among good feeders at Douglas Lake in September, 1937, one refused food at 60° F. Several others fed fairly readily at temperatures from 57° to 60° F. The lowest temperature at which any fed was 52° F. Two accepted a fish with some hesitancy and swallowed it laboriously. (One of these same snakes refused food at 54° F. on another occasion). When exposed to a temperature of 45° F. for one hour, no specimens would feed.

Collections of snakes taken during, or immediately following, periods of cool weather may be expected to show an extremely low percentage of freshly-taken food—if any is present.

#### POST-GASTRIC DIGESTION

Few observations were made on the duration of post-gastric digestion, and these were made at unfortunately low temperatures (62° to 65° F.) at Douglas Lake, Michigan, in the early fall of 1937. However, they suggest certain probable features. The crude "marker" method was used. A wad of indigestible mouse fur was inserted within the body cavity of the small fish (minnow) that made up each meal. The time elapsing from the completion of gastric digestion until the first appearance of fur in the excreta was then recorded. In one instance all the marker material was passed in one fecal sample. In several others, periods varying from 22 to 38 hours elapsed between first and last passages of the marker. This method presents the obvious danger (especially in poorly fed snakes) that the marker may be retained within the body after it has reached the colon and is actually ready to be passed. This difficulty may be avoided by feeding a second meal soon after the "marker meal" has left the stomach.

In five instances the time required for post-gastric digestion (in the above sense) varied from 40 to 113 per cent. of that required for gastric digestion, averaging 71 per cent.

In terms of temperatures in the middle 70s (F.), with a gastric digestion time of about two days, roughly a day and a half would be added

to this for post-gastric digestion, thus amounting to three and one-half days for total digestion or total passage of the alimentary canal. Extensive variation either way is to be expected.

#### SEASON OF FEEDING ACTIVITY

During several seasons at Ithaca, New York, I was able to make fairly extensive collections of water snakes throughout the entire season of activity of the snakes. The food findings from these collections suggested that during the average summer in this region, June, July and August were all months of heavy feeding. Food taken during all the remaining months combined (April, May and September) tended to total considerably less than that for any one of the three mid-summer months.

#### CONTROL MEASURES

Snakes should, of course, be guarded against in fish hatchery situations. Lagler (1939) has pointed out that intensive efforts during one or two seasons of collecting may effectively reduce local water snake populations for several succeeding years. This idea was borne out by experience at the Cornell University hatchery some years ago. It was also supported by my own extensive collecting in certain limited snake habitats along streams of the Ithaca region.

Frederick Tresselt, of Thurmont, Maryland, told me (conversation) some years ago that he had decided success in trapping water snakes on his 17 acres of goldfish ponds. His traps were of a cylindrical minnow-trap type, constructed of wire mesh, about 2 feet long by 10 inches diameter, and with funnel entrances (one removable) at the ends. (This trap was rather similar to that described by Fitch in 1951 if the projecting bibs be left off of the latter). Traps were set in shallow water with the surface of the water cutting across the entrances, so that a snake could swim in with its head above water. Snakes would explore and enter these traps even though they were unbaited. Mr. Tresselt believed that he trapped more than 1,000 snakes in a dozen traps in 1936 and about 500 snakes in more traps in 1937. In 1938 snakes were relatively scarce.

#### SUMMARY

Contents of the stomachs of 207 New York and Michigan water snakes (*Natrix sipedon sipedon*) were tabulated according to frequencies, volume and habitats of collection. Fishes comprised 79 per cent. of the food items taken (with minnows, darters, sculpin and suckers predominant), amphibians 21 per cent. Food is listed for 73 young snakes of the first year. Minnows, darters and amphibians together comprised 80

per cent. of the food items captured. Capture of prey involves so-called groping and direct attack methods. Prey may be taken in relatively deep water. Prey may, or may not, be brought ashore for swallowing. Food organisms were swallowed headfirst in 80 per cent. of 200 cases. This snake appears to be well fitted for either diurnal or nocturnal feeding activity, apparently being more diurnal in cooler habitats, more nocturnal in warmer ones. It seems to be most active at temperatures between 70° and 80° F. Food amounting to 40 per cent. of the weight of the snake may be taken at one time, but a meal is usually considerably smaller. Two hundred and seven stomachs in nature contained 1 to 7 food items, but averaged only 1.2 items per stomach. Examples are presented of amounts of food taken experimentally by good feeders during a period of a number of weeks. Four first-year specimens consumed food averaging 61 per cent. of the original weight of the snake per week, or 247 per cent. per month. Corresponding figures for 4 adult snakes were 43 per cent. of the original weight of the snake per week or 174 per cent. per month. Increases in gross length during this experimental feeding period averaged about the same for first-year specimens as for the fifth and sixth year adults: 7 mm. per week or 28 mm. per month. Increase in gross weight was much more rapid in the adults than in the young. However, weight increase in terms of percentage increase over the original weight of the snake was approximately twice as rapid in the young. Young individuals consumed about 3 grams of food for each gram of gain in weight. The adults consumed half again as much (4.5 grams) per gram of gain in weight. Moderate meals required about 2 days for gastric digestion to be completed at mid-summer temperatures. Post-gastric digestion required somewhat less time. In the central New York region June, July and August were the months of heavy feeding by snakes in nature, with much more moderate food consumption during late April, May and September.

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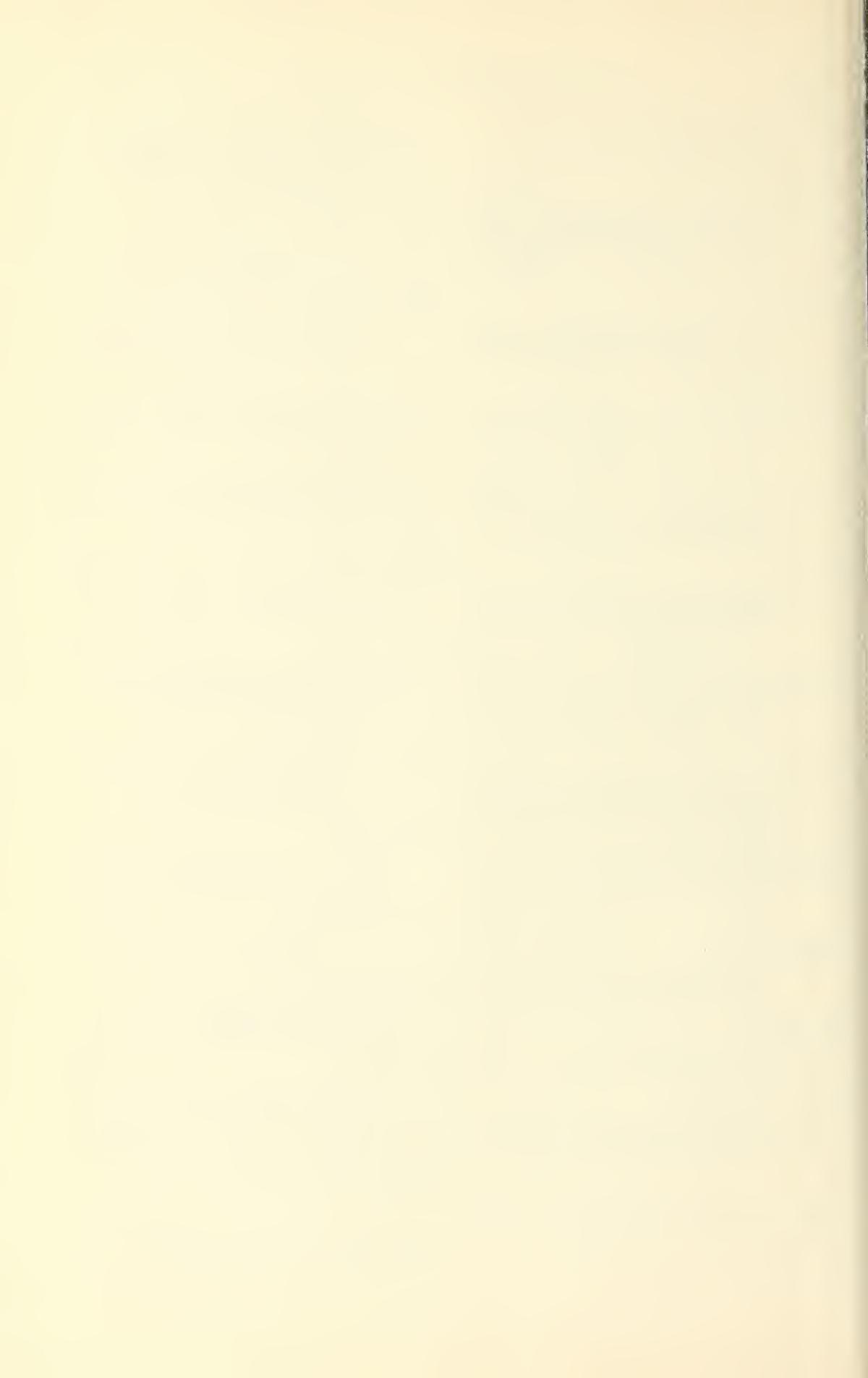
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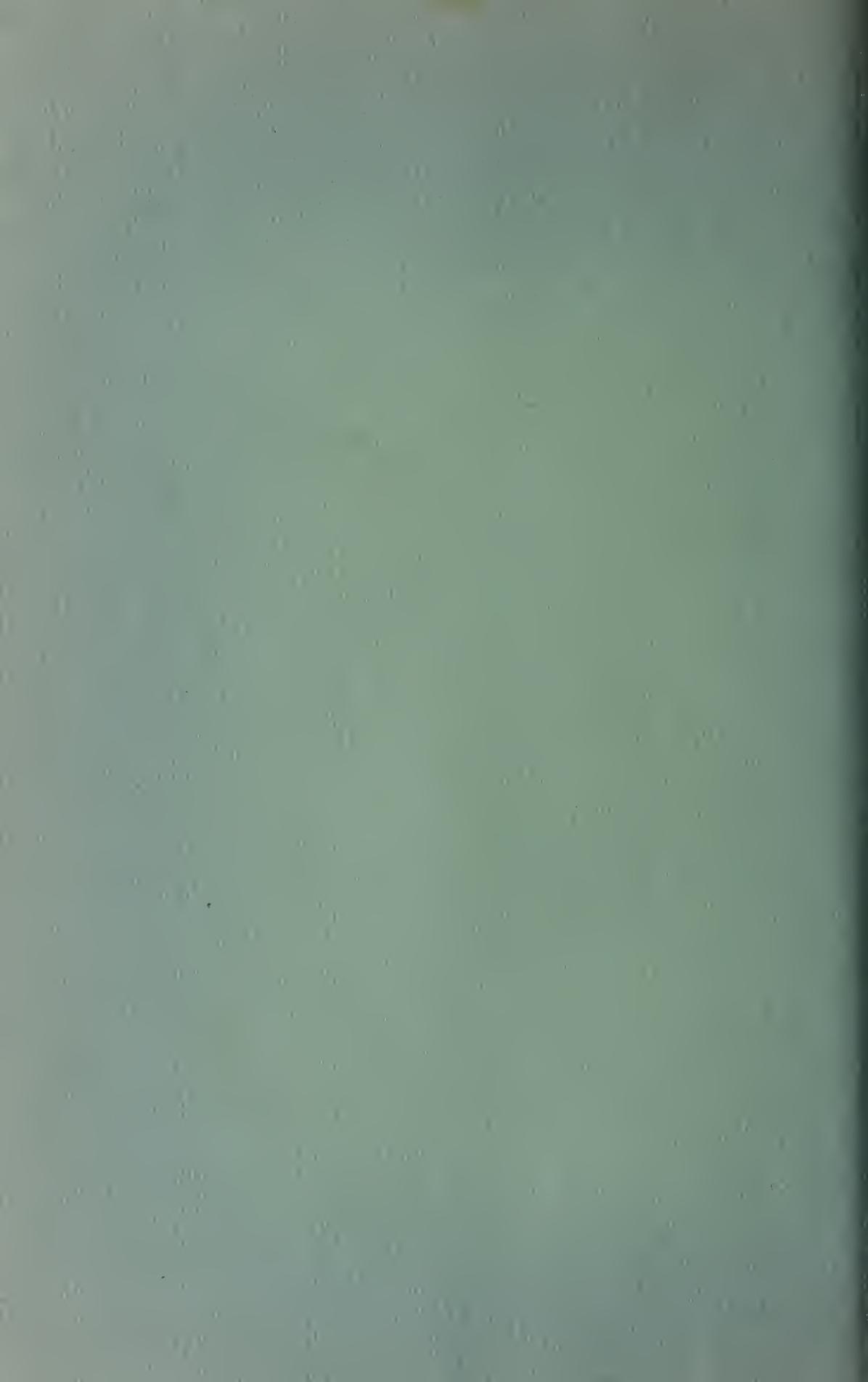
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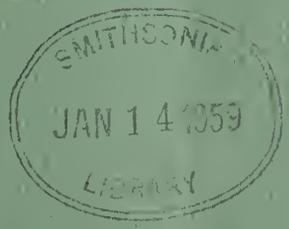


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## Uptake and Turnover of a Single Injected Dose of $I^{131}$ in Tadpoles of *Rana clamitans*<sup>1,2</sup>

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(Text-figures 1-3)

### INTRODUCTION

IN 1941 Gorbman & Evans first demonstrated by means of radioautographs that the thyroid of an anuran tadpole, *Hyla regilla*, can accumulate, in organic combination, radioactive iodine placed in the water as iodide. Dent & Hunt (1952), also employing radioautographs, have mapped the radioiodine distribution in *Hyla versicolor*. Later, Hunt & Dent (1957) studied, by quantitative techniques, the radioiodine uptake and turnover in frog tadpoles in whose environmental water radioiodide was placed. Money, Lucas & Rawson (1955) and Saxén *et al.* (1957) have conducted similar studies with tadpoles of *Rana pipiens* and *Xenopus laevis* respectively.

None of the observations on thyroidal radioiodine accumulation in radioiodide-immersed animals gives a clear idea of the metabolism of a single tracer dose of the isotope. Since absorption from the environment must occur in immersed animals, various additional physiologically variable factors are interposed between the thyroid function one wishes to measure and the tracer iodine. It is not possible, with any degree of assurance or precision, to express the thyroidal  $I^{131}$  in terms of per cent. uptake of a given dose since the amount of  $I^{131}$  which actually enters the animal is difficult to evaluate and varies from one animal to the next. Furthermore, the effect of number and/or size of

animals per unit volume of environmental water and of the amount of "carrier" iodide in this water is not easily determined.

For these reasons the present study was undertaken. The purpose of these observations was the determination of the fate of a single dose of carrier-free radioiodide injected into the tadpole.

### MATERIALS AND METHODS

Premetamorphic tadpoles of *Rana clamitans* of 6-8 cm. in length with hind legs of less than 6 mm. were used (Taylor & Kollros, 1946). Prior to experimentation they were kept in tap water and fed on *Elodea* and corn meal. During the experimental period the tadpoles were kept in tap water, 7 animals per three liters, at 22° C. They were not fed. Into each animal a single dose of 5 microcuries of carrier-free radioiodine ( $I^{131}$ ) in a 0.05 cc. volume was injected intraperitoneally, the needle being inserted through the tail musculature.

At time intervals of 2, 10, 20, 40, 72 and 120 hours after injection, 6 of the 7 animals in each group were anesthetized by immersion in 0.1% M.S.-222 (Tricaine-methane-sulfonate, Sandoz). Each tadpole was then dissected into a planned number of parts, each of which was placed in a closed vial containing 1 cc. of 0.7 % NaCl. The weight and the  $I^{131}$  content of each part was recorded so that the localized concentration of iodine could be followed over a period of time. Measurements of radioactivity were made in a well-type gamma ray scintillation counter (and were corrected for physical decay of the isotope).

### RESULTS

Per cent. uptake of the injected  $I^{131}$  was calculated for the total animal, thyroid and eyes.

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<sup>2</sup>Physical facilities were provided by the Department of Zoology, Barnard College, Columbia University, New York.

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Concentration was calculated as per cent. uptake per mg. of tissue  $\times 100$  (for convenience) for the thyroid, eyes, ventral white skin, tail (both skin and musculature), carcass of head, dark skin of carcass, coiled intestine and remaining viscera. Thyroids were dissected out under the binocular microscope. The small size of the glands obliged us to include small pieces of cartilage, which were necessarily weighed along with the glands.

In Text-fig. 1 the per cent. uptake curve of the eyes, as a typical body tissue, reaches a peak at about the same time as the per cent. uptake curve of the whole animal, whereas the thyroid curve reaches its peak at 72 hours.

Although total thyroid uptake is low, the concentration per mg. of tissue is exceedingly high as compared with the other body tissues in Text-fig. 2.

It is interesting to note in Text-fig. 3 that the curves of  $I^{131}$  concentration for the various body tissues fall into three groups: tail, eyes and carcass of head in one group; ventral white skin and dark skin of carcass in a second group; and coiled intestine and remaining viscera in a third group.

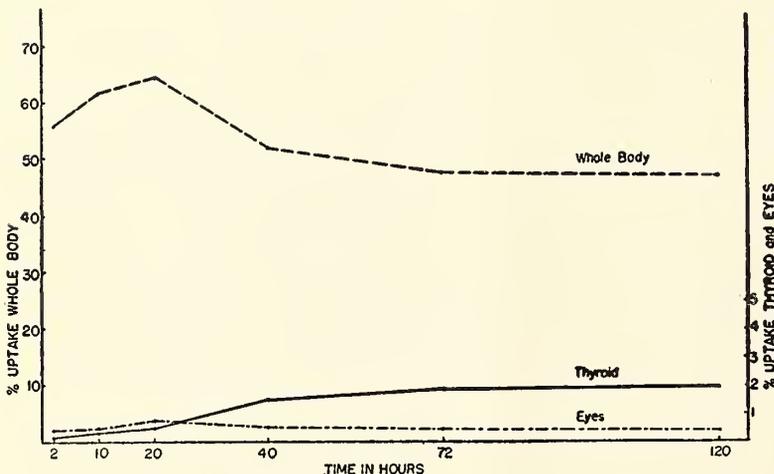
#### DISCUSSION

In this study iodine accumulation by the thyroid slowly reached a level of 2 % of the injected dose at 72 hours and remained at this value until the end of the experiment. This level in the thyroid is reached only after the values for the other body tissues have decreased, as indicated by the curve for the pair of eyes in Text-fig. 1. Very possibly the thyroid continues to take up radioiodine from the blood stream after the iodine has been distributed throughout the body. Unpublished data of Gorbman & Dundee show that *Eurycea*, a neotenic form of salamander,

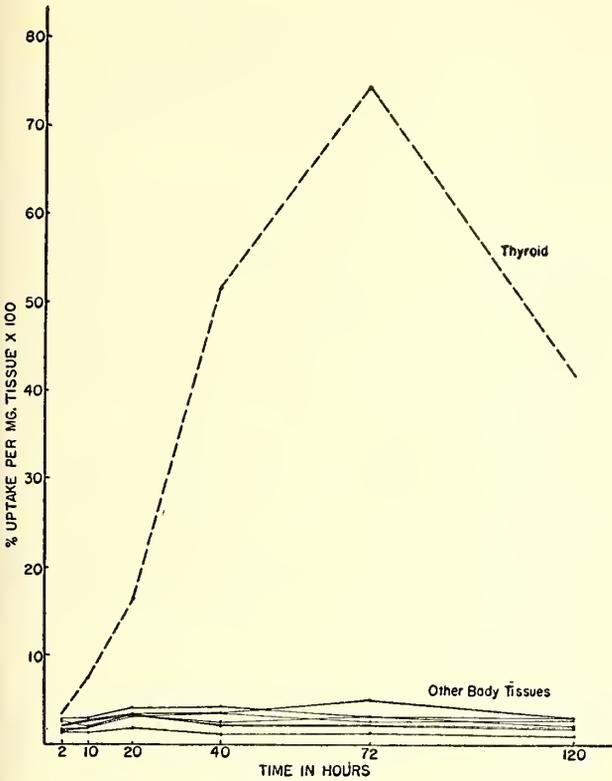
also has a low iodine turnover, so that at the end of 7 days the thyroid still contains about 50 % of its peak value of 2.5 % achieved at about 24 hours.

Text-fig. 2 clearly shows that the thyroid is the most potent of all tissues in concentrating radioiodine. Since the dissected thyroid piece includes the weight of the thyroid, as well as the cartilage upon which it rests, the values obtained for concentration are considerably lower than the real values. The peak for thyroid, which is at least 7 times greater than any other value, comes at a time when the majority of other body tissues have reached an equilibrium (Text-fig. 2). Other experiments with anuran tadpoles have not provided information concerning the relative concentrations of iodine in the thyroid and the remainder of the body. The chemical form of the thyroïdal iodine in tadpoles is as yet unknown since chromatographic studies have not been done. However, radioautographs indicate that it is bound in an organic form (Dent & Hunt, 1952).

Money, Lucas & Rawson (1955), using an alternative technique of immersing *Rana pipiens* tadpoles of different ages for a definite period of time in a solution of  $I^{131}$ , find a value of close to 10-20 % of environmental  $I^{131}$  localized in the block of thyroid tissue at the end of five days (MLR Fig. 2). When they injected tadpoles lower thyroïdal  $I^{131}$  accumulation was found (5-10 %), which still exceeded the values we have observed in *Rana clamitans*. Such data illustrate the differences to be found between single administrations of tracer  $I^{131}$  and continuous absorption from the environment. The fact that continuous absorption varies with stage and therefore cannot be used as a standard value is shown also in the work of Saxén *et al.* (1957).



TEXT-FIG. 1. Uptake for whole body, thyroid and eyes. Each point on the curve represents the average of determinations done on six animals.

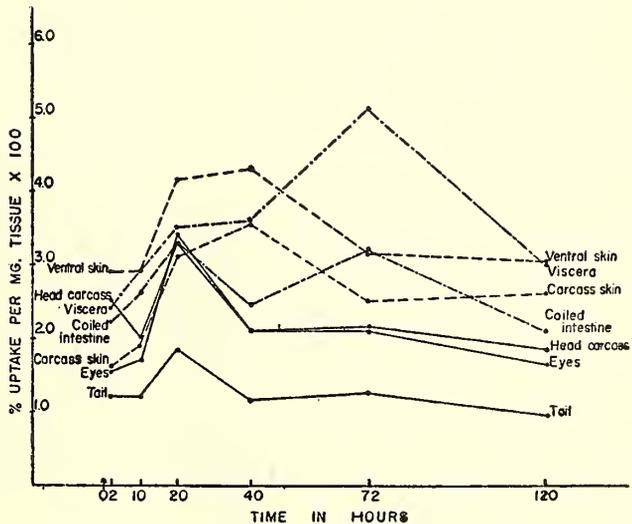


TEXT-FIG. 2. Concentration of  $I^{131}$  in the thyroid and other body tissues. Concentration calculated as per cent. uptake per mg. tissue  $\times 100$ . Average values determined the same as in Text-fig. 1.

The apparently continued increase in total body  $I^{131}$  to 65 % at 20 hours after injection (Text-fig. 1) is at first difficult to interpret. The only apparent explanation is that up to that time a considerable part of the injected dose remained unabsorbed in the body cavity and/or blood stream of the tadpole. The whole body value of the administered dose was found by summing

the values obtained for individual body parts. After 20 hours the amount of radioiodine decreases gradually to 47 % and appears to maintain itself at that level. This seems to indicate that extrathyroidal areas, which retain a considerable amount of the injected dose, also have a low turnover. These data agree, in general, with those provided for *Rana pipiens* tadpoles

TEXT-FIG. 3. Concentration of  $I^{131}$  in the various body tissues other than thyroid. Average determinations the same as in Text-fig. 1.



by Money, Lucas & Rawson (1955).

Data obtained by Hunt & Dent (1957), who administered  $I^{131}$  by a short period of immersion in  $I^{131}$  solutions, indicate that after 2 days the total amount of iodine absorbed in *Hyla versicolor* tadpoles decreases from approximately 50 % to 10 % whereas our values during the same period remain near 47 %.

Dent & Hunt in 1952 pursued a study of the  $I^{131}$  distribution by radioautographing sections of various tissues. However, their study was not primarily quantitative. By actually measuring the fraction of the administered dose accumulated in various parts of the body by means of a well-type gamma ray scintillation counter, our study has allowed a quantitative description of the distribution of the radioiodine.

It is interesting to note that the curves for the body tissues appear to fall into three sets of parallel curves (Text-fig. 3). The group composed of ventral white skin and dark skin of carcass, unexpectedly, shows higher values for the ventral white skin, which would be expected to contain much less tyrosine. Dent & Hunt (1952) found a denser radioautograph in the region of the skin. They attributed this to the binding of iodine by the tyrosine of the melanin pigment. The tail, with less skin and more musculo-skeletal tissue per unit weight, contained much lower iodine concentration, indicating that such tissue probably does not serve as a storage area for iodine. Both viscera and coiled intestine continue to concentrate  $I^{131}$  even at a time when the other tissues seem to be reaching an equilibrium. Entero-hepatic recirculation is an important mode of excretion of thyroid hormones through the liver and intestine. The higher values for these organs may be a reflection of such excretion, since the peaks occur at the same time as the thyroidal peak. This may be taken to indicate that the thyroid in the tadpole does have a turnover, although a low one.

Our experimental data indicate much individual variation, as also shown by both Hunt & Dent (1957) and Money, Lucas & Rawson (1955). Because each group of animals was kept in a large volume of water, the possibility of  $I^{131}$  reabsorption is negligible. Hunt & Dent (1957) also feel that the concentration of iodine in the water and the amount of food ingested by the tadpole do not effect the release of iodine. An extension of the experimental period beyond five days would have been desirable.

#### ACKNOWLEDGEMENTS

The authors of this paper wish to thank Professor Aubrey Gorbman for his guidance and criticism in the execution of this experiment.

#### SUMMARY

1. Per cent. uptake of injected  $I^{131}$  was calculated for the whole body, thyroid and eyes of premetamorphic *Rana clamitans*.
2. Distribution of iodine was studied by comparison of  $I^{131}$  concentration in the thyroid to the concentration of  $I^{131}$  in the other body tissues over a period of five days.
3. Total body per cent. uptake of  $I^{131}$  reaches a peak of 65 % at 20 hours and decreases to an equilibrium of 47 % at 72 hours.
4. The fraction of administered dose of  $I^{131}$  accumulated by the thyroid reaches a maximum of approximately 2 % at 72 hours.

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## Oral Incubation in the Cichlid Fish *Geophagus jurupari* Heckel

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(Plate I)

### HISTORICAL RÉSUMÉ

**A**LTHOUGH reproductive habits of the cichlid fishes assigned to the genus *Geophagus* were described as early as 1855, 1863 and 1865, our knowledge of them has remained, to this day, in a state of disconcerting confusion.

In 1855 Castelnau described how his new species, *Geophagus (Chromys) lapidifera*, carried pebbles in its mouth to form a nest in which the eggs were laid (Pellegrin, 1903). In 1862 the Reverend J. C. Fletcher and Sr. Henrique Antonii collected specimens of one or two species of *Geophagus* that had eggs or young in their mouths (Putnam, 1863; Fletcher & Kidder, 1866). In 1865 Louis Agassiz also obtained a species of *Geophagus* in the mouth of which eggs and young in various stages of development were found (Agassiz, 1865), and within a year he had discovered additional species in a similar condition (Agassiz, 1866; Agassiz & Agassiz, 1868.)<sup>2</sup> The seeds of confusion, however, were already sown by these pioneers. Agassiz never identified or described his fishes in any detail, and some 14 bottles of unidentified *Geophagus* from the Thayer Expedition to Brazil, the one on which Professor Agassiz collected his fish, are stored at the Museum of Comparative Zoology.

Similar limitations afflict most subsequent observations on the group. Too often one cannot be certain of the identity of the fish concerned. Pellegrin (1903) recognized 17 species of *Geophagus*, while Regan (1906) accepted 12. Of these, three or four appear to have become

generally known. viz. *Geophagus brasiliensis* (Quoy & Gaimard), *G. jurupari* Heckel, *G. surinamensis* (Bloch) and perhaps *G. gymnogynys* Hensel, but one would be hard put to explain the different reproductive habits that have been ascribed to each of them except on the basis of misidentification of the form under observation. Without the background of a much needed taxonomic revision of the genus, as well as an attempt critically to identify each fish in question, it would be pointless to list the observations of all the amateur and professional workers who have described their reproductive behavior. Our purposes will be served by a brief consensus, with mention of the most important papers and the most notable exceptions.

At least ten different accounts of the breeding of *Geophagus brasiliensis* in captivity agree that the eggs and young are cared for by both parents in typical cichlid fashion. Hensel (1870), however, described how a specimen in nature took young into its mouth when disturbed and how these were found crowded into its mouth after the fish had been killed or stunned by a shot.<sup>3</sup> Adloff (1922) similarly reported that he had seen the young of a freshly caught *G. brasiliensis* flee into the mouth of the parent several times. Von Ihering (1883, 1920) and Brüning (1931) stated that this species was a mouthbreeder, but their opinions appear to be based on the observations of others. None of these authors mentioned the sex of the fish involved. Guimarães (1930) says nothing about oral incubation in his description of the reproductive habits of this species, both in aquaria and in nature.

Similarly, at least six aquarists have agreed

<sup>1</sup> The junior author is Associate Curator, New York Aquarium, New York Zoological Society.

<sup>2</sup> These five publications appear to be the first to mention oral incubation in the cichlid fishes.

<sup>3</sup> The fish was said to belong to Hensel's newly described species, *Geophagus scymnophilus* sp. nov., which Pellegrin (1903) and Regan (1906) have both synonymized with *G. brasiliensis*.

that *Geophagus gymnogenys* reproduces itself in typical cichlid fashion, but Haseman (1911a, b), who declared that a subspecies of *G. brasiliensis* was not a mouthbreeder, attempted to catch a female *G. gymnogenys* which was surrounded by small fish. These disappeared into her mouth and reappeared later. When the fish was finally caught, her mouth was full of young. On another occasion, a recently captured specimen of his released young from its mouth.

Although two aquarists have mentioned no signs of oral incubation in their breeding pairs of *Geophagus surinamensis*, Eigenmann (1912) collected a wild specimen carrying young, Beebe & Tee-Van (1922) two specimens similarly encumbered,<sup>4</sup> and Puyo (1949) two females with eggs in their mouths. Eigenmann (1912) also found a specimen of *G. jurupari* that was sheltering young, while Beebe & Tee-Van (1922) caught two fish of the same species that, following capture, spewed out 58 young between them. Another fish was found to have taken up some 60 young with which it had been placed in an aquarium five days previously, the fish apparently being parent and offspring that had become separated at the time of capture.<sup>4</sup> Professional ichthyologists and home aquarium fanciers are less at odds with regard to *G. jurupari*; Härtel (1936) and Dvoskin (1955) have described how the female orally incubated both eggs and young in aquaria. Leitholf (1917), however, did not notice any mouthbreeding behavior in his breeding pair of this species.

Among the less well known species of *Geophagus*, Eigenmann (1922) collected a female *G. pellegrini* carrying young. Brüning (1918) described how a male *G. acuticeps* gave shelter to his offspring whenever danger threatened in an aquarium. Two other home aquarium reports on the latter species, however, do not mention mouthbreeding.

Brüning (1918) and Haseman (1911a) erroneously believed that *Geophagus* shelters only the young in its mouth, never the eggs. As to the sex of the incubating parent, what little data there are implicate the female more often than the male, with a single observation that might well indicate that both members of a pair were simultaneously engaged in carrying young (Beebe & Tee-Van, 1922). The statements of Pellegrin (1908) and Miles (1947) that the male typically performs the nursing duties are therefore hard to justify.

<sup>4</sup> We thank Drs. William Beebe and John Tee-Van for permitting us to use these unpublished data, which were gathered at the station of the Department of Tropical Research, New York Zoological Society, formerly located at Kartabo, British Guiana.

There appears to be no question about the identity of the fish of Eigenmann (1912), Beebe & Tee-Van (1922) and Puyo (1949), but it would be reassuring to check those of Haseman (1911a, b). Our opinion is that *Geophagus jurupari* and *G. surinamensis* are mouthbreeders, while *G. brasiliensis* is not. About the other species we hesitate to commit ourselves. The need for further, more detailed, observations on all species of *Geophagus* is obvious.

#### PRESENT OBSERVATIONS

The two fish whose behavior is the subject of this paper were kept in standing freshwater aquaria at the home of the senior author for 13 months before their first spawning. At that time the male was about five and one-half inches in total length, the female slightly more than five. About five months previously, the first signs of sexual dimorphism had appeared, accompanied by aggressive behavior on the part of the male. Most notable were the more pointed extension of the posterior rays of the male's dorsal fin and the much more conspicuous elongation of the anterior rays of his pelvics (Plate I). It was the latter outgrowth that seemed to indicate that the fish belonged to the species *Geophagus acuticeps* Heckel (Reid, 1956), but Dr. George S. Myers has recently examined the two fish and found that they belong to the species *G. jurupari* (Register Number, Stanford University, SU 49836).

Ten spawnings have been recorded (Table 1), but the bulk of the observations were made during three of them (Nos. I, III and IV). Details of methods of care and feeding are given in Reid (1956, 1957). Since the senior author was unable to make systematic observations throughout the day or at regular times on successive days, the data do not lend themselves to quantitative treatment. Nevertheless, sufficient time was devoted to observing the activities of the fish to reveal the general pattern of reproductive behavior as well as a number of interesting details.

*Typical sequence of events.*—Both male and female clean the surface on which the eggs are to be laid, within a few hours of spawning. The spawning act itself does not differ from that of many cichlids, the female laying many small batches of adhesive eggs, each batch being fertilized, in sequence, by the male. The eggs are guarded by both parents. Roughly 24 hours after laying, the eggs are picked up and orally incubated, by both parents or by the female alone. Although our observations cannot be considered conclusive on this point, we believe that the eggs

TABLE 1. SUCCESSIVE SPAWNINGS OF A PAIR OF *Geophagus jurupari* HECKEL

No.	Date 1955-1956	Time	Place <sup>1</sup>	No. Eggs (approx.)	Behavior	Outcome
I	March 5	Morning?	Flat, red shale, 2½x1½ inches	150	Both parents cooperated in care of eggs and young	All young eventually lost, by seventeenth day
II	April 19 or 20	?	?	?	Female alone at time of spawning	Swallowed eggs on fifth or sixth day
III	May 10 <sup>2</sup>	9:15-10:45 A.M.	Flat, red shale, 2¼x1½ inches	?	Both parents guarded eggs; female carried them	Swallowed eggs (or young?) on fourth day
IV	May 24	Daytime	Flat, red shale, 2¼x2¾ inches	200	Both parents cooperated in care of eggs and young	Parental care ceased on or shortly before forty-first day; 105 young remained
V	July 9 or 10	?	?	?	Female carried eggs	Swallowed eggs
VI	July 26	Daytime	?	?	Female alone during spawning, separated from male by pane of glass	Eggs eaten on second day
VII	October 6	About noon	Flat, green shale, 1½x1½ inches; few on gravel	350	Both parents cooperated in care of eggs	Swallowed eggs on third day
VIII	November 1	11:20 A.M. —?	Flat, red shale, 2x1¼-2¾ inches; few on gravel	275- 325	Female carried eggs; separated from male on second day	Swallowed brood on eighth day
IX	November 29	Morning	Large piece shale	?	Both parents guarded eggs, which were removed on second day	Artificial incubation unsuccessful, although eggs hatched in two to three days at 81°F.
X	April 24	?	Three small pieces shale, one green, two red, as well as gravel	?		Eggs eaten

## FOOTNOTES TO TABLE 1

<sup>1</sup>The first spawning occurred in a 20-gallon home aquarium, 24 × 12 × 16 (high) inches; subsequent spawnings took place in one of similar capacity, 30 × 12 × 12 inches. The former was a community tank, while in the latter the *Geophagus* were maintained alone with the infrequent exception of a small catfish or two.

<sup>2</sup>On May 3, the female seemed to have eggs in her mouth, but no signs of a nest or other eggs could be found, and subsequent events yielded no clue as to whether a spawning had actually taken place.

are not released from the mouth. On the other hand, one- or two-day-old young are released into depressions dug in the bottom and may be transferred back and forth between the pair. Sometimes the male, sometimes the female, and most frequently both sexes carry the brood. Free-swimming young are released (undoubtedly to feed), and they return to the mouth, and are gathered up by the parents as well, at times of disturbance and at night. Parental care may be exercised for as long as 37 days.

*Selection and preparation of spawning site.*—Selection of the nest site may be a function of the male, but our data provide only a suggestion that this is so. On the first spawning (I), the male tugged at the stone on which the eggs had been laid, as if attempting to move it. This occurred when the senior author had inadvertently disturbed the fish. At one time (April 24), when the male was being kept in a community tank without his mate, he dug a deep depression in the gravel and attacked the senior author's hand when it was put into the water. Five days before a spawning (III), the male was seen to drag a piece of shale across the tank for about 25 inches, and on the day of the event (III), he dragged another stone to the front of the tank, this stone being the object that both fish subsequently cleaned and used as a spawning place.

Cleaning of the spawning site immediately preceded the false "runs" in which the female engaged just prior to actual egg laying (III). First the pair cleaned the flat stone with their mouths, then they covered it with gravel and again cleaned it off with their mouths. They repeated this procedure over and over, perhaps as a means of thoroughly cleansing the future egg site.

It is possible that this behavior is related to the fact that on four occasions (I, III, IV and VII), a sprinkling of gravel was found on the eggs during part of the time they remained at the spawning site. Härtel (1936) stated that a few hours after spawning, his pair of *G. jurupari* had covered their eggs entirely with sand.

*Oviposition and fertilization.*—Eggs were laid during daylight hours—so far as definitely known, during the forenoon or early afternoon (Table 1). On two occasions (III and VIII), spawning was observed. On the first, the female swam over the stone several times, her extended ovipositor touching it. After each false "run," she unsuccessfully attempted to drive the male toward the stone. When she began to lay her eggs, in closely packed rows, the male followed, fertilizing each row in turn. On the second occasion (VIII), the male harried the female while she was laying the

eggs by nipping her. The female in turn attacked the male after laying each row, giving him little opportunity to fertilize the eggs. When he followed close behind her, he was able to pass over the newly laid row, but this occurred only once in every five or six rows laid.

*Guarding the eggs.*—On four occasions when the behavior of the fish was observed during the late afternoon or evening of the day on which the eggs were laid (III, IV, VIII and IX), the female alone guarded the eggs, keeping the male away. Once (VII) it appeared that both might have been so engaged with the female closer and more attentive to the spawn. On the first spawning, it is not known how long the eggs had been laid before they were discovered, but it was the protective behavior of both parents that led to their detection; they attacked the siphon introduced into the aquarium by the senior author. (On the basis of the schedule of events of other spawnings, it is extremely likely that the eggs had been laid that morning).

On another occasion (III), the female was guarding and vigorously fanning the eggs with her pectoral fins and keeping her mate away, when some methylene blue was added to the tank. The male immediately approached the eggs and both parents then guarded them. Later the female again chased the male away. On still another occasion (IX), the female was guarding the eggs on the day of spawning, when water and chemicals were added to the tank. During this operation, both fish guarded the spawn, but the next morning the female alone was doing so.

From this and other behavior to be described subsequently, we conclude that the male would have cared for the eggs from the start, had the female permitted him to do so. On the evening of one spawning day (IV), the female was guarding the eggs alone, but the male persisted in his attempts to take part in this activity. As the male came near the spawn, the female tried to block his approach with her body, but as he became more aggressive, he was able to get past her and settle at the opposite side of the stone. Each time this happened, she chased him away, and he then swam about the bank, foraging through the gravel (displacement activity?) and sometimes returning to the spawn. After a while, the female began to tolerate the male's presence; they then assumed a head-to-head position, lips almost touching while they both fanned the eggs. The following morning they were still fanning in the same position, but later on they began to chase each other, circling about and nipping each other's tail. While guarding the spawn (I) in a community tank, which contained

two *Pterophyllum*, two *Helostoma*, four *Corydoras*, four *Gymnocorymbus* and two loricariid catfish, the parents took positions at opposite corners of the rectangular stone, facing in. When one parent changed position to ward off a potential threat, the other changed position accordingly so that both were continuously guarding the spawn. They first thrust themselves at the intruding fish, and if necessary, they placed their bodies directly between the eggs and the intruder. Finally they would vigorously chase the intruder, although they never actually left the spawn to follow a retreating fish. Their teamwork appeared highly efficient.

*Picking up the eggs.*—The eggs were picked up during the day after spawning in all instances where observations were made covering this phase (I, III, IV, VII and VIII). The actual performance was seen but once (VII). At 1:00 P.M. both parents began to pick up the eggs in their mouths. While one was so engaged, the other swam about the tank, rolling eggs in its mouth. The fish took turns, picking up only a few eggs at a time, and the procedure required about three hours. Occasionally the two circled about, chasing each other. Both sexes carried eggs after two other spawnings (I and IV), but the female alone gave evidence of having eggs in her mouth during another (III), and during one spawning (VIII) it was impossible to determine whether or not the male ever carried any eggs. On at least some occasions, all of the eggs were not picked up; 50 were left unattended in spawning I, 2 in spawning III, and 45 in spawning IV.

Eggs that were artificially incubated at 81° Fahrenheit hatched in somewhat less than three days. During the course of the present observations, the temperature ranged from 80° to 84° F. These fish have never been observed to spit out unhatched eggs, but Dvoskin (1955) reported that his female regularly did so as late as ten days after spawning. In the light of the above observations, as well as the senior author's experience in confusing with eggs some recently hatched young which had been released from their parents' mouths for the first time, because the young were immobile and their tails practically invisible, we conclude that Dvoskin's fish was manipulating young, not eggs.

*Incubation of young.*—The young fish were first seen outside the parents' mouths on the sixth (I) and on the eighth (IV) days. The temperature in both cases had been about 84° F. In the latter instance the young were further developed, although still not free-swimming. In both cases the tiny fish were released into a depression dug

in the sand, but in the latter each parent simultaneously used a different depression. The female, who had the greater part of the brood, tried to keep the male away, but he managed to pick up a few strays from her complement.

