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TRANSACTIONS

OF THE

LINNAEAN SOCIETY

OF

NEW YORK

Volume VIII

Development of Behavior in Precocial Birds

By Margaret Morse Nice

New York

July, 1962

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Illustrated with Line Drawings by the Author

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To Albert Hochbaum
without whom this book would
never have been written

PREFACE

For four seasons—from 1951 to 1954—my daughter Constance and I were privileged to study the early development of precocial chicks at the Delta Waterfowl Research Station at Delta, Manitoba. The primary object was to compare the development of behavior in precocial birds with that in altricial birds—a subject on which I had concentrated earlier.

Those were rich experiences at Delta beside the great marsh and its wildlife, so vividly described by Albert Hochbaum (1944). The friendly, eager atmosphere of staff and students, engaged in the study of waterfowl life, and the visits of biologists from the Old and New Worlds were most stimulating.

We are deeply indebted to Albert Hochbaum, Director of the Station, for his generous welcome to us and his unfailing assistance in our problems. We owe much to Peter Ward, Superintendent of the Hatchery, to Norman Godfrey, and to many of the fellow students who brought us eggs of different species and showed us nests they had found. Helen Hays was especially helpful.

Fruitful consultations were held with Frank McKinney, Nicholas Collias, and especially William H. Elder, whose help was invaluable in working out a scheme of classification of birds with eight categories from the most precocial to the altricial, namely, Table 2.

I sketched our subjects directly from life, sometimes in pencil, sometimes in ink. (As might be expected, the scale is not always consistent.) In this activity Albert Hochbaum gave me excellent criticisms and suggestions.

Working up of the results of our studies was delayed by other projects: an excursion into development of mammalian behavior (Nice *et al.*, 1956) and especially an investigation of the history of statements on incubation periods from Aristotle to the present day (Nice, 1954a, 1954b). Both these lines of research shed light on the studies at Delta. When I was able to turn my whole attention to these, I found that the original subject had broadened. Having discovered so many analogies between the behavior development of precocial and altricial birds and between them and mammals, it seemed wise to devote an introductory chapter to the functions of parental care throughout the Animal Kingdom. Here Konrad Lorenz, visiting this country in 1954, gave me excellent suggestions, as did Lars von Haartman two years

later. The scientist to whom I am most indebted for the validity of Chapters I and II is the late Karl P. Schmidt, Director of Zoology at the Chicago Natural History Museum, whose broad knowledge, especially of herpetology, enabled him to criticize what I had collected from the literature and to give me additional information.

Many ornithologists have helped through reading and criticizing portions of the manuscript: Chapters I through IV—Emmet R. Blake, John Emlen, Louise de Kiriline Lawrence, S. Charles Kendeigh, Austin L. Rand; Chapters I through V and Chapter XIV—George A. Bartholomew, Jr.; Chapters V and XIV—Thomas R. Howell; Chapter VI, Section A—Albert Hochbaum, Frank McKinney; Chapter VI—Milton Weller; Chapter VII—Derek Goodwin, Eckhard Hess; Chapter VIII, Section A—K. E. L. Simmons; and most of the chapters—Laidlaw Williams. To all of these friends I am deeply grateful; from each one I received help, even though I did not follow all of their suggestions. Special thanks are due to Anne Wachenfeld and Eugene Eisenmann for their editorial labors.

To my daughter Janet I am indebted for the typing of the manuscript. To Constance my debt is great indeed; she took the major part of the care of the baby birds; she shared the watching, and often contributed illuminating insights into the meaning of various actions of our subjects.

I am extremely grateful to the Wildlife Management Institute of Washington, D. C., sponsors of the Delta Waterfowl Research Station, for financial assistance in publishing this study.