The young always spent the night in the mouths of their parents. Even as long as 37 days after spawning (IV), when the bulk of the brood was too great to be thus accommodated, the parents appeared to carry as many young as they could at night. The amount of light influenced the activity of the parents and whether or not they released or carried their brood. Often the morning opening of the blinds of the room in which their tank was kept was followed by swimming activity by the parents and then the release of the young into a dish-shaped depression, 5-6 inches in diameter and 1½ inches deep at the center. On the other hand, during the day bright light on either tank (I and IV), seemed to make the parent fish exceedingly wary, and for this reason the electric lights immediately above the tank were usually kept off during daylight hours. Putting on the room lights at night rarely brought about the release of the young, however.

Frequently the initial release of the young was not a simple matter but consisted of ejecting and retrieving the small fish several times, sometimes as rapidly as possible. This might continue for a minute or more before the young would finally be permitted to remain outside. The young were usually more active when first released and the parents had greater difficulty keeping them together, but whether the above-described parental behavior was solely the result of a stimulus-response situation, we cannot say.

Either one or both parents incubated the young. In the first spawning, when the number of young soon became reduced to about 50, there were times when one or the other would carry the whole brood for a day or more while the unencumbered fish swam about and ate. They alternated fairly regularly. In a later spawning (IV), with more than twice as many young to care for, both male and female carried some young every day, although they did not necessarily share the burden equally. If any choice could be made, the female was the more assiduous in orally incubating the offspring. We have already seen that what little information was previously known about this species, as well as other orally incubating species of *Geophagus*, indicates that the female performs the duty with greater frequency than the male.

As the young fish became older, they spent less and less time in their parents' mouths until finally they remained free except in times of disturbance and at night.

The orientation or exact location of the young inside the parent fish was never discerned, but they might be expelled through the mouth or operculi or all three openings at the same time. The female was noted to employ all these methods, while the male rarely released his young except by way of the mouth. The young emerged from under the operculi head or tail first, seemingly at random.

*Feeding of parents and young.*—Unlike all other orally incubating cichlids known to us, *G. jurupari* takes in food while in the act of carrying young. The pair under observation fed on and off during the entire period of parental care except the three or four days that the eggs were being incubated, but even during this interval the female was observed to suck in tubificid worms while rolling eggs about in her mouth (II and VIII). Considerable numbers of worms were taken on five successive days in the latter case, but in the former, worms were seen to be taken but once, and then they were ejected through the operculi shortly afterward. Both sexes were seen eating while guarding the eggs, after spawning and before they were picked up. The taking of food with young in the mouth was first noted five days (I) and six days (IV) after the day of spawning. In the former instance, which was the first occasion that the young had been seen outside the parental mouth, the female was observed to suck in tubificid worms during the process of picking up the small fish. In the latter instance, the female took in tubificid worms on the day before the young were first seen. Following that occasion, both sexes gingerly took some blood worms after they had picked up all of their brood. Other instances of similar behavior were also noted.

Whether this combined feeding and oral incubation was for the purpose of nourishing parent or offspring is not known. In several instances, the food taken in was obviously too large for the young fish to engulf. Frequently when the young were expelled, a few tubificid worms were also ejected. These were picked up and swallowed while the young were outside the mouth. It is possible that the parents did not swallow any worms when there were young in their mouths, but "saved" them for moments like these. On the other hand, the fish appeared to possess fine powers of oral discrimination between fry and other small objects. For example, on the sixteenth day after spawning (I), each parent was observed to engulf a young fish while in the process of eating daphnia, but the small fish soon emerged through the gill openings. Once the male was observed to pick up a few

fry and then take a little gravel into his mouth and commence chewing movements. After a minute, a few fry and some of the gravel were ejected through the gills and the remainder were spit out (one month after spawning IV).

The observations of Härtel (1936) are in some ways similar to the present ones: "On the fourteenth day a few of the young appeared through the gill openings; they could not swim and were immediately picked up by the mother. Accidentally, I saw the female with a bunch of mosquito larvae in her mouth; she crushed them against the side of the tank and inhaled the 'juice.' The following day enchytrae were fed. They were at once taken by the female, chewed and, when she believed herself to be unobserved, ejected in a cloud together with the young. I could see the latter feeding in the cloud." The observations of Dvoskin (1955), on the other hand, are strikingly different. The female carried the brood, and for about ten days she did not eat. The male then began to chew mouthfuls of worms which he spat out in the direction of his mate. She took this into her mouth, presumably to feed the young there.

In the pair observed by us, the most vigorous feeding was performed by either parent while the other was engaged in caring for the entire brood, and the division of labor seemed to be fairly equal. From about the twelfth day after spawning (I and IV) on, the young frequently swam into the cloud of detritus and sediment that the adult fish passed out by their gills during their grubbing on the bottom. (As in all the *Geophagus* known to us and as they had done since their earliest days, the adults frequently took a mouthful of gravel and after chewing it, presumably to extract food, expelled the material through their gill openings and mouth). At first it could not be seen whether the fry were eating or not, but later this was definitely seen to be the case. Since the parents sometimes sifted through the gravel at places in the aquarium far from the young, there did not seem to be any special behavioral mechanism to insure the feeding of the young in the above fashion, but rather a satisfying of the needs of the one by the unmodified self-satisfying behavior of the other.

*Return of young to the mouth.*—The return of the young *G. jurupari* to the parental mouth definitely results from the interaction of the behavior of both parents and offspring. During the earlier stages of development, the parents, rather than the young, seemed to initiate the return, and since the young could not swim when first released, the parents perforce had to accomplish the deed alone. At this time they did so with

an inhaling, vacuum-cleaner action, and even though the young might be blown back out through the mouth or through the opercular openings, the handling of the fry appeared to be a gentle procedure.

Roughly eight to ten days after spawning (I and IV), the young had become active although they were still not able to maintain themselves indefinitely in mid-water. They usually seemed hardest to control when released for the first time in the morning. The parents were kept busy picking them up as they spread out over the bottom of the aquarium. After a while, the young turned toward the parent fish and began swimming about their heads trying to get back into the oral cavity, or even the gill chambers. Usually the parents picked up the young leisurely, over a period of five to twenty seconds, but if there was any danger, real or no, they were able to secure all the fry within about two seconds. The parents then tilted their heads toward the young, opened wide their mouths, and in a state of high excitement with all fins spread wide, they sucked in the young. The fry also cooperated by swimming to their mouths. Ordinarily the male and female kept their ventral fins close to their bodies while standing guard over the brood, but their pectorals were constantly moving as they apparently fanned (or signaled?) the young. Occasionally when the nearer parent rose a bit in the water, the young also rose in a swarm with it. When one parent moved away to ward off an intruding fish, the young did not follow it, but moved closer to the other parent. On the basis of our observations, however, we are unable to state whether any particular action on the part of the parents served to "call" the young or whether it was an assemblage of visual, and perhaps auditory or mechanical, stimuli that was responsible.

During the later stages, the young usually seemed to make the moves initiating a pick-up. They streamed like a swarm of bees toward the mouth of the nearer parent, who did not always take them in. Whether this behavior was the result of some action on the part of the parent fish or of some other stimulus is not known. On several occasions the parents were seen to refuse to open their mouths even though the young persistently swam about their heads. (It might also be noted that as late as 34 days after spawning (IV), the young still tried to gain ingress through the operculi, although they were never seen to enter either parent by these openings). If the parent fish closed its mouth while there were still a few stragglers outside, these would keep swimming about the head until taken in or until their sibs were released.

One anatomical structure whose role in the picking-up process needs elucidation is the oral valve. This was seen to vibrate rapidly while fry were being returned to the oral cavity.<sup>5</sup>

*Cooperation between parents.*—That female and male cooperated in cleaning the egg site, guarding the newly laid eggs and orally incubating eggs and young has already been indicated. Coordinated efforts in guarding their brood were naturally more apparent during the course of spawning I, which took place in a community aquarium. We have already noted (p. 80) how effective was the teamwork the pair displayed in guarding the eggs in this situation. As mentioned before, either one or both parents might carry the brood, but as the young grew, it became impossible for a single fish to encompass all of them. Exchange of young took place by means of a depression dug in the gravel into which the young were ejected and from which they were picked up. While the brood was being carried about, the parents did not pay any attention to the other fishes in the aquarium, but when they were about to release the fry they drove all fishes away from the depression they were to use, before ejecting any young. For example, on the morning of the eighth day after spawning I, the male spit all the fry into the depression and the female joined him in picking them up. The male then spit his out again, and while the female was picking them up, he patrolled the area, warding off intruders and picking up any strays missed by the female. Again and again he returned strays to the depression, where they were picked up by the female. After the female had been carrying all the fry for a few minutes, she blew them out through her gills and the male again helped her pick them up. The female then took up the young and ejected them several more times, while the male stood guard, rolling his complement about in his mouth.

As in guarding the eggs, the cooperation between parents was remarkably well developed. When one parent was tending the young alone, the other sometimes seemed to ignore its mate and swam about the tank foraging through the gravel. Even while thus engaged, however, the

<sup>5</sup> Another structure whose relation to the habit of oral incubation needs elucidation is the pharyngeal gland. The presence of a pair of papillae or compressed lobes on the first branchial arch is considered a generic characteristic of *Geophagus* (Pellegrin, 1903; Regan, 1906). Pellegrin believed it most likely that these structures served some purpose connected with mouth-breeding, and Shaw & Aronson (1954) presented certain additional evidence supporting this view. At least one member of the genus, however, *G. brasiliensis*, does not seem to be an oral incubator.

fish appeared to keep a wary eye homeward. If the tending parent had to rise from the fry to ward off an intruder, the free-swimming parent immediately dashed back to the young.

On one occasion (18 days after spawning IV), each parent fish appeared to be leading a separate group of fry about the entire aquarium. At that time there were about 140 young. Whether such a splitting up of the brood would ever occur under natural conditions is hard to say.

*Breakdown of parent-young relationship.*—On two occasions events culminating in the termination of the parent-offspring bond were witnessed. On the seventeenth morning after spawning I, there were seven fry left and when they were expelled they immediately tried to return to the parents' mouths. They practically bounced back in as if they were on rubberbands. The parents then began to pick up and expel the young rapidly. One of the fry became injured and began to spiral around. The male picked it up several times, but when it stopped moving he ignored it. The remaining six then began dashing about the tank out of control. Two were eaten by other fishes, and the parents vigorously chased the last four, who showed no response but fled as any small fish might while trying to escape a large one. In a short time all the young had disappeared. The parents roamed the tank apparently searching for them and while doing so they grabbed and tugged at plants in a haphazard fashion.

One month after spawning IV, the more than one hundred young were seen swimming about the aquarium obviously not under the immediate supervision of their parents. When an attempt was made to net some of them, however, both parents hastily picked up the brood in the usual way. The following day it was noted that the parents seemed unable to close their mouths completely when carrying the young. They swam about with their mouths partly open, rhythmically opening them wider in breathing. Three days later the male did not pick up his share of the young even when disturbed with a catching-bell that was carefully manipulated near him in order to remove ten fry from the aquarium. Instead, he retreated toward the bottom and the young nestled about him. Later the same evening, however, he did pick up almost all of the small fish not already being carried by his mate. On the evening of the following day the male was seen to refuse entry to some of the young, continuing to feed on daphnia that had just been put into the aquarium. The next night the male attempted to pick up his share of the brood when the senior author approached the aquarium, but he ap-

peared physically unable to do so. The young remaining outside persistently swam about his head, and he soon released those inside his mouth. Both parents were seen with their mouths crammed with young at midnight, but there were still quite a few others gathered in small groups throughout the aquarium. Four days later, after dark, neither parent was found to be carrying any young, which instead were scattered about the aquarium. Some daphnia were fed, and both parents and young commenced to feed on them. When the female approached one of the small fish, she quickly pursued it and the youngster fled from her. The male, on the other hand, paid no attention to his offspring, nor did they seem afraid of him. Adults and young were kept together for four more days during which the small fish generally stayed away from their parents, occasionally fleeing from them, but sometimes they swam directly in front of their mouths or under their bellies without being molested.

Härtel (1936) also recorded an unusually long period of parental care, more than 30 days, and Schreitmüller (1936b) called attention to the sharp contrast between this and the other, shorter periods exhibited by other cichlids.

*Recognition of young by parents.*—As noted above, the pair of *G. jurupari* under observation did not eat any young, even after all ties with them had seemingly been broken. In fact, at no time were these specimens seen to attempt to eat any kind of small fish. Although eggs or young might be swallowed early in the sequence of reproductive events (Table 1), the young were never, to the best of our knowledge, eaten later on. The adults were well fed at all times on non-living, dry or wet prepared foods, as well as live tubificid worms, chironomid larvae (blood worms), daphnia, cut-up earthworms, brine shrimp and "mikroworms." On at least three occasions it was noted that dead fry were ignored, not eaten, and that dying fry might either be ignored or repeatedly picked up until they ceased moving.

In order to test the parents' reactions to small, strange fish, two six-day-old black mollies (*Mollienesia*) were put into the aquarium on the twenty-eighth day after spawning (IV). No attention was paid to them, and they were removed after a few days. Four days previous to this, a young fish from the same brood—which had been raised in a separate aquarium with three others like it for 18 days—was returned to its parents' aquarium. This young fish was at the time considerably larger than those being raised by the

parents.<sup>6</sup> It seemed frightened and stayed motionless near a rock. When the female finally saw it, she swam toward it. The youngster fled to a corner, as if to hide. The senior author then chased it out toward the group of young being tended by the parent fish. The parents were excited by this action and they picked up all of the fry. When the male spotted the lone small fish, he went after it, his mouth full of young. It appeared obvious that his intention was to pick up the newcomer. By evening the small fish was still in hiding and was removed.

#### DISCUSSION

Many cichlids, belonging to nearly a score of genera, are known to practice oral incubation. Nevertheless, the patterns of reproductive behavior shown by the species that have been studied in sufficient detail may be separated into three major types (Table 2). Two of these groups are represented by a single species—although a few close relatives, not yet well enough known, should undoubtedly be grouped there also—while the bulk of the cichlid oral incubators seem to belong to the third group. Outstanding differences among these three types involve the sex of the principal parent incubating eggs and young, the length of time elapsing before the eggs are picked up and orally incubated, and whether the young ever return to the parental mouth after being released for the first time. That these differences are correlated functionally remains to be seen. We believe it possible that some of the features of oral incubation peculiar to *Geophagus jurupari* are associated with young that are provided with relatively little yolk, as compared with other orally incubating cichlids, and which therefore must begin feeding soon after hatching. Young *G. jurupari* are less well developed at the time of first release than are *Tilapia* and *Haplochromis*, for example, but this fact is at best only indicative of a poor endowment of yolk. A comparative study of eggs and young is needed to help establish this point.

Greenwood (in Lowe, 1957) reported that the period of parental care in *Tilapia leucosticta* extends for about 32 days, which appears to be longer than in any other fish belonging to the third group. Lowe pointed out that the eggs of this species are smaller and more numerous than those of many other African mouthbreeding

<sup>6</sup> After 27 days in a separate 7½ gallon aquarium (35 days after being spawned), these four young were almost one inch long, while their sibs of the same age being raised by the parent fish were only about half that length.

TABLE 2. COMPARISON OF THREE MAJOR TYPES OF ORAL INCUBATION AMONG CICHLID FISHES<sup>1</sup>

Type	Spawning Location	Interval of time from spawning until:			Sex of principal parent: <sup>2</sup>		
		First eggs picked up	Hatching from mouth	First release from parental care	Preparing egg site	Carrying eggs	Carrying young
<i>Geophagus jurupari</i>	On flat stones	About 24 hours	About 3 days	About 6-8 days	30-37 days	Male and female, or female	Male and female
<i>Tilapia macrocephala</i>	In depression on bottom	20-130 seconds	6-10 days	8-20 (mean 14) days	8-20 (mean 14) days	Male	Male
<i>Tilapia</i> spp., <i>Haplochromis</i> spp.	In depression or other nest on bottom	From less than one to a few minutes	2½-6 days	4-20 (mode 14) days	10-32 (mode 20) days	Female, or male and female	Female, or male and female

#### FOOTNOTES TO TABLE 2

<sup>1</sup> The figures are tentative, with the exception of those concerning *T. macrocephala* which are taken from the ample studies of Aronson (1949) and Shaw & Aronson (1954).

<sup>2</sup> In those species studied in detail, cases in which the opposite sex has been found to perform the duties are usually on record. For example, female *Tilapia macrocephala* and male *Haplochromis multicolor* occasionally orally incubate.

cichlids. Again a correlation between provision of yolk and length of parental care is suggested.

Because of the conflict of reports as to whether the various species of *Geophagus* do or do not practice oral incubation, we at one time entertained the idea that this habit was a direct response to outside interference, or threat of interference, and that this would explain why species known to orally incubate in the wild had not been reported to do so in captivity. The present observations lend no support to this idea; the pair of *G. jurupari* incubated their eggs and young just as assiduously when kept alone as when living in a community aquarium with several good-sized fishes of other species. One difference was apparent, however. The amount of chasing, nipping and other molestation between mates was noticeably greater when the pair bred alone.

Two peculiarities of mouthbreeding in *Geophagus* that may well have misled aquarists are the relatively long delay before the eggs are picked up and the undeveloped state of the young when first liberated (see p. 81).

That *G. jurupari* waits practically a whole day before picking up and orally incubating its spawn, in the meantime guarding and fanning it in typical cichlid fashion, poses the question whether this state of affairs could represent a stage in the evolution of the other two major types of cichlid oral incubation (Table 2). Such a stage is not incompatible with the mode of origin of piscine oral incubation suggested by Darwin (1871), Breder (1933, 1934), Myers (1937), and, in part, Ogilby (1916), but not essential to it. At any rate, it does not appear necessary to consider that the habit of mouthbreeding indicates any phylogenetic relationship between the neotropical genus *Geophagus* and the other, African, genera that contain orally incubating species, because of the probability of multiple origin of this habit within the Family Cichlidae.

We believe that further studies of reproductive behavior in *Geophagus jurupari* and its close relatives would be especially revealing because of the long association of parent and offspring and the relatively undeveloped state at which the young are first released from the mouth, in addition to the sharing of duties by male and female and the evident variability in their feeding behavior during the period of parental care. An extensive program, such as the one Dr. Lester R. Aronson of the American Museum of Natural History in New York has carried out with *Tilapia macrocephala*, is called for, but first of all standardized conditions that result in a high fre-

quency of spawning in *G. jurupari* must be developed. It is unfortunately true that spawning pairs of this species have seldom become established under the prevailing conditions of captivity.

#### SUMMARY

1. Reports on the reproductive habits of several cichlid fishes assigned to the genus *Geophagus* disagree as to whether or not oral incubation is practiced. On the basis of a review of the literature, it is believed that *G. jurupari* and *G. surinamensis* are mouthbreeders, but that *G. brasiliensis* is not.

2. Extended observations on a breeding pair of *G. jurupari* confirmed its status as an oral incubator.

3. Instead of picking up the eggs soon after spawning, as do other mouthbreeding cichlids, both parents guarded them for about a day before commencing oral incubation. Both sexes or the female alone carried the eggs.

4. The young were given shelter in both parents' mouths for more than thirty days, a much longer period of parental care than is exercised by other mouthbreeding cichlids.

5. Both parents fed through most of the period of parental care, even while in the act of carrying the young and, occasionally, the eggs.

6. The significance of these features in connection with the evolution of oral incubation and the amount of yolk provided for the young is briefly discussed.

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## EXPLANATION OF THE PLATE

## PLATE I

- FIG. 1. The pair of *Geophagus jurupari* Heckel whose reproductive behavior formed the basis for the present report. The male is on the right. Photographed on October 18, 1955, by S. C. Dunton, Staff Photographer, New York Zoological Society.
- FIG. 2. The male, showing the extensions of the

pelvic (ventral) fins. These continued to grow, and at the time of death, in January, 1958, one had reached approximately the middle of the caudal fin. The other previously had been broken off. Photographed as above.

- FIG. 3. Two of the young from spawning IV. Age, 3½ months. Photographed by S. C. Dunton.

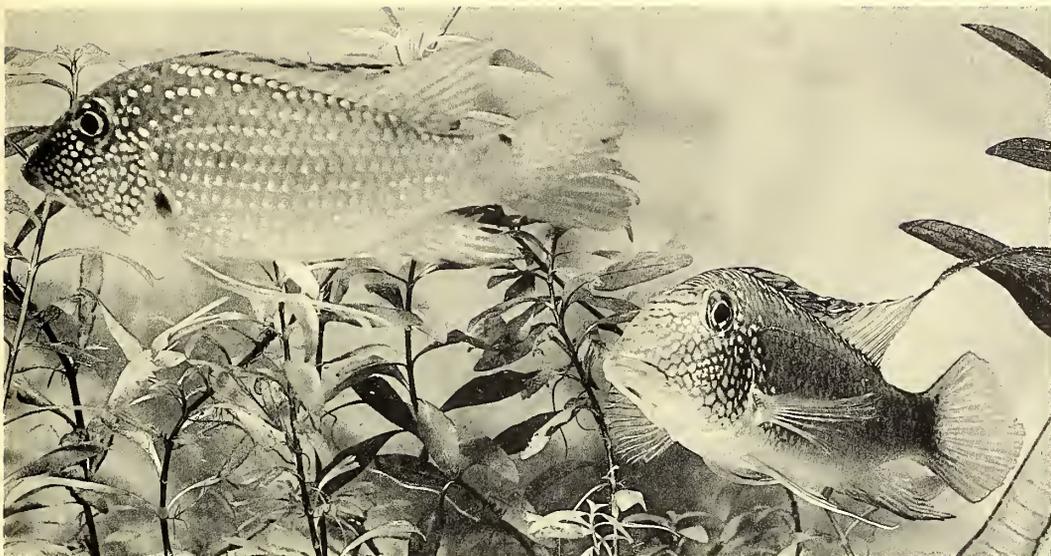


FIG. 1

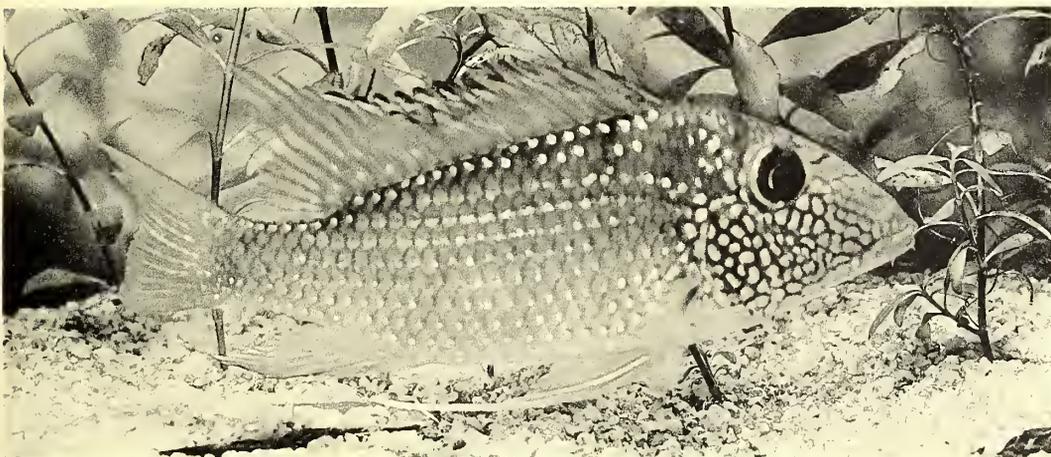


FIG. 2

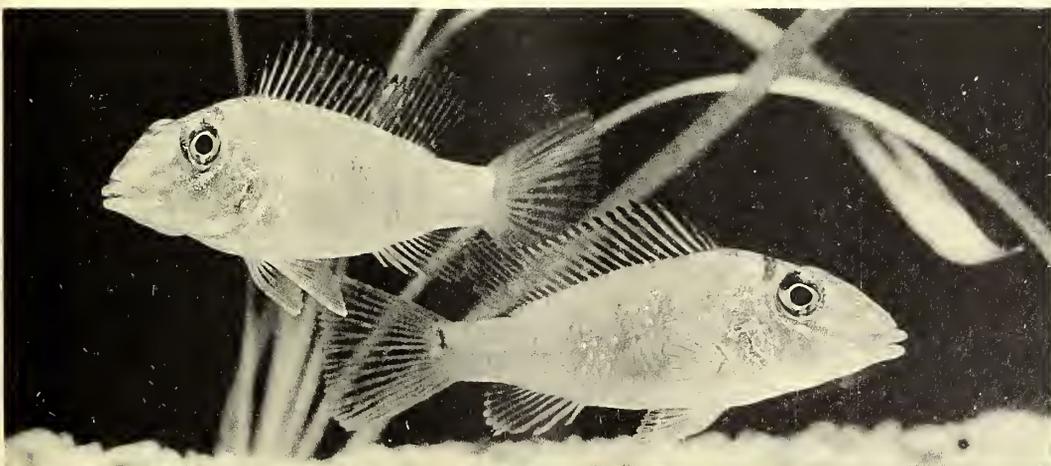


FIG. 3

ORAL INCUBATION IN THE CICHLID FISH *GEOPHAGUS JURUPARI* HECKEL



The Specific Distinctness of the Fiddler Crabs *Uca pugnax* (Smith)  
and *Uca rapax* (Smith) at Their Zone of Overlap  
in Northeastern Florida<sup>1</sup>

RICHARD E. TASHIAN & F. JOHN VERNBERG

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(Plate I)

THE fiddler crab *Uca pugnax* (Smith), has been described as ranging from the northeastern United States to the southern coast of Brazil near Rio de Janeiro. Systematically, this species is currently divided into three subspecies: the northern, nominate race extending from Cape Cod, Massachusetts, to southern Florida (?); the southern race, *rapax*, from southern Florida to Angra dos Reis, Brazil; and a localized race, *brasiliensis*, from Baía de Guanabara, Brazil. *Uca pugnax* and *Uca rapax* were originally described as separate species (Smith, 1870) and later reduced to subspecies by Rathbun (1901, 1918). The form *brasiliensis* (Oliveira, 1939) may have been based on aberrant individuals (Jocelyn Crane, personal communication) and is therefore of doubtful validity. On the basis of evidence to be presented in this paper, the forms *U. p. pugnax* and *U. p. rapax* apparently should be restored to full specific status, and will therefore be designated in the following pages as *U. pugnax* and *U. rapax*.

We are very thankful to Miss Jocelyn Crane of the New York Zoological Society for her many helpful suggestions during this study as well as for having critically read the manuscript.

#### DISTRIBUTION IN NORTHEASTERN FLORIDA

Although the eastern coast of Florida has been arbitrarily designated as the most probable region where the northern and southern subspecies of *Uca pugnax* intergrade, the actual area has never been studied. In the course of a preliminary survey of the ecology of fiddler crabs

from the Atlantic coast of the Americas, the authors visited the eastern coast of Florida in July of 1957 for the purpose of establishing, if possible, the area of supposed intergradation between the two forms.

It was believed that the northern Indian River region of east-central Florida would be a good point from which to begin observations. Here, at the town of Shiloh, the forms all proved to be typical *U. rapax*. Collections were then made progressively north of Shiloh at New Smyrna Beach, Flagler Beach, Crescent Beach, Vilano Beach and Jacksonville Beach. *U. rapax* was found from New Smyrna Beach to Crescent Beach, and *U. pugnax* from Crescent Beach north. From these findings it can be seen that the two forms meet in the general region of Crescent Beach which is located some ten miles south of St. Augustine, Florida.

It is interesting to note that another tropical fiddler crab, *Uca thayeri*, was found as far north as Vilano Beach, immediately northeast of St. Augustine, thus paralleling the northern extension of *U. rapax*.

The question now arises as to whether there is any evidence of intergradation, or do two distinct species overlap where the ranges meet? In order to clarify this point, the following observations were made on the forms from the Crescent Beach region and adjacent areas.

#### ECOLOGY

The forms of *U. rapax* at Crescent Beach were all found above the high tide level in sandy soil with tall grass cover, whereas *U. pugnax* was seen in situations approximating those of northern regions, that is, in relatively open, intertidal

<sup>1</sup>This study was supported by a grant from the National Science Foundation (G-2509).

mud flats. During some two hours of observation at Crescent Beach we saw no indication of overlap between these two forms; *Uca pugilator*, however, characteristically an intertidal species of the open sandy beach, was seen to overlap *U. pugnax* much as it does in other areas where their habitats adjoin. The *U. rapax* which we had observed at Key Biscayne (five miles south of Miami, Fla.), Flagler Beach, New Smyrna Beach and Shiloh were almost invariably found in sandy habitats with grass or mangrove cover. Although Crane (1943a) found *U. rapax* from Venezuela often frequenting a sandy or pebbly habitat, either in the open or among grass tussocks, it should be borne in mind that *U. rapax* from the Caribbean region (Venezuela, Jamaica and Trinidad) has been observed by the authors and Miss Crane more typically to inhabit either muddy or sandy mud situations.

#### SIZE

The *U. pugnax* taken and observed by us at Crescent Beach, Jacksonville Beach and Vilano Beach averaged much smaller than typical *U. pugnax* from more northern areas (Table 1). It would seem that there is a tendency toward a decrease in size for *U. pugnax* at the southern limit of its range. *U. rapax*, however, from the northern limits of its range does not appear to exhibit a correspondingly marked decrease in size. Truly tropical *U. rapax* does nevertheless average larger than any of the Florida forms observed; we have recorded maximum weights of 8.5 gms. from Trinidad and 13.5 gms. from Jamaica, B.W.I.

#### COLOR

On the basis of color, the *U. pugnax* from Crescent Beach could be readily separated from the *U. rapax* with no evidence of integradation. The *U. pugnax* specimens all had the dark greenish-olive carapace of typical *pugnax* with the characteristic frontal blue area between the ocular peduncles. The major cheliped (large claw) of the male was also typically *pugnax* in having the palm (hand) lighter olive green than the carapace with light brownish-yellow at the articulations and the fingers light yellow.

All the specimens of *U. rapax* from Crescent Beach possessed the characteristic coloring of that form, the ground color of the carapace being a creamy or dusky white with the posterior quarter usually dark vinaceous brown and the remainder mottled variously with grayish or brownish patterns, varying from very sparse mottling to a solid dark brown. Light reddish spotting in the frontal region was quite often

apparent between the ocular peduncles. The ground color of the major cheliped was a light apricot orange, mottled or diffused with light brown on the propodus and becoming white or creamy white on the fingers. The legs varied from brownish-white to dark reddish or vinaceous brown. The description of *U. rapax* by Crane (1943a) from Venezuela agrees closely with our Florida material, thus showing good homogeneity of coloration within that form.

#### MORPHOLOGY

One of the most obvious differences between the males of the two forms is the relatively chunky appearance of the major cheliped of *U. rapax* as compared to the generally more slender claw of *U. pugnax*. Representative claws from both typical and overlap populations are figured in Plate I. The length of the entire propodus in *U. rapax*, as measured from the tip of the immovable finger to the proximal edge, is usually less than twice the length of the palm, as measured from the lower point of articulation with the movable finger to the proximal edge. Table 1 gives the ratios of the palm length to the propodus length for some of the populations studied. About 80 per cent. of the 37 males of the *pugnax-rapax* assemblage at Crescent Beach, with ratios greater than 2.0, could be separated as *U. pugnax*, and about 88 per cent. of those with ratios less than 2.0 could be separated as *U. rapax*.

There is also a tendency to have the fingers of the major cheliped in *U. rapax* shorter and less slender than in *U. pugnax*, with the distal fourth of the immovable finger invariably curved up, whereas in *U. pugnax* it is most often straight or even curving slightly down.

Other differences, such as the angle of the eyebrow and variations in the granulation of the inner surface of the palm, have been discussed by Rathbun (1918).

#### BEHAVIOR

Crane (1943b) has described the display waving of the large claw in the males of *U. pugnax* and *U. rapax* as being quite distinctive. We have likewise observed this difference, which becomes markedly apparent when the two forms are seen displaying side by side in laboratory aquaria. Miss Crane further remarks (personal communication) that "an outstanding fact concerning all other widespread fiddler species has proved to be the constancy of their display characteristics throughout their range, along with the absence of any noticeable tendency to subspeciate."

TABLE 1. RATIO OF LENGTH OF PALM TO PROPODUS IN THE MAJOR CHELIPED OF *Uca pugnax* AND *Uca rapax* FROM SEVERAL POPULATIONS

Locality and Form	Sample Size	Range in Length of Propodus (mm.)	Propodus Length* Palm Length	
			Range	Mean $\pm$ S.E.
Beaufort, N. C. ( <i>U. pugnax</i> )	50	14.8-44.3	1.72-2.43	2.12 $\pm$ .023
Jacksonville Beach, Fla. ( <i>U. pugnax</i> )	23	16.5-29.7	1.72-2.38	2.12 $\pm$ .020
Crescent Beach, Fla. ( <i>U. pugnax</i> )	19	10.9-27.4	1.87-2.31	2.06 $\pm$ .023
Crescent Beach, Fla. ( <i>U. rapax</i> )	18	22.7-35.4	1.70-2.04	1.86 $\pm$ .020
Shiloh, Fla. ( <i>U. rapax</i> )	18	10.8-34.2	1.50-1.91	1.77 $\pm$ .028
Key Biscayne, Fla. ( <i>U. rapax</i> )	50	13.1-38.4	1.62-2.08	1.85 $\pm$ .016
Jamaica, B.W.I. ( <i>U. rapax</i> )	34	14.4-33.7	1.61-2.15	1.94 $\pm$ .022

\*See text for exact limits of measurement.

#### SUMMARY AND CONCLUSIONS

Because of the lack of any color, morphological or behavioral intergradation between the northern (nominate) and southern (*rapax*) subspecies of the fiddler crab, *Uca pugnax*, in the region where the two forms come together in northeastern Florida, it appears evident that the two forms are actually separate species rather

than subspecies as had been previously thought. In view of this evidence, therefore, the name *Uca pugnax* (Smith) is retained for the species ranging from Cape Cod, Massachusetts, to the St. Augustine region of northeastern Florida, and the species ranging from northeastern Florida to Angra dos Reis, Brazil, then becomes *Uca rapax* (Smith).

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## EXPLANATION OF THE PLATE

## PLATE I

- FIG. 1. Major cheliped of *Uca pugnax* from Beaufort, North Carolina.
- FIG. 2. Major cheliped of *Uca pugnax* from Crescent Beach, Florida.
- FIG. 3. Major cheliped of *Uca rapax* from Crescent Beach, Florida.
- FIG. 4. Major cheliped of *Uca rapax* from Shiloh, Florida.

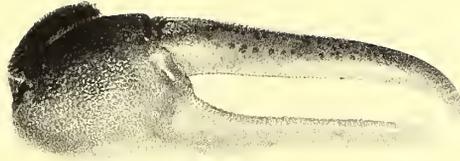


FIG. 1



FIG. 2



FIG. 3

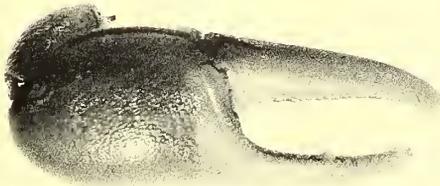


FIG. 4

THE SPECIFIC DISTINCTNESS OF THE FIDDLER CRABS *UCA PUGNAX* (SMITH) AND *UCA RAPAX* (SMITH)  
AT THEIR ZONE OF OVERLAP IN NORTHEASTERN FLORIDA



## A Practical Method of Obtaining Blood from Anesthetized Turtles by Means of Cardiac Puncture

CHARLES P. GANDAL

*Veterinarian, New York Zoological Park*

(Text-figure 1)

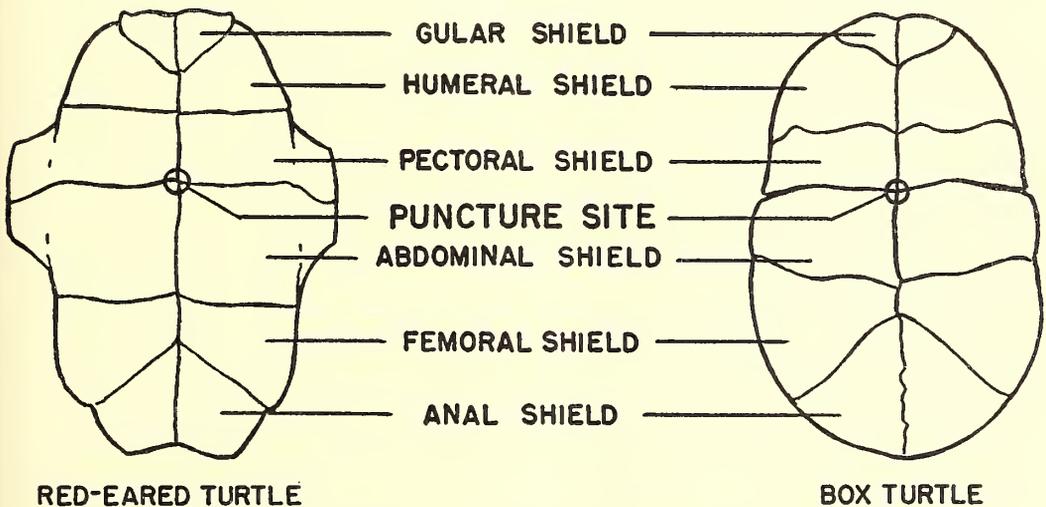
A successful technique for withdrawing blood from turtles under nembutal (a 6% solution of pentobarbital sodium "Abbott") anesthesia has been developed in the Animal Hospital of the New York Zoological Park. Species to which the technique has been applied are the box turtle, *Terrapene c. carolina*, and the red-eared turtle, *Pseudemys scripta elegans*, but it is believed that this method is applicable to many other species.

### PROCEDURE

Each turtle was weighed and given a subcutaneous injection of nembutal at the rate of 0.1 grain per 240 grams of body weight (see Table 1). In order to avoid any possible slough-

ing (which may occur at the site of a subcutaneous injection of nembutal), sterile distilled water was added to the prescribed dosage to make 1 cc. of total injected fluid. None of the turtles showed any signs of sloughing afterward. Satisfactory anesthesia was attained in approximately 45 minutes and recovery was uneventful with no fatalities.

Withdrawal was effected by a 1.5-inch 18-gauge needle attached to a 5 or 10 cc. lock-tip syringe. The subject was held in dorsal recumbency and the puncture area was thoroughly cleaned with alcohol. The needle was then inserted through the plastron on the midline at the junction of the pectoral and abdominal shields (Text-fig. 1), with a gentle rotating



TEXT-FIG. 1. Plastron diagram of box turtle, *Terrapene c. carolina*, and red-eared turtle, *Pseudemys scripta elegans*, showing puncture sites.

TABLE 1. WEIGHT, ANESTHESIA AND WITHDRAWAL OF BLOOD FROM TURTLES

Subjects	Weight range (grams)	Nembutal dose range (grains) @ 0.1 grain per 240 grams	Minimum & maximum amount of blood withdrawn (cc.)	Average amount of blood withdrawn (cc.)
22 Box turtles	359-800	0.15-0.33	0.5-6.5	3.2
5 Red-eared turtles	516-1745	0.22-0.73	2.0-14.0	7.6

motion. A fair amount of downward pressure must be applied to make the puncture, and the necessary rotating motion makes it important to use a lock-tip type of syringe. The point of entry corresponds to the osseous as well as the dermal sutures and therefore passage of the needle into the body cavity is facilitated.

The needle used for perforating the plastron frequently became plugged. Routinely it was replaced with a new needle of the same size to effect the actual cardiac puncture. (If available a similarly sized stillette may be substituted for the first needle.)

The needle was inserted postero-dorsal at an angle of about 20 degrees from the vertical, and pierced the cardiac ventricle when it was

inserted half an inch to an inch. Gentle suction was then applied.

Blood cannot be withdrawn continuously, but comes in spurts every 5 to 8 seconds, as would be expected in view of the functioning of the reptilian heart. Withdrawal pressure should not be applied during the intervening "heart filling" phase.

After two or three withdrawals at 5- to 8-second intervals, a clot may occlude the lumen of the needle. If this happens, the needle may be withdrawn and a new one inserted in the same aperture.

#### SUMMARY

A practical method of cardiac puncture in turtles anesthetized with nembutal is described.

## Observations on the Breeding in Captivity of a Pair of Lowland Gorillas

WARREN D. THOMAS

(Plates I-III; Text-figures 1 & 2)

ON December 22, 1956, a pair of lowland gorillas, *Gorilla gorilla gorilla* (Savage & Wyman), gave birth to a healthy female baby in the Columbus Zoological Garden, Columbus, Ohio. This was the first reported birth of a gorilla bred and born in captivity. As a student of veterinary medicine at Ohio State University I have had the good fortune to observe the parents of this baby from the time of their arrival at the Zoo to the present, and also to observe the baby in the first few minutes of its life and subsequently. The major facts concerning the development of the parents in captivity, their breeding behavior and the birth of their offspring are recorded here in an effort to cast some light on the propagation of gorillas in captivity.

### PRE-BREEDING HISTORY

The Columbus Zoo's gorillas are known as "Baron" and "Christina." They were captured near the end of 1950 in the French Cameroons, by the late Bill Said of Columbus, Ohio, and arrived in New York on December 22, 1950. Shortly thereafter they were bought by the Columbus Zoo and arrived in Columbus on January 8, 1951.

On arrival, Baron weighed approximately 72 pounds and was estimated to be a little more than four years old. Christina weighed about 21 pounds and was estimated to be a year and a half old. A third gorilla was received at the same time, a small male named "Christopher," about the same age and weight as Christina.

All three were in poor condition. They were suffering from severe upper respiratory infections and in addition Christopher had gunshot wounds in one arm and one leg. However, they were immediately treated by the Zoo Veterinarian and after a time responded well to treatment.

The only quarters available at the time of their

arrival were temporary ones with poor lighting and sanitary facilities and with very irregular temperature control. Baron was placed in one cage, and in the adjoining cage, with only bars separating them, Christina and Christopher were housed together. During the whole of their stay in these quarters they could see each other at all times, but they were never allowed to enter each other's cage.

In the spring of 1954 they were moved to semi-permanent quarters in another building, and early in the summer Christopher was traded to a European zoo. Facilities were much better in the new quarters, which were constructed of concrete block and steel bars. Again Baron and Christina were placed in adjoining cages, this time separated by a solid wall with a barred door through which they could always see each other and through which they could pass their fingers. It was in these quarters that they began to exhibit some sexual activity.

Baron and Christina remained in this semi-permanent installation until the late summer of 1956 when they were moved to their permanent quarters in the newly-built Ape House. Here they have essentially the same housing arrangements as in the semi-permanent quarters.

When they first arrived at the Zoo they were reluctant to eat, but little by little regained appetite. They were placed on a varied diet which was competently adjusted to their daily routine by Don Jones, their regular keeper. Table 1 gives their typical meals.

In addition to the items shown in Table 1, a commercial vitamin preparation was usually given to both animals once a day. The diets were increased and adjusted as the animals grew older and larger, but the diet in Table 1 is typical for 1951 to 1953.

According to his hypothetical birth date of

TABLE 1. TYPICAL MEALS OF YOUNG GORILLAS, 1951-1953.

	Baron	Christina
<i>Morning</i>		
Cereal (Rice, Cream of Wheat or Rolled Oats, Raisins)	3 to 4 cups	3 to 4 cups
Lettuce	½ to 1 head	½ to 1 head
Carrots	4	3
Apples	3 to 4	2
Bananas	8 to 10	3
Grapefruit	1	½ to 1
Eggs (raw in milk)	2	2
Pear	1	1
Milk	1 to 2 pints	1 to 2 pints
Bread	½ to 1 loaf	½ loaf
<i>Noon</i>		
Peanut or applebutter sandwiches	1 to 2	1
Navy beans, cooked	1 pint*	1 pint*
Prunes	4	4
Meat (chicken or beef, broiled)	¼ pound	¼ pound
<i>Evening</i>		
Lettuce	½ to 1 head	½ head
Bread	1 loaf	½ loaf
Apples	3	2
Carrots	6	4
Sweet potato, baked	6*	6*
Irish potato, baked or boiled	6	4
Celery	12 stalks	6 stalks
Oranges	1 to 2	1
Bananas	10 to 15	8 to 12
Grapes	¼ pound	¼ pound
Milk	1 pint	1 pint

\*Two to three times a week.

October, 1946 (Yerkes, 1951), Baron was 4 years and about 2 months old when he was received at the Columbus Zoo. He had an unusually prognathous appearance for a lowland gorilla, and his head has always been disproportionately large in relation to his body. It has always been noticeable that the facial and cephalic features of Baron and Christina are decidedly different, over and above their sexual differences, but it is well known that there is wide variation among gorillas (Coolidge, 1929).

Baron's saggital and occipital crests began to develop when he was about 5½ years old and were fully developed at the age of 10. He lost his deciduous incisors at 6½ years and his canine teeth at 10½. He progressed steadily in weight and in December, 1956, weighed about 300 pounds, ± 10 pounds. His appearance at that

time is shown in Pl. I, Fig. 1. As gorillas go, Baron has always been inclined to leanness.

According to her hypothetical birth date of August, 1949 (Yerkes, 1951), Christina was about 1½ years old when she came to the Columbus Zoo. She lost her deciduous incisors at 5 years. She has always been rather small and had a tendency to obesity even when on a restricted diet. She weighed approximately 200 to 210 pounds at the time of the birth of her baby. Her appearance on December 22, 1956, is shown in Pl. I, Fig. 2.

From the beginning Baron was playful and quite active. Every inch of his cage was used for exercise. He had acquired the habit of pounding his chest when he arrived at the Zoo, and indulged in it frequently. He became used to his daily routine and any deviation from it resulted in severe diarrhea. He had a dislike for water from a hose, but not a fear of it. Toward strange objects in his cage he demonstrated inquisitiveness but rarely what could be interpreted as fear.

Christina was always quieter than Baron, but could not be trusted as far as he could. When the hand or arm of anyone but her regular keeper got too close, she sometimes appeared slightly vicious. She was always much less physically active than Baron. Unlike him, she developed a fondness for standing in a stream of water. Any change in routine resulted in diarrhea, and strange objects in or out of her cage appeared to frighten her at first, but if they were exposed long enough she became accustomed to them and accepted them.

Both Baron and Christina regularly and easily regurgitate large portions of each meal and then reconsume it. This practice began when they were four to five years old. It is apparently normal in gorillas (Dr. Leonard J. Goss, Moody J. R. Lentz: personal communications).

#### BREEDING BEHAVIOR

##### *The Female*

The first activity between the two animals began as playing through the bars of their adjoining cages, and this was a fairly constant thing from the time of their arrival at the zoo. The first observations of sexual play were made in the spring of 1954 when Christina was about five years old. At that time she began to "present" for the male. Baron would sit on one side of the bar door and she would back up to the bars on all fours, after which the male would carry on digital intercourse with her through the bars. She would emit a low grunt and stand for him. Her sexual drive was variable and no particular pattern was determined. Her menstrual cycle

was also difficult to determine because the only evidence was a few drops of blood on the cage floor, and these could easily be overlooked.

### *The Male*

Baron showed no exceptional interest in Christina until after the other male in the original trio, Christopher, left the Zoo, and then his interest became more active. When the female "presented" for him and he carried on digital intercourse, he emitted a staccato series of grunts which built up to a climax of guttural sounds. In this kind of intercourse he used the third finger of, more often than not, his left hand. He has never been observed to masturbate.

### *Intercourse*

After this sexual play had been observed for some months it was decided to put the two animals together for short periods of time in hope that they would mate. They were first put together on August 10, 1954. They played together for some time, and intercourse was attempted but was not successful, and they were separated. On several other occasions they were put together with the same result. Successful coitus was not achieved until January 9, 1955.

The two animals were turned in together only when the female showed signs of sexual activity by "presenting," and they were usually separated after coitus if the male showed signs of playing rough, which was not infrequently. Sometimes, even though Christina showed signs of sexual activity, she would not stand for the male and this resulted in their fighting and subsequent separation.

Two positions of intercourse were used: dorso-ventrally (Pl. II, Fig. 3) and ventro-ventrally (Pl. II, Fig. 4). At first they used only the dorso-ventral position but as time went on both positions were used about equally.

The male's penis, erect, is about 14 cm. in length and about 1.5 cm. in diameter halfway posterior from the glans penis.

### *Breeding Record*

Records were kept of the sexual activity of the two gorillas and most of the information below was supplied by Keeper Don Jones. It may be summarized as follows:

1954

- |              |   |
|--------------|---|
| July 17      | Positive signs of sexual activity.            |
| August 10    | Put together; unsuccessful attempt at coitus. |
| September 27 | Put together; unsuccessful attempt at coitus. |
| October 2    | Put together; unsuccessful attempt at coitus. |

- |            |   |
|------------|---|
| October 31 | Signs of sexual activity, but not put together. |
| December 5 | Signs of sexual activity, but not put together. |

1955

- |              |   |
|--------------|---|
| January 8    | Signs of sexual activity, but not put together. |
| January 9    | Successful coitus.                              |
| January 10   | Coitus.   |
| February 5   | Put together; no coitus.                        |
| February 11  | Coitus.   |
| February 12  | Signs of sexual activity, but not put together. |
| February 13  | Signs of sexual activity, but not put together. |
| March 9      | Coitus.   |
| April 6      | Coitus.   |
| April 7      | Coitus.   |
| April 8      | Coitus.   |
| May 10       | Signs of sexual activity, but not put together. |
| June 6       | Signs of sexual activity, but not put together. |
| August 28    | Signs of sexual activity, but not put together. |
| September 24 | Coitus.   |
| December 5   | Put together; no coitus.                        |
| December 16  | Coitus.   |
| December 17  | Coitus.   |

1956

- |             |                          |
|-------------|--------------------------|
| January 15  | Coitus.                  |
| January 16  | Coitus.                  |
| January 17  | Coitus.                  |
| January 18  | Coitus.                  |
| February 15 | Coitus.                  |
| February 16 | Coitus.                  |
| February 17 | Put together; no coitus. |
| March 11    | Coitus.                  |
| March 12    | Coitus.                  |
| March 13    | Coitus.                  |
| April 6     | Coitus.                  |
| April 7     | Coitus.                  |
| April 8     | Coitus.                  |

### PREGNANCY AND PARTURITION

#### *Physical Changes*

Conception probably took place on April 6, 7 or 8, 1956; this supposition is based on the fact that soon afterward Christina ceased to show signs of sexual activity, menstrual flow was no longer observed and her temperament changed radically. At this time she was approximately 7 years old and thus, according to present belief, not physically mature. Consequently when changes occurred during her pregnancy it was difficult to differentiate between those of maturity and those of pregnancy.

Pregnancy tests were made at about 120 days of pregnancy under the direction of Robert W. Vesper, DVM, the Veterinarian of the Colum-

bus Zoo. Sixteen *Xenopus* frogs were inoculated with a urine sample. Four frogs died and the remaining twelve showed negative. One rabbit was inoculated with urine but died in six hours. At 200+ days Cuboni tests were made and the results were again negative.

Changes in the female which beyond reasonable doubt can be classified as due to pregnancy were:

*Abdomen.*—There were no appreciable changes until she had progressed about 120 days, at which time there was a gradual increase in size out of proportion to the rest of her development.

*Feet and Ankles.*—A definite edema became apparent after about 210 to 220 days of pregnancy; this persisted until almost three weeks after parturition.

#### *Temperamental Changes*

Changes in temperament shown by Christina during pregnancy were very noticeable.

She became sullen, irritable and at times even belligerent. She had long periods of depression and lethargy. Whereas once her keeper could scratch her and play with her through the bars, she now stayed quite distant from him. She was acutely responsive to loud noises and was continually irritated by the commotion caused by Baron in an adjoining cage.

Her appetite decreased and remained at a low level all during pregnancy and for about a week after parturition. She began to regurgitate more frequently and only a small portion of the regurgitation was reconsumed.

Her activity declined to a very low point. She frequently sat for long periods of time and stared off into space.

#### *Convulsive Attack*

Christina underwent a convulsive attack on December 8, fourteen days before parturition. The timetable of the attack follows:

- 3:00 p.m. A central nervous seizure was noticed by the keeper on duty. Its onset was fairly gradual. There was a shaking of her head and body as if she were taken by chills. She climbed up into her rest cage and sat down, then turned around and slid backwards down onto her bench where she remained, leaning into her rest cage, with both feet on the bench.
- 3:10 p.m. She showed no volitional control of her body. The only reflex found was an eye reflex. She perspired and sali-

vated profusely. No indications of cyanosis were found. She was still standing on her bench, leaning into her rest cage. At this time she was boosted up into the cage by her keepers, and in this new position she lay without moving.

- 3:40 p.m. Volitional control of the right hand, and then of the right arm, began to return.
- 3:50 p.m. Volitional control of the left hand and arm began to return.
- 4:05 p.m. The left leg showed volitional control.
- 5:00 p.m. The right leg showed volitional control.
- 6:00 p.m. She staggered down out of the rest cage and moved with a reeling gait.
- 9:00 p.m. At this time she was in complete control of her faculties. She showed only a small appetite.

#### PARTURITION

The first signs that were noted, indicative of impending parturition, were on December 20, 1956. She refused her morning feeding and ate only a small part of her evening meal. In the afternoon a clear, serous, vaginal discharge was observed. She was very restless and paced the cage all day.

On December 21 her appetite had not improved but she appeared to be more calm. There was no vaginal discharge.

On the morning of December 22, 257 to 259 days after probable conception, she was offered food at 8 o'clock. At this time she was standing on all fours in her "rest cage," a small cage four feet above the floor of the main cage and behind and adjoining the main cage. She made no attempt to come down and investigate her food.

She was checked again at 8:30 a.m. and her food was untouched and she was still standing quietly, in the same position.

At 8:50 a.m. she was checked for a third time and found to be in the same place, but in the middle of the floor of the main cage was the newborn gorilla, still encased in the amniotic sac with about two and one-half feet of umbilical cord stringing out behind it. During all this time she had not been heard to utter an audible sound. She had a dazed, glassy expression on her face.

She was quickly locked in her rest cage. The baby was then removed from the cage floor and taken to the kitchen of the building. The amniotic sac, in which the baby was still encased,

had a grayish-white, translucent appearance, and had about a five-inch hole in it where it had apparently pulled away from the placenta. The umbilical cord passed through this hole. The cord had a loose knot in it, apparently tied *in utero*. The placenta was later found in the rest cage, with about three inches of cord attached.

The amniotic sac, which still contained a fair amount of fluid, was quickly removed. On examination, the baby did not show respiration and there was a definite cyanosis. A large, thick, mucous plug was manually extracted from the mouth. The baby was then held upside down and struck sharply on the back, with the palm of the hand. It gasped twice, then ceased to respond.

At it was getting progressively more cyanotic, artificial respiration was resorted to, by gently blowing into its mouth. After a minute or two it gasped again and began breathing erratically.

The baby proved to be a female. She was cleaned and placed in an improvised incubator consisting of a cardboard box and a 150-watt bulb, and later in a commercially built incubator for human babies. The Zoo's Veterinarian, on his arrival about an hour after the birth, tied the cord with 00 medium chromic gut and treated the umbilicus with diluted Lugol's solution.

Christina remained in her rest cage until around 1 p.m., after which she began to move about slowly. She lost blood steadily, although relatively little in relation to her size, until close to 1 p.m. From this time on the loss of blood diminished, and by 6 p.m. it had ceased. She passed some clotted blood for the next 24 hours.

About 5:30 pm. on December 22 she ate all of her evening feed. She had one normal bowel movement and urinated frequently and profusely. All the rest of that day she appeared to be nervous but quite exhausted.

She appeared depressed and lethargic for about five or six days and then gradually became more alert and active. Three weeks after parturition she had regained her pre-pregnancy level of activity and her appetite returned. She became less irritable, much more docile, and again enjoyed playing with her keepers through the bars.

After parturition the size of her lower abdomen decreased slightly. In about a week to ten days the edema in her feet and ankles had disappeared.

In approximately 36 hours after parturition her mammae became engorged and lactation began. The Zoo's Veterinarian administered 10 mg. of methyl testosterone in her feed, which brought about a cessation of lactation in about five days.

Throughout pregnancy her bowels functioned normally. By about a week after delivery the amount and frequency of urination decreased to a normal level.

About a month after delivery she began to show some sexual activity by "presenting," but when placed with the male she refused to accept him. Finally, seven months after parturition, on July 23, 1957, she accepted the male for the first time since conception early in 1956.

#### OBSERVATIONS ON THE INFANT

##### *At Birth*

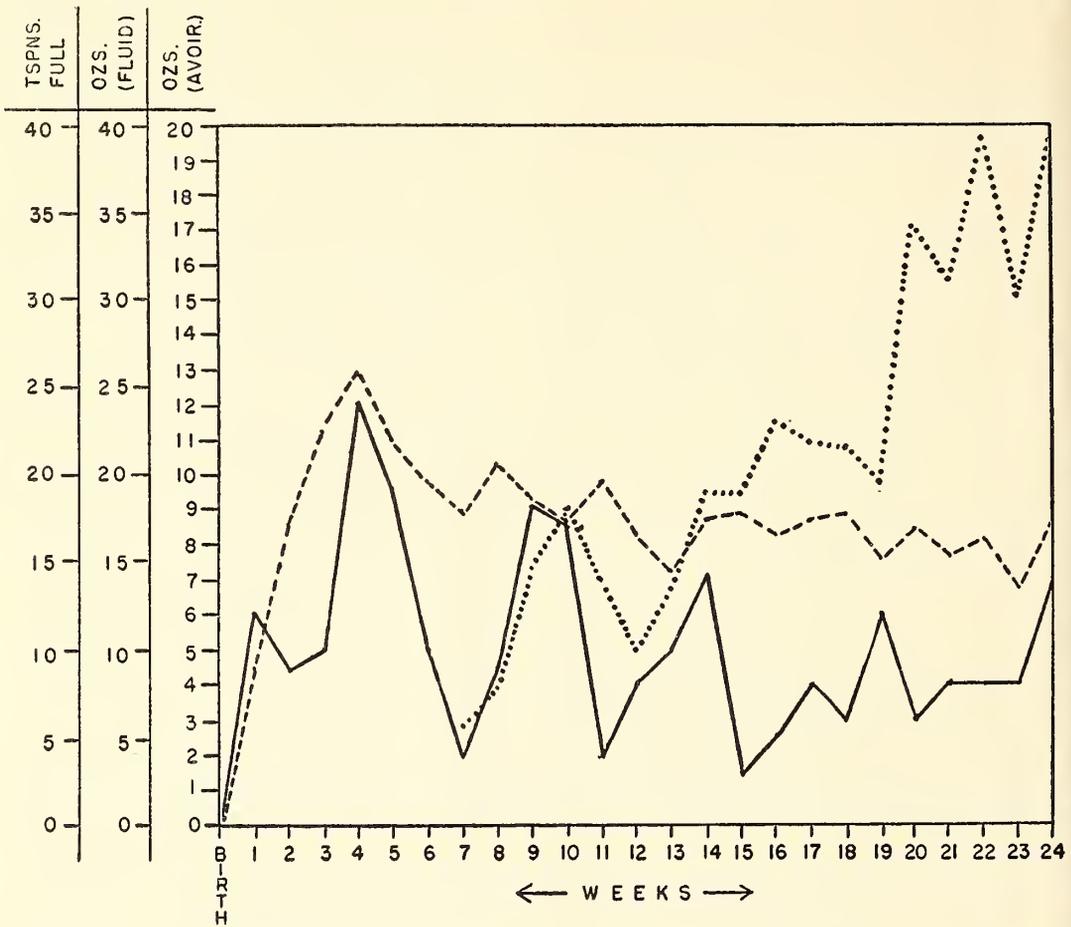
Unfortunately, no accurate measurements were taken at birth. The infant weighed approximately 4 lbs. 2 oz. and had the appearance of a shriveled mass of skin and bone (Pl. III, Fig. 5). Both size and weight were about what could have been expected (Schultz, 1945 (1950)). Her arms were quite long in proportion to the rest of the body. The legs were short and she maintained them flexed at about a 45° angle at the knee. Her head was roughly oval-shaped, sloping down in front, uninterrupted by ocular ridges, to form her face.

She did not open her eyes until about an hour after birth. Her eyes were brown. Her skin was loose and lay in wrinkles, and was of a medium chocolate-brown color. The palms of her hands, the soles of her feet and her face and chest were devoid of hair. The rest of her body, except the top of her head, was sparsely covered with black hair about half an inch long. The hair on top of her head was much denser than on the rest of her body, and was about twice as long. It also was black. Her eyebrows were sparse and measured about two and one-half inches in length. Her fingernails and toenails were even with the ends of her digits.

Her mucous membranes, which at first were blanched and slightly cyanotic, changed to the characteristic watermelon-pink color. Her genitalia had a normal appearance. The clitoris was quite enlarged. Her mammary glands were enlarged and very prominent; the nipple rested on an enlarged, button-like area of swelling which was about 17 mm. in diameter and about 3 to 4 mm. thick.

##### *The First Six Months*

*Weight Gain, Growth and Food.*—Several interesting points are to be noted in reference to the infant's gain in weight. During the first 24 hours her weight dropped to 3 lbs. 4 oz. After this she never had a week in which she exhibited a negative total gain. The maximum gain was 12 oz. in her 4th week, the minimum was 1½ oz.



TEXT-FIG. 1. Weight gain and food consumption of the infant lowland gorilla. Weight: **solid line** indicates total weight gain by week in ounces. Food consumption (fluid): **dash line** represents average daily

(24 hr.) consumption calculated on a weekly basis in fluid ounces. Food consumption (solid): **dotted line** represents average daily (24 hr.) consumption calculated on a weekly basis in teaspoons full.

in her 15th week when she had an attack of enteritis. Her over-all average gain was 5.1 oz. a week.

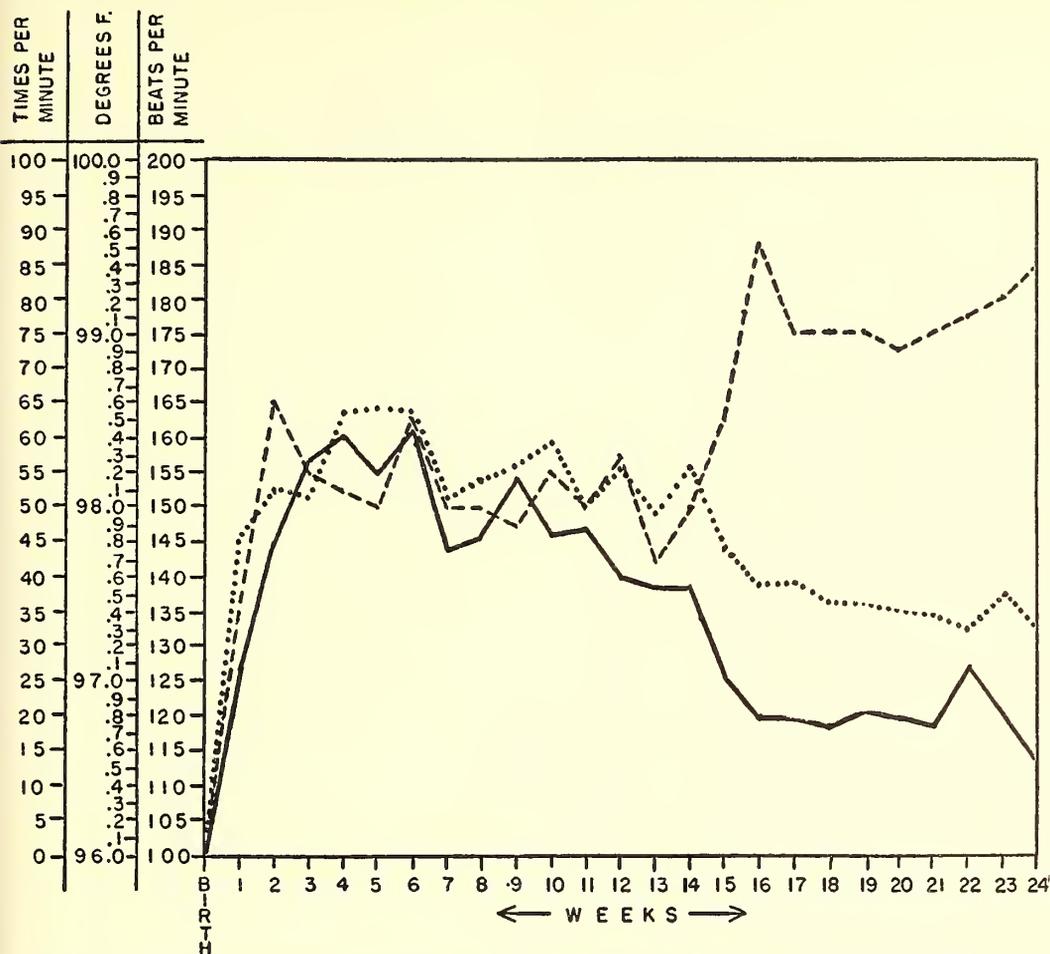
Three definite and severe drops in gain will be seen in Text-fig. 1. The first occurred during the infant's 5th, 6th and 7th weeks just before she was given solid food. The second occurred in the 11th week during a time when four teeth erupted in a period of five days. The third and most severe drop in gain came in the 15th week during the attack of enteritis.

During the first six months the baby received no water alone, only formula ("Olac," Mead Johnson) and water. It will be noted in Text-fig. 1 that her formula consumption reached its peak in the 4th week and then declined, leveling off to a relatively constant rate.

Solid food (strained baby foods and cereal) was started in her 7th week. Her appearance shortly before this time is shown in Pl. III, Fig. 6. As Text-fig 1 shows, her consumption of food increased steadily as she grew older, except during her 11th and 12th weeks when she was teething. In her 20th week there was a sharp rise in consumption. It was at this time that she was moved into new quarters which gave her a great deal more room to move around and her activity increased considerably.

During the period when she had enteritis, her fluid consumption remained fairly constant and her solids intake remained constant and then increased.

*Heart Rate, Temperature and Respiration.*—Her heart rate climbed steadily until her 4th



TEXT-FIG. 2. Heart rate, temperature and respiration of the infant lowland gorilla. Heart rate: **solid line** represents weekly average in beats per minute. Tem-

perature: **dash line** represents weekly average in degrees Fahrenheit. Respiration: **dotted line** represents weekly average in beats per minute.

week and from then until her 12th week it was rather erratic. There was a sharp drop during her 15th and 16th weeks, the period of enteritis during which she was relatively inactive. Her maximum was 180 beats per minute, recorded on January 28, 1957; her minimum was 100 per minute on the day after birth. See Text-fig. 2.

Her temperature rose sharply until the 2nd week. It was very erratic until the 15th and 16th weeks when it reached its maximum. After the attack of enteritis at this time the temperature was much less erratic. Maximum (rectal temperature) was 101.1° F. on April 9, 1957, and minimum was 96° F. on December 24, 1956.

Respiration reached its peak in the 5th week, was erratic for a time, and finally settled down to an even, declining rate.

*Bowel and Urinary Functions.*—For the most

part, bowel and urinary functions were relatively regular and normal during the first six months. There were some short periods of constipation but these were not considered significant.

*Hormonal Function.*—The mammary development described at birth persisted for about a month. There was no mammary secretion. At the age of four days there was a vaginal discharge of a bloody, mucoid consistency. This continued off and on until she was about two weeks old, when it ceased.

*Common Integument and Its Appendages.*—*Skin:* The baby's skin peeled twice during her first two months. The first time it came off in large sections, the second time in small flakes. Her skin was light to medium brown at birth but pigmentation gradually increased until, at the

age of two months, she was the characteristically purplish-black of the adult gorilla.

*Hair:* The hair at birth was uniformly black except for a white patch around the anus, and remained thus until she was about a month and a half old, when the hair on the top of the head began to turn lighter. At two and a half months this was light buff to dirty orange, almost identical with the hair on top of her father's head.

In her 2nd week the amount of hair on her body began to increase and at 3 months the amount and distribution were similar to the adults. The texture of the baby's hair remained soft and silky with the exception of that on top of her head, which was inclined to be bristle-like.

*Dentition:* The order of eruption of the deciduous teeth followed, generally, the expected pattern (Schultz, 1930). Eruption dates were:

*Lower*

Left Central Incisor	Jan. 30, 1957
Right Central Incisor	Jan. 30, 1957
Left Lateral Incisor	March 8, 1957
Right Lateral Incisor	March 20, 1957

*Upper*

Right Lateral Incisor	March 6, 1957
Right Central Incisor	March 9, 1957
Left Central Incisor	March 10, 1957
Left Lateral Incisor	February 12, 1957
Left First Molar	June 8, 1957
Right First Molar	June 8, 1957

Measurements and weight records taken at intervals during the first six months are shown in Table 2.

CARE OF THE INFANT

*Feeding*

*Formula.* — The first feeding was given nine hours after birth and the baby was started on a weak mixture of one teaspoon of Olac (Mead Johnson) to four ounces of water. This formula was maintained until the 3rd day, when she was gradually changed to a stronger mixture of one teaspoon of Olac to two ounces of water. This stronger formula then became standard, only the quantity varying. The baby did very well on such a mixture, with a minimum of digestive dis-

TABLE 2. PERIODIC MEASUREMENTS OF INFANT GORILLA DURING FIRST SIX MONTHS

Date	Head			Appendages					Trunk		Weight
	Circumference* (in mm.)	Width of Nostrils (in mm.)	Length of Ears (in mm.)	Arm Span† (in mm.)	Hand Length (in mm.)	Hand Width (in mm.)	Leg Length (in mm.)	Foot Length (in mm.)	Circum. of Chest (in mm.)	Sitting Height (in mm.)	
Jan. 6, 1957	272	..	28	554	R-80 L-81	R-38 L-39	R-206 L-206	R-88 L-89	290	282	4 lb. ½ oz.
Jan. 13, 1957	278	..	29	577	R-80 L-83	R-39 L-41.5	R-206 L-206	R-88 L-89	296	290	4 lbs. 6 oz.
Jan. 20, 1957	285	34	29	591	R-82 L-84	R-40 L-42	R-206 L-206	R-90 L-91	311	305	5 lbs. 4 oz.
Jan. 27, 1957	290	34	30	618	R-85 L-90	R-45 L-48	R-218 L-222	R-104 L-105	320	314	5 lbs. 9 oz.
Feb. 3, 1957	302	35	30	625	R-87 L-90	R-45 L-48	R-218 L-222	R-104 L-105	324	325	6 lbs.
Feb. 10, 1957	315	38	30	625	R-91 L-92	R-49 L-50	R-225 L-226	R-104 L-105	326	325	6 lbs. 2 oz.
Mar. 3, 1957	320	38	32	660	R-97 L-100	R-51 L-53	R-227 L-229	R-110 L-111	340	360	7 lbs. 3 oz.
May 5, 1957	330	41	..	690	R-108 L-110	R-52 L-53	R-... L-...	R-121 L-121	370	387	9 lbs. 11 oz.
June 8, 1957	350	46	50	695	R-108 L-111	R-54 L-55	R-231 L-236	R-124 L-124	405	395	10 lbs. 15 oz.

\*Frontal-occipital measurement.

†From tip of right third digit to tip of left third digit.

turbance. She had to be "burped" at least twice during each feeding.

*Solids.*—Solid-food feeding was started in the 7th week. It consisted of dry cereals (Pabulum, Mead Johnson; and other types) mixed with the Olac-and-water formula. She was first given Rice Cereal, then an Oat Cereal, and finally Mixed Cereal, and took all of these very well. Prepared baby foods of strained fruits, meats and vegetables were also used. The formula was given on a demand feeding system.

Cereal and fruit were given in the morning and vegetables, meat and fruit at the evening feeding. Among the foods given were:

Chicken	Peas
Liver	Beets
Beef and beef heart	Squash
Vegetables and beef	Orange pudding
Vegetables and lamb	Custard pudding
Vegetables and liver	Bananas
Vegetables and chicken	Applesauce
Vegetables and bacon	Peaches
Lamb	Pears
Green beans	Pineapple
Spinach	Plums
Carrots	Apricots

Except for preferences in taste, she took all the foods offered very well. During her 2nd week she was started on vitamins (0.3 to 0.6 cc. ABDEC, Parke Davis).

#### *External Environment*

When first placed in the commercial incubator, the baby was kept at a temperature of 90° F. This was gradually lowered over a period of about a month to room temperature close to 70° F.

Humidity was kept relatively high, between 65% and 85%.

All bottles, nipples and the like were sterilized in boiling water. Sanitary disposable diapers were used. Disinfectant was employed liberally around the baby's quarters, an aerosol sterilizer was placed in the quarters and for the first several weeks attendants wore face masks.

From birth she was bathed in olive oil once or twice a day, and after the first month she was

bathed once a day in tepid water and mild soap.

After she was moved from her incubator, she was placed on display in a glass-fronted wooden cage. Later a permanent nursery was built for her.

About two months after birth, the baby was given the name "Col-o," in honor of the place of birth, Columbus, Ohio. Her appearance at the age of one year is shown in Pl. III, Fig. 7.

#### SUMMARY

On December 22, 1956, a pair of lowland gorillas, *Gorilla gorilla gorilla* (Savage & Wyman), gave birth to a healthy female baby in the Columbus Zoological Garden. It was the first recorded birth of a gorilla bred and born in captivity. The gestation period, as determined from the probable time of conception, was 257 to 259 days. At the time of the birth the male and female gorillas were, respectively, a little more than 10 and 7 years old.

The captivity history of the parents is presented, including housing and care, diet, growth changes, temperament, sexual behavior, pregnancy of the female and parturition.

The appearance, care, diet and development of the infant during its first six months are reported.

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1951. Gorilla census and study. J. Mamm., 32: 429-436.

## EXPLANATION OF THE PLATES

## PLATE I

- FIG. 1. Male lowland gorilla, "Baron," at the age of 10 years, on December 24, two days after the birth of Col-o. *Columbus Dispatch* photograph by Gene Wells.
- FIG. 2. Female lowland gorilla, "Christina," on December 22, 1956, two hours after the birth of her baby. Photograph by Stephen Kelley.

## PLATE II

- FIG. 3. Dorso-ventral position in coitus. Photograph by Phillip Amorose.

- FIG. 4. Ventro-ventral position in coitus. Photograph by Phillip Amorose.

## PLATE III

- FIG. 5. The infant gorilla, "Col-o," 15 minutes after birth. Photograph by Stephen Kelley.
- FIG. 6. Col-o at the age of 4 weeks. *Columbus Dispatch* photograph by Tom Richards.
- FIG. 7. Col-o at the age of 1 year. Photograph by Dr. N. Ebert.



FIG. 1

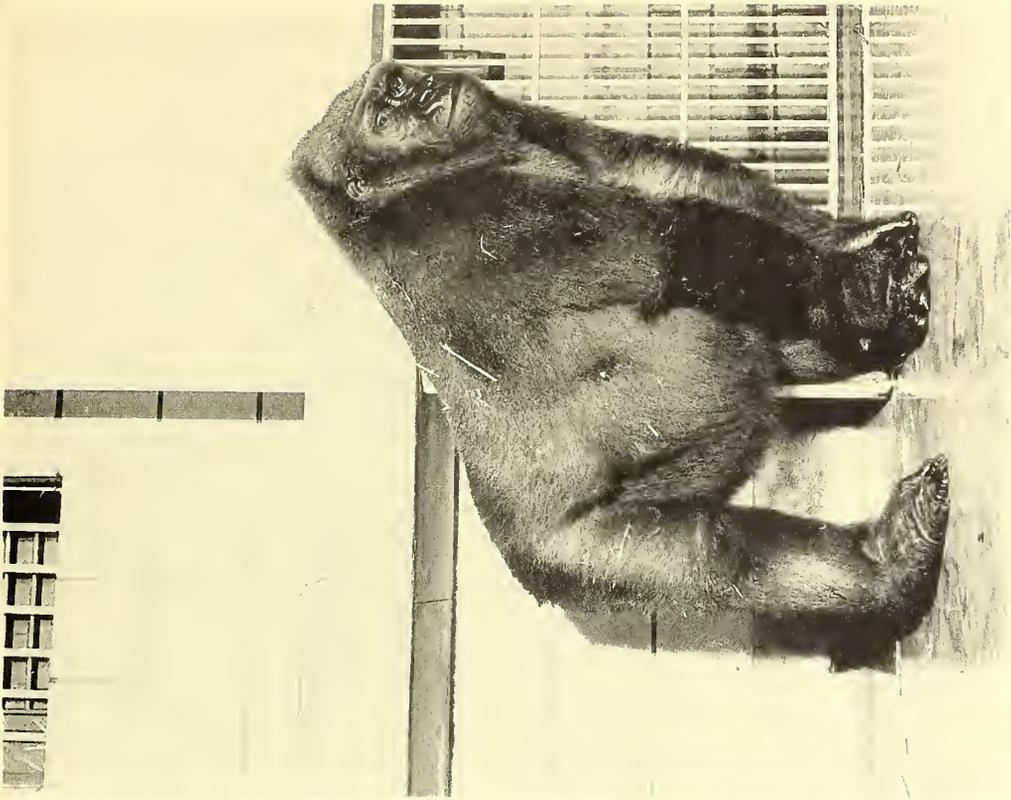


FIG. 2

OBSERVATIONS ON THE BREEDING IN CAPTIVITY  
OF A PAIR OF LOWLAND GORILLAS



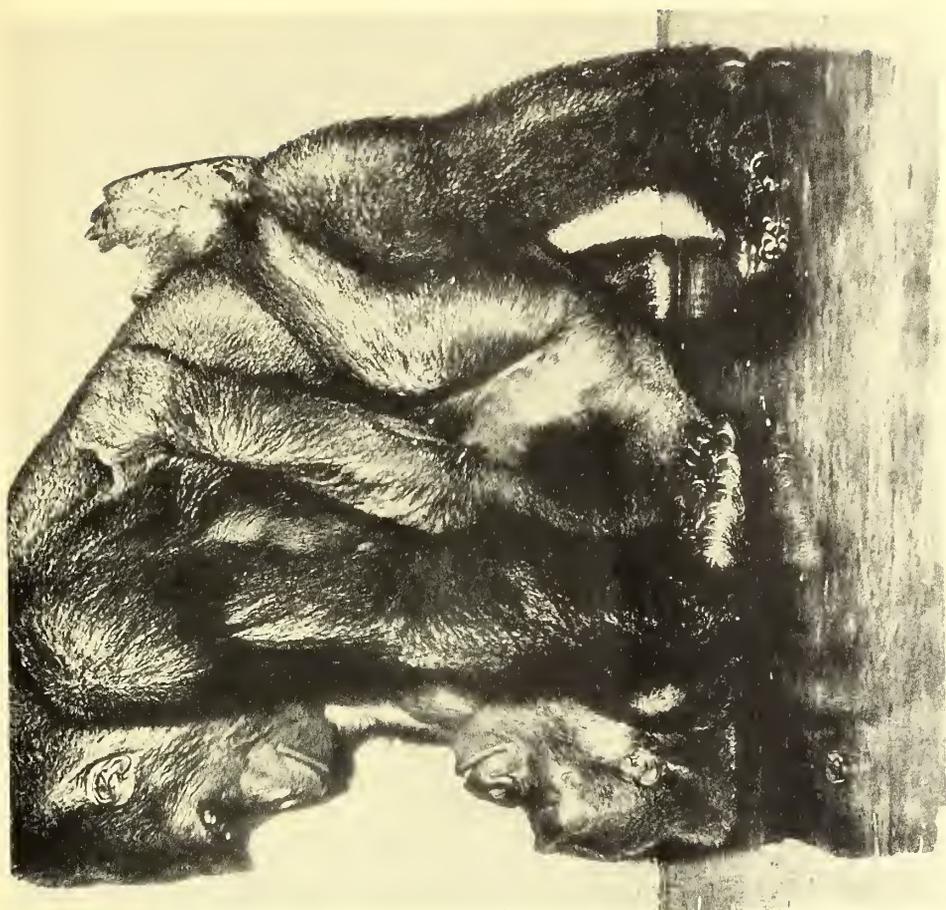


FIG. 4



FIG. 3

OBSERVATIONS ON THE BREEDING IN CAPTIVITY  
OF A PAIR OF LOWLAND GORILLAS





FIG. 5



FIG. 6

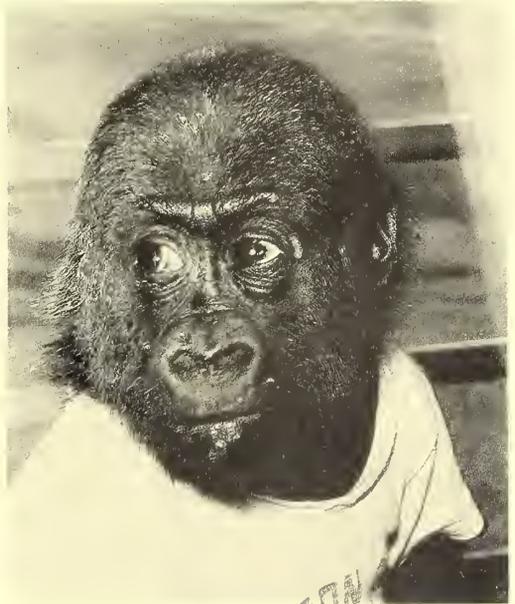


FIG. 7

OBSERVATIONS ON THE BREEDING IN CAPTIVITY  
OF A PAIR OF LOWLAND GORILLAS



The Morphology of *Renicola philippinensis*, n. sp.,  
a Digenetic Trematode from the Pheasant-tailed Jacana,  
*Hydrophasianus chirurgus* (Scopoli)

HORACE W. STUNKARD<sup>1</sup>, ROSS F. NIGRELLI<sup>2</sup> & CHARLES P. GANDAL<sup>3</sup>

(Plate I; Text-figures 1-3)

A SPECIMEN of the pheasant-tailed jacana, *Hydrophasianus chirurgus* (Scopoli), was acquired by the New York Zoological Park on October 31, 1956, and died on January 15, 1957. The native habitat of this virtually omnivorous species is southeast Asia and the present specimen was taken in the Philippine Islands, but it had been kept in California for about two months before coming to the Zoological Park. At autopsy, the kidneys contained about fifty sexually mature worms, clearly referable to the trematode genus *Renicola*. Insofar as known, no fish was given the bird during its stay in California, and at the Zoological Park it was fed on North American smelts that had been frozen for a long period, some for several months. It is likely that the bird acquired the infection in the Philippines before its capture and this supposition is strengthened by the facts that no juvenile or immature worms were present in the kidneys, no rhodometopous cercariae or metacercariae have so far been reported on either the Atlantic or the Pacific coast of North America and no other birds in the New York Zoological Park have been found infected with *Renicola*, although large numbers of smelt and other Atlantic fishes are used as food.

Another specimen of *H. chirurgus* received at the same time as this bird subsequently died but showed no trematode infection in the kidneys or elsewhere.

The diseased bird was emaciated and languid when first examined, but exhibited only mild anorexia. It was treated with prednisolone par-

enterally and aureomycin topically for a pea-sized, bumblefoot lesion on the ventral surface of the right foot. The left tarsus was somewhat swollen and was treated with an intra-articular injection of prednisolone. Two weeks later the lesion was healed but the symptoms remained the same and the bird died the day after the bandage was removed from the right foot, that is, 15 days following initial treatment.

Macroscopically and microscopically, the lesions had the general appearance of polycystic kidneys in which the cystic spaces (enlarged renal tubules) were filled with worms (Pl. I, Figs. 1, 4, 5). As in congenital polycystic kidneys which are seen in mammals and other animals, the cysts were lined with low columnar epithelium (Pl. I, Figs. 4, 5) that had been flattened by pressure from the worms. The tubules and glomerular tufts adjacent to the cysts were compressed and in some areas atrophied (Pl. I, Figs. 4, 5). Extensive regions of the kidneys, however, were normal in appearance and in this respect the pathological condition in the bird differs from typical polycystic kidneys, in which very little cortical tissue is present.

The worms, although hermaphroditic, occurred usually in pairs in the cysts. They were oriented indiscriminately, with about one-half of the body of each overlapping that of the other. All were sexually mature and their uteri were filled with enormous numbers of eggs. Since *Renicola* has not previously been reported from this host or from southeast Asia, a description of the worms is presented. They manifest distinct differences from all previously described species, and are described provisionally as a new species for which the name *Renicola philippinensis* is proposed.

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<sup>2</sup>Pathologist, New York Aquarium, New York.