A word as to the organization of this volume. It is a study of behavior development in animals with chief emphasis on the Class Aves, particularly on representative precocial birds. The first four chapters are introductory. They include: a brief survey of the functions of parental care and of its occurrence throughout the Animal Kingdom; a summary of some aspects of behavior development in five classes of vertebrates; a classification of birds according to maturity at hatching; and a discussion and comparison of stages in behavior development of an altricial bird, a mammal, and a precocial bird. Chapter V is concerned with megapodes, the most precocial of all birds. Chapters VI through XI are devoted to the birds studied by us, mostly at Delta, and Chapter XII to generalizations founded on these studies. Chapters XIII and XIV are largely based on research—anatomical and physiological—of other workers.

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CHAPTER I

Functions of Parental Care

Evolution has followed two widely differing techniques for ensuring the survival of species. One depends upon a multiplicity of offspring launched upon their own from the start; the other upon a smaller number of offspring cared for in greater or less degree by the parents during the vulnerable stages.

The fundamental functions of parental care are defense and the provision of nourishment. Supplementary functions consist in guidance, sanitation, and provision of heat. The performance of these functions might be called "passive" or "indirect" on the one hand, or "active" or "direct" on the other.

In the Plant Kingdom the more primitive plants "reproduce by spores or by sperm-and-egg methods," but the highest group—the Spermatophytes—surround the embryo with stored food and protective coats. "So successful has the seed habit been, that at least half of the plant kingdom belongs to this phylum. . . . It is the care for the nourishment, protection and dispersal of the embryonic plant which has given the Seed Plants their great advantage over all other groups of land plants" (Hylander, 1943:6, 11). In these phanerogamic plants "some species have many seeds with small food-stores, while others have few seeds with large food-stores" (Lack, 1954:149). Devices for the scattering of seeds are many and varied. One might call the parental functions of plants passive defense, anticipatory provision of nourishment, and a primitive kind of guidance—an attempt to help the offspring away from home into more favorable environment than under the parental shade.

In the Animal Kingdom "reduced fecundity, coupled with some degree of parental care, is found in some species of all the main phyla" (Burton, 1949, I:94). Marine invertebrates with a high degree of brood-protection lay 20 to 100 eggs, those with a primitive type of brood-protection lay 100 to 1,000 eggs, and those with no brood protection lay 1,000-500,000,000 eggs (Thorson, 1950:4). Lack (1954) emphasizes the contrast between many small eggs poor in yolk with few large eggs rich in yolk, giving examples from copepods and insects to fish and lizards. Protection from enemies may be provided by retention of

the eggs until hatching within or on the parent's body, such devices serving as passive defense.

In vertebrates parental care may or may not occur in fishes and amphibians. It is present in all reptiles to some degree and in birds and mammals without exception.

A. Parental Care in Invertebrates

In those invertebrates which exhibit parental care, passive defense of the eggs may be effected by their retention within the body, as with the Porifera and Coelenterata, some Platyhelminthes, Nemathelminthes, Trochelminthes, Bryozoa, Pelecypoda, and Crustacea. Or it may be brought about by attention paid to the place where the eggs are laid—in the ground, in crevices, etc. "Sometimes nests or artificial shelters are formed, as in some Diplopoda and Insecta; cocoons, as Oligochaeta; or egg sacs, as in the Arachnida" (Kendeigh, 1952:301).

Passive defense of the young is seen in some annelids and arthropods. The young of many leeches "attach themselves to the under surface of the parent's body" (Regan, 1936:65). Among isopods, the mother wood louse, *Porcellio scaber,* is found surrounded by young. The female crayfish, *Cambarus affinis,* carries her eggs and young on her pleopods until the second stage. Mother scorpions carry their young on their backs. Some male Pycnogonids transport the eggs on their legs and in some arctic and antarctic species the larvae remain clinging to their father until well developed (Hedgpeth, 1952:788). The trap-door spider carries her bag of eggs out in the sunshine and back into her den; later she shares her food with the young.