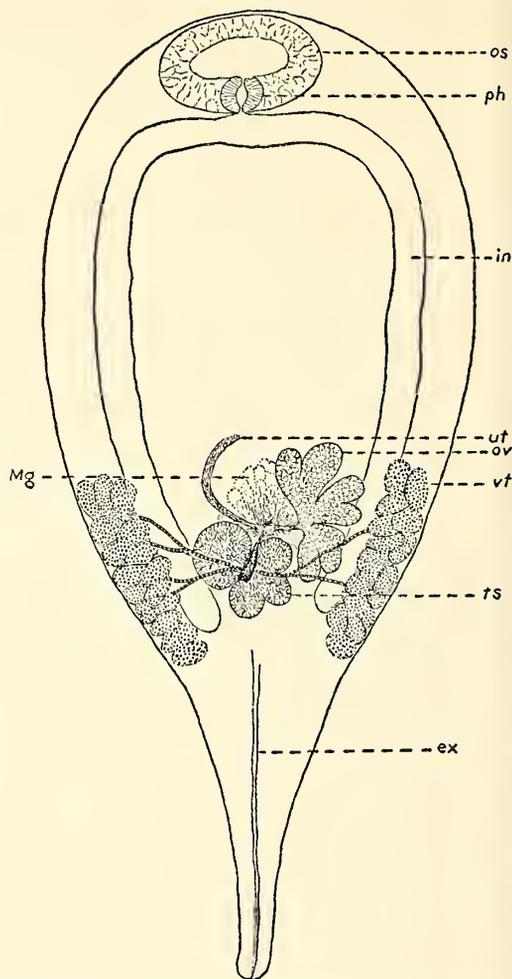
<sup>3</sup>Veterinarian, New York Zoological Park.

***Renicola philippinensis*, new species****DESCRIPTION**

The body is ovate to pyriform, rounded anteriorly and more or less attenuate posteriorly. The terminal portion may be extended as a narrowing tail-like structure. This region, which is posterior to the digestive ceca and the reproductive organs, may be retracted until it is a mere knob-like protuberance or extended to a length of 0.25 mm. An average and a somewhat extended specimen are presented in Pl. I, Fig. 2. The structural details, coils of the uterus omitted, of the longer worm are shown in Text-fig. 1. The specimens, all gravid, measured 1.7-3.6 mm. in length and 1.0-1.8 mm. in width. The cuticula (Pl. I, Fig. 5; Text-fig. 2) bears relatively slender, distinctly separated, sharp spines. The musculature of the body wall is very weak and movement of the worms was slow rather than vigorous. The acetabulum is shallow, 0.1-0.12 mm. in diameter, and is situated at the testicular level, directly below the vitelline receptacle, about 0.1 mm. posterior to the genital pore. The acetabulum and genital pore are rarely visible in whole mounts, as the enlarged terminal portion of the uterus, filled with dark-colored eggs, lies immediately above these structures and obscures them.

The mouth is subterminal, the oral sucker is usually wider than long and measures 0.4-0.5 mm. in diameter. It is shallow and weak and the tissue is vacuolated, without distinct radial fibers. There is no prepharynx; instead, the pharynx, which measures 0.08-0.11 mm. in diameter, appears to be embedded in the wall of the sucker, with the anterior opening of the pharynx at the base of the concavity of the sucker (Text-fig. 1). The pharynx is provided with radial and circular muscles. From the pharynx, the intestinal ceca follow the lateral contours of the body and terminate at a level between the posterior limits of the testes and vitellaria. The posterior portions of the ceca are compressed between the vitellaria and the gonads. The walls of the ceca are membranous and the epithelium is so flattened that in places it is hardly recognizable. The lumen contains a fibrous precipitate, obviously of a fluid, and no cell fragments were observed. It appears, therefore, that the worms take nourishment in liquid form, by sucking lymph or plasma from the tissues rather than by ingestion of cells.

The excretory pore is terminal, the vesicle is Y-shaped, the bifurcation is immediately post-testicular, at the base of the tail-like portion of the body. Both the stem and crura of the vesicle bear lateral evaginations, although those of the stem are indistinct when the posterior end of the

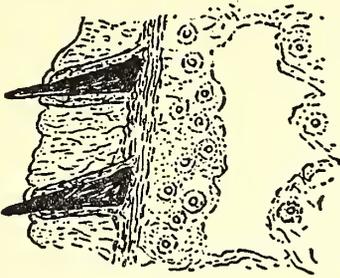


TEXT-FIG. 1. Morphological details of longer specimen shown in Pl. I, Fig. 2; uterus omitted, dorsal view. Specimen as mounted 2.46 mm. long.

**Abbreviations:** OS = oral sucker; PH = pharynx; IN = intestine; UT = initial portion of uterus; OV = ovary; VT = vitellaria; TS = testis; EX = excretory vesicle; MG = Mehlis's gland.

body is extended (Text-fig. 1). The flame-cell pattern was not studied.

The reproductive organs are compressed into a small region near the posterior end of the body (Text-fig. 1). The testes are opposite to oblique, usually contiguous or overlapping, just anterior to the caudal portion of the body. They are spherical to oval to reniform, entire, indented or lobed, 0.2-0.5 mm. in diameter; in the specimen shown in Text-fig. 1 the left testis is entire, almost spherical, whereas the other is distinctly trilobed. Sperm ducts lead mediad and ventrad, uniting to form a small seminal vesicle from



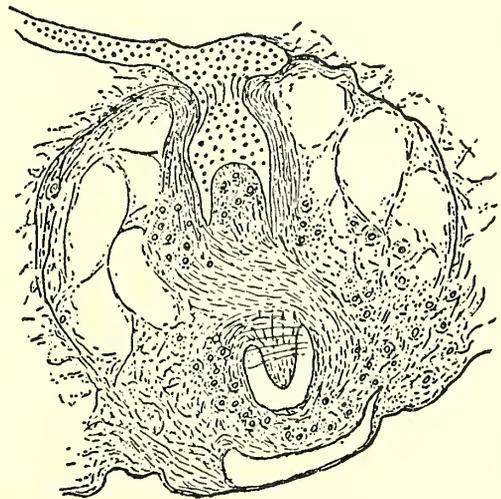
TEXT-FIG. 2. Section of body-wall, showing spines embedded in thick cuticula, and weak musculature; cf. Pl. I, Fig. 5.

which a short duct leads ventrad and opens as a small papilla into a shallow genital atrium (Text-fig. 3). There is no true cirrus-sac, but the initial portion of the ejaculatory duct is enclosed by a few secretory cells and the duct with its surrounding parenchyma is bounded by a membranous covering (Text-fig. 3). The ovary is trilobate, with each lobe more or less divided; it is located on the right side of the body, slightly anterior to but overlapping the testicular zone. It is larger than either testis and measures 0.3-0.5 mm. in greatest dimension. The oviduct arises from the medial face and bears a small evagination, the seminal receptacle, filled with spermatozoa; it then receives the short, common vitelline duct, and expands to form the ootype, surrounded by the cells of Mehlis's gland. The initial bend of the uterus, with colorless eggs, passes forward and mediad as shown in Text-fig. 1. The uterus extends in loops and coils, chiefly on the ovarian side of the body, from the vitelline follicles to the anterior end, courses around the oral sucker and posteriad to the vitellaria of the antovarian side; it then forms a conspicuous mass of coils and the distended terminal end of the uterus discharges through a very short metratermal portion into the genital atrium. The metraterm is only three or four times the length of an egg. The genital pore is ventral to Mehlis's gland. As the eggs traverse the uterine coils, the shells become darker in color. All portions of the uterus, with the exception of the black, terminal, median portion, are pretesticular. The vitelline follicles are oval to clavate, 0.06-0.13 mm. in length; they are lateral and extend forward almost to the level of the anterior lobe of the ovary and backward slightly beyond the ends of the intestinal ceca. Multiple ducts pass mediad, those from either side joining above the testes to form a vitelline receptacle from which the common duct leads anterior and ventrad to join the oviduct at the beginning of the ootype. The eggs (Pl. I, Fig. 3), produced in enormous numbers, are operculate,

embryonated, and measure 0.025-0.027 by 0.012-0.014 mm.

#### DISCUSSION

*Specific Identity.*—The number of valid species in the genus *Renicola* is problematical. Dollfus (1946) listed nine species but noted, "Chacune de ces espèces, sauf *lari*, n'a été vue qu'une seule fois, quelques-unes seulement en un ou deux exemplaires, aussi n'ont-elles pas pu être toutes suffisamment bien caractérisées, décrites et figurées." He found only slight differences between *Renicola glandiloba* Witenberg, 1929, *Renicola lari* Timon-David, 1933, and the type species, *Renicola pinguis* (Mehlis in Creplin, 1846). The specimens of Mehlis were from the crested grebe, *Colymbus (Podiceps) cristatus*, and the species was named type of the new genus *Renicola* by Cohn (1904), who found the acetabulum and removed the species from the then accepted genus *Monostomum*. In this paper Cohn made the significant observation that trematodes from closed cavities have reduced and atrophied suckers and that monostomes may be derived from distomes. In addition to the nine previously named species, Dollfus described but did not name specimens from *Mergulus (Plotus) alle* killed at Wimereux, Pas de Calais. Although Dollfus recognized *Stamparia* Neslobinsky, 1926, as a valid genus, Caballero y Caballero (1953) suppressed the name as a synonym of *Renicola* and from the present study it is clear that the grounds on which Dollfus accepted *Stamparia*, viz., the shape and location of the testes, are much too variable to warrant generic recogni-



TEXT-FIG. 3. Section through the genital atrium showing, above, the union of the sperm-ducts and below, the male papilla.

tion. A key to the species of *Renicola* was prepared by Dollfus, based largely on the extent and location of the vitellaria. This feature is a conspicuous one and undoubtedly significant; it appears that the extension of the uterus into the caudal region of the body is also an important and distinguishing specific feature. Callot (1946) reported but did not name specimens of *Renicola* from *Sterna cantiaea*, "provenant des côtes de la Manche." He stated that the specimens did not correspond to any of the species described by Dollfus (1946).

A number of species in the genus *Renicola* have been described since 1946. Sudarikov (1947) described *Renicola pandioni* and *Renicola undecima*, both from *Pandion haliaetus* in the Gorkovsk Province of Russia. Bykhovskaya-Pavlovskaya (1950) described *Renicola mediovitellata* from the ducks, *Anas strepera*, *Nyroca ferina* and *Spatula clypeata* in Siberia, and *Renicola magnicaudata* from the barn swallow, *Hirundo rustica*, also in Siberia. From *Branta canadensis* McIntosh & Farr (1952) described *Renicola brantae*, a species in which the arrangement of the vitelline follicles is the same as in *R. mediovitellata*, one of whose hosts, *Spatula clypeata* is common in America. Timon-David (1952) described *Renicola bretensis* from the magpie, *Pica pica*, on the Mediterranean coast. Bykhovskaya-Pavlovskaya (1952) described *Renicola nana* from *Tringa totanus* in Siberia. Caballero y Caballero (1953) announced the identity of *R. lari* Timon-David, 1933, and *R. glandiloba* Witenberg, 1929. He described specimens from *Pelecanus occidentalis* as a new species, *Renicola thapari*. Wright (1954a) described *Renicola cruzi* from *Sterna maxima* and *Sterna hirundacea* in Brazil. He also listed but did not describe three additional species from Brazilian birds. One of them, from the white-bellied gannet, *Sula leucogaster*, is presumably identical with *Renicola mirandaribeiroi*, described from the same host by Teixeira de Freitas (1955). In a second paper, Wright (1954b) described specimens of *Renicola* from birds in British zoological gardens. Two new species were named: *Renicola pelecani* from *Pelecanus phillipensis* of Ceylon and *Pelecanus onocrotalus* of Calcutta, and *Renicola sloanei* from two penguins, *Pygoscelis antarctica* and *Eudyptes chrysolophus*, and from the common guillemot, *Uria aalge*, taken in Sussex, England. Three additional species were described briefly, but not named; also the species reported but not named by Hamerton (1934) was described from the original specimens. More recently, Wright (1957) reported two kidney-flukes from Sudanese birds. One of the worms was found in a cyst

in the kidney of the Goliath Heron (*Ardea goliath*) and was described as a new species, *Renicola goliath*. The bird had been shot at least 1,000 miles from the sea coast, and for this and other reasons, Wright speculated on the possibility that some members of the genus *Renicola* may pass their life cycle in fresh water.

Wright (1956) reported on the life history and ecology of species in the genus *Renicola*. He discussed the morphological criteria on which species have been distinguished and the value of these criteria. He found that variation among specimens from a single host was so great that it could be explained only on the basis of multiple infections or the failure of previous workers to realize the extent of variation that may occur within a single species. A study of records of hosts and parasites convinced him that "host-specificity in the sense of a group relationship does not apply in this genus." Supplementing the accounts of earlier authors, he described the histo-pathological details of the infected kidney. He found cellular debris and excretory material from the birds in the ceca of the worms.

It is clear that existing descriptions have assumed a morphological rigidity that does not exist, but until experimental studies have measured the variation that may occur in a single, natural species, it is impossible to determine with assurance which of the presently described species are valid and which should be rejected. Because of the incomplete and unsatisfactory nature of many specific descriptions, it is impracticable to attempt a detailed comparison of the present specimens with previously described ones, but the present specimens do not correspond to existing descriptions in one or more of the following characters: extent and location of vitellaria, extent of uterus, location of acetabulum and gonads, total size and size of organs, especially the suckers, which are not influenced by the state or degree of reproductive activity.

*Life History.*—Stunkard (1932) described the excretory vesicle and flame-cell pattern of *Cercaria rhodometopa* Pérez, 1924, a parasite of *Turritella communis* at Roscoff, France. He predicted that "the excretory system is apparently well developed and probably has already attained the definitive form which will persist through all succeeding stages in the life-cycle of the species. The system is so peculiar and characteristic that it will afford a quick and certain criterion for the identification of later stages in the life-history, and may, indeed, lead to the correlation of this larva with an adult trematode having the same excretory pattern." Miriam Rothschild (1935) described four additional species of rhodometopous cercariae: *C. pythio-*

*nike*, *C. herpsyllis*, *C. doricha* and *C. nicarete* from *T. communis* at Plymouth, England, and two additional ones, *C. ampelis* and *C. ranzii*, from the same host-species at Naples, Italy. Behavior as well as morphology was recorded by Miss Rothschild. All infection attempts failed, and wide search for the metacercariae proved fruitless although Miss Rothschild correctly surmised that the second intermediate host is a fish. Rothschild & Sproston (1941) found encysted metacercariae in *Gadus luscus* and *Gadus merlangus* which agreed morphologically with the rhodometopous cercaria that Miss Rothschild had described as *C. doricha*. They reported earlier attempts to induce these larvae to penetrate *Gadus merlangus* and suggested that the infection of the fish results from ingestion of the cercariae. They stated, "The search for the final host should now be considerably narrowed as there are relatively few fish which both consistently prey upon *G. merlangus* and *G. luscus* and are common over the Rame Mud. . . . The fact that the intermediate host is found at a depth of 20 fathoms or more, and is yet commonly infected with *Rhodometopa* cercariae makes it exceedingly unlikely that the final host is a bird." Yamaguti (1939) described and figured *Renicola umigarasu* and *Renicola keimahuri*. Stunkard (1946) called attention to the virtual identity of structure between the excretory vesicle of these species and that of *Cercaria rhodometopa* Pérez, 1924. Referring to his earlier description and prediction, he declared that there is strong presumptive evidence that *C. rhodometopa* is the larva of a species of *Renicola*. Wright (1953) reported that the excretory vesicle of young specimens of *Renicola* which Campbell and Sloane had found in penguins hatched in the Edinburgh zoo, and which he subsequently described as *Renicola sloanei*, was similar to that of the *Rhodometopa* Group of cercariae described by Rothschild (1935). Shortly after Wright's publication, Timon-David (1953) reported metacercariae from the pyloric ceca, the intestinal wall and mesenteries of sardines in the Mediterranean; these parasites being similar morphologically to the rhodometopous cercariae, particularly in the excretory system. He stated, "Les affinités de cette métacercaire avec le groupe *rhodometopa* s'imposent, mais il est plus difficile de préciser à quelle forme elle correspond . . . C'est peut-être avec la forme type *C. rhodometopa* Pérez que la métacercaire de la Sardine présente les affinités plus accusées." Wright (1956) noted that the only common feature of the species which serve as final hosts of *Renicola* is their fish-eating habit.

The morphological agreement between the

rhodometopous cercariae and the metacercariae from fishes, and of the excretory pattern of these larvae with that of members of the genus *Renicola*, provided clear evidence of genetic relationship. Only experimental confirmation of the life cycle and specific identification of the larvae and adults remained. In the examination of 1,400 specimens of *Turritella communis*, Wright (1956) found natural infections with three of the species described by Rothschild (1935), viz., *C. doricha*, *C. pythionike* and *C. nicarete*; also two additional species which he described as new, *C. doricha-pigmentata* and *C. cooki*. The first of these species, *C. doricha*, was associated by Rothschild & Sproston (1941) with the metacercariae found in *Gadus luscus* although they acknowledged that "Without experimental proof, however, it is difficult to assign metacercariae with certainty to any of the closely related species." Wright (1956) found that the eggs of *Renicola* spp. will not hatch in fresh, brackish or sea water but do hatch in the intestine of *T. communis*. He described the miracidia as pyriform, tapering anteriorly, with long cilia restricted to a collar or band situated about midway along the tapering anterior end. No eye-spots are present but two large cells of somewhat irregular outline are located just behind the anterior end. The eggs were ingested by snails, and specimens dissected 24 to 72 hours after exposure to the eggs had lesions on the outside of the intestinal wall, each of which consisted of a surrounding membrane and a number of cells, some of which stained intra-vitally with neutral red. It was suggested that these structures may have been early mother sporocysts. Other attempts were made to infect the molluscan host. Since it is impossible to raise *T. communis* from eggs past the veliger stage, the snails to be used for experiments were isolated for periods of two and one-half to four and one-half months. Wright (1956) named the birds from which the eggs of the parasite were obtained, but the species of *Renicola* were not identified. In the first experiment, 42 snails that had been isolated in the laboratory for four and one-half months were exposed overnight to eggs of *Renicola* sp. from *Colymbus arcticus*. The snails were dissected at intervals and one dissected at the end of three and one-half months contained very immature sporocysts in the gonad. In a second experiment, 69 snails, tested previously for a period of four months, were exposed to eggs of *Renicola* sp. from *Puffinus puffinus*. Sample snails were dissected over a period of three months but no infection was found. In a third experiment, 60 snails that had been tested for two and one-half months were exposed to eggs of the parasite from *P. puffi-*

*mus*. Dissection during three and one-half months failed to disclose infection, but four female specimens out of eight alive at the end of six months contained sporocysts, more advanced than those found in the first infection. No naturally emerged cercariae were obtained, but it is well known that many snails are not properly nourished under laboratory conditions and that the development of trematode parasites is delayed or suspended when the host is deprived of essential nourishment or kept under deleterious conditions. Apparently no attempt was made to infect fishes, although metacercariae of natural infections were compared with the bodies of cercariae and with juvenile worms from the intestine of naturally infected birds. Attempts to infect avian hosts were limited to the feeding of large numbers of metacercariae to a chick, a duckling and a gull, all of which were fruitless. However, the laboratory infection of the molluscan host is a distinct contribution to knowledge of the renicolid trematodes and together with other corroborative evidence demonstrates that the rhodometopous cercariae are indeed the larval stages of these trematodes and that fishes serve as intermediate hosts. Information is yet too uncertain to permit precise specific correlation of larval with adult stages.

#### SUMMARY

Trematodes from cyst-like enlargements of the renal tubules of the pheasant-tailed jacana, *Hydrophasianus chirurgus* (Scopoli), are described provisionally as a new species, *Renicola philippinensis*. This is the first record of a *Renicola* from southeast Asia. Specific identity and life history in the genus *Renicola* are considered.

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## EXPLANATION OF THE PLATE

## PLATE I

- FIG. 1. Photograph of kidneys of *H. chirurgus*, showing cystic enlargements.
- FIG. 2. Two specimens of *R. philippinensis*. The morphology of the longer one is shown in Text-fig. 1.
- FIG. 3. Eggs of *R. philippinensis*.
- FIG. 4. Section of renal tubule, showing the two worms in the dilated portion.
- FIG. 5. Portion of the area depicted in Fig. 4, higher magnification, to show body-wall and spines of the parasite, and the intact epithelium of the renal tubule.

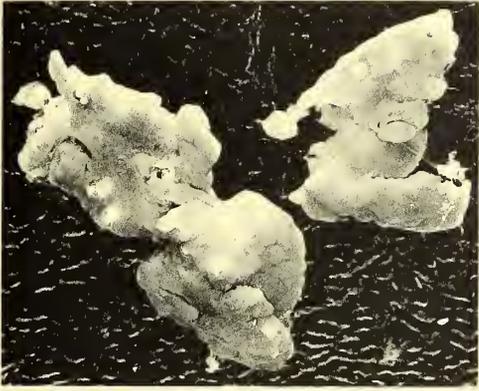


FIG. 1

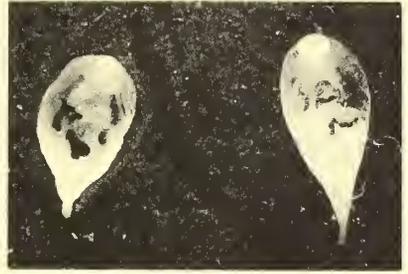


FIG. 2



FIG. 3

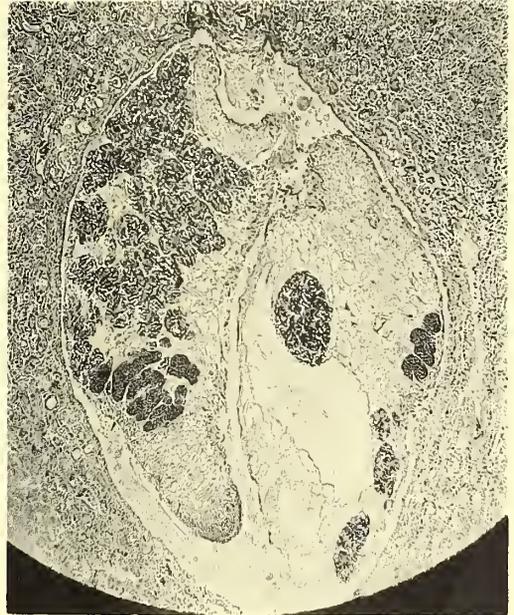


FIG. 4

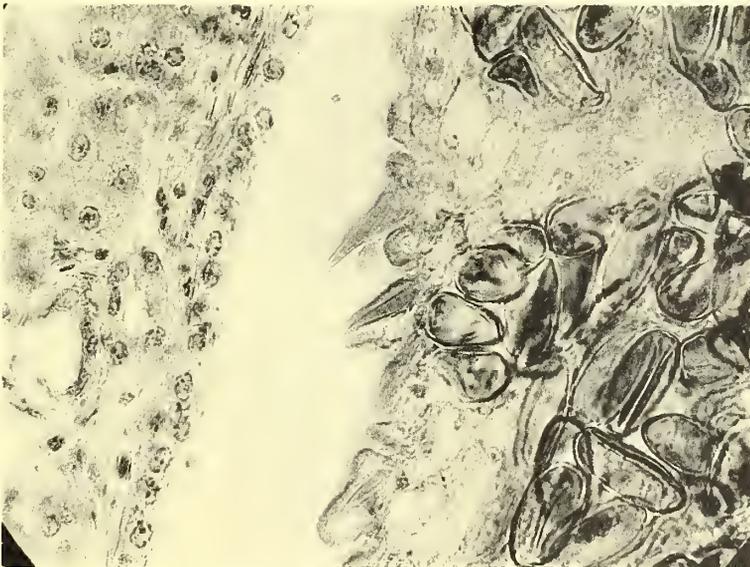
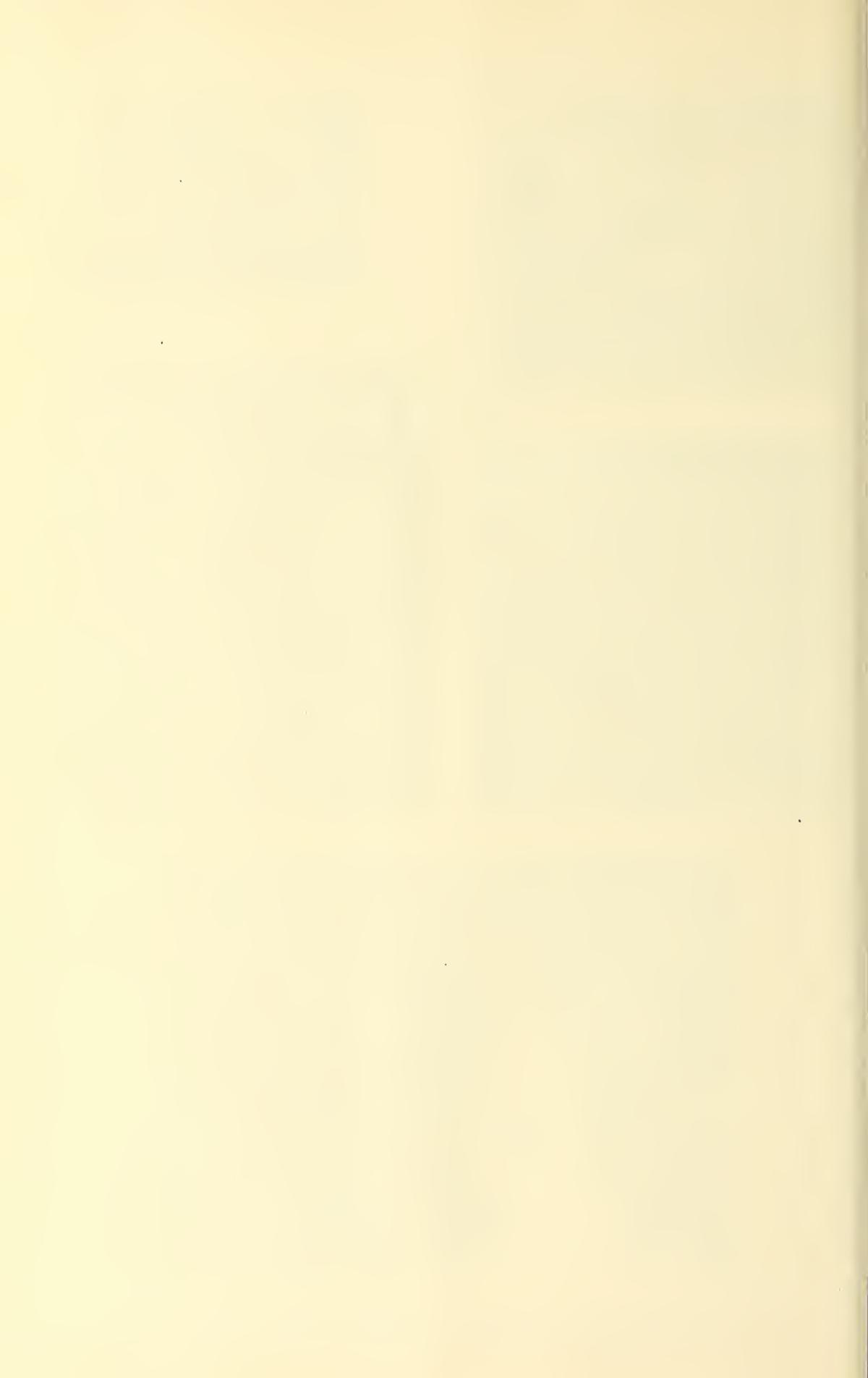


FIG. 5

THE MORPHOLOGY OF *RENICOLA PHILIPPINENSIS* N. SP., A DIGENETIC TREMATODE FROM THE PHEASANT-TAILED JACANA, *HYDROPHASIANUS CHIRURGUS* (SCOPOLI)



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# Aspects of Social Behavior in Fiddler Crabs, with Special Reference to *Uca maracoani* (Latreille)<sup>1, 2</sup>

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(Plate I; Text-figures 1-5)

[This paper is one of a series emanating from the tropical Field Station of the New York Zoological Society at Simla, Arima Valley, Trinidad, British West Indies. The Station was founded in 1950 by the Zoological Society's Department of Tropical Research, under the direction of Dr. William Beebe. It comprises 200 acres in the middle of the Northern Range, which includes large stretches of undisturbed government forest reserves. The laboratory of the Station is intended for research in tropical ecology and in animal behavior. The altitude of the research area is 500 to 1,800 feet, with an annual rainfall of more than 100 inches.

[For further ecological details of meteorology and biotic zones see "Introduction to the Ecology of the Arima Valley, Trinidad, B. W. I.," William Beebe. (Zoologica, 1952, Vol. 37, No. 13, pp. 157-184.)]

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## I. INTRODUCTION

**T**HIS paper is a preliminary report on recent studies of social behavior in tropical fiddler crabs, conducted both in the field and in captivity. It is concerned with activity rhythms determined principally by light and tide, with changing phases of behavior under internal control, and with expressions of agonistic and

epigamic behavior. All of these topics will be more fully developed in a monograph on the genus *Uca*, now in preparation.

A general account of the field work undertaken in the present study has been given in a recent paper (Crane, 1957), in which it is stated that observations and motion picture records on the behavior of many species were made in Southeast Asia, the South Pacific and the neotropics. Since then a summer has been spent on the east and west coasts of Africa.

Throughout the previous seasons of the work the need for supplementary observations on captive crabs was felt with increasing force. Because so much territory had to be covered, stays in one locality of more than a week were infrequent. More leisurely study periods, ranging from ten days to two months in length, were accomplished in Panama, Tahiti, Fiji, Singapore, Zanzibar and Angola, but even during these periods certain observations were necessarily meager. Everywhere the deficiencies were felt particularly in data concerning behavior sequences in individual crabs and in those concerning territoriality.

Accordingly, during the winter and spring of 1958 a group of four local species of *Uca* was established in captivity in Trinidad. The species selected were *maracoani*, *thayeri*, *rapax* and *cumulanta* (Table I). All four live sympatrically on mudflats that are surrounded by mangroves and adjacent to the open waters of the Gulf of Paria. The locality, known as Cocorite Swamp, lies in the suburbs of Port-of-Spain.

The data reported in the present paper are altogether observational. Experimental studies, paralleling those of Brown and his co-workers (1954, and refs.) on the diurnal, tidal and semi-

<sup>1</sup>This study has been aided by a grant from the National Science Foundation.

<sup>2</sup>Contribution No. 989, Department of Tropical Research, New York Zoological Society.

TABLE 1. SPECIES, AUTHORITIES, REFERENCES AND RANGES OF *Uca* MENTIONED IN THIS CONTRIBUTION

Species	Taxonomic Reference and Comment	Range
<i>annulipes</i> (Latreille)	Barnard, 1950, p. 97	East Africa to Philippines
<i>chlorophthalmus</i> (Milne-Edwards)	The African form, as characterized by Barnard, 1950, p. 95	East Africa
<i>cumulanta</i> Cranc	Crane, 1943, p. 42	Tropical Western Atlantic
<i>latimanus</i> (Rathbun)	Rathbun, 1918, p. 422	Tropical Eastern Pacific
<i>maracoani</i> (Latreille)	Rathbun, 1918, p. 378	Tropical Western Atlantic
<i>marionis</i> (Desmarest)	Barnard, 1950, p. 90	East Africa to Samoa
<i>pugilator</i> (Bosc)	Rathbun, 1918, p. 400	Eastern & Southern United States
<i>pugnax</i> (Smith)	Rathbun, 1918, p. 395	Eastern United States south to Northern Florida
<i>rapax</i> (Smith)	Tashian, 1958, p. 89 Syn.: <i>pugnax rapax</i> Rathbun, 1900, p. 7; 1918, p. 397	Western Atlantic: North Florida to Brazil
<i>stenodactylus</i> (Milne-Edwards & Lucas)	Rathbun, 1918, p. 416	Tropical Eastern Pacific
<i>thayeri</i> Rathbun	Rathbun, 1918, p. 406	Western Atlantic: North Florida to Brazil
<i>urvillei</i> (Milne-Edwards)	The African form, as characterized by Barnard, 1950, p. 93	East Africa

lunar influences on chromatophore expansion and oxygen consumption, have not yet been undertaken.

Particular thanks are due to my co-workers, Dr. William Beebe, Mr. Henry Fleming and Dr. D. W. Snow, as well as to Mr. M. Woodbridge Williams of the National Geographic Society, for advice and cooperation in the inauguration and operation of the outdoor terrarium at the Trinidad Field Station of the New York Zoological Society.

## II. MATERIAL AND METHODS (Plate I)

The method of maintaining the crabs far from the sea at the laboratory's altitude of 800 feet proved to be surprisingly simple. A cement-lined lily pond, measuring 5½ by 14 feet in area and 16 inches in depth, was emptied of all plants and drained. Tubfuls of mud from the crabs' native swamp were heaped across one end of the pool which, in one corner, was adjacent to a small, fresh-water marsh. The latter, established for the original lily pond, was maintained for the crab terrarium in order better to conserve moisture in the marine mud during the dry weather. The mud was fashioned into a gently sloping bank measuring about 40 square feet in area and having a maximum depth of 11 inches. Narrow strips of window glass were thrust into the mud against the cement walls of the pool, framing it on three

sides to provide a surface which could not be scaled by the crabs. Since the fiddlers, once they had settled in, never wandered along the bottom more than a few inches, it was unnecessary to line the sides completely.

A "tide" was found to be essential in order to induce a level and variety of social activity adequate for the work. However, an exceedingly rough approximation of natural tidal conditions proved adequate for the present purpose. Briefly, it was sufficient merely to fill and empty the pond with a garden hose on an approximately 25-hour schedule that resembled the daylight tidal schedule in Cocorite, the local swamp.

In practice the system worked as follows: The artificial mudbank was always completely exposed at the hour of local daylight low tide, as well as, variously and irregularly, for one to three hours both before and after that time. No attempt was made to drain or fill the pool in accordance with the natural tidal rate, since this factor was found not to affect noticeably the crabs' activities. Filling of the pool required between two and one-half and three hours and drainage about forty minutes.

In the first two weeks of the work spring and neap tides were roughly simulated on the appropriate dates, but this too proved to be a refinement unnecessary for the present study. Although the height of high tide was made slightly

and irregularly to vary, a small area at the top of the bank was always left exposed.

After the first few days no attempt was made to shift the tides twice daily; only the daytime low tide was represented. Every two weeks, however, as low tide coincided roughly with dawn and dusk, the water level was either kept low for some eighteen hours (as from 3 P.M. to 9 A.M.), or else two natural 12-hour-plus tides were provided for that particular 25-hour period; this arrangement made the shift from a late afternoon to an early morning "low." No attempt was made to make the shift at a particular corresponding tide fortnightly; it was simply done as convenient when the local tide occurred between five and eight o'clock. This shift was purposely made differently, at different hours, from fortnight to fortnight, to avoid establishing any artificial rhythms; no trace of such a result was evident, and the behavior of the captive crabs remained in harmony with that of the source populations in the mangrove swamp. Field trips were made to that area for comparative observation at frequent intervals throughout the four and one-half months of the observations.

Fresh water piped from mountain springs, used for all purposes at the Station, was provided for the pool. A sample, as tested by the Government Chemist's Department of Trinidad, contained 0.288 parts per thousand of dissolved salts. This was in contrast to 34.5 parts per thousand of dissolved salts at high tide, during the dry season, of the Gulf of Paria at the point where the water was flooding into Cocorite Swamp. At the height of the rainy season water from crab holes and an adjacent ditch, at low tide, proved almost as salty—33.7 and 33.8 parts per thousand, respectively. Swamp water tested earlier (Crane, 1943) in a Venezuelan habitat of the same species gave much lower salinities, ranging from about 5 to 7 parts per thousand during the rainy season. None of these species, however, was ever found in fresh water.

Their ready adaptation to tap-water tides in the crabbery was explained when water from these burrows was analyzed. Although the mud had been unchanged for several weeks before each analysis, and was subjected to gentle flooding daily, samples taken in March, April, May and June contained respectively 7.73, 8.36, 13.2 and 8.15 parts per thousand of dissolved salts. All these figures, judging by the previous Venezuelan analyses, are within the normal toleration of the species. Since only pure mud from the native swamp was used in the crabbery, it was originally strongly impregnated with salts and held them well; the drainage was in fact so poor that water remained standing in the lower parts

of the burrows even on hot and dry days when the pool had been otherwise drained for an entire tidal period.

In spite of this poor drainage, the mud never gave off any odor of decay. Most of the few crabs that died did so on top of the flat. No food material was ever added to the mud, and the crabs fed normally by sifting organic matter from it. Aside from the daily draining and filling of the pool, the only maintenance performed was the addition, once every three or four weeks, of a fresh layer of mud from Cocorite Swamp. Although the material was always spread very roughly over the existing bank, which had become lowered by erosion, within a day the crabs and the changing water levels removed all traces of disturbance.

Marine toads (*Bufo marinus*) proved to be the only nuisance, since they came in crowds to the pool at night. The extreme top of the bank was always exposed, and they did minor damage by knocking over burrow markers, leaving slime and eggs and, probably, eating occasional small crabs whose disappearance was otherwise unexplained. A foot-high fence of copper netting, soon erected, kept the toads out.

Garden plant flags, made of magnesium and marked with waterproof ink, identified burrows for territorial studies. Individual crabs were painted for recognition with spots of quick-drying lacquer in various colors and positions. Marks on the anterior part of the carapace and outer edge of the major cheliped were best for both visibility and durability. Providing the paint was not applied to pilous or tuberculous areas, the marks remained distinct for about a month.

Observations were conducted principally from an eight-foot-high platform standing near the pool. A 20-power monocular enabled even minor mouthpart motions to be seen. From this position the crabs were undisturbed by the observer's movements, and the entire mudbank could be easily overlooked.

It was found that the optimum population level was not more than about 5 to 7 males and a similar number of females of *U. maracoani*, the largest species. A total of 35 crabs of all species was never exceeded at any one time.

The success of the terrarium for these species is attested by the following facts: two *maracoani* survived healthily the entire period of observation, which comprised more than four and one-half months; fifteen of three species were kept between one and three months. The only losses were as follows: senility or disease (six), accidental poisoning by the addition of unseasoned lime blocks, escape of small crabs up the glass which had been coated with mud by splashing

during heavy rains and, apparently, predation by marine toads. Other specimens were killed after various periods for drawing and dissection. All species displayed and courted, all except *cumulanta* were seen to mate from one to four times; several immature *maracoani* females molted to the adult stage; and, finally, at least five *thayeri* females and one *maracoani* laid eggs.

Throughout the study the behavior of the original populations in Cocorite Swamp was checked at least once every ten days for comparison with the activity level in the terrarium.

Henceforth the term "crabbery" will be used for the converted lily pond described above.

### III. TIDAL AND SEMILUNAR RHYTHMS IN ACTIVITY

The activity levels of fiddler crabs are influenced by the following major factors of the external environment: light, tide, temperature, surface moisture and rain. The general conditions for high activity in populations are known to any observer who has repeatedly watched these crustaceans. As a whole the crabs are most active during several hours before and after low tide on warm, sunny days; the optimum time of day, other factors being favorable, is often the mid-morning. As with many intertidal animals, spring tides are especially favorable to species living close to either low- or high-tide levels. With one or two exceptions the crabs are diurnal. Conversely, adverse conditions include darkness, submersion of the habitat by the tide, temperatures unfavorable to the species, extreme drying of the habitat and heavy showers. If one external factor becomes strongly unfavorable, all activity in a population is suppressed, the crabs retiring underground and remaining there for any required period, from minutes to a season, until conditions improve.

Laboratory investigations have shown that some of the chromatophores in *Uca pugnax* and *pugilator* expand in accordance with at least two of the aforementioned external factors favorable to activity—daylight and the hours of low tide. Under ordinary conditions, these *Uca* are typically darker by day and paler by night, showing a distinct 24-hour rhythm (Welsh, 1938; Brown & Webb, 1948; Webb, 1950; Brown & Stephens, 1951; Brown & Hines, 1952). Superimposed on this daily rhythm is a tidal rhythm which effects a secondary daily expansion of the chromatophores at the time of low tide. In normal tidal cycles, therefore, this secondary expansion occurs on the average some forty-nine minutes later every day. Accordingly the two superimposed chromatophoric schedules come into synchrony every fortnight, resulting in a

semilunar rhythm (Brown, Fingerman, Sandeen & Webb, 1953; Brown, 1954; Brown, Webb, Bennett & Sandeen, 1954; Fingerman, 1956). The rate of oxygen consumption shows similar diurnal and tidal rhythms (Brown, Bennett & Webb, 1953). The various rhythms have been shown to persist in the laboratory over considerable periods, and are independent of a wide range of temperatures. They appear to be established originally by local conditions of light and tide, probably early in the life of the young crab.

Recent studies reveal additional complexities. Fingerman (1957) found that the tidal rhythm in *pugilator* varies with the height of the burrows above low water; chromatophores in crabs from the higher levels expand earlier, apparently in accordance with their earlier uncovering by the tide.

*Tidal Rhythms.*—The work in the Trinidad crabbery showed that behavior in fiddlers, and particularly their social behavior, is also influenced by light and tide. If the induced daytime tide did not correspond roughly with the natural hours of ebbing and flowing at Cocorite, the native habitat of the captive crabs, feeding activity was much reduced and social behavior almost or wholly absent. If the water level in the crabbery was kept constant, at any level, evidence of the crabs' original activity rhythm was clearly apparent: although activity was far below normal, the crabs emerged from their burrows, fed and, for several days, waved and fought almost entirely during the normal periods of maximum activity at Cocorite.

In spite of the unnatural and irregular 25-hour rhythm under which the crabs were eventually maintained for more than four months, and the abnormal rapidity of the raising and lowering of the tides, traces of this natural rhythm were shown by the oldest inhabitants of the crabbery to the end of the period of observation.

Since the purpose of the crabbery was merely to supplement field observations on social behavior, no attempt was made to condition the crabs to a different tidal rhythm. It is hoped that this preliminary study will lead to experimental inquiries conducted under appropriately controlled conditions.

*Semilunar Rhythms.*—A related result of the crabbery work was the observation that a semilunar rhythm also exists in the social behavior of *Uca* and is also governed by a time-clock that is largely independent of external conditions. The factors responsible for this rhythm seem unquestionably to be a particular combination of time of day with time of low tide. That is, there is evidence of a fortnightly rhythm in social behavior corresponding to that found in the be-

havior of the crabs' chromatophores. It appears also to be similar to some of the semilunar rhythms concerned in the breeding and other behavior of numerous marine animals (Korringa, 1947, and refs.).