It is among the insects that parental care is most highly developed. The beginnings are seen in subsocial insects (Michener, C. D. and M. H., 1951:43-56), where parental care has been observed among Hemiptera, Coleoptera, Orthoptera, Dermaptera and Embioptera. Active defense of the brood is shown by some species in all these orders; at least three of the bugs (a stink bug, shield bug and negro bug) brood their eggs and young; with some roaches, earwigs and webspinners the young remain with the mother for a while and are defended by her. Both male and female of the tenebrionid beetle, *Phrenapates,* and the burying beetle, *Necrophorus,* feed their young, while a scolytid (an ambrosia beetle) brings fresh food—pieces of fungus—to the young and removes waste material.

Guidance of the young is reported for two forms. When the young scarabs of the genus *Copris* "emerge as adults, the parents escort them to the surface of the ground" (Michener, 1951:47). The egg-plant lace bug, *Gargaphia solani,* "leaves her eggs only to feed. Later she shepherds her flock of over two hundred nymphs as they move from leaf to leaf. She hurries about, apparently guiding and urging them on with her long antennae. A mother lace bug has been seen to dart out, wings outstretched, seemingly to frighten off a hunting ladybird beetle" (Michener, 1951:44).

The social Hymenoptera (ants, bees and wasps) and Isoptera (termites) typically exhibit both passive and active defense of offspring and provision of food, and in some cases provision of heat, sanitation and guidance, all five functions of parental care.

B. Parental Care in Vertebrates

As with invertebrates, the two classes of cold-blooded vertebrates that reproduce in the water—fishes and amphibians—may lay many small eggs and give them no care or may lay a few large eggs and protect the brood during early stages. The higher vertebrates have reduced their number of offspring. "With the advent of the reptiles a new type of eggs developed, carrying very large stores of yolk in solid shells." Many were deposited on land, others were "retained in the oviducts for a long time. . . . The developing young of today's amniotes (reptiles, birds, mammals) have become the objects of more and more prolonged parental care" (Witschi, 1956:9).

Fishes and reptiles may be oviparous, i.e., they lay eggs; or they may be ovoviviparous, in which case the young are born alive, having been nourished by the egg yolk, and hatched while still within the reproductive tract of the mother. Many sharks are truly viviparous, for the embryo is nourished by a placenta. (Aristotle on this basis thought sharks and mammals were related.) Viviparity has arisen independently in at least eight large groups of teleost fishes (Turner, 1947). The young of fishes and reptiles are precocial and able to change location at birth or hatching, and this is true of most amphibians. The young of birds and mammals may be precocial or altricial; in the latter condition they are unable to change their location.

1. Fishes

The ling may lay over 28 million eggs, a cichlid 20 eggs. "Where there is courtship and pairing the males are often brightly coloured, and have large and ornamental fins. Fishes of this type as a rule have a relatively small number of eggs, and one or both parents, generally the father, may guard the eggs and young" (Regan, 1936:204). The male pipe-fish carries eggs and young in his marsupium, releasing the tiny fishes to swim about and taking them in again in face of danger. The male stickleback builds a nest for the eggs, defends and aerates them, and protects the young for some time (Tinbergen, 1953b:Chaps. I, III).

The Baerends (1950) tell how the cichlid *Tilapia natalensis* retains the eggs in her mouth for 10 to 12 days after spawning; the little fishes are "completely developed some days before they leave the mouth of the female." She leads her young slowly about and when danger threatens, she may furiously attack the intruder, butting and biting it; the young come to her mouth, which "they actively penetrate or are passively taken up by the female" (p. 193).

In various species of *Hemichromis* the parents stay together, guarding the eggs and attacking intruders. They aerate the eggs, thus increasing the oxygen supply, and carry off infertile specimens; they also aerate the young and carry them in their mouths to new pits. They lead the young with special slow movements, and some species collect the brood into pits at night. Young may follow their parents till 13, 15 and 18 days of age.