Field observations in the Indo-Pacific area during the past several years suggested that the highest levels of social activity in fiddler crabs, particularly in more primitive species, appear fortnightly and that the periods of maximum activity occur at different times of the day, depending on the species. In general the primitive crabs become active earlier in the morning than more advanced forms, and hence would be optimally suited by an earlier hour by low tide.

As a notable example three species may be cited which live contiguously on the Island of Pemba, East Africa. The primitive narrow-front, *urvillei*, reached the height of its display period by 8:30 A.M. and its waving practically ceased by 10 A.M., regardless of the favorableness of the tide. In contrast the moderately advanced species, *annulipes*, although its burrows, being higher on the shore, were uncovered earlier than those of *urvillei*, did not display fully until around 10 o'clock. Display then continued even during the heat of the day, at temperatures which often temporarily inhibit waving in other species, and stopped only in the late afternoon when the tide was lapping at the burrows. The third species, *chlorophthalmus*, fell between the other two in hours of waving; its phylogenetic position also appears intermediate between those of *urvillei* and *annulipes*.

Obviously the waving period of the primitive *urvillei* was limited to a low-tide hour falling between 6 and 9 A.M., since it lived on mudflats exposed less than four hours daily, and since, like other fiddlers, it did not become fully active before about 7 A.M. Whether its midday activities were curtailed by light intensity or temperature or both, or by some other factor, is unknown; also, unfortunately, my stay was not long enough to observe its behavior when low tide occurred during the late afternoon.

In Trinidad the four species under special observation were found to have similar differences of maximum activity in respect to tide and time of day (Table 2). The most primitive of the crabs, *U. thayeri*, was most active socially when low tide in its native swamp was reached between 6 and 9, field observations being made as appropriate in either the late afternoon or early morning. In previous years, before it was known either that this crab is primitive and so displays relatively little, or that its diurnal pattern is distinct, I had rarely and incompletely observed its

display and had formed erroneous ideas of its display season.

The other three species observed at Cocorite Swamp and in the crabbery showed similar distinctions in maximum display activity. Optimum low tides for *maracoani* were found to occur between 8 and 10 A.M., while for *rapax* and *cumulanta* the corresponding times are somewhat later, approximately between 8 A.M. and noon, although the evidence is not so complete.

Tides occurring between noon and 5 P.M. are disadvantageous to all four Trinidad species, and to the majority observed in other parts of the world. The few exceptions seem to be confined to the highly developed species, particularly in the Pacific neotropics. For example, when physiological conditions, weather and tides are all favorable, *stenodactylus* and *latimanus* display strongly at any time of the day from mid-morning to near sunset, with only brief respites during exceptionally hot midday periods.

Enough has been said to show that various species are most active socially at various combinations of light, tide and, almost certainly, temperature. The activity is not purely a prompt response to external conditions, however, since crabs both at Cocorite Swamp and in the crabbery behaved in accordance with favorable and unfavorable periods of the fortnight regardless of light and temperature. On cool afternoons at low tide, the crabs showed no notable increase in waving behavior, nor did cloudy (but not densely overcast) mornings decrease the amount of waving during their optimum hours of activity. Similarly, on brilliantly sunny days the crabbery remained mostly in the shade, being only intermittently and briefly dappled with sun, until 1:30 P.M., while the surface temperature stayed virtually unchanged between 9 and 1:30. This temperature, ranging between the mid-seventies and the low eighties (approximately 24°-29° C.) is the optimum for waving activity in *thayeri* and *maracoani*. Yet, except for rare individuals of exceptionally low threshold, waving in both species virtually ceased when low tide fell after 11 A.M. Repeated observations at Cocorite, on relative degrees of waving under various conditions, corroborated the observations made on the miniature population in the crabbery.

#### IV. PHASES OF BEHAVIOR UNDER INTERNAL CONTROL

A rough diurnal sequence of activities is usually apparent in any population of *Uca*. Feeding, display and, again, feeding combined with burrow repairs typically follow in sequence as the dominant activity during any low-tide period (Crane, 1941; Altevogt, 1955.2, 1957).

TABLE 2. INDICATIONS OF SEMILUNAR RHYTHMS IN THE DISPLAY OF *Uca* spp. IN CAPTIVITY

Moon	Date	Tide (Day Low)	Display	Moon	Date	Tide (Day Low)	Display	Moon	Date	Tide (Day Low)	Display	
Last Quarter	Feb. 10	15:58	-	Last Quarter	Mar. 12	16:39	-	Last Quarter	Apr. 10	16:11	-	
	11	17:17	-		13	18:24	M		-	11	17:38	m
	12	18:45	-		14	7:00	-		-	12	6:34	m
	13	6:58	-		15	8:13	M		T	13	7:48	M
	14	8:08	M		16	8:51	T		R	14	8:26	M
	15	8:53	M		17	9:15	M		T	15	8:49	M
	16	9:23	M		18	9:31	m		t	16	9:07	M
	17	9:46	?		19	9:49	m		t	17	9:28	M
	18	10:07	M		20	10:12	m		r	18	9:54	M
	19	10:30	-		21	10:41	m		T	19	10:25	M
	20	11:00	-		22	11:16	m		-	20	11:01	M
New	21	11:35	m	t	23	11:54	-	r	21	11:40	-	
	22	12:14	-	T	24	12:36	m	t	22	12:24	m	
	23	12:58	m	t	25	13:22	m	-	23	13:08	m	
	24	13:45	-	r	26	14:14	-	-	24	13:58	m	
	25	14:42	m	-	27	15:18	-	-	25	14:55	-	
	26	15:51	?	?	28	16:42	-	r	26	16:04	-	
	27	17:12	?	?	29	18:10	-	T	27	17:25	-	
	28	18:23	-	-	30	6:28	-	T	28	6:08	m	
	29	6:48	-	T	31	7:33	M	T	29	7:11	m	
	30	7:50	-	T	Apr. 1	8:21	M	T	30	8:02	m	
	First Quarter	1	8:39	-	T	Apr. 2	9:04	M	T	May 1	8:46	m
2		9:23	m	?	3	9:47	M	T	2	9:29	m	
3		10:07	-	r	4	10:31	M	t	3	10:13	m	
4		10:52	-	R	5	11:18	m	t	4	10:58	M	
5		11:40	-	-	6	12:07	m	-	5	11:45	m	
6		12:31	-	r	7	12:58	m	t	6	12:34	-	
7		13:25	-	r	8	13:55	m	-	7	13:26	M	
8		14:23	-	-	9	14:56	-	-	8	14:19	M	
9		15:29	-	r					9	15:17	M	

KEY

m: Display, usually infrequent and of low intensity, by minority of *maracoani*.  
 t: Display, usually infrequent and of low intensity, by minority of *thayeri*.  
 r: Display, usually infrequent and of low intensity, by minority of *rapax*.  
 M: High display activity by half or more *maracoani*.  
 T: High display activity by half or more *thayeri*.  
 R: High display activity by half or more *rapax*.  
 -: No display in *maracoani* when bar is on left, *thayeri* when bar is in center, *rapax* when bar is on right.  
 ?: Observations inadequate.

NOTE

From five to nine adult males of each species formed the daily basis of the data. Because of the number of variables a numerical analysis of this material seems unwarranted. Nevertheless, inspection of the table clearly shows a preponderance of display activity on dates when low tide occurred during the morning hours. The atypical pattern in May was probably the result of five days of high rainfall that began on April 28 and marked the end of the dry season. Data on the display of the fourth species, *U. cumulanta*, were insufficient for inclusion.

When the behavior of individual crabs is observed, however, wide variations are shown in the amount of time spent in feeding, fighting, wandering about and display. Many do not display at all, some remain almost inactive, others feed more than usual and a few wander through the population repeatedly dispossessing other males of their burrows and then passing on. Observation of the same individuals over successive days shows that there is often an overnight shift in the dominant type of activity. The first evidence of these shifting phases was obtained in Panama (Crane, 1941, pp. 160, 196). Similar observations (unpubl.) have since been made on a number of additional species in both hemispheres.

Attempts to keep track of individuals in the field by marking them with paint were made in Panama, Singapore and Zanzibar. Little success was attained; the great majority of the crabs were not seen again after two or three days. Another difficulty was the limited study time available for any one locality. Altevogt, on the other hand, working principally with *annulipes* and *marionis* in India (1955.2, 1957), secured good results in measuring the distances traveled by marked *marionis* between successive low tides. He was also able to keep track of certain individuals well enough to determine that they usually retained their paint for two to three weeks. Although these specimens showed the usual daily sequence of activities, with wandering or waving-and-fighting sometimes accentuated, sequential phases in the present sense were apparently not noticeable in either of his species.

*Phase Characteristics.*—One of the principal reasons for establishing the Trinidad crabberly was to keep individuals under close observation for long periods. In each of the four species maintained in the crabberly, five or six distinct phases were apparent. Although data were accumulated on individuals in each species, close and continuous daily observations were confined to adult male *U. maracoani* (Text-fig. 1). In this species the phases and their characteristics are as follows:

1. *Underground Phase.* The crab does not emerge from the burrow during at least one entire period of low tide.

2. *Phase of Maintenance Activity.* Activity is confined to feeding and repair of original burrow. Aggressive or defensive behavior is lacking, the crab always giving way to an intruder without threat postures or fighting (Text-figs. 2, 3); no apparent attention directed toward females; no display.

3. *Non-aggressive Wandering Phase.* At its

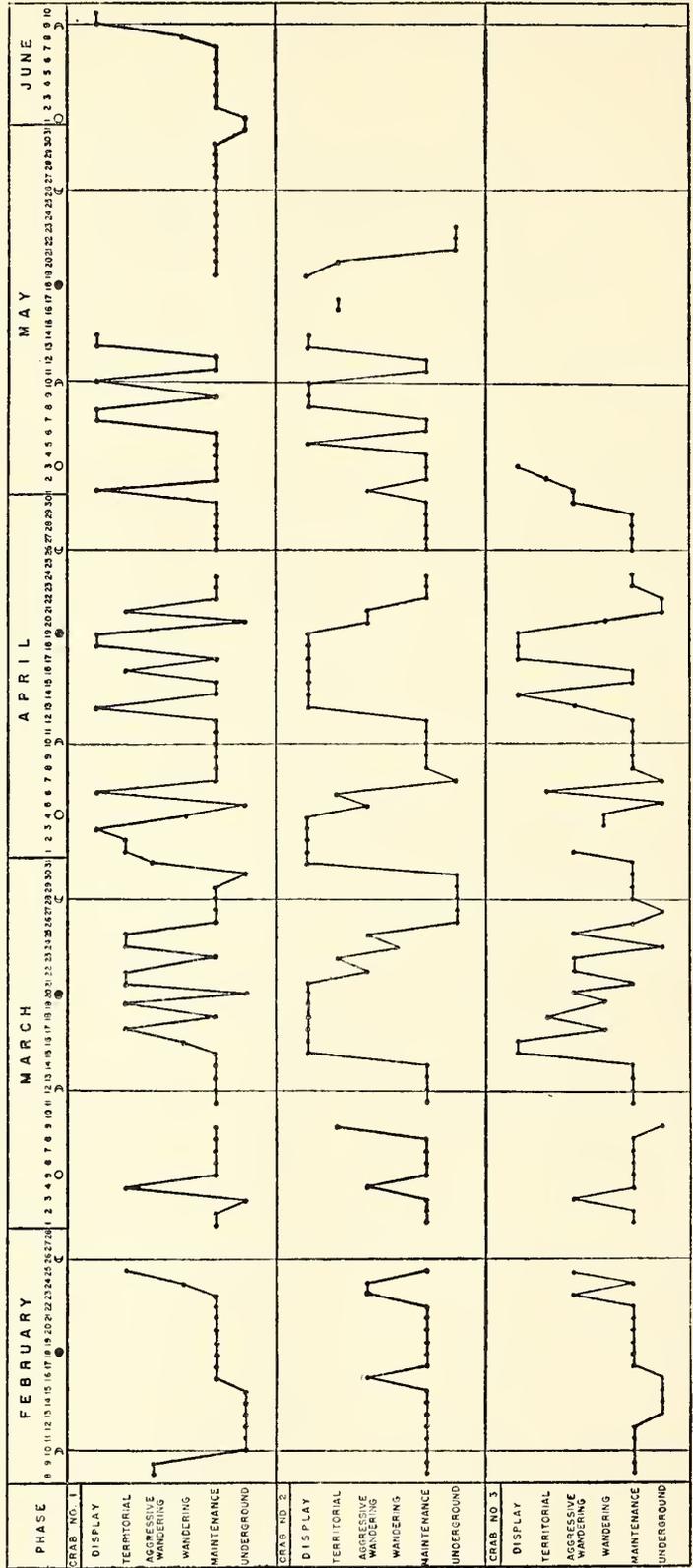
peak this phase is characterized by almost ceaseless walking during low-tide periods, punctuated by periods of feeding. Feeding is often near the water's edge, rather than in the vicinity of burrows. In the crabberly no fixed route is followed, although it is often roughly circular, embracing the entire circumference of the mudbank and obviously limited by the barriers. When in the vicinity of the walls, the crab often attempts to climb the glass repeatedly, clawing at the smooth surface for minutes at a time. Only crabs in this phase and the one following ever show this behavior. As in Phase 2, defensive, aggressive and display behavior, as well as overt responses to females, are altogether lacking.

4. *Aggressive Wandering Phase.* In this phase the crab covers almost as much territory as in the preceding, but the wanderings are punctuated with attacks on burrow-holding males. These attacks may or may not be successful: the tenant, if he is in one of the foregoing, non-aggressive phases, usually abandons the burrow and goes promptly away, although he may hold out for a while by retiring underground. In encounters between males in any of the higher phases the result is uncertain. Typical of this phase is the abandonment of the newly-won burrow by the aggressor, usually very soon after the departure of the former tenant. Pursuit of females, followed by covering and ritualized feeding from their carapaces (p. 127 and Text-fig. 4), begins in this phase, although mating does not take place.

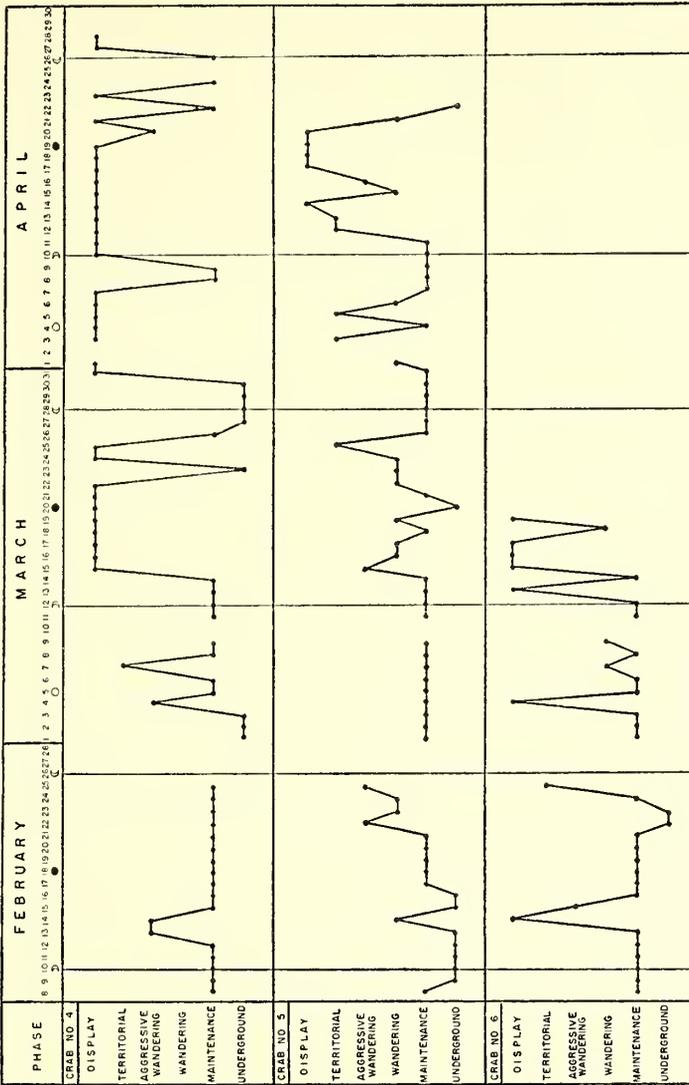
5. *Territorial Phase.* In this phase, usually brief, a crab takes possession of a burrow and attempts, often successfully, to ward off aggressors with threat and fighting. Preliminary courtship, as in the preceding phase, occurs without display.

6. *Display Phase.* A crab that displays during any time of a given day is considered to be in the display phase. Complete courtship, including copulation, is confined to individuals that display at some time of the same day, although waving does not always in this species immediately precede mating in surface courtships, and there is no display except in the immediate vicinity of a burrow held by the displaying crab. As in many species observed in the field, the burrows of displaying crabs are usually on the higher part of the bank. Such a burrow, which may be held by the same individual for a number of days during the display phase, is often the same one taken over by the crab during its territorial phase.

*Sequence Characteristics.*—To a certain extent these phases are recapitulated each day and during every semilunar period. Even crabs at



TEXT-FIG. 1 (part). See caption below.



TEXT-FIG. 1. Phase sequences in the behavior of six adult male *Uca maracoani* in captivity. The position of each dot indicates the highest type of activity attained by an individual on a particular date, when these types are arranged in a series from least social to most social. The complete natural sequence appears to range from uninterrupted inactivity underground, through simple maintenance (feeding and digging) activities, wandering, aggressive wandering, territoriality and, finally, display. See text, p. 117 ff.

Gaps in the diagrams represent days when observations were missing or inadequate. The graph of each individual's activity ends with the day before its death.

These specimens were selected for illustration because of their longevity. The shorter records of fifteen other individuals showed similar characteristics.

the height of a display phase feed briefly, often away from the burrow near the water, and all crabs spend inclement periods underground.

Ideally the phases may be traced, in sequence, over a period of days or weeks in individual crabs. In practice, however, one or more phases are frequently omitted, curtailed or superimposed on the preceding. The territorial phase is very often curtailed, emerging abruptly from the end of the aggressive wandering phase and almost at once giving way, on the same day, to a display phase. These changes on single days are not indicated in Text-figure 1, which shows only the highest type of activity attained by an individual on a particular date, when these types are arranged in the series described above from least to most social.

At the end of a display phase the sequence is rarely reversed. Rather, the crab frequently subsides abruptly into a maintenance phase, which may or may not deteriorate further into a period passed underground.

It will be noted that in all six individuals illustrated, more days were passed at the maintenance level than in any other single phase, although the periods spent in this manner were as variable as the other phases. In fact, a principal characteristic of the phases was their variability in occurrence and duration, both in the same individual and among members of the group.

*Dominance Hierarchies.*—Hierarchies among crustaceans under laboratory conditions have been reported for hermit crabs (Allee & Douglis,

1945), lobsters (Douglass, 1946) and crayfish (Bovbjerg, 1953, 1956; Lowe, 1956). In the crabbery, also, male *maracoani* arrange themselves daily in a dominance hierarchy, although this type of behavior is still too incompletely known to warrant comparison with the hierarchies in the previously-mentioned crustaceans. The following characteristics were, however, plainly evident throughout the period of observation.

Individual *maracoani* in the display phase are dominant to other individuals. Active crabs in the categories showing no aggressive behavior (Phases 2 and 3) always give way to all individuals in the higher categories; no agonistic behavior whatever is shown when individuals in these two categories meet. Among displaying individuals size often but not always determines dominance, and only straight-line hierarchies have been observed. Finally, a long-dominant or very large individual that has recently subsided into a maintenance phase may still dominate an aggressor in the aggressive wandering phase or even, rarely, a crab in the display phase.

A low-tide observation period of about two hours proved to be more than sufficient to determine the phase for that day of every male in the group, and to arrange them in the hierarchy applicable for the day. The same hierarchy never held for more than several days in succession. During the more inactive portions of the semilunar periods social activity was at such a low level that the hierarchy system was scarcely discernible.

Because of the importance of wandering individuals in the hierarchy, it seems that dominance relationships between individuals can rarely be established in the field to the extent they are noticeable in the crabbery; here the wanderers are forced repeatedly to encounter the same individuals.

*Territoriality.*—Altevogt (1957) reported that territoriality in the restricted sense of defending or remaining attached to a single burrow for a prolonged time does not exist in the species he was studying (*annulipes* and *marionis*). My own observations agree with his, particularly in the case of *marionis*. In this species, as in many primitive and semi-primitive species, waving takes place whether or not a burrow is, at the moment, being held.

In highly evolved species territoriality is much better developed. In *maracoani*, as in a number of other advanced species in different branches of the genus, a particular burrow may be defended by the same individual throughout a single display phase, often lasting a number of days. In these species no waving takes place

before the crab has taken over a burrow either through its own aggression or through default by a previous tenant; this burrow is then defended from approaching aggressors, either by threat postures or by physical combat (p. 125 ff.) No waving occurs except within a few inches of the burrow, and in some small species the mouth of the burrow itself appears to comprise the entire territory, the crab normally threatening and displaying only when one or more tarsi are actually touching the rim of the hole. Even when a display-phase crab has defended a given burrow for several days, it does not wave during its infrequent periods away from the territory. Unless pursuing a female or briefly attacking a neighboring male slightly lower in the hierarchy, these absences usually consist, in *maracoani*, of direct trips through the population to the water's edge to feed; they are followed by returns, equally direct, to the burrow.

It is of course true that fiddlers in the non-aggressive phases (1-3 in *maracoani*) all occupy burrows at least during high tide, and that fiddlers of almost all species typically feed in the vicinity of the burrows, down which they descend when alarmed or at the approach of the tide. These burrows are, however, never defended against aggressors and there seems, at present, to be no definable bond between such a crab and a particular burrow. In these cases there appears to be no question of territorial behavior in the usual zoological senses of the word.

Many burrows, however, are held and defended for very short periods by crabs which, although physiologically in one of the upper phases (5 and 6 in *maracoani*), are yet rather low in the day's hierarchy and so easily dispossessed. Yet, during these periods of occupancy the tenant often shows territorial behavior as emphatically as do long-established tenants. It thus remains difficult and probably unrewarding to place a lower limit on the time a burrow shall be defended in order to qualify the occupant as a territory-holder.

The widely varying degrees to which territoriality is developed in *Uca*, and its fluctuations within individuals as described in the preceding pages, make its comparative study within this group of special biological and evolutionary interest. Until the completion of this aspect of the work, Thorpe's definition of territory as "any defended area" will remain particularly useful.

*Activity Phases in Relation to External Conditions.*—Under adverse external conditions individual response is related to activity phase. As conditions deteriorate, socially inactive crabs are the first to be affected. Vice versa, crabs in full display condition are exceedingly tolerant of

poor environmental conditions of various kinds. Such low-threshold individuals often display in spite of dull weather, high temperature, imminent tides or adverse days of the semilunar period. In any field population numerous crabs are of course simultaneously in this low-threshold condition. Their conspicuousness is misleading, and makes casual observations on activity levels in relation to external conditions of little value.

A preliminary series of dissections shows that there is a gradual development and decline of the reproductory organs over a period of months, so that the short behavior cycles cannot be attributed directly to the seasonal development of gonads, nor is evidence available that the production of a spermatophore is involved. Almost certainly, however, the phases will prove to be hormonally controlled, whether through the activity of the sinus or other glands or through neural hormones. A phenomenon possibly related to the wandering phase of *Uca* was reported by Bliss (1953), when she observed that eyestalkless land crabs (*Gecarcinus*) were hyperactive.

Seasonal rhythms were apparent in various parts of the ranges in some of the common, widespread species of *Uca*: *marionis* in Fiji, Australia, Singapore, Zanzibar and Mozambique; *annulipes* in Singapore, Ceylon and Africa; *inversa* in Eritrea, Zanzibar and Mozambique, and a number of species, particularly *rapax*, in the neotropics. All of these show evidence that populations near the beginning of the breeding season include on any day more individuals in the aggressive wandering phase, and that more fighting takes place, than later in the season, when waving is at its peak.

#### V. POSTURES AND MOTIONS ASSOCIATED WITH SOCIAL BEHAVIOR IN *Uca maracoani*

Through the work in the crabberly, a special study was made of the postures connected with social behavior in *U. maracoani*, a species which is highly developed socially. Many of the postures and motions have been observed in most or all of the other species studied in the genus in either identical form (as in high-intensity fighting) or with slight variations; others appear to be more restricted.

In any case, Text-figures 2-5 inclusive, in association with the explanations below, should serve as a useful standard and comparison for equivalent behavior in other species of the genus.

Text-figure 2. *Agonistic Behavior in Uca maracoani*. In A-D inclusive the activities illustrated are not necessarily associated with the

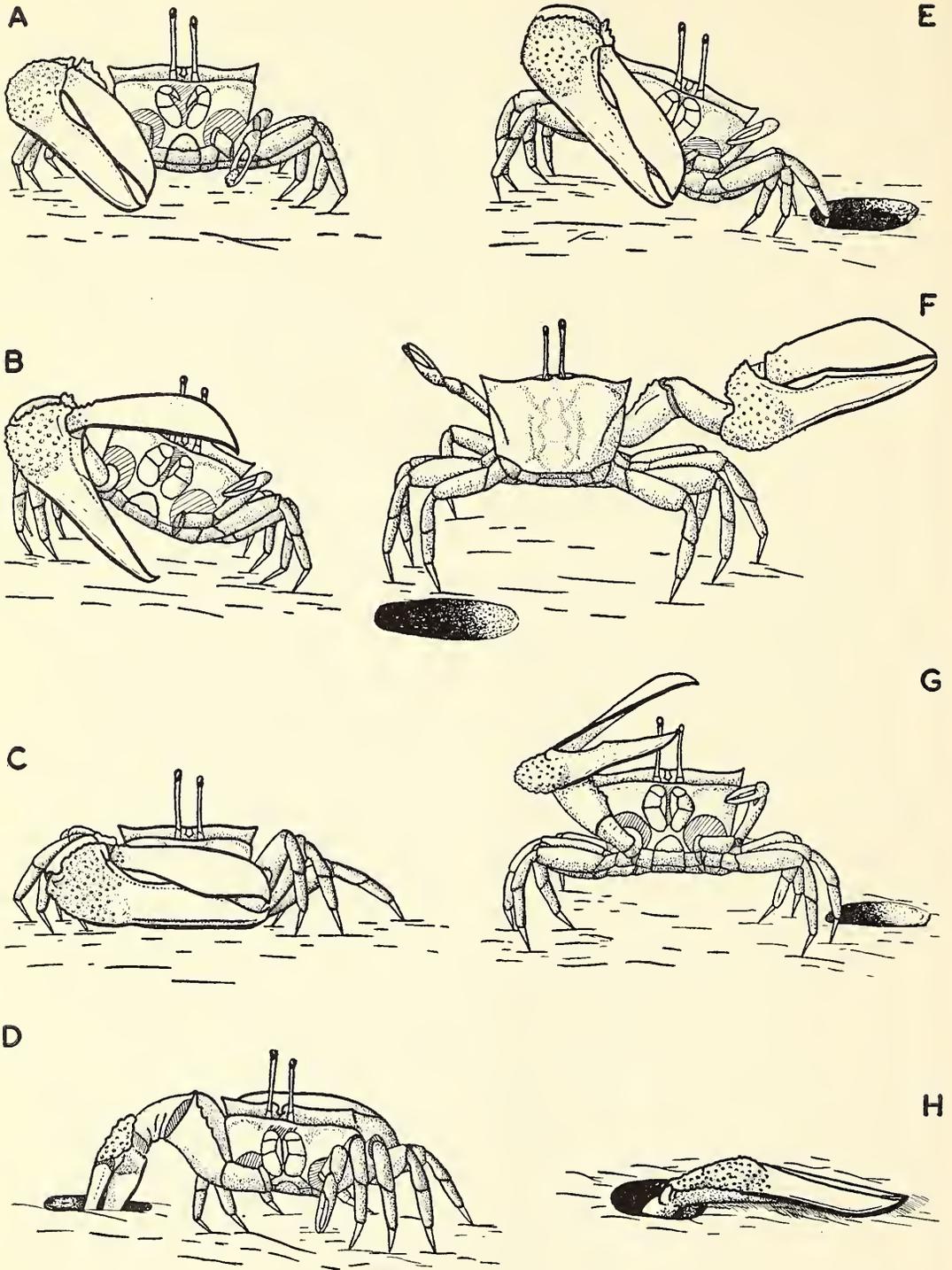
tenancy of a burrow. In E-H inclusive the individual always shows attachment, however temporary, to a particular hole.

A. *Threat: Lowest Intensity. Posture*: Body scarcely or not at all elevated; base of major manus slightly raised, not over-reaching height of erect eye. Chelae closed, the tips touching ground or nearly so. *Motion*: Cheliped moved back and forth, forward and slightly sideways, in narrow arc; true feeding usually continued. *Occurrence*: This behavior may occur in males in the three upper phases, when feeding at a distance from a burrow, usually at the water's edge; it occurs when the feeding crab is crowded or approached by another individual, male or female.

B. *Threat: Medium to High Intensity. Posture*: Major side of body and base of major manus moderately elevated; pollex pointed obliquely down, chelae widely opened. *Motion*: Walking present or absent. *Occurrence*: Assumed by males in either aggressive wandering or display phases, in either aggression or defense. An aggressive wanderer may employ it in approaching any burrow held, however temporarily, by a male in any phase, that is standing close to it. It is also often used by a burrow's tenant, in a display or predisplay territorial phase, at the approach of another male. By whichever crab it is inaugurated, it often elicits the same posture in the opponent. Pressure of the apposed open chelae follows more rarely (as in Text-fig. 3A or 3B) and linked chelipeds (3C) most rarely of all.

C. *Submissive-escape Behavior. Posture*: Body and major cheliped barely clear ground. *Motion*: Walking, usually with the major cheliped leading. *Occurrence*: Characteristic of males in the maintenance or wandering phases, or of a display phase male which has been displaced from his burrow by threat or by prying out, by another individual higher in the dominance hierarchy. Finally, it is sometimes assumed by the retreating loser following an actual fight (Text-fig. 3).

D. *Exploratory Behavior. Posture*: Major cheliped inserted in burrow, body partially elevated. *Motion*: Slight thrusting movements of chelae. *Occurrence*: May be performed by any male about to enter a strange burrow or its own burrow after an absence, apparently when there is at least a possibility of its occupancy by another crab, male or female. Also performed as a preliminary motion to pry out another crab, male or female, as when a dominated individual such as illustrated in C, having been pursued, has escaped down a burrow. Actual entering of a burrow and prying out are almost always



TEXT-FIG. 2. A-H, Agonistic behavior in *Uca maracoani*. For explanation, see text, p. 123 ff. Drawings by Julie C. Emsley.

accomplished by the ambulatories of the opposite (minor) side, the crab first withdrawing the large cheliped and turning completely around.

**E. Burrow Defense: Low Intensity. Posture:** Similar to A, the non-territorial equivalent, but base of major manus and entire major side are well elevated. Often the minor ambulatories are half concealed in burrow. **Motion:** None, except to face potential opponent. **Occurrence:** Assumed only by display-phase males when adjacent to their currently occupied burrows. The stimulus is the approach or near passing of another male in any phase.

**F. Burrow Defense: Medium Intensity. Posture:** Body elevated, chelipeds outspread horizontally. **Motion:** None, except to present vertically tilted carapace to potential opponent. **Occurrence:** Usually follows preceding posture, E, as the stimulating crab passes to the side and/or rear of the burrow's tenant. In that case, E shifts smoothly into F. Alternatively, F is assumed when a potential aggressor approaches from the rear. As in E, only a male in the territorial or display phase assumes this posture.

**G. Burrow Defense: High Intensity. Posture and Movement:** This is true display, typical of the species, with the cheliped making a somewhat circular "wave" and not returning to the ground between displays. Body and cheliped both moderately elevated, the tips of the chelae reaching their maximum somewhat above eye level. There is no walking during display, although the crab may turn to remain facing the stimulus. The high elevation of the body contrasts with its low level in the submissive individual shown in C. Although the display represents the highest intensity of burrow defense behavior short of fighting, it is low intensity as far as display is concerned. The cheliped is rotated slowly, with an outward, up and down movement typical of lateral displays except that the cheliped is not brought to the ground between waves. In contrast to high-intensity courtship (Text-fig. 5B, C) the tempo is slow, the circular "windmilling" of the chelae is not accented, both the stretch of the ambulatories and the reach of the cheliped are moderate, the carapace is not tilted so far back as to be vertical and the crab always faces its opponent, if any. **Occurrence:** Found, by definition, only in display phase males, and then only when they are within a short distance of their burrows, usually several inches or less.

The display described above often occurs within an apparent vacuum—that is, without apparent stimulus from another individual, even of another species. This is best seen during adverse tides or weather in the crabbery, when

occasionally only a single individual—a *maracoani* in full display phase—is on the surface. Such individuals customarily erupt rapidly from their burrows and commence display at once. The vacuum character of such displays is understandably nearly impossible to establish under field conditions, because the excellent eyesight of the crabs makes the range extent of possible stimuli difficult to determine. Display also is frequently initiated at the approach of males and apparently by distant or motionless females. Often it precedes or follows E or F, or the sequence E, F, or, with equal frequency, B, when the crab is a burrow tenant.

**H. Burrow Defense and/or Individual Defense, Lowest Intensity. Posture:** Only the cheliped, the chelae usually completely closed, is left flat outside the burrow. **Motion:** None. **Occurrence:** This behavior is characteristic of crabs in the beginning of a territorial phase, when approached by an aggressively wandering male, particularly one in B posture. It also occurs in display phase males when approached by an aggressive wandering or display phase male higher in the hierarchy. Under the latter conditions this behavior is sometimes even preceded by low intensity display as in G.

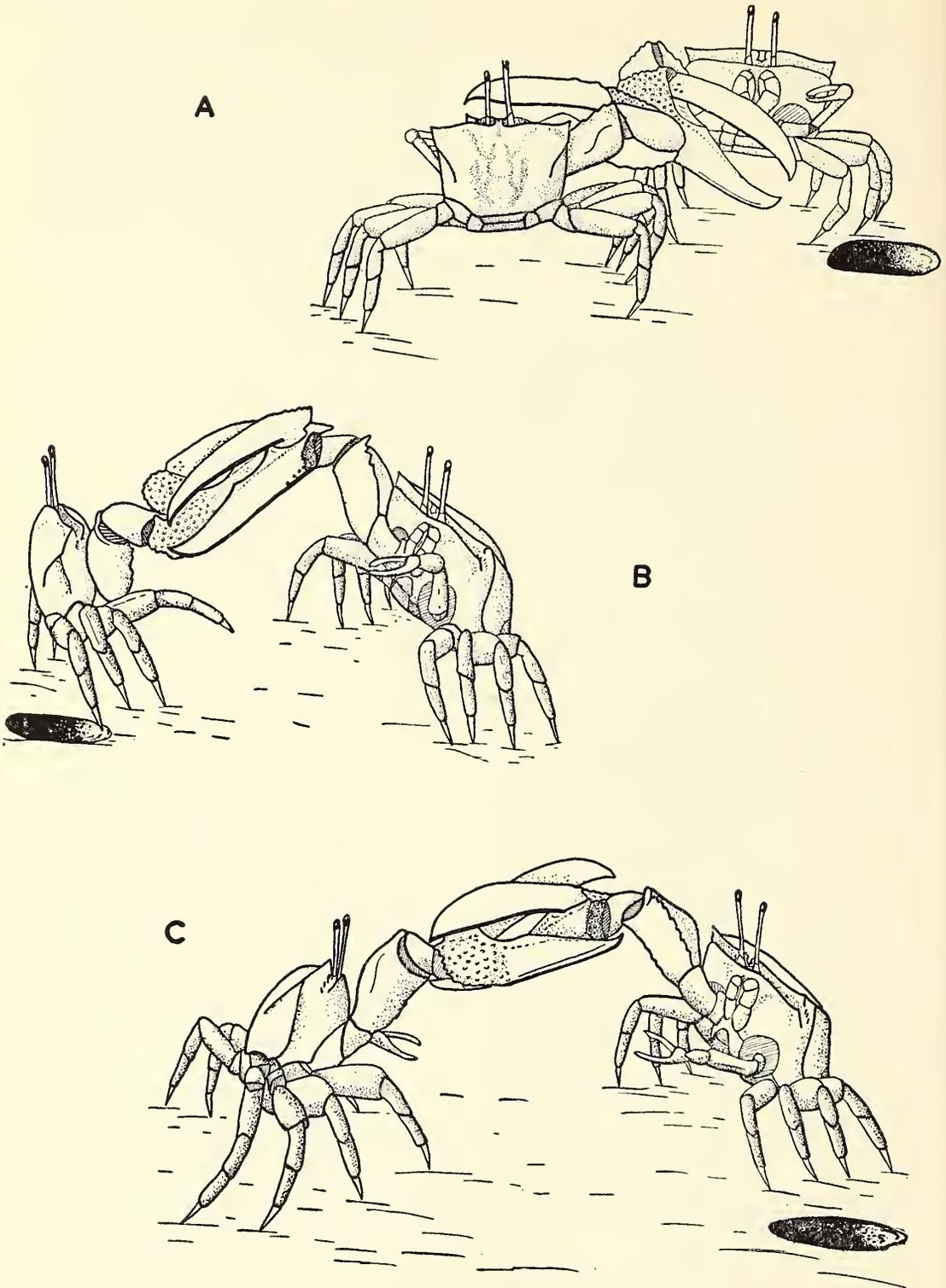
Text-figure 3. *Fighting in U. maracoani.* Fighting, as opposed to mere threat, is here defined as any behavior between two males in which the major chelipeds are brought into contact. No fights occur in this species unless one of the crabs is close to a burrow of which he is the tenant. All of the types of fighting are much rarer than any of the threat gestures previously described, and only crabs in the aggressive wandering, territorial or display phases are involved.

Altevogt's illustrations (1957, pp. 64-65) of one threat gesture and two kinds of fighting in *marionis* clearly show corresponding postures in another species.

**A. Low Intensity: Manus-to-manus Pushing.** The direction is back-and-forth. Maximum result: One crab is forced backward, and retreats, often in a hasty skid.

**B. Medium Intensity: Manus-to-pollex Pushing.** The curved, externally concave end of the pollex fits under the heel-like, tuberculous surface of the lower base of its opponent's manus, giving good leverage. Obviously this position is impracticable when opponents have claws of opposite sides enlarged. A complete upsetting by this means has not been observed, although one of the crabs is often thrust off balance and rapidly retreats.

**C. High Intensity: Chelipeds Interlocked.** Of relatively rare occurrence. Crabs push back and



TEXT-FIG. 3. A-C, Fighting in *Uca maracoani*. For explanation, see text, p. 125 ff. Drawings by Julie C. Emsley.

forth and pry upward. The ultimate, exceedingly rare climax is the complete overturn of one of the crabs. No physical damage of any kind has ever been observed in any of these types of fighting.

Text-figure 4. *Courtship Away from Burrow of Male.*

A. *Rejection Posture of Female:* At the approach of a male, an unwilling female partially descends her burrow, leaving the legs of one side projecting stiffly above the ground. Successful efforts to pry out and court such a female have not been observed.

B. *Ritualized Feeding.* The male climbs on top of a female and makes plucking motions at frontal, suborbital and especially the tuberculous antero-lateral regions of her carapace. The male's minor chelae are brought to his buccal region as in feeding, but actual feeding, from the scanty mud clinging to the female, does not take place; often the cheliped is not brought all the way to the mouth and no pellet (dropped or wiped away in true feeding) is ever formed at the base of the maxillipeds. In addition to the ritual feeding the male's ambulatories sometimes stroke the female's carapace and legs, in addition to the male's obvious ultimate motions involved in turning her over into the position shown in C. At the beginning of ritualized feeding the female may be struggling, her body held high on rigidly braced legs. She gradually relaxes into the quiescent position shown in B.

C. *Copulation at Surface.* The position of the major cheliped varied in the half-dozen surface copulations seen in this species, but it played no particular part in holding the female and the chelae only once touched her at all.

Text-figure 5. *Courtship Display at Mouth of Male's Burrow.*

A. *Routine Low Intensity Display* (as in Text-fig. 1G). This behavior occurs by the hour in males at the peak of the display phase. When directed toward an individual, whether male or non-approaching female, the crab always faces in that direction.

B. and C. *High Intensity Courtship Display.* Elicited only by an approaching female. Compared with A, the carapace is held higher and tilted vertically back, the cheliped reaches higher and rotates faster in a much wider arc, the chelae are widely opened and one or two ambulatories, first on one side and then on the other, are elevated, in accordance with the momentarily shifting balance of the great claw. During the high intensity display the crab always presents the carapace toward the approaching female, who generally does not approach steadily but

in spurts interrupted by pauses. These pauses do not interrupt the male's display. The female after such an approach usually bypasses the male, in which case the quality of his display subsides to low intensity (as in A) or ceases altogether almost at once. Occasionally, however, a female approaches almost beneath him (C) whereupon he swiftly descends the burrow (minor side first, as usual). The female then either passes on or follows the male at once. In the latter case she may or may not stay below, presumably copulating.

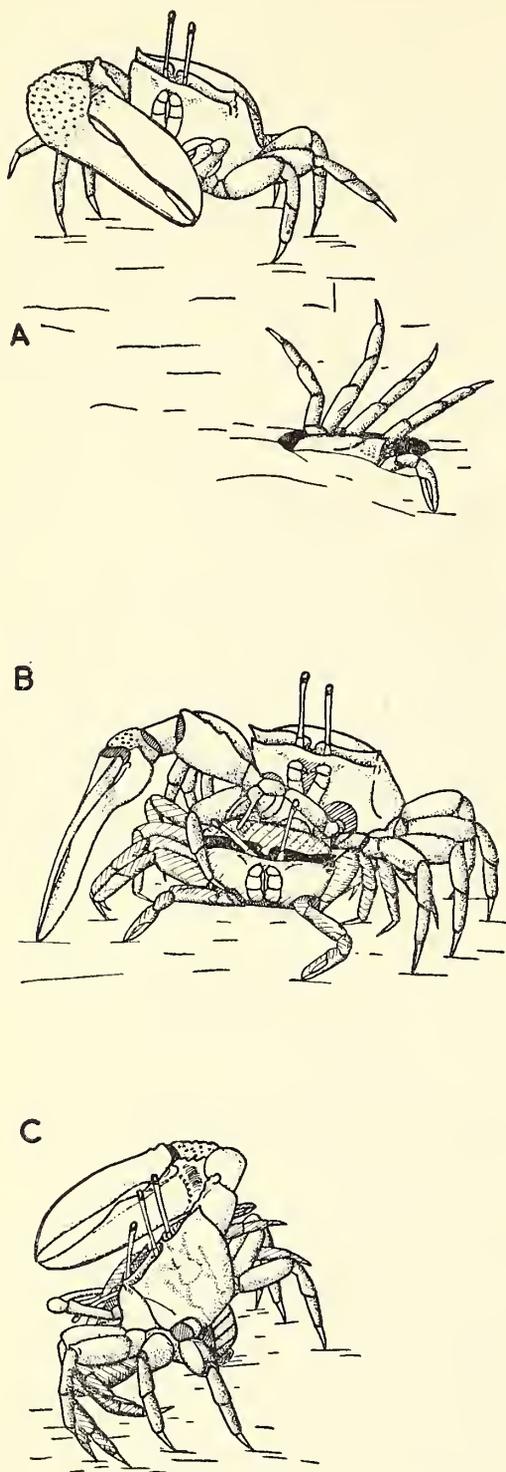
In *maracoani* the behavior illustrated in Text-figure 4 seems to be characteristic of pairs where the female is less ready to mate than the male. It is the only type of mating found in the primitive species of the genus (Crane, 1957). Also, 4B often occurs where the male is not in full display phase; in these latter instances copulation has never been observed to follow.

The behavior illustrated in Text-figure 5, on the other hand, is in this advanced species the more typical. There is evidence that it is females which have recently molted, although hardened, that are in the wandering phase that stimulates high intensity waving. It also seems likely that odor plays a minor role, since at least in this species not all moving females stimulate strong waving from males. Nevertheless in many other advanced forms a male without major cheliped, or a dried female on a string, is enough to release high intensity waving (Burkenroad, 1947; Altevoigt, 1957; Crane, unpub.).

## VI. SUMMARY

In order to supplement field observations on comparative social behavior in the genus *Uca*, four species were maintained in an out-of-doors terrarium in Trinidad. Throughout a period of four months detailed records were kept of the daily activities of individual *U. maracoani*, while additional data were assembled on *cumulanta*, *rapax* and *thayeri*.

All the species showed strong tidal and semilunar rhythms in their social activities, similar to those known partially to control the expansion of chromatophores in northern species. The successful use of the terrarium depended on an arrangement of tides and observation schedules roughly in accordance with these rhythms. No attempt was made either to determine their periods with laboratory precision or to alter them experimentally. The semilunar rhythms apparently depended on a favorable juxtaposition of time of day with local hours of low tide. Differences among the species were evident in the timing of the optimum period of social activity each fortnight.



TEXT-FIG. 4. A-C, Courtship in *Uca maracoani*. For explanation, see text, p. 127. Drawings by Julie C. Emsley.

Apart from behaving in accordance with the above rhythms, each individual adult male showed cycles of social behavior that culminated in a display phase. In *maracoani* the preceding stages lead from a period of inactivity underground, through a simple maintenance routine (feeding and digging), a wandering phase, one of aggressive wandering and a phase in which a burrow was defended as a territory. The subsequent display phase, which sometimes persisted for a number of days and occurred several times a season, occasionally culminated in full courtship and, rarely, in mating. The phases were highly variable in duration both within single individuals and among members of the group, and in any cycle one or more phases were often superimposed or omitted.

A special study was made of social postures and motions in *maracoani*. The males showed an extensive repertory, the various components being elicited in response to specific situations of an agonistic or epigamic character. Most of the postures have their equivalent in other species of the genus; some are characteristic only of species in which territoriality is more or less developed; a few, including one fighting pattern and display itself, are specifically distinct.

Under terrarium conditions a distinct dominance hierarchy was found to occur in *maracoani*. The order was never maintained for more than several days at a time, apparently because of the changing phases of the individuals. Crabs at the top of the day's hierarchy were almost always in the full display phase. Rarely an individual just past a long-maintained display phase was still dominant to one or more displaying males which he had previously dominated. The hierarchy showed in encounters even when both males were in the display phase, the same crab being dominant at least during a single low-tide period. Between such individuals which were well matched in phase, comparative size was usually but not always a factor of importance. Between two individuals well separated in the hierarchy the lower individual always retreated without fighting, and usually in a low-crouching position. Because of the prevalence of wandering phases it seems probable that most hierarchies in the field are even more temporary than in the terrarium.

The governing influences and specific variety of characteristics controlling social behavior in the crabbery are certainly prevalent throughout the genus. Before the start of the Trinidad work, field studies on many species in both hemispheres had already given preliminary evidence of the existence of tidal and semilunar rhythms, the occurrence of phases in individuals and the wide

variety of postures and motions characteristic of highly evolved species. The prolonged observations of individuals in captivity provided an invaluable supplement to basic studies of wild populations.

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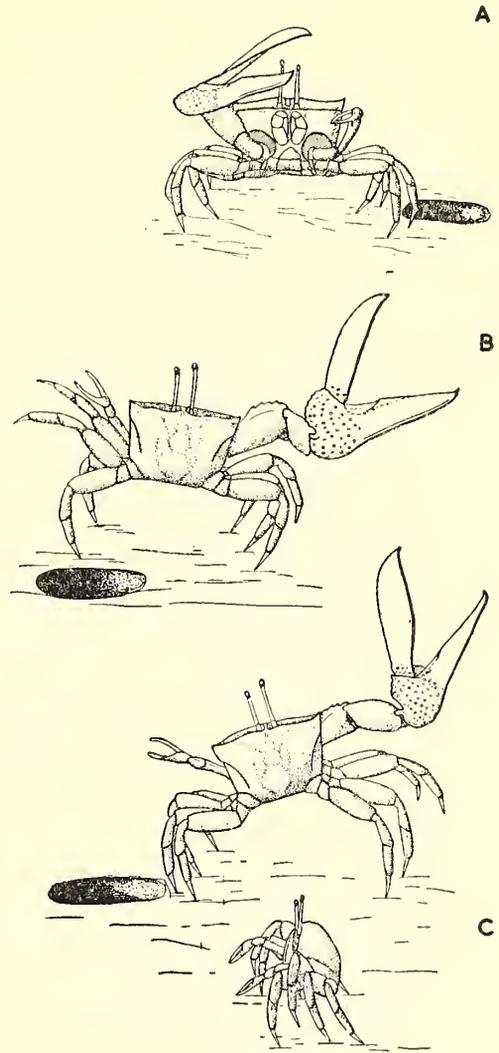
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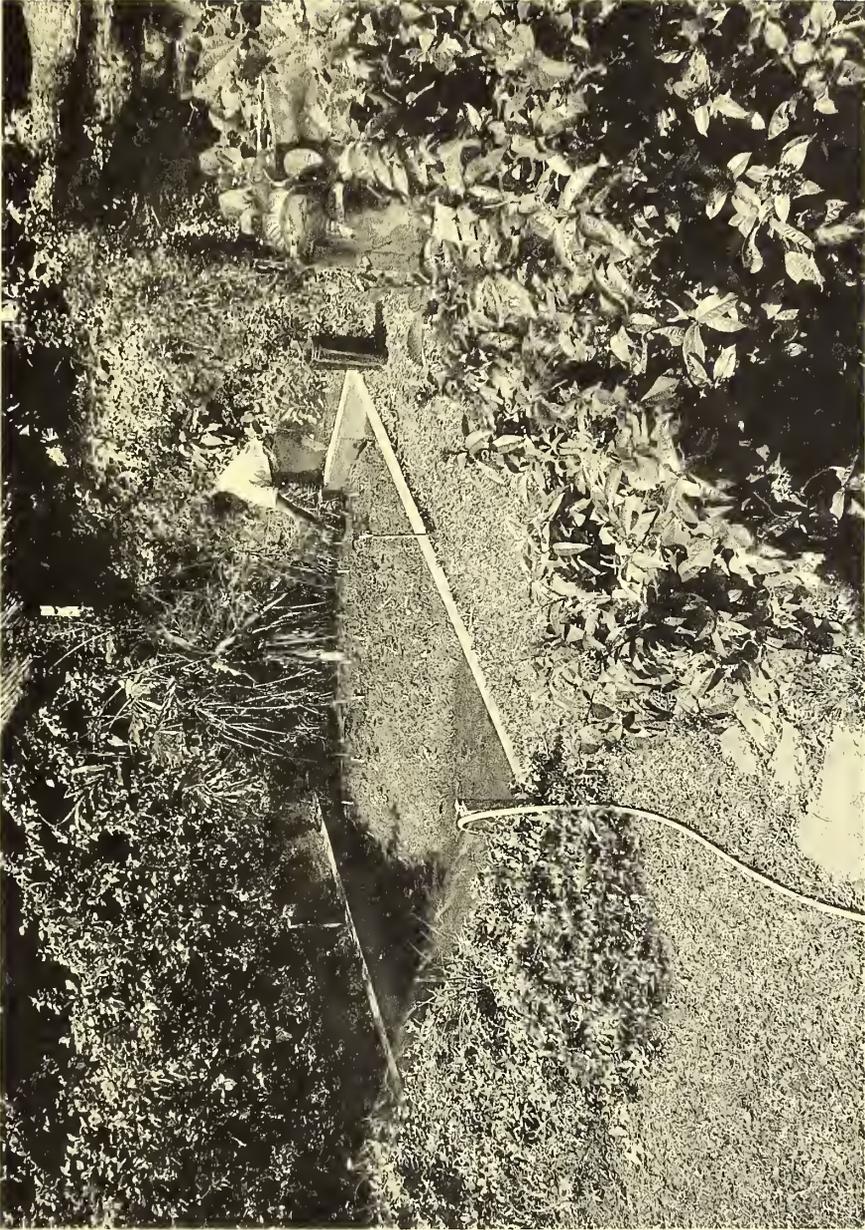
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## EXPLANATION OF THE PLATE

## PLATE I

Outdoor terrarium for fiddler crabs, showing mud-bank with burrow markers, fence of wire netting to keep out toads, and hose for raising water level to simulate a rising tide. See text, p. 114 ff.



ASPECTS OF SOCIAL BEHAVIOR IN FIDDLER CRABS, WITH SPECIAL REFERENCE  
TO *UCA MARACOANI* (LATREILLE)



A Catalog of the Type Specimens of Fishes Formerly in the  
Collections of the Department of Tropical Research,  
New York Zoological Society<sup>1</sup>

GILES W. MEAD<sup>2</sup>

**D**URING the past thirty-five years the Department of Tropical Research of the New York Zoological Society, under the direction of Dr. William Beebe, has contributed much to the study of fishes. The active field program resulted in large collections which were maintained and studied in the Department's laboratory in the Zoological Park and in a long series of technical publications. In recent years, Dr. Beebe has donated parts of this collection to several institutions, where they continue to contribute to ichthyological research. The distribution of the Department's collection of fishes was completed in 1957 with the transfer of the remaining specimens to the U. S. National Museum and the Natural History Museum, Stanford University. The type material resulting from the Department's work is now in the collections of these two institutions and four others to which specimens were given prior to 1957.

The list which follows has been prepared, at Dr. Beebe's request, primarily to make known the present location of this type material. Its compilation was simplified by the catalogs and indices maintained by Dr. Beebe and through the cooperation of the curators of the several museums that now contain collections assembled by the Department of Tropical Research.

The list is alphabetical, and all species are listed under the genus in which they were first described, regardless of subsequent transfer. Four species of deep-sea fishes were described by Dr. Beebe from sight observations from the bathysphere. These four, *Bathysphaera intacta* (Beebe, 1932, *Bull. New York Zool. Soc.*, 35

(5): 175), *Bathycerantias trilychnus*, *Bathyembryx istiophasma* and *Bathysidus pentagrammus* (Beebe, 1934, *ibid.*, 37 (6): 190-192), have been omitted.

The following abbreviations have been used:

NYZS—New York Zoological Society. KOH—New York Zoological Society number assigned to specimens which were cleared in potassium hydroxide and stained with alizarine for osteological study. USNM—United States National Museum. SU—Natural History Museum, Stanford University. AMNH—American Museum of Natural History. CAS—California Academy of Sciences.

*Acanthemblemaria arborescens* Beebe & Tee-Van, 1928, *Zoologica* (N.Y.), 10 (1): 244. Lamentin Reef, Port-au-Prince Bay, Haiti; Feb. 22, 1927. Type: (NYZS 6923) USNM 170566.

*Acanthemblemaria crockeri* Beebe & Tee-Van, 1938, *ibid.*, 23 (3): 310. San Lucas Bay, Lower California, Mexico; April 2, 1936. Type: (NYZS 24824) SU 46497.

*Acanthemblemaria variegata* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 247. Lamentin Reef, Port-au-Prince Bay, Haiti; May 8, 1927. Type: (NYZS 7464) USNM 170569.

*Aceratias edentula* Beebe, 1932, *ibid.*, 13 (4): 102. 13 mi. south of Nonsuch, Bermuda; 1,000 fms.; June 2, 1931. Type: (NYZS 20571, misprinted as 20751 in text; KOH 871) USNM 170951.

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<sup>1</sup>Contribution No. 990, Department of Tropical Research, New York Zoological Society.

<sup>2</sup>Ichthyological Laboratory, United States Fish and Wildlife Service, U. S. National Museum, Washington 25, D. C.

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- Cirrhitichthys corallicola* Tee-Van, 1940, *ibid.*, 25 (5): 58. Gorgona Island, Pacific off Colombia; 2° 58' N., 78° 11' W.; March 30, 1938. Type: (NYZS 28710-A) SU 46504.
- Citharichthys gordae* Beebe & Tee-Van, 1938, *ibid.*, 23 (3): 302. Outer Gorda Bank, Lower California, Mexico; 60 fms.; April 23, 1936. Type: (NYZS 25785) SU 46496.
- Corythoichthys bermudensis* Beebe & Tee-Van, 1932, *ibid.*, 13 (5): 113. Nonsuch Island, Bermuda; Aug. 18, 1930. Type: (NYZS 9326) USNM 170913.
- Cremnobates argus* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 238. Lamentin Reef, Port-au-Prince Bay, Haiti. Type: (NYZS 7375) USNM 170904.
- Cyprinodon bondi* Myers, 1935, *ibid.*, 10 (3): 303. Étang Saumâtre, Haiti; Feb. 20, 1933. Type: USNM 100960.
- Cypselurus antarei* Beebe & Hollister, 1931, *ibid.*, 12 (9): 83. 200 mi. north of Sombrero, B.W.I.; 21° 50' N., 63° 32' W.; June 30, 1932. Type: (Antares Exp. no. 6) USNM 170921.
- Dasyatis pacificus* Beebe & Tee-Van, 1941, *ibid.*, 26 (3): 262. Port Parker, Costa Rica; Jan. 22, 1938. Type: (NYZS 26120) AMNH 15661, 15662, 15663 (three pieces of the body) and 15710 (lower jaw).
- Diabolidium arcturi* Beebe, 1926, Bull. New York Zool. Soc., 29 (2): 80. Pacific; 4° 50' N., 87° W.; 514-900 fms. Type: (NYZS 6144; number on vial containing type: 6333) SU 46505.
- Dicrolene gregoryi* Trotter, 1926, Zoologica (N.Y.), 8 (3): 116. Pacific; 4° 50' N., 87° W.; 844 fms.; May 31, 1925. Type: (NYZS 6063) AMNH 7511.
- Dixonina pacifica* Beebe, 1942, *ibid.*, 27 (8): 43. Port Culebra, Costa Rica; 10° 31' N., 85° 40' W.; Jan. 24, 1938. Type: (NYZS 26131) SU 46486.
- Dolichopteryx binocularis* Beebe, 1932, *ibid.*, 13 (4): 49. 14 mi. southeast of Nonsuch, Bermuda; 400 fms.; Aug. 4, 1931. Type: (NYZS 21867; KOH 960) USNM 170933.
- Dolopichthys gladisfenae* Beebe, 1932, *op. cit.*, p. 86. 6 mi. south of Nonsuch, Bermuda; 700 fms.; May 28, 1930. Type: (NYZS 15490) USNM 170944.
- Dolopichthys tentaculatus* Beebe, 1932, *op. cit.*, p. 88. 10 mi. southeast of Nonsuch, Bermuda; 600 fms.; Sept. 7, 1931. Type: (NYZS 23170) USNM 170945.
- Emblemaria micropes* Beebe & Tee-Van, 1938, *ibid.*, 23 (3): 308. Inez Point, Santa Inez Bay, Gulf of California, Mexico; April 9, 1936. Type: (NYZS 24895) SU 46499.
- Eucinostomus mowbrayi* Beebe & Tee-Van, 1932, *ibid.*, 13 (5): 115. Nonsuch Island, Bermuda; Sept. 30, 1930. Type: (NYZS 9328) USNM 170909.
- Eupomacentrus beebei* Nichols, 1924, *ibid.*, 5 (4): 63. Eden, Indefatigable Island, Galapagos; April 1, 1923. Type: AMNH 8270.
- Eupomacentrus rubridorsalis* Beebe & Hollister, 1933, *ibid.*, 12 (9): 85. Chatham Bay, Union Island, Grenadines, B.W.I.; July 9, 1932. Type: (NYZS-Antares Exp. no. 97) USNM 170922.
- Eustomias satterleei* Beebe, 1933, Copeia 1933 (4): 164. 8 mi. south of Nonsuch, Bermuda; 1,000 fms.; Sept. 10, 1929. Type: (NYZS 13457) USNM 170927.
- Eustomias schiffi* Beebe, 1932, Zoologica (N.Y.), 13 (4): 54. 6 mi. south of Nonsuch, Bermuda; 600 fms.; May 29, 1930. Type: (NYZS 15653) USNM 170935.
- Exonantes marginatus* Nichols & Breder, 1928, *ibid.*, 8 (7): 429. Pacific east of the Galapagos; 2° 36'-2° 8' N., 85° 1'-86° 31' W. Type: AMNH 9234.
- Exonantes nonsuchae* Beebe & Tee-Van, 1932, *ibid.*, 13 (5): 112. Near St. David's Island, Bermuda; May 15, 1929. Type: (NYZS 9983) USNM 170912.
- Gambusia beebei* Myers, 1935, *ibid.*, 10 (3): 305. Étang de Miragoâne, Haiti. Type: (NYZS 7168); missing.

*Gobiosox daedaleus boreus* Briggs, 1955, Stanford Ichthyol. Bull., 6 (1): 111. Conchaguita Island, Gulf of Fonseca, El Salvador; Dec. 22, 1937. Type: (NYZS 27550) SU 17392.

*Gobiosox stenocephalus* Briggs, 1955, *op. cit.*, p. 92. Puerto Parker, Costa Rica; Jan. 14, 1938. Type: (NYZS 27872) SU 17408.

*Gigantactis perlatus* Beebe & Crane, 1947, Zoologica (N.Y.), 31 (4): 167. Pacific off Jicaron Island, Panama; 500 fms.; March 20, 1938. Type: (NYZS 28621) SU 46487.

*Gillellus quadrocinctus* Beebe & Hollister, 1935, *ibid.*, 19 (6): 222. (Also spelled *quadrocintus*, a lapsus). Union Island, Grenadines, B.W.I.; July 12, 1934. Type: (NYZS-Antares Exp. no. 180); missing.

*Gobiosoma chancei* Beebe & Hollister, 1933, *ibid.*, 12 (9): 87. St. George's Bay, Grenada, B.W.I.; July 4, 1932. Type: (NYZS-Antares Exp. no. 22) USNM 170955.

*Gobiosoma macrodon* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 226. Lamentin Reef, Port-au-Prince Bay, Haiti. Type: (NYZS 7462) USNM 170896.

*Haplophryne hudsonius* Beebe, 1929, *ibid.*, 12 (2): 23. Hudson Gorge; 600 fms.; July 7, 1928. Type: (NYZS 7696; KOH 26) USNM 170954.

*Himantolophus azurlucens* Beebe & Crane, 1947, *ibid.*, 31 (4): 155. Pacific off Cape Mala, Panama; 7° N., 79° 16' W.; 500 fms.; March 25, 1938. Type: (NYZS 28641) SU 46507.

*Hypleurochilus bermudensis* Beebe & Tee-Van, 1933; *ibid.*, 13 (7): 155. Marshall Island, Bermuda. Type: Harvard Mus. Comp. Zool. no. 33070.

*Iridio bathyphilus* Beebe & Tee-Van, 1932, *ibid.*, 13 (5): 117. 1 mi. south of Nonsuch, Bermuda; 510 feet; Sept. 30, 1929. Type: (NYZS 9050) USNM 170910.

*Labrisomus albigenys* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 233. Lamentin Reef, Port-au-Prince Bay, Haiti; May 9, 1927. Type: (NYZS 7372) USNM 170899.

*Labrisomus haitiensis* Beebe & Tee-Van, 1928, *op. cit.*, p. 232. Bizoton, Port-au-Prince Bay, Haiti; March 15, 1927. Type: (NYZS 7170) USNM 170903.

*Lampanyctus septilucis* Beebe, 1932, *ibid.*, 13 (4): 68. 7 mi. south-southwest of Nonsuch, Bermuda; 700 fms.; July 4, 1929. Type: (NYZS 14292-A) USNM 171199.

*Lampanyctus polyphotis* Beebe, 1932, *op. cit.*, p. 67. 5 mi. south of Nonsuch; 900 fms.; May 25, 1929. Type: (NYZS 10151) USNM 171200.

*Lamprotodus angulifer* Beebe, 1932, *op. cit.*, p. 56. 15 mi. southeast of Nonsuch, Bermuda; 500 fms.; July 27, 1931. Type: (NYZS 21667) USNM 170936.

*Lasiognathus beebel* Regan & Trewavas, 1932. Dana Rep. (1928-30 Exped.), 2: 90. Descr. based on Beebe, Bull. N. Y. Zool. Soc., 33 (2): 60 (figure), without reference to specimen. Figure taken from a specimen which should stand as the type: (NYZS 9804; KOH 287) USNM 170956.

*Leptocephalus microphthalmus* Beebe & Tee-Van, 1928, Zoologica (N.Y.), 10 (1): 58. Port-au-Prince

Bay, Haiti; March 19, 1927. Type: (NYZS 7080) USNM 170906.

*Leptophilypnus crocodilus* Beebe & Tee-Van, 1928, *op. cit.*, p. 219. Lamentin Reef, Port-au-Prince Bay, Haiti. Type: (NYZS 7467) USNM 170905.

*Leptostomias bermudensis* Beebe, 1932, *ibid.*, 13 (4): 59. 7½ mi. southeast of Nonsuch, Bermuda; 500 fms.; June 15, 1931. Type: (NYZS 20826) USNM 170937.

*Linophryne brevibarbata* Beebe, 1932, *op. cit.*, p. 94. 9 mi. southeast of Nonsuch, Bermuda; 900 fms.; July 16, 1929. Type: (NYZS 11656; KOH 973) USNM 170947.

*Linophryne quinqueramosus* Beebe & Crane, 1947, *ibid.*, 31 (4): 174. Pacific off Panama; 7° 24' N., 78° 35' W.; 500 fms.; April 4, 1938. Type: (NYZS 28709) SU 46506.

*Lipactis megalops* Beebe, 1929, *ibid.*, 12 (1): 19. Hudson Gorge; 1,000 fms.; July 28, 1925. Type: (NYZS 6633-A) missing since prior to 1932.

*Lophodolus lyra* Beebe, 1932, *ibid.*, 13 (4): 96. 10 mi. south of Nonsuch, Bermuda; 800 fms.; July 27, 1931. Type: (NYZS 21610) USNM 170949.

*Macromastax gymnos* Beebe, 1933, *ibid.*, 13 (8): 162. 8 mi. south of Nonsuch, Bermuda; 1,000 fms.; June 22, 1929. Type: (NYZS 10829) USNM 170960.

*Macrostomias calosoma* Beebe, 1933, *op. cit.*, p. 165. 12 mi. southeast of Nonsuch, Bermuda; 600 fms.; Sept. 15, 1930. Type: (NYZS 18781); missing.

*Megalodoras irwini* Eigenmann, 1925, Trans. American Phil. Soc., n.s., 22 (5): 307-308. Beebe's specimen, Indiana Univ. no. TRS 2567, was made the type of a new species which Eigenmann suppressed in proof when he found it to be a large representative of *M. irwini*, described on the following page. It is evident from his account that he intended a specimen from Iquitos collected by Allen to be the type. Beebe's fish is now in the California Academy of Sciences (CAS 20735).

*Melanocetus megalodontis* Beebe & Crane, 1947, Zoologica (N.Y.), 31 (4): 152. Pacific 145 mi. north of Clarion Island; 500 fms.; May 17, 1936. Type: (NYZS 25791) SU 46488.

*Melanonus unipennis* Beebe, *ibid.*, 13 (4): 74. 10 mi. southeast of Nonsuch, Bermuda; 700 fms.; Aug. 15, 1931. Type: (NYZS 22397) USNM 170940.

*Melauostomias bulbosus* Beebe, 1933, Copeia, 1933 (4): 166. 9 mi. southeast of Nonsuch, Bermuda; 700 fms.; May 30, 1929. Type: (NYZS 10235) USNM 170928.

*Mnierpes macrocephalus catherinae* Clark Hubbs, 1952, Stanford Ichthyol. Bull., 4 (2): 61. Piedra Blanca, Costa Rica; Feb. 4, 1938. Type: (NYZS 27178, misprinted as 28178) SU 46509.

*Mobula lucasana* Beebe & Tee-Van, 1938, Zoologica (N.Y.), 23 (3): 299. San Lucas Bay, Lower California, Mexico. Type: (NYZS 24793) AMNH 15676 and 15675 (two pieces).

- Neonesthes gnathoprora* Cohen, 1956, *ibid.*, 41 (2): 81. South of Nonsuch, Bermuda; 900 fms.; Aug. 17, 1929. Type: (NYZS 12501) SU 46381.
- Neonesthes nicholsi* Beebe, 1933, *Copeia*, 1933 (4): 160. 9 mi. south of Nonsuch, Bermuda; 800 fms.; Sept. 1, 1930. Type: (NYZS 17529) USNM 170925.
- Ophioblennius ferox* Beebe & Tee-Van, 1928, *Zoologica* (N.Y.), 10 (1): 242. Bizoton, Port-au-Prince Bay, Haiti; April 6, 1927. Type: (NYZS 7152) USNM 170901.
- Parabrotula dentiense* Beebe, 1932, *ibid.*, 13 (4): 81. 8 mi. southeast of Nonsuch, Bermuda; 800 fms.; June 12, 1930. Type: (NYZS 16110; published error: NYZS 15882; KOH 556) USNM 170952.
- Paraclinus beebei* Clark Hubbs, 1952, *Stanford Ichthyol. Bull.*, 4 (2): 81. Piedra Bay, Costa Rica. Type: (NYZS 28152) SU 46512.
- Pherallodiscus varius* Briggs, 1955, *ibid.*, 6 (1): 131. Passavera Island, Chamela Bay, Jalisco, Mexico; Nov. 19, 1937. Type: SU 17807.
- Photichthys nonsuchae* Beebe, 1932, *Zoologica* (N.Y.), 13 (4): 61. 7 mi. south-southwest of Nonsuch, Bermuda; 600 fms.; May 3, 1929. Type: (NYZS 9793; published error: NYZS 9973) USNM 170938.
- Photonectes biflifer* Beebe, 1933, *Copeia*, 1933 (4): 167. 9 mi. south of Nonsuch, Bermuda; 800 fms.; May 19, 1930. Type: (NYZS 15146) USNM 170929.
- Photonectes cornutus* Beebe, 1933, *op. cit.*, p. 169. 10 mi. south of Nonsuch, Bermuda; 600 fms.; Sept. 4, 1930. Type: (NYZS 17875) USNM 170930.
- Photostylus pycnopterus* Beebe, 1933, *Zoologica* (N.Y.), 13 (8): 163. 9 mi. southeast of Nonsuch, Bermuda; 800 fms.; May 30, 1929. Type: (NYZS 10217) USNM 170959.
- Pomacentrus freemani* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 196. Sand Cay, Port-au-Prince Bay, Haiti; May 7, 1927. Type: (NYZS 7269) USNM 170898.
- Prionotus teaguei* Briggs, 1956, *Quart. Journ. Florida Acad. Sci.*, 19 (2-3): 101. 14 mi. southeast of Judas Point, Costa Rica; 9° 19' 32" N., 84° 29' 30" W.; March 1, 1938. Type: SU 46380.
- Psanmobatus spinosissimus* Beebe & Tee-Van, 1941, *Zoologica* (N.Y.), 26 (3): 259. Pacific south of Cocos Island; 765 fms.; June 3, 1925. Type: (NYZS 6132) SU 46500. Station data given in text do not agree with *Arcturus* station 72, the published number, but with station 74.
- Pseudoscopelus stellatus* Beebe, 1932, *ibid.*, 13 (4): 75. 8 mi. southeast of Nonsuch, Bermuda; 300 fms.; July 7, 1931. Type: (NYZS 21555) USNM 170941.
- Quassiremus goslingi* Beebe & Tee-Van, 1932, *ibid.*, 13 (5): 110. Castle Roads, Bermuda; 30 feet; March 21, 1929. Type: (NYZS 8700) USNM 170563.
- Runula albolinea* Nichols, 1924, *ibid.*, 5 (4): 64. Indefatigable Island, Galapagos. Type: AMNH 8271.
- Rypticus bornoi* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 132. Lamentin Reef, Port-au-Prince Bay, Haiti; April 27, 1927. Type: (NYZS 7206) USNM 170572.
- Saccopharynx harrisoni* Beebe, 1932, *ibid.*, 13 (4): 63. 10 mi. southeast of Nonsuch, Bermuda; 900 fms.; June 11, 1931. Type: (NYZS 20802) USNM 170939.
- Scorpaenodes cortezi* Beebe & Tee-Van, 1938, *ibid.*, 23 (3): 304. Off San José Island, Gulf of California, Mexico; 24° 55' N., 110° 20' W.; April 8, 1936. Type: (NYZS 24889-A) SU 46503.
- Scorpaenodes russelli* Beebe & Tee-Van, 1928, *ibid.*, 10 (1): 189. Bizoton Reef, Port-au-Prince Bay, Haiti; 12 feet; April 27, 1927. Type: (NYZS 7207) USNM 170573.
- Somersia furcata* Beebe & Tee-Van, 1934, *American Mus. Novitates*, 730: 1. Hungry Bay, Bermuda; Nov. 12, 1933. Type: (NYZS 26165) USNM 170924.
- Stathmonotus corallicola* Beebe & Tee-Van, 1928, *Zoologica* (N.Y.), 10 (1): 249. Lamentin Reef, Port-au-Prince Bay, Haiti; April 22, 1927. Type: (NYZS 7463) USNM 170571.
- Stathmonotus lugubris* Böhlke, 1953, *ibid.*, 38 (3): 145. Port Guatulco, Golfo de Tehuantepec, Mexico; 15° 43' 30" N., 96° 08' W.; Dec. 3, 1937. Type: (NYZS 27236) SU 17748.
- Stomias fusus* Beebe, 1929, *ibid.*, 12 (1): 7. Hudson Gorge; 600 fms.; Aug. 6, 1928. Type: (NYZS 7667) USNM 170953.
- Syngnathus mackayi nesioties* Herald, 1942, *Stanford Ichthyol. Bull.*, 4 (2): 128. Nonsuch, Bermuda. Type: (NYZS 8919) USNM 170915.
- Syngnathus pipulus* Beebe & Tee-Van, 1932, *Zoologica* (N.Y.), 13 (5): 115. The Reach, Bermuda. Type: (NYZS 25152) USNM 170914.
- Tomicodon eos rhadinus* Briggs, 1955, *Stanford Ichthyol. Bull.*, 6 (1): 70. Tangola-Tangola Bay, Oaxaca, Mexico; Dec. 12, 1937. Type: (NYZS 27516) SU 18121.
- Trematorhynchus adipatus* Beebe & Crane, 1947, *Zoologica* (N.Y.), 31 (4): 163. Pacific 71 mi. off Cape Corrientes, Colombia; 500 fms.; March 26, 1938. Type: (NYZS 28770) SU 46494.
- Trematorhynchus moderatus* Beebe & Crane, 1947, *op. cit.*, p. 164. Pacific, off Cape Corrientes, Colombia; 500 fms.; March 26, 1938. Type: (NYZS 28771) SU 46492.
- Trematorhynchus multilamellatus* Beebe & Crane, 1947, *op. cit.*, p. 165. 16 mi. southwest of Narborough Island, Galapagos; 1,900 fms.; June 12, 1925. Type: (NYZS 6321) SU 46490.
- Trematorhynchus multiradiatus* Beebe & Crane, 1947, *op. cit.*, p. 166. Pacific, 11 mi. southwest of Jicarón Island, Panama; 500 fms.; March 20, 1938. Type: (NYZS 28773) SU 46491.
- Trematorhynchus paucilamellatus* Beebe & Crane, 1947, *op. cit.*, p. 166. Pacific, 20 mi. south of Cape Blanco, Costa Rica; 500 fms.; Feb. 7, 1938. Type: (NYZS 28250) SU 46489.
- Ultimostomias mirabilis* Beebe, 1933, *Copeia*, 1933 (4): 174. 12 mi. south of Nonsuch, Bermuda; 900 fms.; June 24, 1929. Type: (NYZS 10865) USNM 170932.
- Xenoceratias nudus* Beebe & Crane, 1947, *Zoologica* (N. Y.), 31 (4): 155. Pacific, 20 mi. south of Cape Blanco, Costa Rica; 500 fms.; Feb. 27, 1938. Type: (NYZS 28402) SU 46495.

## The Influence of Environment on the Pigmentation of *Histrio histrio* (Linnaeus)

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(Plates I-III)

### INTRODUCTION

THE remarkable manner in which *Histrio histrio* (Linnaeus) disappears against a background of sargasso weed, with which it is so closely associated, has long been a matter of comment by both biologists and casual observers. This condition is facilitated by the form of the fish and its pigmentation. While, as noted by Breder (1946), *Histrio* cannot be easily counted among those fishes which closely imitate specific parts of plants in the manner defined by him, its general "ragged" appearance enables it to become extremely inconspicuous against an equivalent appearance which the weed produces, although the latter is considerably different in detail. This effect, so far as form is involved, is greatly enhanced by the fish's innumerable small "tabs" of skin, assisted in a measure by the exerted rays of the pectoral fins. With pattern and coloration these features account for all the physical elements in the near "invisibility" of *Histrio*. The coloration and pattern, almost entirely caused by the arrangement and colors of the chromatophores, are the features to which this study has been chiefly addressed, since it is this system which is basically responsible for the ability of these fishes to render themselves so well concealed.

The general difficulty encountered in finding *Histrio* against a background of sargasso weed has been mentioned in many, often popular, accounts of such matters. See for example, Braam Houckgeest (1774), Ives (1889), Vignon (1931), Gordon (1938) and Breder (1949). Casual observations in the field indicate that not only do these fishes show this general resemblance to *Sargassum* but that usually an individual matches the tan or yellowish color of the

particular clump of weed on which it is found. While the range of coloration in these weeds is not great, there is sufficient variation to make such differences easily noticeable. Normally the fish are not found in other than living clumps of floating weed. Clumps which have been cast on the beach and refloated by a returning tide, after having been killed and dried in the interim, are much darker brown or sometimes nearly black. These have always been found to be devoid of *Histrio*. Thus these fishes are evidently not ordinarily called upon to respond other than to a limited range of color and pattern, as compared with the backgrounds against which most other color-matching fishes are exposed. For this reason, experiments were planned to determine the limits of the range of chromatic changes possible in *Histrio* as compared with the range of background which they ordinarily encounter, and in reference to the kinds and arrangements of the chromatophores with which they were provided.

The related various species of *Antennarius*, which are capable of much greater color and pattern changes, including brilliant reds, greens and yellows, are discussed comparatively with *Histrio*. Originally it had been planned to carry out an identical series of experiments on *Antennarius*, but, as is developed in the concluding remarks of this paper, it became unnecessary to do this for present purposes.

Most of the field observations mentioned herein were made while at The Lerner Marine Laboratory, on North Bimini in the Bahamas. All of the experimental studies were carried on in the laboratories of the Department of Fishes and Aquatic Biology of the American Museum of Natural History in New York. The living

material established there was collected at Bimini, some by Dr. Louis Krumbholz and some by Dr. Vladimir Walters. Dr. Walters also kindly supplied certain field data pertinent to these studies. The necessary sea water was obtained through the kindness of Mr. C. W. Coates, Director of the New York Aquarium, for which we are grateful. The description of the pigmentary systems involved are mostly paraphrased from notes prepared by Miss Priscilla Rasquin who was working at the time on the reproduction and embryology of these same fishes, reported in Rasquin (1958). The plastic films employed in some of the experiments were supplied by the Visking Corporation, New York City, through the kindness of its representative, Mr. Ronald Basso, for which we are most appreciative.

#### EXPERIMENTAL BACKGROUNDS AND RESULTS

All of the following experiments were carried out in seven aquaria, each of which measured 2 ft. long by 1 ft. by 1 ft. These were supplied with the running sea water in a small circulating system set up especially for these experiments and described in detail by Breder (1957). The water used in the laboratory aquaria was obtained locally, most of it through the cooperation of the New York Aquarium at Coney Island. This was concentrated by evaporation to the approximate density of the water in which the fish were received, and held between 24° and 29° C., usually near 25°. The floors of these aquaria were covered about one-half inch deep in whitish calcareous sand from North Bimini. This served a practical maintenance purpose, as described by Breder (1957), and took on a reflected tint of the particular plastic shields employed. It was necessary to clean this sand periodically for both sanitary and chromatic reasons. The illumination used was entirely artificial and consisted of fluorescent tubes, of the so-called "warm white" type which are generally suitable for small aquaria in that they permit the satisfactory growth of green plants. This light source was directly overhead.

As *Histrio* customarily climbs about in sargasso weed, it was felt advisable to provide some sort of structure which would provide approximately similar support for such activity. Most of the larger marine algae, especially *Sargassum*, are difficult to maintain satisfactorily in small aquaria and in any case would interfere with the artificial chromatic arrangements. Therefore artificial supports of small glass rods 8½ in. high were built in the form of a tripod with extended arms of lesser-sized rods, as is shown in several of the plates. These were colorless in themselves

and sanitary and at most reflected or refracted the color of the surrounding plastic shields. The spontaneous growth of adherent algae made it necessary to clean them periodically.

All the fishes were obtained from sargasso weed floating in the sea near Bimini. The smallest were shipped to New York by air express in the conventional plastic bags now in general use by aquarium dealers. Because of their well known voracious appetites, the fishes were kept separated by glass partitions in the tanks. They were fed daily with live *Lebistes reticulatus* Peters, *Astyanax mexicanus* (Filippi) and *Tilapia heudeloti* (Bleeker) of sizes suited to the individual *Histrio*. Most of the individuals were induced to accept cut up pieces of *Tilapia* and *Astyanax*.

Two sets of experiments were carried out, both in an effort to determine the extent of influence of the colors seen by the fishes on their pigmentation. In the first set, sheets of colored plastic were placed against the outside of the four glass walls of the aquaria. Matching strips of plastic were placed inside each corner of the aquaria to mask the blackish aquarium cement used to hold the glass sides in place. This plastic, a vinyl chloride-acetate copolymer to which pigment had been added, was first thoroughly tested, in each of the colors used, for possible biological effects and found to be entirely satisfactory. Since the colored plastic sheets, ¼" stock, were somewhat translucent, transmitted light as well as that reflected from the inner surface of the sheets enhanced the chromatic values obtained.

In the second set of experiments the same aquaria were used, modified in the following way. The protective shields of colored plastic were removed and the tripods were wound with colored strips of polyethylene sheeting of 0.1 mm. or less in thickness. These, too, had been tested for biological effects and found to be satisfactory. A lesser variety of colors was employed for this series, because certain results in the first series had demonstrated some to be quite unnecessary. All other details were identical with those described for the first series except that corner strips were not necessary in the black aquaria, since the corners were already black. The polyethylene fringes for the glass tripods were made as follows. Plastic strips 1¾ in. wide were folded lengthwise. Repeated cuts were made in these at right angles to the fold by small scissors. The cuts were made from the edges which had been pressed together in folding so that the cuts nearly reached the line of fold. One end of such a fringed strip was then knotted to the lower end of the tripod and wrapped up

it spirally. Others were attached to the cross rods. The finished appearances of these structures are shown in Plate I. It was found that the fishes made considerably more use of the tripods when so decorated and frequently nestled in this imitation sargasso weed, often disappearing as completely as they do when nestled in the natural plant.

The purpose in the design of these two series of experiments was to make a distinction, if any existed, between a general over-all coloration of the environment as compared with the details of the weed in which the fish nestle. In a state of nature, all that these fish normally view is the more or less checkered sargasso weed and its other closely matching attendant organisms in the bluish void of the lateral viewing of the open ocean. This is only interrupted by the comparatively infrequent appearance of some passing larger fish or smaller food object. In the first case it was the general over-all water color that was changed by the slightly translucent

plastic shields, while in the second case the colors of the "weed" itself were modified.

A schedule of the period of days in which the various individuals occupied the different aquaria is given in Table 1, covering both the first and second series. In all, 42 individuals were used in these experiments, 19 of which may be considered as controls, that is, fishes kept in clear glass aquaria and not exposed to specific colors as previously described. The 23 remaining fishes were exposed for varying times and under other differing conditions to these especially prepared colors. In addition to black and white, four colors were employed for this purpose: red, yellow, green and blue. There was one aquarium so shielded by each of the six plastic shields above named. No attempt to define these colors in terms of wave length has been made, since this refinement appeared to be quite unnecessary for the purposes of the project, and as it was well known in advance that these fishes could match a fair range of sargasso

TABLE 1. EXPOSURE OF *Histrio* TO VARIOUS COLORS, IN DAYS

Fish number	Aquaria						
	Clear	White	Yellow	Red	Green	Blue	Black
1	54						←85
2	19➤	83					
3						20	
4						66	
5						13	
6				183			
7				14			
8				178			
9			48		80➤		48➤yellow
10			54		80➤		48➤yellow
11			42		80➤		48➤yellow
12			128➤blue		25	←29	
13			127				
15	3➤black				101		←77
16	2➤	18					
19	5➤	118					
21	5➤					62	
23	5➤		147➤32f				
26	5➤						71➤82f
32	3➤					48➤114f	
35	3➤						54➤82f
36	3➤	101					
37	3➤		55➤117f				

NOTE. Arrows indicate direction of change to another color, named where necessary.

"f" indicates tripod has fringe of color indicated.

In addition to the above 23 numbered individuals there were 19 controls as follows: 14, 17, 18, 20, 22, 24, 25, 27-31, 33, 34, 38-42.

There is no indication of number of companions,

if any, nor of shifts without color change, incident to operations in this tabulation.

The fishes arrived and were placed in the aquaria indicated according to the following tabulation.

Nos. 1 to 3, 3/22/56	Nos. 29 to 37, 12/25/56
Nos. 4 to 16, 5/1/56	Nos. 40 to 41, 5/27/57
Nos. 17 to 28, 12/6/56	No. 42, 6/23/57

weed hues. The fringed tripods were prepared in yellow, blue, black and clear, while red developed spontaneously by the overgrowth of a red alga on a tripod fringed with clear plastic. Five fish were used in connection with these decorated tripods, most of which had been previously exposed to plastic shields of the same color. The days spent under each condition and the sequence of change are given in Table 1. Other details are given in the text where they are pertinent. The missing numbers of individual fishes refer to the controls, which were maintained in ordinary aquaria up to 193 days.

The details of the experiments indicated in summary in Tables 1 and 2 are as follows, arranged by color and followed by those concerned with changed colors.

**Black.**—The four fish exposed to black in the manner described all gave clear and definite reactions. They all were very dark by the time they had been continuously exposed for 2 to 3 weeks. The resulting darkening for Fish No. 1 and Fish No. 26 is shown in Plate I after exposures of 30 and 103 days respectively.

**Yellow.**—The ten fish exposed to yellow all showed an appropriate change in a more yellow over-all appearance and a lessening of pattern detail. This was, however, not nearly as pronounced as in the case of the black backgrounds, partly, at least, because the yellow backgrounds called for less of a change from the initial condition of the fishes than in the former. In Plate I, Fish No. 13 and Fish No. 37 are shown with plain and fringed tripods. These illustrations were made after the fish had been exposed for 38 and 85 days respectively.

**Red.**—The differences between the unexposed fish and those exposed to red were slight and somewhat uncertain and could not be detected in a black-and-white photograph. Consequently no illustrations are given covering these three fishes.

**Green.**—While there was no evident response to green, three fish which were simultaneously exposed to green for 79 days are shown in Plate II. These three fish, Nos. 9, 10 and 11, all showed different basic patterns when introduced into this single partitioned aquarium and maintained them throughout the study. The possible significance of these patterns differs. Two other fish, Nos. 12 and 15, the latter having first been exposed to black, were also exposed to green, making a series of five fish. All performed in an essentially similar manner, including the black fish, No. 15, which, while lightening slightly, agreed with the rest in showing no direct response to green. The lightening was very limited, as would be expected because of the size

TABLE 2. SIZES OF VARIOUS INDIVIDUAL *Histrio* AT PARTICULAR TIMES

Fish number	Size on arrival	Size when photographed	Date when photographed	Figure number
1			4/20/56	1
26	18	65	3/19/57	2
13			6/7/56	3
37	25	77	3/19/57	4
9			7/18/56	5
10			7/18/56	5
11			7/18/56	5
2			5/2/56	6
14			5/2/56	7
28	15	48	1/4/57	8
29	43	65	2/26/57	10

NOTE. All measurements are given as millimeters in total length. Dates of measurements are approximate.

and age of the fish which had long passed its peak of maximum response to background colors.

**Blue.**—Six fish, Nos. 3, 4, 5, 12, 21 and 32, were exposed to blue and showed absolutely no tendency to approach that color. It seemed that the fishes did not thrive nearly as well in the blue aquarium as in the others, several early deaths appearing which it was thought might have been in some obscure fashion connected with the color involved.

**White.**—The four fish exposed to white, Nos. 2, 16, 19 and 36, all showed either a definite lightening or an evident great increase in brilliance in the white spots made up of crowded leucophores, or both. There was no close approach, however, to white in any real sense. Indeed, this would have been very difficult, for even if all the chromatophores could be reduced, it would require a tremendous overgrowth of leucophores to mask the underlying tissue colors. Plate II, fig. 6, shows Fish No. 2.

**Clear.**—In addition to the two fish, Nos. 1 and 2, there were 19 "control" fish not listed in Table 1 which were kept in similar aquaria. The long series of fish kept in clear aquaria from 2 to 5 days were held there merely preparatory to transfer and the periods were too short to have any bearing on these experiments. All these fish changed less than those which were exposed to colored backgrounds, which gives support to the significance of the colors to the chromatic changes observed on the experimental fishes. Plate II, fig. 7, and Plate III, fig. 8, show Fish No. 14 as kept in an ordinary clear glass aquarium and Fish No. 28 in association with clear fringe.

## THE PIGMENTARY SYSTEM AND ITS LIMITATIONS

The following descriptions cover the kinds and distribution of the chromatophores and related structures as viewed on the living fishes through stereoscopic dissecting microscopes. These features cover the mechanism by which color and pattern changes are effected in *Histrio* and the cellular types present give an effective measure of the limitations present in their particular chromatophore system.

The pigment cells present are of three kinds only, melanophores, xanthophores and leucophores. The xanthophores are deep yellow, nearly approaching orange. The leucophores show no iridescence, all being of the milk white type.

The typical condition found in *Histrio*, with little variation, is as follows. The most deeply pigmented patches in the dermal pattern seem to be composed entirely of melanophores and xanthophores. If there are any leucophores present in these areas they are evidently completely obscured by the overlaying of the more deeply colored cells. Both the melanophores and xanthophores are small in size, but exceedingly numerous and very closely crowded together in the darker areas of the skin. The sharpness of the pattern shown by *Histrio* is accentuated by the abrupt ending of the more heavily pigmented areas, which have very sharp lines of demarcation between them and the lighter areas of the pattern. In the latter there are few, if any, straggling melanophores or xanthophores. Some leucophores are present in these clear areas, but they are sparse, to the point where the vascularization of the dermis can be easily distinguished. The coloration of these lighter areas is based to a large extent on the nature of the underlying tissues, including principally a reddish suffusion of the blood, a pale yellowish from fat and a whitish tint from the muscles. The opaque white spots are composed entirely of tightly packed leucophores. All these features are displayed in the post dorsal area of skin shown in Plate III, fig. 9. Although this picture was taken of a freshly formalin-fixed fish, it is still typical of the living animal.

In fishes which have become nearly entirely black, as Fish Nos. 1 and 26 of Plate I, figs. 1 and 2, there has clearly been an enormous increase in the number of melanophores. The greatly reduced clear areas contain straggling cells of both melanophores and xanthophores and the line of demarcation between the originally dark and clear areas is not nearly as sharp as in the lighter-colored fishes. Some of the remaining white spots contain xanthophores as well as leucophores while others remain as colonies of pure leucophores.

Fishes which have become more yellow, as Fish No. 37 of Plate I, fig. 4, show more clear spaces than the controls. Straggling xanthophores are found in these spaces but no melanophores. None of either were found in the white spots. The xanthophores are of a particularly brilliant orange hue.

It seemed that fishes which had been kept in a red aquarium just barely suggested a slightly reddish hue, but this was too indefinite to be rigidly established. Fish No. 8, which had been kept in a red aquarium for 178 days, was such a case and its faint but seemingly reddish hue was evidently caused by its deeply colored xanthophores, combined with many black melanophores. The particular adjustment between them may indeed have been as far as the fish was able to go in the direction of matching a red background with its rather limited chromatophore system. The yellow fish above mentioned has its intense yellow caused, not by paler xanthophores, but by more of them and fewer melanophores than Fish No. 8. Xanthophores on the black fish, No. 1, are mostly covered by the very numerous melanophores, but what few were visible were definitely paler than on the other fishes.

It should be noted in these connections that the presence of the white patches formed of massed leucophores sometimes gives a false sense of color, as they take on the hue of their surroundings, making a fish on yellow, for instance, appear to be yellower than it actually is. This effect helps enhance background matching in a purely passive way. Because of this condition, caution was taken in the observations to make necessary allowances, often by viewing the fishes against a neutral gray background instead of the background of the colored containers.

While it is clear that the colors can and do change considerably in reference to the background, differences in pattern, which are evidenced in the smallest individuals obtained, do not vary to any noticeable extent except as certain markings may be obliterated by masking, as in the very dark color phases. The basic design on each fish seems to be fixed for life. Whether this pattern is largely genetic or largely fixed at a very early stage, at sizes as yet not obtainable, is still unknown.

As in all fishes showing marked ability to change their coloration, there are two elements in the response which must be distinguished in order to proceed with a satisfactory discussion. The rapid changes, sometimes almost instantaneous, are all due to prompt reactions involving the dispersal or concentration of the chroma-

tophore pigment granules. These, while striking in their speed and extent, are not as profound as those which take a longer time to appear, covering periods of weeks or months. The first kind are under the immediate control of the nervous and hormonal systems and the reactions are at speeds consistent with those systems. The slower type is based on the development of more color cells and thus involves a true morphological modification. The color changes here under consideration all refer to the second or morphological changes, as many days are involved in their development. *Histrio* is capable of making sudden changes in coloration but it is not, as a species, especially marked in this direction. When sudden change does occur, it is more apt to be associated with some influence other than background—as for example during breeding periods when radical changes in coloration sometimes appear for short periods. These changes are sometimes striking to the eye but are not nearly as fundamental as the great increase in the numbers of melanophores which an individual will develop against a black background.

#### DISCUSSION

It is shown in the preceding sections that *Histrio* responds rather slowly, but very definitely, to colors in its surroundings. These responses are evidently rather severely restricted to the colors found in sargasso weed, or perhaps with little extensions of them into blacks and yellows. This situation is evidently a matter of the physical limitations of the chromatophore system. Whether there is also a behavioral limitation involved, of course, cannot be verified by direct experimentation. Since, however, the not distantly related *Antennarius* can, in various of its species, show a much greater range of chromatic adjustment and necessarily has a larger number of types of chromatophores, it would seem that *Histrio*, if not so restricted by its chromatophore system, should be able to do as well. This view is supported by the excellent matching effect which *Histrio* attains with its limited chromatic abilities within the environment with which it is normally associated.

Nearly all of the individuals of *Histrio* encountered in the field are found in close association with *Sargassum*, both from personal observation and the reports of collectors and the literature. The initial observation, which prompted the undertaking of the experiments herein described, was made in an aquarium in the Lerner Marine Laboratory. This tank, which had a light sand bottom, had been painted black on its back and two ends. Into it had been inad-

vertently dropped a very small *Histrio* incident to some entirely unrelated operations, on November 15, 1954. The only other contents of this  $3 \times 1\frac{1}{2} \times 1\frac{1}{2}$  foot aquarium were the light sand bottom and a dozen or so small *Sardinella*. There was no *Sargassum* or other floating weed. The small *Histrio* usually was to be seen wedged in a corner near the surface. This fish, originally of the usual coloration and pattern, by December 3 was a perfect match for the dead black background against which it had been living. Not only was the black background matched perfectly but there appeared on the sides of the fish a few small milk-white spots, which were the size and shape of a scattering of equally white volunteer calcareous growths on the black glass. The resemblance of the white spots to the growths may have been purely accidental, as these fishes normally display some milk-white spots which usually go unnoticed in their otherwise mottled pattern. However, as was noticed in the later experiments, the very smallest fishes made the most striking adjustments to background, whereas the larger in no case did nearly so well. It is possible that the size and shape of the white spots on the fish above described were pattern adjustments, beyond the capabilities of the considerably larger fishes studied later. It may be that much greater adjustment to both colors and pattern of background is a capability of these fishes at sizes well below those ordinarily obtainable. It would certainly be desirable to work from the transparent planktonic larvae just before they settle in the *Sargassum* in any attempt to analyze the potentialities of smaller fish. Such material is not obtainable by any presently known means.

Aside from this fish that turned black in an aquarium, there appears to be no previous record of black *Histrio*. Three years later the following observations were made near the laboratory. These constitute the only known occurrences of black *Histrio* in a state of nature and have a very distinct bearing on the present experiments. Dr. Vladimir Walters, working on other matters, collected three such black *Histrio* on March 30, 1957, in one of the passages through the mangrove stands along the south side of South Bimini. The specimens were subsequently lost in shipment, but he described them as closely resembling the most thoroughly black fishes developed in the laboratory. Although many persons working out of the Lerner Marine Laboratory had collected in this same place and in many others basically similar to it, there have been no other reports of *Histrio* in these places whatever. In the present case, rotenone was used in collecting, which may be responsible for find-

ing them at all. It is to be noted that especially heavy weather the preceding month had brought quantities of sargasso weed closer to the mangrove stands than usual.

The presumed fate of these black *Histrio*, stranded in a mangrove swamp and living against a very black background, would seem to be obvious enough even if the precise reasons are not clear. In the light of aquarium observations, it would seem that such fish should be able to manage well enough, by taking on the habits of an *Antennarius*, which is something they may approximate in an aquarium without artificial weed. That they are not very successful in mangrove swamps is evidenced by their normal absence from such places. At least, it would appear that this is not based on any inability to match the mangrove background. It could be that there is some element in the mangrove association with which they are unable to cope. This could conceivably be the frequent abundance of large callinectids, so often found in such associations. If actual destruction of the fishes did not take place by some such means, it is conceivable that the fish might escape back to their normal environment, a seemingly unlikely event. The general reluctance of fishes to leave a background to which they are chromatically adjusted would have to be overridden at some stage in any attempt to work out of a mangrove stand. There are no available step-by-step environmental niches through which they could make an easy transition from mangrove-black to sargasso-mottled, especially in view of the sluggishness of their chromatic adjustments.

The ability of *Histrio* to assume the behavior usually associated with *Antennarius*, as above noted, was nicely demonstrated by one that was placed in an aquarium where the sole fitting was a small shell, *Melongena*. This it associated with to the extent of spending much time huddled against it or even within the mouth of the shell. A typical posture of this fish is shown in Plate III, fig. 10. Not only were the postures reminiscent of *Antennarius* but often the movements of the pectorals and the creeping about on the aquarium floor resembled the movements of that genus rather than *Histrio*. As might be expected, the darker markings of this fish took on a brown hue very close to that of the brown markings around the lip of the shell.

The formal experiments agree well with the field observations and of course show that *Histrio* is well able to make chromatic adjustments involving mottled patterns from black through various brown and yellowish tans to a fair yellow. Also because of the islands of leucophores,

they are able to take on the appearance of overlaid whitish patches, not unlike various of the sessile epizootics on *Sargassum*. Actually this range goes little further than covering the range of possibilities of this somewhat variable weed but to which can be added any dominantly black environment such as a mangrove swamp. Other backgrounds do not yield such striking results. Green and blue, which are the backgrounds which one would expect to call for the presence of iridophores and combinations of chromatophores into chromatosomes, yielded no recognizable response. Red, which might be expected to call for erythrophores, which too, are absent, yielded only questionable response of a slight sort. Actually what appeared to be a slight response was caused by a particular mixture of melanophores and xanthophores. This indeed may have been a tendency to produce a red color but one impossible of attaining any real success with the pigments present. White and clear, the latter in the form of plastic fringes, caused only a general lightening of the fish, *i. e.* a reduction in the number of melanophores and xanthophores with perhaps some increase in the number of leucophores. While this results in a better matching than red, green or blue, it is not in the same class at all with the effects induced by black or yellow.

It is interesting in the above connections to consider the three fish shown in Plate II, fig. 5. Not only do they show marked differences in pattern but also at least equally marked differences in amounts of pigmentation. As may be seen in the photograph, the fish at the left showed a comparatively heavily pigmented pattern of broad blotches while the central fish showed conspicuously less pigmentation and the right hand fish showed pigmentation comparable to that of the left hand fish but in a much finer pattern. It would seem almost that these fishes either reacted in no way at all to the green color and retained whatever tendency they had been impressed with before capture, or that they each reacted in a distinctly different manner to a common background which was neither very light nor very dark. It is evident in any case that this color green, to which so many fishes respond by matching, is evidently completely out of the chromatic reactivity of these fishes which respond so markedly to the yellow browns of the weeds which they normally inhabit.

In these studies, several fish showed aberrations in their chromatic behavior that are not easily explained, the details of which are given in the preceding section. These would all appear to be due to some derangement in the complex system responsible for fishes responding with

their pigmentary effectors from colors thrown on the retina, as the mediating receptor. This is too poorly understood and too complex a matter to be discussed in present connections, except to suggest that these sometime reverse responses may be at the basis of the cause which impels a fish to change from a background-matching habit to one of background-opposing. Influences bearing on these two diametrically opposed reactions to background are further discussed by Breder & Rasquin (1955) and Breder (1955) in reference to other fishes.

While it has been impossible to obtain sufficient material of *Antennarius* to perform a set of parallel experiments, observations on these fishes show them to have chromatic possibilities far exceeding that of *Histrio*. Barbour (1942) and Schultz (1957) indicated the highly variable coloration and pattern differences seen in these fishes. Individuals of *Antennarius multiocellatus* (Cuvier & Valenciennes) have been seen to vary through shades of red, vivid green, brilliant yellows, black and gray or brown mottlings. These are believed to represent only a few of the chromatically possible arrangements of which this particular species is capable. Not only does this species, at least, show such background-matching proclivities, but may alternate it with background-opposing coloration. The behavior of one individual in regard to this latter feature is discussed by Breder (1949). It is to be noted in reference to the above that this behavior in *Antennarius* was found to occur in environments where a variety of other fishes also show the background-opposing response.

An examination by Dr. Walters, of the pigmentary system of a freshly fixed specimen of *Antennarius ocellatus* (Bloch & Schneider) from the Dry Tortugas, showed the following conditions. This fish, still pinkish in coloration, possessed melanophores, erythrophores and leucophores, but no xanthophores or iridophores. A full study of the presences and absences of the various chromatophore types should be interesting and illuminating.

These considerations lead to the idea that *Histrio* certainly descended from some form less restricted as to habitat, that it had an ancestor with greater chromatic range, perhaps similar to that found in *Antennarius*, and that therefore the condition presently found in *Histrio* is to be considered one of loss of certain pigmentary elements. Schultz (1957) considers *Histrio* and *Antennarius* as derived separately from what he calls "antennariid stock" rather than as having any closer relationship. That these retained pigmentary elements permit the fish little ability to change color outside the range of those found in

*Sargassum* certainly suggests a long-time association between the two. Also in reference to the *Histrio* in the mangrove swamp, it further suggests that such occurrences are probably very rare and are likely terminal wastage rather than some obscure but normal alternative open to these fishes in the ordinary run of their lives.

#### SUMMARY

1. *Histrio* has little ability to match backgrounds outside of the range of colors displayed by *Sargassum*.
2. Black is well matched and yellow not quite so well while with other colors attempts to match are absent or negligible.
3. The only chromatophores present in the integument of *Histrio* are melanophores, xanthophores and leucophores, a condition which in itself is perhaps sufficient to explain the restricted chromatic ability of these fishes.
4. The related *Antennarius* is capable of much greater chromatic adjustment because of the presence of other types of chromatophores and is found to inhabit places which expose it to backgrounds which show a correspondingly greater range of colors.
5. It is inferred that *Histrio* descended from a chromatically more competent ancestor and the present chromatophore complement is one of loss and indicates a long association with *Sargassum*, in which these present elements have sufficed.

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## EXPLANATION OF THE PLATES

Note. In all photographs of living *Histrio* a temporary background of a neutral gray card was substituted for colored plastic shields, except in Plate 2, fig. 5, in which the green plastic shield was left in place. In all but the excepted case this was necessary to make these fish sufficiently visible for photography. It is to be especially noted that in reduction to monochrome the pictures lose much of the effective resemblance these fishes exhibit toward their colored backgrounds.

## PLATE I

*Histrio* after exposure to black and to yellow

- FIG. 1. Fish No. 1 after 30 days behind black shields.  
 FIG. 2. Fish No. 26 after 82 days with black-fringed tripod.  
 FIG. 3. Fish No. 13 after 38 days behind yellow shields.  
 FIG. 4. Fish No. 37 after 85 days with yellow-fringed tripod.

## PLATE II

*Histrio*; various exposures

- FIG. 5. Fishes Nos. 9, 10 and 11 after 79 days behind green shields, showing basic pattern differences.  
 FIG. 6. Fish No. 2 after 23 days behind white shields.  
 FIG. 7. Fish No. 14 the day after arrival, for comparison with the experimental fishes.

## PLATE III

*Histrio*; chromatic and behavior details

- FIG. 8. Fish No. 28 after 85 days with clear-fringed tripod.  
 FIG. 9. Magnified area at dorsal base on the right side of Fish No. 12 showing the main features of chromatophore cell types.  
 FIG. 10. Fish No. 29 after 64 days' association with a shell.



FIG. 1



FIG. 2

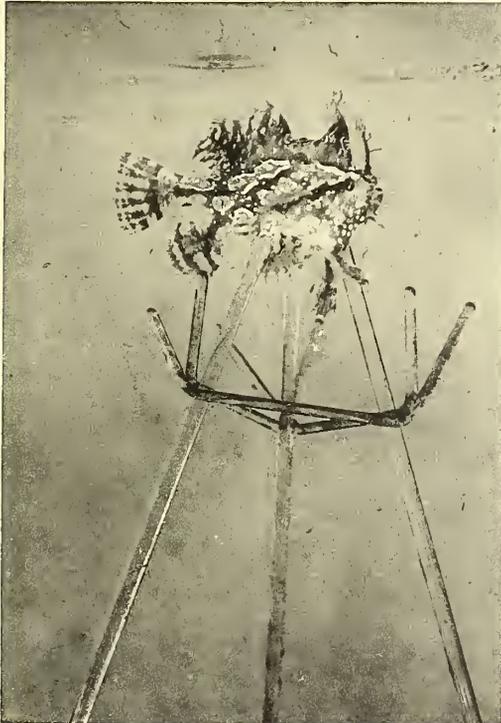


FIG. 3



FIG. 4

THE INFLUENCE OF ENVIRONMENT ON THE PIGMENTATION OF HISTRIO HISTRIO (LINNAEUS)



FIG. 5

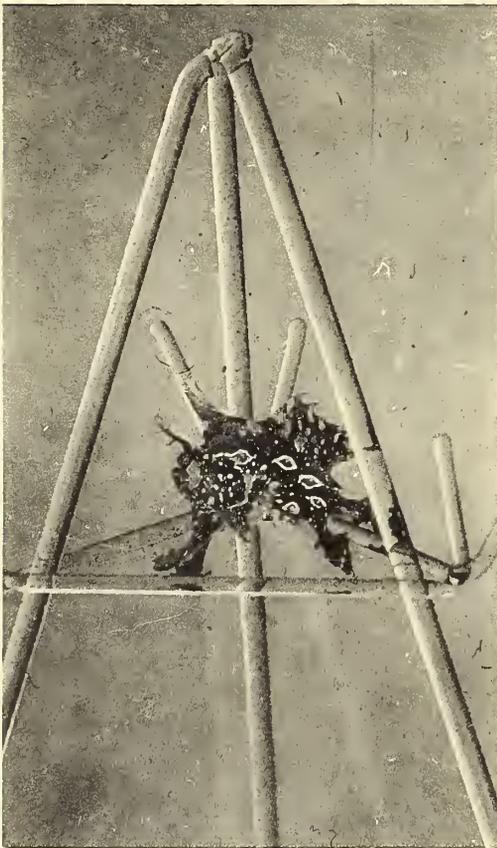


FIG. 6

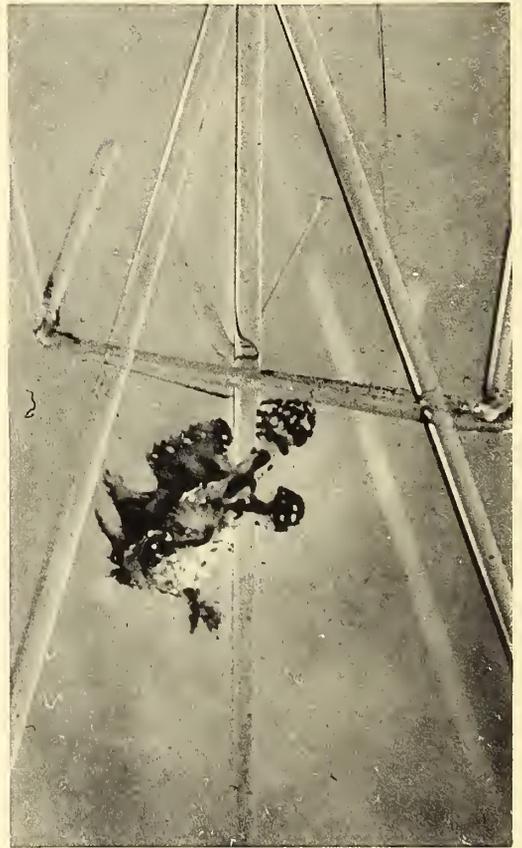


FIG. 7

THE INFLUENCE OF ENVIRONMENT ON THE PIGMENTATION OF HISTRIO HISTRIO (LINNAEUS)

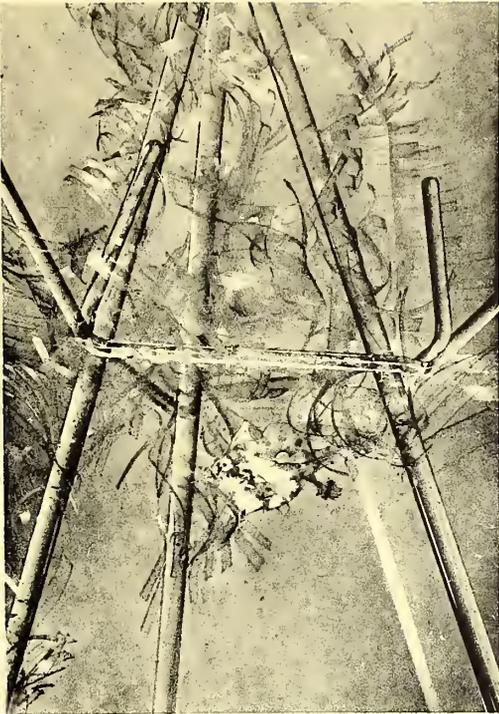


FIG. 8

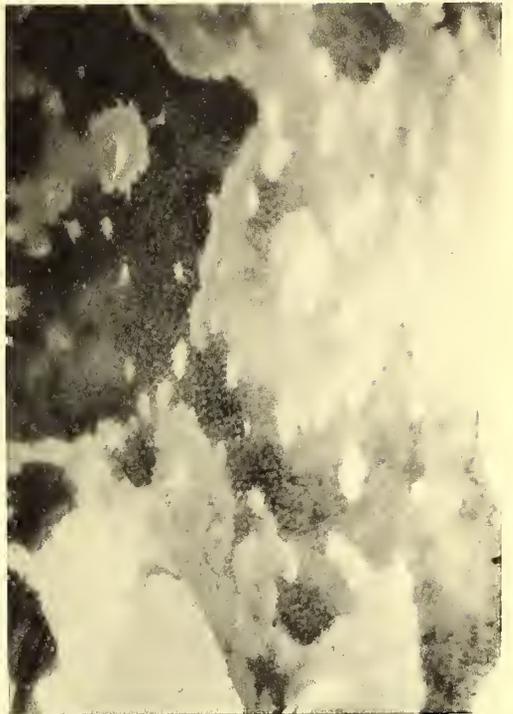


FIG. 9

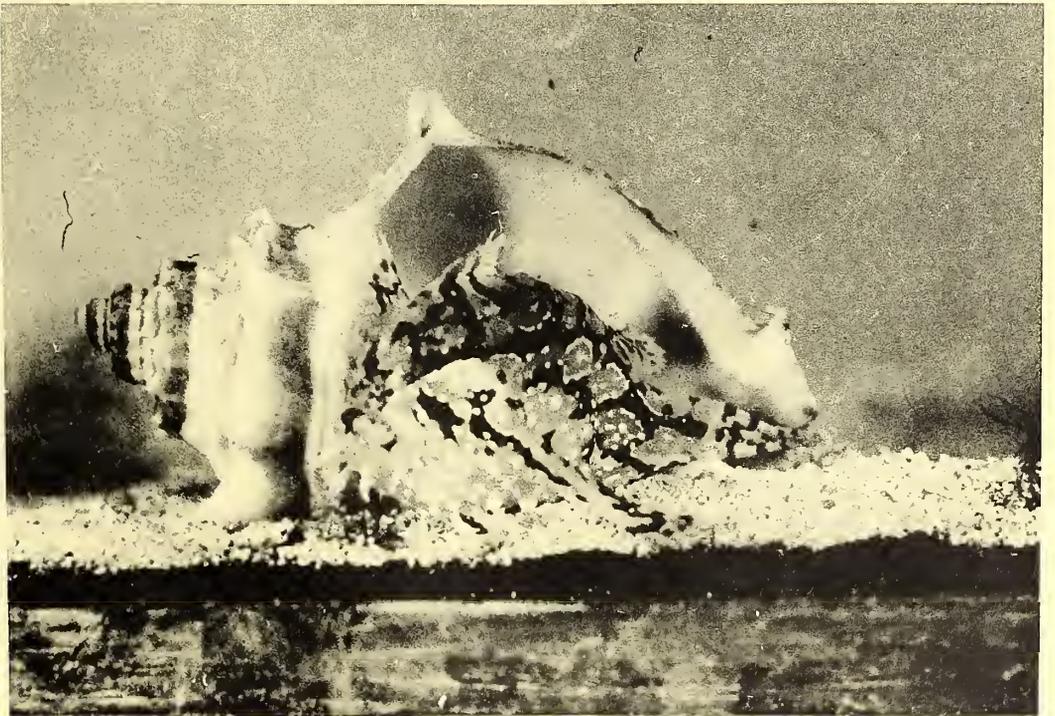


FIG. 10

THE INFLUENCE OF ENVIRONMENT ON THE PIGMENTATION OF HISTRIO HISTRIO (LINNAEUS)



Studies on the Histology and Histopathology of the Rainbow Trout,  
*Salmo gairdneri irideus*. I. Hematology: Under Normal  
 and Experimental Conditions of Inflammation<sup>1</sup>

EVA LURIE WEINREB

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(Plate I)

**M**OST studies in comparative hematology have been limited to descriptions of the staining properties of fixed cells. The present study was made on living blood cells of the rainbow trout, *Salmo gairdneri irideus*, using phase contrast microscopy, to further elucidate physiological as well as morphological changes under experimental conditions. Such changes were compared with similar effects reported in more common laboratory animals.

The circulatory system of the rainbow trout is sensitive to foreign stimuli and reflects the homeostasis of the animal. Changes in the blood picture were used, therefore, as criteria of systemic response to experimental conditions. Before such changes could be evaluated, the normal blood picture had to be determined and a standard established.

Descriptive studies of teleost blood cells of various species have included perch (Yokoyama, 1947), carp and brook trout (Dombrowski, 1953) and salmon (Watson *et al.*, 1956). Detailed reports on rainbow trout have not been found. The response of leukocytes to various irritants has been described for many laboratory animals including dogfish shark (Reznikoff & Reznikoff, 1934), turtle (Charipper & Davis, 1932; Ryerson, 1943), perch (Yokoyama, 1947), mice and rats (Harlow & Selye, 1937). The influence of adrenal cortical hormones and ACTH on circulating leukocytes in mice, rats and rabbits has also been described (Dougherty & White, 1944; Palmer *et al.*, 1951). The rela-

tion among leukocytes, ACTH and adrenal cortex was reviewed by Sayers (1950).

Although the blood-forming centers in fish differ from those found in mammals, and the individual cells vary between the classes, the author is retaining such terms as myeloid, myelocyte and lymphoid in order to be consistent with literature on fish hematology and to describe the various stages in granulocyte maturation in the fish as compared to similar well-defined stages in mammals. The prefix myelo- in this text is used not in reference to bone marrow, but to granulocytic as distinct from lymphoid elements.

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#### NORMAL BLOOD PICTURE

##### Materials and Methods

The animals used for all studies were from the same hatching group (October 9, 1953). Fish were delivered from the Nevins State Fish Hatchery, Madison, Wisconsin, to the University of Wisconsin Lake Laboratory and maintained in oxygenated water at 12-12.5°C. for several days so they might become acclimated to the experimental tanks. The trout, of both sexes, averaged 15 cm. fork length and 50 gm. weight. The age ranged from 12 months at the start of this study to 21 months at its completion.

<sup>1</sup>A revised portion of the thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Wisconsin.

Since the variability of cell counts is great, each experimental group consisted of animals kept under the same conditions and of the same age and approximate size. After severing the tail, blood samples were collected from the haemal vessels, using no anticoagulants, and each animal was autopsied, with particular attention being paid to the hemopoietic structures. All trout used were in normal condition as far as could be determined.

Living blood cells were studied and counted by phase contrast microscopy, using a dark contrast-medium oil immersion objective. Wright's stained smears were used for comparison (Plate I). The former method was found to afford greater accuracy of identification and precision in counting, the artefacts of staining and loss of fragile heterophils being minimal. Total red and white cell counts were made (Yokoyama, 1947), in order to determine the total number variability in different animals under normal and experimental conditions. Since the erythrocyte count did not exhibit significant change, it was used as the basis for the differential leukocyte counts: all leukocytes within the range of 300 red blood cells were counted. The cells counted included heterophils, lymphocytes and thrombocytes; the number of eosinophils and basophils was negligible, and monocytes were absent.

## Results

The criteria for cell identification in phase studies include size, shape, degree of motility, nuclear-cytoplasmic ratio, nuclear size and shape, chromatin pattern, cytoplasmic granulation and mitochondria.

The mature erythrocyte is oval and nucleated, with abundant cytoplasm containing many very small, motile mitochondria. The smaller, rounder polychromatophilic erythrocyte differs in having less hemoglobin and a heavier nuclear membrane, similar to that of the lymphocyte. Lymphocytes are the most abundant, being smaller and rounder than the red cell, often exhibiting pseudopod formation. The round or slightly indented nucleus is surrounded by a thin rim of cytoplasm with motile, rod-shaped mitochondria. The outstanding feature of the lymphocyte is the nuclear pattern; the chromatin forms a distinct network of alternately dark and highly refractile, light areas.

In the highly amoeboid heterophil, the partially lobed nucleus is in almost continuous rolling motion, while, after staining, the nucleus is lobed or ribbon-like. The cytoplasm, which exhibits continuous streaming and pseudopod formation, is filled with granules and filamentous

mitochondria. Cells comparable to myelocytes and metamyelocytes are not uncommon and may be distinguished from the mature heterophil by being less motile and round to oval in shape, with a more rounded nucleus and less granulation. The myelocyte is smaller and more rounded than either of the older cells. In both immature cell types the nucleus exhibits a folding motion with wrinkling of the surface, rather than the distinct roll of the heterophil.

Although thrombocytes are usually in the blebbed state, intact cells are visible. Young cells are similar to lymphocytes, although smaller and rounder. Mature thrombocytes are elongated. In contrast to the lymphocyte, the cell may be identified by its indistinct chromatin network, paucity of cytoplasmic granules and barely motile mitochondria.

Occasional eosinophils and basophils are seen. Eosinophils are slightly larger than lymphocytes, with numerous, extremely refractile, spherical granules. The basophil, which is the largest leukocyte, has an eccentric spherical nucleus, indistinct chromatin and a very prominent nucleolus. The large, round cytoplasmic granules are characterized by an internal, laminated or striated pattern.

Macrophages, which are not usually found in a normal blood smear, are prominent in bacterial and other infections. These cells are the largest in the circulation, being twice the size of the basophil. They contain abundant debris.

Leukocyte counts were made on 10 normal rainbow trout. The number of fish leukocytes, particularly lymphocytes and thrombocytes, varies. In order to establish a normal standard, the mean  $\pm$  standard error of mean (S.E.) and the range of mean, where range is the distance between the upper and lower 95% confidence limits, were determined for each cell type. The mean  $\pm$  S.E. and range of mean for the heterophil, lymphocyte and thrombocyte are  $2.3 \pm 0.66$  (0.98-3.62),  $20.5 \pm 2.31$  (15.88-25.12) and  $11.1 \pm 2.33$  (6.44-15.76), respectively.

## EFFECTS OF TURPENTINE, CORTISONE AND ACTH ON LEUKOCYTES

### Materials and Methods

Trout were injected intraperitoneally under the pelvic fin with 0.2 cc./100 gm. of turpentine, N.F. Controls were given injections of 0.6 cc./100 gm. of Ringer-Locke solution (0.65%). The animals were divided into two series; the first was sacrificed after 1, 3, 5, 7 and 24-hour intervals, the second after 1, 3, 5, 6, 7, 10, 24, 48, 60 and 72-hour intervals. Differential leukocyte counts were made after each time interval. Total

red and white cell counts were also made 6 and 24 hours after turpentine injection.

To study the effect of cortisone on leukocyte response, trout were divided into two series; each received 0.2 cc./100 gm. of turpentine. Those in series 1 were given intraperitoneal injection of cortisone (Cortone Acetate, Merck and Co.) in saline suspension concurrently with the turpentine, while series 2 received cortisone 24 hours in advance of the turpentine. Animals were subdivided into dosage groups, receiving 0.3, 0.6 and 1.0 mg./cc., respectively. Controls were injected with 1.0 mg./cc. of cortisone without turpentine. Blood samples were taken 6 and 24 hours after turpentine injection as well as after the control cortisone injection.

To determine whether administration of ACTH would stimulate adrenal tissue to secrete a hormone eliciting the same leukocyte response as cortisone, another group of trout was injected with ACTH (Corticotropin, ACTH, Armour Laboratories) in Ringer-Locke solution. Dosages of 2 U. S. P. units (I. U.) were used and blood samples taken after 6 and 24 hours.

Leukocyte counts were made and the 95% range of the mean in normal and experimental trout compared. Data were considered statistically significant when two ranges failed to overlap.

## Results

Injections of Ringer-Locke solution resulted in no significant change in either heterophil or lymphocyte counts. The slight increase in heterophils encountered in a few animals was attributed to handling and other unknown factors. Turpentine injection elicited a marked response. Total red cell counts did not differ significantly from normal, while total leukocyte counts were notably increased. Leukocyte counts of the first series, over a 24-hour period, are given in Table 1; those for series 2, over a 72-hour period, in Table 2.

In response to injected turpentine, the heterophil count rose significantly within 5 hours, reached its peak at 6 hours and remained high for 60 hours. The lymphocyte count dropped significantly in 6 hours, and remained low for 72 hours. No significant change occurred in thrombocyte number in the first 24 hours, but decreases occurred at 48 and 60 hours. The early increase in heterophils is mainly due to release of myelocytes and metamyelocytes into the circulation.

The mortality rate following turpentine injection averaged 30%, the greatest loss occurring between the second and fourth post-injection hours.

Leukocyte counts of trout following cortisone and concurrent injections of turpentine and cortisone are listed in Table 3. Counts taken after prior injections of cortisone are given in Table 4.

Cortisone alone had little effect on the heterophil count; the change in lymphocyte count, however, was marked. Lymphopenia was noted 6 and 24 hours after injection, accompanied by thrombocytopenia. Cortisone, when given concurrently with turpentine, resulted in less heterophilia than did turpentine alone, the increase being due to a preponderance of mature heterophils. The effect of cortisone was most apparent when injected in advance of the irritant. Although the largest dose yielded the maximum effect, little difference existed between dosage groups.

After prior injection of cortisone, lymphopenia and thrombocytopenia were greater than that noted after concurrent injections. A comparison of mortality rates indicates that cortisone has a significant effect. Concurrent injections in series 1 maintained the average (30%) mortality rate. However, prior injections in series 2 average only 16%, a reduction of almost one-half.

ACTH injection resulted in lymphopenia and thrombocytopenia, as did cortisone. In addition, heterophilia, due to increased mature cells, resulted. Leukocyte counts are given in Table 5.

## DISCUSSION

The blood response elicited in trout by turpentine is similar to that reported in other animals, including the dogfish (Reznikoff & Reznikoff, 1934), turtle (Ryerson, 1943), chicken (Bradley, 1937) and perch (Yokoyama, 1947). Comparable effects were also reported in mice and rats after injections of adrenalin or formaldehyde (Harlow & Selye, 1937).

The response of the trout was not limited to the irritant, but was also an expression of the shock reaction to the toxin. The high mortality seen in the first hours is attributed to this. The leukocyte response to pituitary and adrenal cortical hormones in trout is comparable to that noted in mammals. A decrease in leukocytosis (due to neutrophilia) was reported by Palmer *et al.* (1951) in turpentine-injected rats after administration of cortisone and ACTH, with the greater reduction following cortisone. The time relationship between administration of cortisone and turpentine was more important than cortisone dosage. Maximal inhibition of inflammation was obtained after prior injection of cortisone, which permitted adequate time for absorption. The effect on mortality also appears to

be dependent upon absorption sufficient to inhibit shock.

The heterophilia noted in trout after administration of ACTH is similar to the neutrophilia elicited by ACTH in intact and adrenalectomized rats (Palmer *et al.*, 1951) and in rats, mice and rabbits following ACTH or foreign protein (Dougherty & White, 1944). The neutrophil or heterophil, therefore, is not under direct adrenal cortical control, but is subject to various influences.

Lymphopenia following cortisone or ACTH is a more specific response. This reaction, reported absent after adrenalectomy or injection of other proteins (Dougherty & White, 1944), results from many unrelated stimuli, including turpentine, and is due to increased adrenal cortical activity initiated by ACTH. Decreased lymphocyte number with stress or hormone treatment in intact animals appears to follow adrenal cortical inhibition of the lymphoid organs.

In rainbow trout, lymphopenia and thrombocytopenia resulted from stress, cortisone and ACTH, while heterophilia followed stress and ACTH injection. Therefore, the mechanism of leukocyte control, as well as the physiological response of each cell type, in the trout is comparable to that in the mammal. Since significant heterophilia was not caused by cortisone, it is inferred that granulocyte-forming centers are not under adrenal cortical control, as may be the case with lymphocytes and thrombocytes. In the trout, where granulocyte- and agranulocyte-forming tissue are located in the same hemopoietic organs, multiple controls exist.

#### SUMMARY

1. Living blood cells from rainbow trout are described, and differential counts made, using phase contrast microscopy. In normal blood the predominant leukocyte is the lymphocyte, the heterophil is scarce, and eosinophils and basophils are seen only occasionally.
2. Changes in blood picture are used as criteria of systemic response to experimental conditions; the effects of turpentine, cortisone and ACTH on the leukocyte counts are determined.
3. Turpentine produced a sterile inflammation, resulting in heterophilia, lymphopenia and thrombocytopenia. Blood counts, made over a 72-hour period, revealed marked heterophilia at 6 hours due to release of myelocytes and metamyelocytes.
4. Cortisone, given concurrently and in advance of turpentine, reduced the inflammatory

TABLE 1. LEUKOCYTE COUNTS OVER 24-HOUR PERIOD FOLLOWING INJECTION OF 0.2 CC./100 GM. TURPENTINE

Time interval (hr.)	Heterophil			Lymphocyte			Thrombocyte		
	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range
1	10.0	8.5 $\pm$ 1.5	5.5-11.5	21.0	20 $\pm$ 1	18-22	12.0	13 $\pm$ 1	11-15
	7.0			19.0			14.0		
3	14.0	16.5 $\pm$ 2.5	11.5-21.5	13.0	19 $\pm$ 6	7-31	5.0	15.5 $\pm$ 10.5	0-36.5
	19.0			25.0			26.0		
5	30.0	22.5 $\pm$ 7.37	7.76-37.24	25.0	21.5 $\pm$ 3.5	14.5-28.5	31.0	17.5 $\pm$ 13.5	0-44.5
	15.0			18.0			4.0		
7	14.0	12.0 $\pm$ 2	8-16	4.0	6 $\pm$ 2	2-10	4.0	5 $\pm$ 1	3-7
	10.0			8.0			6.0		
24	19.0	14.0 $\pm$ 5	4-24	7.0	3.5 $\pm$ 3.5	0-10.5	12.0	11.5 $\pm$ 0.05	11.4-11.6
	9.0			0			11.0		

TABLE 2. LEUKOCYTE COUNTS OVER 72-HOUR PERIOD FOLLOWING INJECTION OF 0.2 CC./100 GM. TURPENTINE

Time interval (hr.)	Heterophil			Lymphocyte			Thrombocyte		
	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range
1	3.0			21.0			8.0		
	7.0	3.5 $\pm$ 1.44	0.62-6.38	11.0	10.5 $\pm$ 3.98	2.54-18.46	8.0	10.5 $\pm$ 3.24	4.02-16.98
	0			2.0			15.0		
	4.0			8.0			11.0		
3	17.0			17.0			6.0		
	1.94	11.49 $\pm$ 4.98	1.53-21.45	17.48	14.24 $\pm$ 3.98	6.28-22.2	10.68	7.17 $\pm$ 1.32	4.53-9.81
	5.0			2.0			6.0		
	22.0			20.0			6.0		
5	15.0			18.0			3.0		
	14.0	18.26 $\pm$ 2.18	13.9-22.62	2.0	9.32 $\pm$ 3.29	1.74-16.9	17.0	6.21 $\pm$ 3.65	0-13.51
	22.04			9.27			3.83		
	22.0			8.0			1.0		
6	24.0			7.0			7.0		
	43.0	28.81 $\pm$ 4.86	19.09-38.53	7.0	4.74 $\pm$ 1.45	1.84-7.64	10.0	5.92 $\pm$ 2.11	1.7-10.12
	33.0			4.0			0		
	15.24			0.96			6.67		
7	34.2			6.84			10.75		
	15.0	21.3 $\pm$ 4.43	12.44-30.16	0	1.96 $\pm$ 1.64	0-5.24	7.0	8.94 $\pm$ 1.12	6.7-11.18
	20.0			0			7.0		
	16.0			1.0			11.0		
10	17.36			0			1.93		
	33.0	21.34 $\pm$ 2.54	16.26-26.42	5.0	1.75 $\pm$ 1.49	0-4.73	10.0	5.73 $\pm$ 1.76	2.21-9.25
	15.0			2.0			7.0		
	20.0			0			4.0		
24	11.0			2.0			4.0		
	18.0	11.87 $\pm$ 2.09	7.69-16.05	2.0	1.24 $\pm$ 0.48	0.28-2.2	10.0	6.66 $\pm$ 1.25	4.16-9.16
	9.46			0.95			6.62		
	9.0			0			6.0		
48	6.0			0			3.0		
	9.68	8.66 $\pm$ 1.41	5.84-11.48	16.45	4.68 $\pm$ 1.93	0.82-8.54	9.68	5.37 $\pm$ 1.26	2.85-7.89
	12.15			1.25			2.80		
	6.82			1.0			6.0		
60	5.0			1.0			7.0		
	7.81	10.86 $\pm$ 4.75	1.36-20.36	7.0	3.5 $\pm$ 1.75	0-7	3.0	5.17 $\pm$ 1	3.17-7.17
	5.62			0			6.75		
	25.0			6.0			4.0		
72	16.0			2.0			10.0		
	0	6.25 $\pm$ 4.91	0-16.07	0.95	3.74 $\pm$ 2.43	0-8.57	10.41	6.85 $\pm$ 2.03	2.79-10.91
	3.0			1.0			5.0		
	6.0			11.0			2.0		

TABLE 3. LEUKOCYTE COUNTS FOLLOWING INJECTION OF 0.2 CC./100 GM. TURPENTINE AND CORTISONE ADMINISTERED CONCURRENTLY

Time interval (hr.) after turpentine	Cortisone dosage mg./cc.	Heterophil		Lymphocyte		Thrombocyte				
		n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range
(Control, no turpentine)										
6	1.0	6.0	3.5 $\pm$ 2.5	0- 8.5	1.0	8 $\pm$ 7	0-22	6.0	3 $\pm$ 3	0-9
		1.0			15.0			0		
6	0.3	15.57	10.98 $\pm$ 4.14	2.7 -19.26	18.51	13.25 $\pm$ 5.24	2.77-23.73	9.74	7.27 $\pm$ 2.04	3.19-11.35
		6.38			7.98			4.79		
6	0.6	25.0	14.5 $\pm$ 5.57	2.86-25.14	7.0	8 $\pm$ 1	6-10	14.0	9.33 $\pm$ 2.6	4.13-14.53
		10.0			10.0			5.0		
		7.0			7.0			9.0		
6	1.0	11.0	10.18 $\pm$ 4.45	1.28-19.08	6.0	6.45 $\pm$ 0.67	5.11-7.79	10.0	7.48 $\pm$ 2.48	2.52-12.44
		6.71			4.79			1.92		
		25.0			7.0			13.0		
		8.0			8.0			5.0		
(Control, no turpentine)										
24	1.0	6.0	5 $\pm$ 1	3-7	0	2 $\pm$ 2	0-6	2.0	3 $\pm$ 1	1-5
		4.0			4.0			4.0		
24	0.3	4.0	-	-	2.0	-	-	2.0	-	-
		5.0			3.0			1.0		
24	1.0	10.0	7.6 $\pm$ 1.51	4.58-10.62	6.0	4.92 $\pm$ 0.94	3.04-6.8	0	3.64 $\pm$ 2.72	0-9.08
		4.81			5.77			1.92		
		8.0			3.0			9.0		

TABLE 4. LEUKOCYTE COUNTS FOLLOWING INJECTION OF 0.2 CC./100 GM. TURPENTINE AND CORTISONE ADMINISTERED 24 HOURS IN ADVANCE

Time interval (hr.) after turpentine	Cortisone dosage mg./cc.	Heterophil			Lymphocyte			Thrombocyte		
		n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range
		6	1.0 8.0 9.0	6 $\pm$ 2.18	1.64-10.36	3.0 4.0 4.0	3.67 $\pm$ 0.33	3.01-4.33	0 9.0 6.0	5 $\pm$ 2.65
6	10.0 9.0 6.0	8.33 $\pm$ 1.2	5.93-10.73	2.0 5.0 4.0	3.67 $\pm$ 0.88	1.91-5.43	11.0 10.0 3.0	8 $\pm$ 2.52	2.96-13.04	
6	10.0 4.87 10.0 13.0	9.47 $\pm$ 1.48	6.51-12.43	6.0 0.97 1.0 3.0	2.74 $\pm$ 1.2	0.34-5.14	4.0 1.95 7.0 5.0	4.49 $\pm$ 1.27	1.95-7.03	
24	0.3	5.0 6.0	5.5 $\pm$ 0.5	4.5-6.5	0 0	0 0	1.0 4.0	2.5 $\pm$ 1.5	0-5.5	
24	0.6	9.0 4.0 2.0	5 $\pm$ 2.09	0.82-9.18	3.0 5.0 0	2.67 $\pm$ 1.45	0-5.57	4.33 $\pm$ 0.88	2.57-6.09	
24	1.0	7.0 4.0 10.0	7 $\pm$ 1.73	3.54-10.46	2.0 7.0 1.0	3.33 $\pm$ 1.86	0-7.05	5 $\pm$ 0.57	3.88-6.14	

TABLE 5. LEUKOCYTE COUNTS FOLLOWING INJECTION OF 2 U.S.P. UNITS OF ACTH

Time interval (hr.)	Heterophil			Lymphocyte			Thrombocyte		
	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range	n	Mean $\pm$ S.E.	95% Range
6	8.0			10.0			11.0		
	1.88			6.39			7.52		
	6.42	7.08 $\pm$ 1.88	3.32-10.84	13.74	10.53 $\pm$ 1.37	6.79-14.27	0	5.63 $\pm$ 1.79	2.05-9.21
	12.0			12.0			4.0		
24	2.0			3.0			5.0		
	3.0			2.0			2.0		
	6.0	6.42 $\pm$ 2.65	1.12-11.72	1.0	2.97 $\pm$ 1.09	0.79-5.15	12.0	6.24 $\pm$ 1.98	2.28-10.20
	14.7			5.88			2.94		

response, while advance injection also reduced mortality by almost 50%.

5. Lymphopenia and thrombocytopenia resulted from stress, cortisone and ACTH, while heterophilia followed stress and ACTH injection.
6. Decrease in lymphocyte number appears to be in direct response to adrenal cortical stimulation initiated by ACTH. Heterophilia is not under direct adrenal cortical control, but subject to a wider range of influencing factors.
7. The mechanism of leukocyte control, as well as the physiological response of each cell type, in the trout is comparable to that in mammals.

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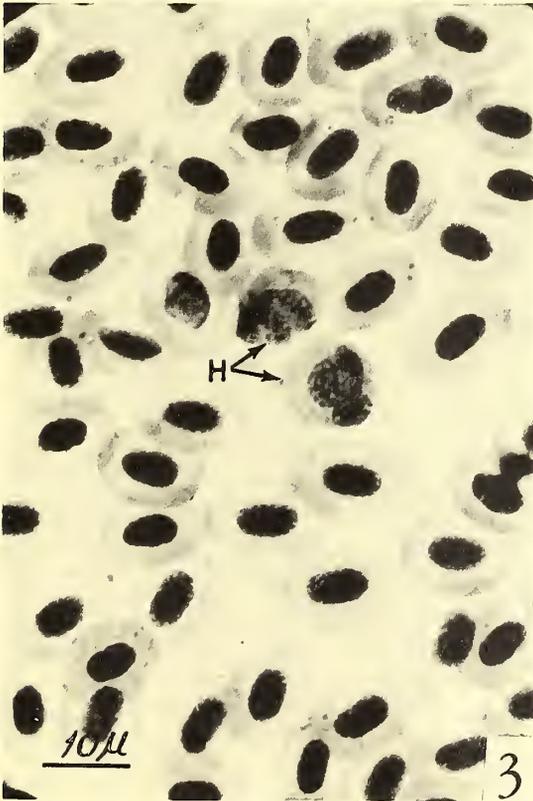
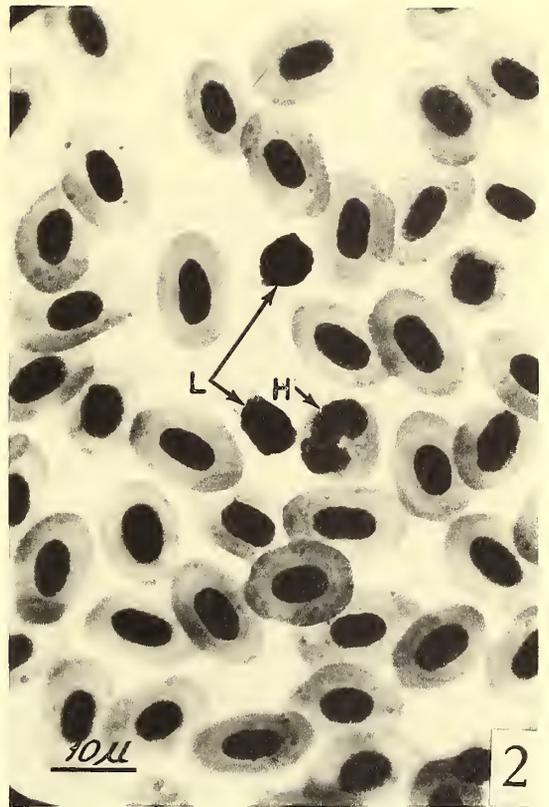
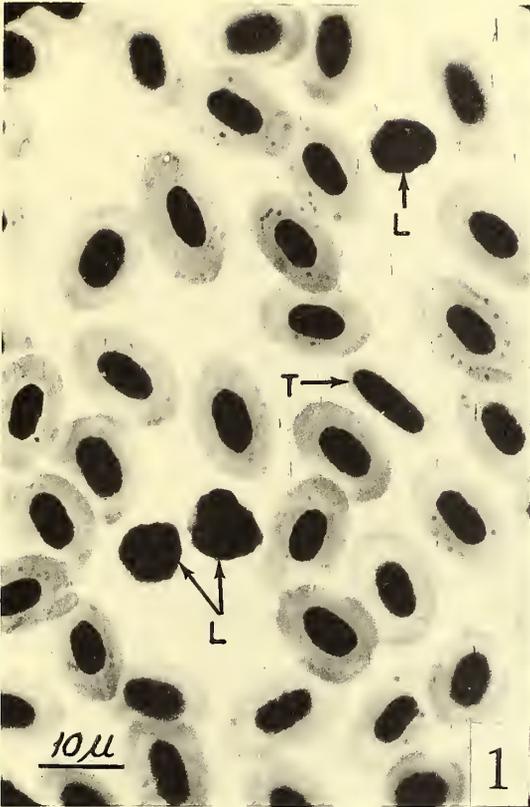
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## EXPLANATION OF THE PLATE

## PLATE I

Typical fields showing leukocyte distribution in blood of normal and turpentine-injected trout. Note scarcity of heterophils and prevalence of lymphocytes in adjacent fields in normal blood (FIGS. 1, 2), compared with reversed condition seen in adjacent fields after turpentine injection (FIGS. 3, 4.). Heterophil, **H**; lymphocyte, **L**; mature thrombocyte, **T**. Wright's stain.



STUDIES ON THE HISTOLOGY AND HISTOPATHOLOGY OF THE RAINBOW TROUT, SALMO GAIRDNERI IRIDEUS. PART I



## Radiobiology of the Newt, *Diemictylus viridescens*. Hematological and Histological Effects of Whole-body X Irradiation<sup>1</sup>

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(Plates I-III; Text-figure 1)

### INTRODUCTION

Attempts to alter the course of pseudoerythroplastic anemia, a condition of the red cells found only in *Diemictylus viridescens* to date, (Jakowska & Nigrelli, 1952), newts were exposed to various amounts of X irradiation. Preliminary observations indicated that these animals survived for a comparatively long time after such treatments and that the normal and abnormal peripheral blood elements showed only slight changes even though the hemopoietic and other organs were extensively damaged.

Various species of amphibians have been used in radiobiological investigations, but we are not aware of any work relating to the radiation pathology of the newt, a salamander often used in studies on development, regeneration and hemopoiesis. The present studies, therefore, were made to determine the extent and nature of the radiation damage and, if possible, to indicate the factors that may be responsible for the apparently high degree of resistance of these animals to X irradiation.

### MATERIALS AND METHODS

Large adult male *Diemictylus viridescens* (= *Triturus viridescens*), weighing from 2.5 to 3.5 gm., obtained from Illinois, were used. Groups of ten animals each were exposed to X rays at room temperature (22-23° C.) in a specially constructed circular lucite container with a total of ten compartments, in which each animal was confined during treatment to a wedge-shaped area. The radiation factors were as

follows: 250 kv; 30 ma; 0.5 mm. Cu and 1 mm. Al filters; target distance 40 cm.; dose rate 140-160 r/min. The doses administered were: 200, 950, 1700, 2450, 3200, 3950 and 4700 r for the animals kept at room temperature following irradiation. Doses of 200 and 1400 r were given to other groups used for experimental infection with *Pseudomonas hydrophila* and *Mycobacterium ranae*, and doses of 200 and 1700 r to animals with confirmed pseudoerythroplastic anemia. Other groups of animals, subsequently stored at 5° C., received 1700, 3000, 4700, 6000 and 9000 r. Following irradiation, all newts were maintained unfed in individual plastic containers, each with a small volume of tap water.

Mortality was recorded daily and random samples of blood and tissues from representative groups were obtained from sacrificed newts at weekly intervals, unless stated otherwise. Films stained with Wright's method were examined for specific absence of or increase in a cell type, or specific damage to cells. Differential counts were made from a number of cases. Paraffin sections of liver, kidney, spleen, intestine, testis, lungs and skin were stained with Hematoxylin-eosin, Giemsa, Masson's and Maximow's techniques.

### OBSERVATIONS

#### *Post-irradiation Behavior*

Irradiated newts showed no cataracts, color changes or excessive skin shedding over the period of the observations. The animals were lively when aroused and demonstrated excellent muscle tonus even shortly before death. Treated animals differed from controls in that they spent more time out of water, climbing on the sides of the containers and remaining on the walls in a

<sup>1</sup> A portion of this work was carried out at Brookhaven National Laboratory under the auspices of the U. S. Atomic Energy Commission.

vertical position. They exhibited a mild hyperemia of the throat region and a very pronounced "buccal-pump" respiratory action, which was characterized by a rapid movement of the floor of the mouth. Both non-irradiated controls and irradiated newts stored at 5° C. remained lethargic, with some tendency to climb. Otherwise their condition appeared good, even five months following exposure to heavy doses of X rays.

#### *Survival at Room Temperature*

There was no significant statistical<sup>2</sup> difference in the survival of well-fed newts or those after a preliminary fast of one month, when exposed to 3200 r. With the assumption that the highest dosages act similarly in these unfed animals, the results of two sets of experiments were considered collectively. Statistical analysis showed highly significant differences between doses and a highly significant linear trend. The linear relationship between dose and number of days of survival fitted the equation  $y = 24.8 - .003432(x - 3008)$ . The above equation was used to determine the LD 50/30 days for 50 of the treated animals kept at room temperature and was found to be 1486 r. The animals which received 200 r survived for four months or more at room temperature and the 200 r dose was omitted from the analysis.

#### *Survival at 5° C.*

Animals exposed to 1700, 3000, 6000 and 9000 r and kept at 5° C. remained alive for as long as five months. The mortality was negligible and the animals selected at random to be sacrificed appeared in good condition, although they remained lethargic in the cold room most of the time. These newts were large and robust and apparently in an excellent nutritional state when they were irradiated. After remaining unfed for five months at 5° C., most animals still had large fat-bodies and fat deposits around the cloaca. Blood was abundant and normal in color; the liver was firm, but the spleen paler and more fragile than in the controls; the lungs were pinkish and partly edematous.

#### *Peripheral Blood*

The blood of the irradiated newts did not clot as rapidly as that of the controls although no accurate data are available. This may have been related to the abnormalities observed in the thrombocytes; these were swollen, had uneven cellular borders, and stained atypically with poor differentiation of the nucleus and of cytoplasmic granules, within one week following a dose of 200 r. This condition of the thrombocytes was consistently seen throughout the life of the ir-

radiated animals regardless of dosage (Pl. I, Fig. 1).

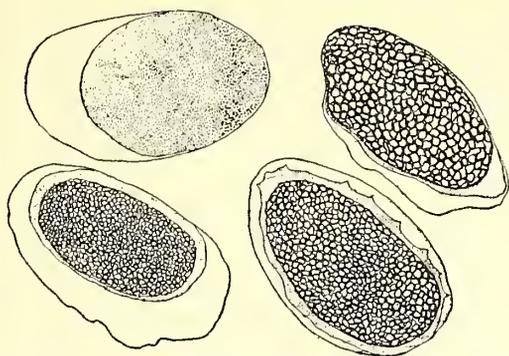
Neutrophils were studied from the peripheral blood and in sections of the liver, which is the chief site of their production. The animals kept at room temperature for 19 days after 200 and 1400 r were challenged with *Pseudomonas hydrophila* and *Mycobacterium ranae* to determine their ability to ward off infections (Jakowska, Nigrelli & Sparrow, 1954). Active phagocytosis, with the participation of numerous neutrophilic leukocytes, was observed 24 hours after the infection was induced on the surface of the tail.

Some neutrophilia, with Classes V and VI predominating, appeared, but only in newts exposed to 200 r. With higher dosages the neutrophils in the animals kept at room temperature were not numerous at any time, but in those kept in the cold for three months following 1700 r or more, obvious neutrophilia with banded (non-segmented) forms predominating was noted (Jakowska & Nigrelli, 1954), together with an increase in the number and in the size of the basophilic granulocytes (Pl. I, Fig. 2). No eosinophils were seen in the peripheral blood of irradiated newts, although these were occasionally seen in the controls.

The erythrocytes did not appear affected, and only occasionally were nuclear fragments seen with a frequency higher than normal (Pl. I, Fig. 3). The nuclear chromatin pattern of the erythrocytes was not basically altered, except in the animals kept for three months in the cold and exposed to the highest dose (9000 r). In these animals the nuclear contents of the erythrocytes appeared somewhat less distinct. Cellular elements of the blood appeared normal in the few newts kept for five months at 5° C. following 6000 r treatment. There was no significant change in the number of erythroplastids (non-nucleated red elements) and microcytes in irradiated animals.

Pseudoerythroplastic anemia (Jakowska & Nigrelli, 1952) was found sporadically in irradiated and non-irradiated unfed newts (Pl. I, Fig. 4). Effects of X irradiation (200 and 1700 r) on the pseudoerythroplastids were studied by exposing such anemic animals. Twenty-four hours after 1700 r, the pseudoerythroplastids of the peripheral blood showed a characteristic separation of the cytoplasm from the cell membrane, possibly indicating that their permeability has been affected (Text-fig. 1). Counts of the early, intermediate and late stages of pseudoerythroplastids before and 24 hours after irradiation failed to reveal numerical differences.

<sup>2</sup> For statistical analysis we are indebted to Dr. Phelps P. Crump of the Brookhaven National Laboratory.



TEXT-FIG. 1. Pseudoerythroplastids of an anemic newt, 24 hours after exposure to 1700 r. Note the separation of the cell membrane from the cytoplasm. From Wright's stained smear. 4000 X.

#### Blood Parasites

Blood parasites were occasionally seen in control and irradiated newts. The cytological appearance of trypanosomes seemed normal even in animals exposed to 4700 r. The trypanosomes also occurred in the blood of some irradiated newts kept in the cold for five months. An exceptionally high degree of infection with *Babesiosoma (Dactylosoma) jahni* (Jakowska & Nigrelli, 1956), a non-pigmented haemosporidian, was found in one animal treated with 950 r and kept at room temperature.

#### Liver

Progressive degeneration of the liver was observed in the animals kept at room temperature. Three weeks after 2450 r, for example, the nuclei of the hepatic cells were pyknotic and the granulocyte-forming perihepatic layer was considerably reduced in thickness and activity. Numerous vacuolated areas in the hepatic cells indicated lipid accumulation. In the animals kept in the cold, the degeneration of the parenchyma was slower but more conspicuous. The perihepatic layer itself was not essentially affected with the lower doses (1700 r) and retained its usual thickness and mitotic activity for about three months (Pl. I, Fig. 5). One month after 4700 r, however, the hepatic capsule was reduced to a thickness of one cell, although the nuclei of the liver cells appeared normal. Exposure to 6000 and 9000 r within one month was followed by the formation of numerous hyalin droplets in the cytoplasm of the parenchyma cells (Jakowska & Nigrelli, 1954). These droplets stained red with Masson and light blue with Giemsa (Pl. II, Fig. 6).

Some recovery in the liver parenchyma was apparent in animals kept for four months in the cold after exposure to higher doses. The cyto-

plasm was finely granular, and, as in the controls, the nuclei did not show pyknosis, but some seemed to contain more than the usual number of nucleoli. A few young leukocytes and occasional macrophages were found scattered in the parenchyma.

#### Kidney

The kidney was very firm in the animals surviving 3000, 6000 and 9000 r for three months or longer in the cold. In animals kept at room temperature, cloudy swelling was seen in the tubular epithelium of the kidney within two to three weeks following 1700 r. The changes progressed further in the animals kept alive for longer periods at 5°C. "Albuminous" material accumulated in the lumen of the tubules (Pl. II, Fig. 7) and in the glomeruli. Later, hyalin droplets were found in the cytoplasm of the cells of the urinary ducts (Pl. II, Fig. 8) and of tubules. These droplets stained similarly to those found in the liver cells (Jakowska & Nigrelli, 1954). The tubular lumen was occluded by homogeneous basophilic material and the lining of the urinary ducts had often been sloughed.

#### Spleen

The spleen of irradiated newts kept at room temperature underwent gradual atrophy. In the animals stored at 5°C., on the other hand, the size of the spleen was consistent with that of non-irradiated controls, showing similar individual variations. Sections, however, revealed large hemosiderin deposits and many destroyed red blood cells. There was a reduction in the hemopoietic tissue and the development of dense fibrous material. Infrequently, a spleen of semi-fluid consistency with a thick fibrous capsule was found (Pl. III, Fig. 9). Such spleens were especially pale in those animals which had received 6000 r, but which had abundant bright red, freely flowing blood. No active erythropoiesis or thrombocytopoiesis were observed. Large numbers of basophilic granulocytes were present.

#### Intestine

Irradiated animals remained unfed throughout the period of observations. There were no changes in the intestinal epithelium indicative of ulcerative damage, nor any desquamation. The margins of the cells of the intestinal mucosa appeared intact. No hemopoiesis was observed in the submucosa.

#### Testes

Animals that were kept for four months in the cold following 3000, 6000 and 9000 r showed no evidence of spermatogenesis, with the majority of the cells pyknotic and with very

little interstitial tissue (Pl. III, Fig. 10). Moderate spermatogenesis was found in the testicular lobes of cold-stored controls.

#### Lungs

The pulmonary vessels of the irradiated animals showed very little blood. There was a profuse exudate in the lungs of newts kept for one month at 5°C. following the highest doses of X irradiation. Even at lower doses, e.g. 1700 r after three months in the cold, exudate containing numerous basophilic granulocytes with coarse irregular granules and microcytes was observed in the lungs. *Hexamita*-like flagellates were occasionally found in such edematous lungs (Pl. III, Fig. 11).

#### Skin

In view of the osmo-regulatory function of the skin in the adult newt, particular attention was given to this organ. Controls kept at room temperature showed an epithelial layer two or three cells in thickness, a highly vascularized corium and actively secreting dermal glands. Controls kept in the cold had thickened epithelium, numerous cells in mitosis, a corium with constricted capillaries and dermal glands filled with secretory granules. Newts exposed to the highest doses of X irradiation and kept in the cold for three months showed slight increase in thickness of the epithelium, no mitosis and considerable keratinization (Pl. III, Fig. 12). There was an increase in the number of dermal glands, associated with an increased stickiness of the body, a condition which disappeared at four and five months. Shedding in all irradiated animals was repeated but not excessive; it occurred in the form of small fragments instead of the usual large epithelial sheets.

#### DISCUSSION

Delayed radiation effects in amphibians were reported by Stearner (1950) for *Rana pipiens* and by Brunst, Sheremetieva-Brunst & Figge (1953) for the axolotl. The absence of early manifestations was attributed to the lower metabolic rate of these cold-blooded animals, or to the greater potential for regeneration.

The data on survival of irradiated newts at room temperature and at 5°C. compare favorably with the results of Patt & Swift (1948) on *Rana pipiens*; the degenerative effects of irradiation in newts were not as rapid as those reported for mammals in similar organs (liver, spleen, lung, intestine, skin, testis, etc.).

Bacteremia was absent at all stages after irradiation in newts. It was apparent that these animals still had ability to mobilize phagocytic neutrophils, as demonstrated by the response of

these elements to experimentally induced infection (Jakowska, Nigrelli & Sparrow, 1954). This is significantly different from the typical acute radiation syndrome in mammals, where fatal infection characterized by a low granulocyte count plays the predominant role (Cronkite & Bond, 1956).

From the present studies, it was evident that the irradiated newts were able to live for a comparatively long time in spite of damage to several vital organs, viz. kidney, liver, lung and spleen. It is well known that cold-blooded animals, especially fish and amphibians, can survive extensive destruction of renal tissue, because a certain amount of osmo-regulation takes place in the gills and skin. Further, it has been shown that newts lived indefinitely with both lungs removed (Philippi, Hausler, Bialy & Jakowska, 1956; Jakowska, Philippi & Nigrelli, 1956). Since considerable skin damage occurred in the irradiated newts, it may be assumed that death was due to the impaired efficiency of the skin in both respiratory and osmo-regulatory functions. Histologically, however, the damage did not involve the formation of abnormal epithelium, as reported by Brunst (1955) in irradiated tadpoles of *Rana catesbeiana*.

In spite of the fact that the principal hemopoietic sites, e.g. the granulocytopoietic layer of the liver and the thrombo- and erythrocytopoietic spleen, were severely injured, the peripheral blood picture remained relatively unaffected. This fact, together with the absence of any mitotic activity in the cells of the peripheral circulation, was indicative of the comparatively long life (approximately 150 days at 5°C.) of the blood elements in this species. The delayed clotting in irradiated newts was probably related to the damage observed in the thrombocytes. The presence of increased numbers of giant basophilic granulocytes, seen in the peripheral blood of newts exposed to 1700 r and kept in the cold for three months or longer, may also have some relationship to the delayed clotting, since it has been shown that basophilic granulocytes (mast cells) in other vertebrates contain heparin (Wilander, 1939; Veil & Quivy, 1950).

#### SUMMARY

Adult newts (*Diemictylus viridescens*) were relatively resistant to high doses of X irradiation, surviving for up to five months following exposure to 9000 r when kept at 5°C. after X ray treatment. At room temperature of 22-23°C., the LD 50/30 days was found to be 1486 r.

There was no appreciable effect on the blood elements of the peripheral circulation, although there was extensive damage to the hemopoietic

organs (erythrocyte- and thrombocyte-forming spleen and granulocyte-forming layer of the liver). No bacteremia was found at any stage and irradiated newts showed the ability to ward off experimental infection by active phagocytosis.

The above may be related to the radioresistance of this species. It is assumed that death was due to the destruction of the osmo-regulatory functions in organs such as the kidney, lungs and skin.

#### ACKNOWLEDGEMENTS

The authors wish to acknowledge the assistance of Mr. L. Schairer with irradiation and dosimetry, and of Mr. R. F. Smith with photography. Dr. L. Z. Saunders commented helpfully on the manuscript.

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## EXPLANATION OF THE PLATES

## PLATE I

- FIG. 1. Damaged thrombocytes in the blood of an animal kept for five months at 5°C. following exposure to 6000 r. Wright's stain. 1800 X.
- FIG. 2. Giant basophilic granulocyte (somewhat flattened), in the blood of a newt kept for three months at 5°C. following exposure to 1700 r. Wright's stain. 1000 X.
- FIG. 3. Erythrocyte with two small, unequal nuclear fragments, found in the blood of a newt kept for one month at 5°C. following exposure to 1700 r. Wright's stain, 2200 X.
- FIG. 4. Normal erythrocytes and pseudoerythroplastids (two early stages are seen in the upper part of the picture and one fully formed, showing surface damage, below center) in the peripheral blood of a newt kept for one month at 5°C. following exposure to 9000 r. Wright's stain. 1800 X.
- FIG. 5. Granulocytopoietic layer of the liver, with several cells appearing to be in mitosis, from a newt kept for three months at 5°C. following 1700 r. Maximow's stain. 900 X.

## PLATE II

- FIG. 6. Hyalin droplets in the liver cells of a newt

kept for one month at 5°C. following exposure to 6000 r. Masson's trichrome stain. 900 X.

- FIG. 7. Degeneration of the kidney tubules in a newt kept for one month at 5°C. following 9000 r. Masson's stain. 600 X.
- FIG. 8. Accumulation of hyalin droplets in the cells of the urinary duct and the occlusion by hyaline material in a newt kept for two months at 5°C. following exposure to 1700 r. Masson's stain. 900 X.

## PLATE III

- FIG. 9. Spleen damage in a newt kept for four months at 5°C. following 9000 r. Hematoxylin-eosin stain. 450 X.
- FIG. 10. Testis of the same newt as in Fig. 9. Note pyknosis and absence of spermatogenesis. Hematoxylin-eosin stain. 450 X.
- FIG. 11. Abnormal basophilic granulocyte, a microcyte and a flagellate found in the lung exudate of a newt kept for three months at 5°C. following 1700 r. Wright's stain. 2000 X.
- FIG. 12. Skin of a newt exposed to 6000 r and kept in the cold for one month. Note the keratinization of the epidermis. Masson's stain. 450 X.



FIG. 1

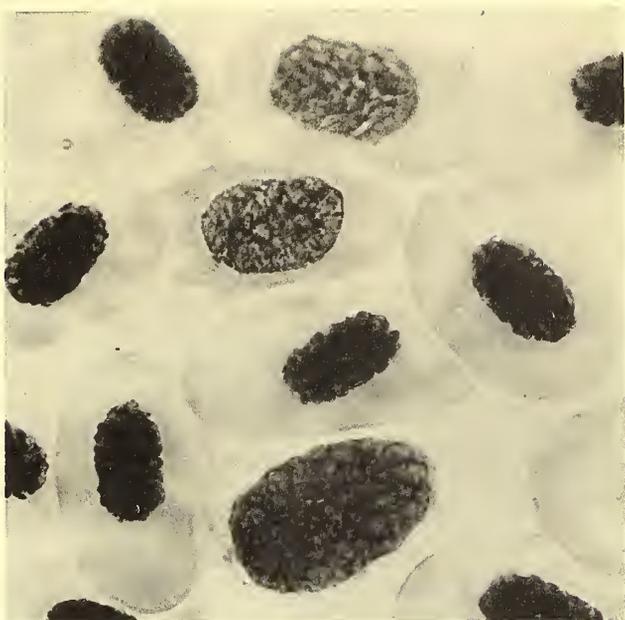


FIG. 4



FIG. 2

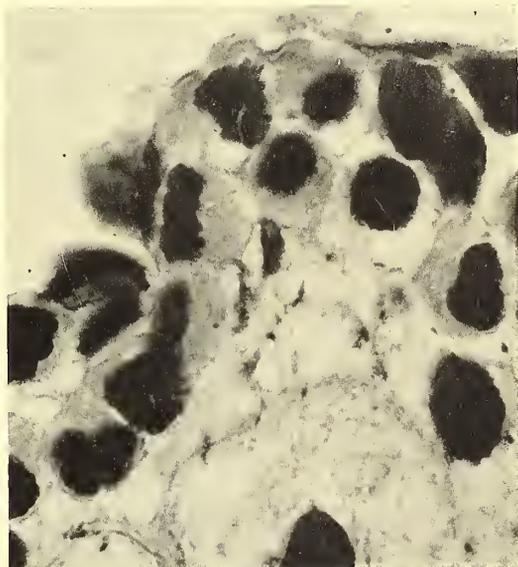


FIG. 5



FIG. 3

RADIOBIOLOGY OF THE NEWT, *DIEMICTYLUS VIRIDESCENS*. HEMATOLOGICAL AND HISTOLOGICAL EFFECTS OF WHOLE-BODY X IRRADIATION



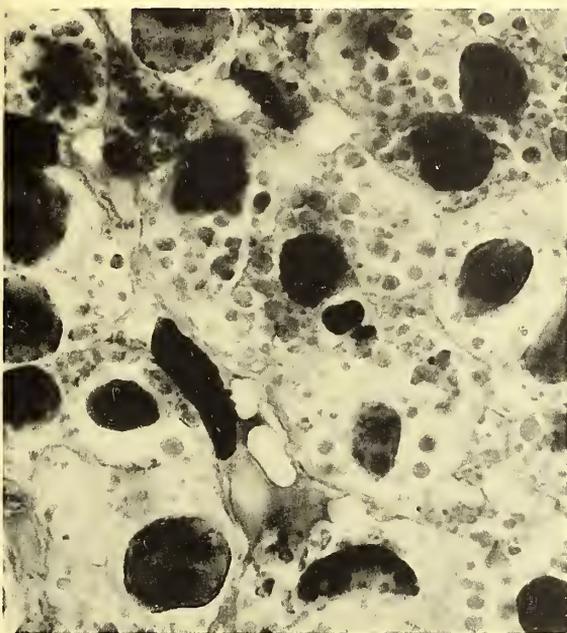


FIG. 6



FIG. 7

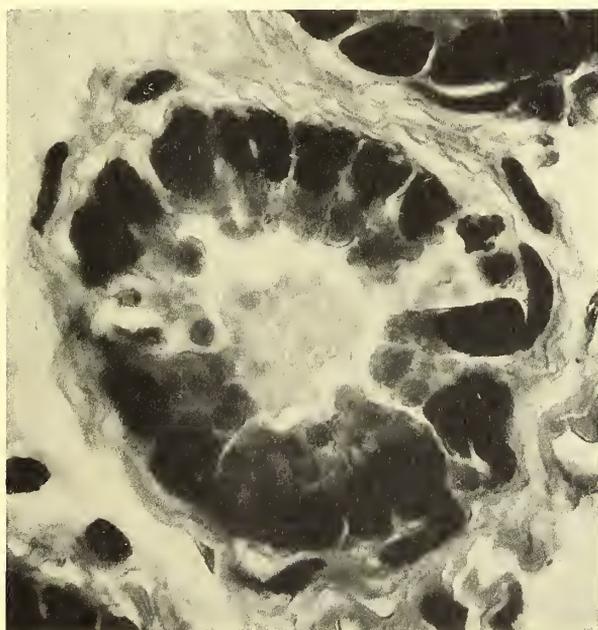


FIG. 8

RADIOBIOLOGY OF THE NEWT, *DIEMICTYLUS VIRIDESCENS*. HEMATOLOGICAL AND HISTOLOGICAL EFFECTS OF WHOLE-BODY X IRRADIATION



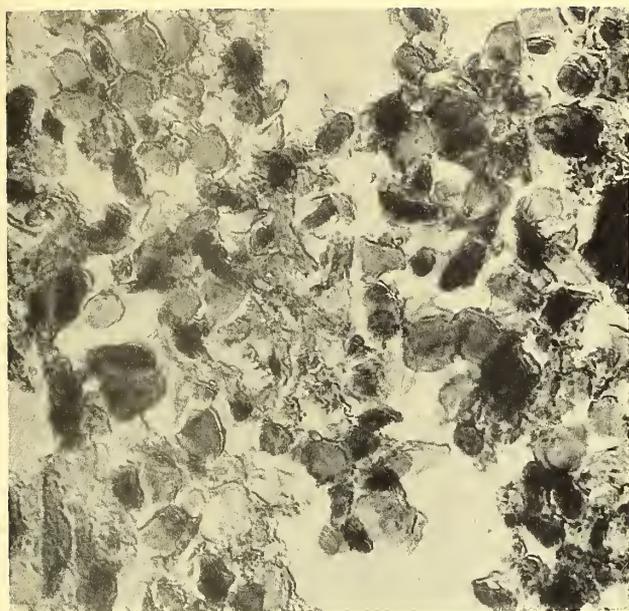


FIG. 9

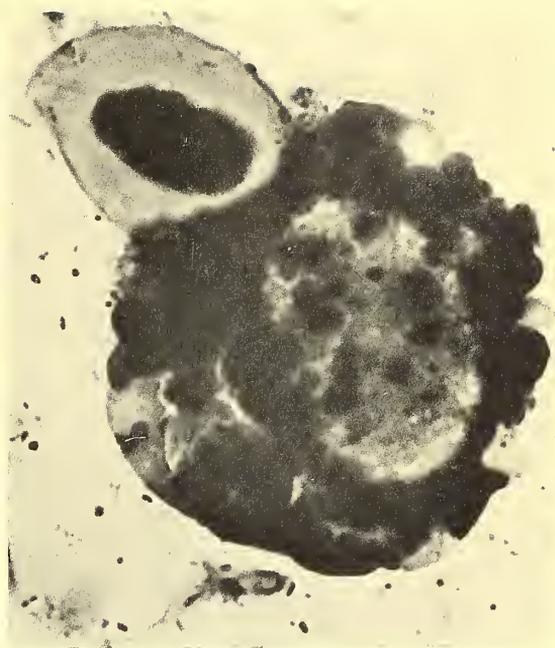


FIG. 11

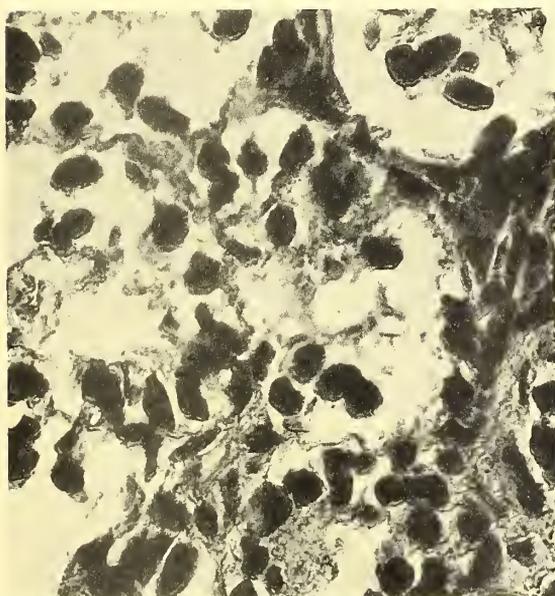


FIG. 10



FIG. 12

RADIOBIOLOGY OF THE NEWT, *DIEMICTYLUS VIRIDESCENS*. HEMATOLOGICAL AND HISTOLOGICAL EFFECTS OF WHOLE-BODY X IRRADIATION



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