Catfishes, the Siamese fighting fish, gobies, mudfish, *Amia,* and many other fishes actively defend their broods. Konrad Lorenz tells me that many cichlids take up food material and drop it down for the young; they also chew up large pieces in the midst of the brood.

It is not always, however, in relation to small numbers of eggs that parental care is shown. The blind goby, *Typhlogobius californiensis,* lives in permanently mated pairs in the burrows of a shrimp; the female lays from 2,500 to 15,000 eggs at a spawning. During the 10 to 12 days of incubation the parents "not only clean and care for the eggs, but will unitedly attempt to defend them against any intruders" (MacGinitie, 1939). The male lumpsucker, *Cyclopterus,* spends weeks, even months, fasting, while he guards and actively defends his clutch of 80,000 to 136,000 eggs (Norman, 1948:311).

It is clear that some fishes show active defense of the brood, provision of nourishment, sanitation and guidance.

2. Amphibians

No amphibian shows as highly developed parental behavior as that of the cichlids just described. Amphibians appear to have relied for protection on the poison glands in their skins and few have developed aggressiveness. Most of our temperate-zone frogs and toads lay many eggs and leave them—the leopard frog, *Rana pipiens,* from 5,000 to 6,000, a Woodhouse toad, *Bufo woodhousei,* 25,644. At the other extreme, the tree frog, *Rhacophorus reticulatus,* in Ceylon carries her dozen tadpoles attached to her under-surface (Regan, 1936:309). Salamanders on the whole lay fewer eggs than frogs; numbers range from 706 eggs in a siren, *Siren intermedia nettingi* (Pope, 1944) to the two young of the Alpine salamander, *Salamandra atra,* that are "born in perfect form, having passed through the larval stage within the parent" (Regan, p. 300).

Adults of all three orders may stay with the eggs. A caecilian in Ceylon, *Icthyophis glutinosa,* coils herself around her mass of eggs. Many other caecilians are ovoviviparous, the young sometimes developing as free larvae in the oviducts; they develop a remarkable type of temporary dentition which has been interpreted as an adaptation for grazing off the proliferating membrane of the oviduct (Karl P. Schmidt, personal communication).

Many salamander females, particularly species that lay on land, remain with their eggs. "The damp body of the parent assures the eggs sufficient moisture, and her dermal secretions apparently prevent mold from growing over them" (Noble, 1931:413). In six out of twelve North American species listed by Oliver (1955:236) the females stay with the eggs. In regard to the dusky salamander, *Desmognathus fuscus,* Wilder (1917) writes of "the extraordinary constancy and devotion of the mother to her offspring during the incubation period." The young after hatching "tend to cling to the mother and would thus be eventually guided by her to the water."

Although the mere presence of the adult with the eggs would often serve to protect them from enemies, active defense seems to have been reported only in cryptobranchids. The male hellbender, *Cryptobranchus allegheniensis,* drives away other hellbenders of both

sexes, seizing them by the head; he defends the eggs, but also eats some of them. "A male in making a valiant defense of the nest protects the eggs, to be sure, but at the same time he guards his own food supply. Thus in the case of *Cryptobranchus* the brooding habit may have its origin in the feeding habit. On account of the slowness of his digestive processes, and the short period during which, it appears, the eggs are available as food, the male hellbender alone is unable to eat more than a small portion of the eggs" (Smith, 1907).

A male giant salamander, *Megalobatrachus japonicus,* in the Amsterdam Zoo aerated the strings of eggs by heaving them up and down, and protected them by driving off the fishes in the aquarium. He attacked his mate so vigorously whenever she approached the eggs that she had to be removed (Kerbert, 1904). There is no mention in this case of eating any of the eggs.

Among frogs, care of offspring has led to many remarkable adaptations in habits and structure of adults, as well as modifications in the life history of young. All of the hundreds of species of the tropical American *Eleutherodactylus* lay a few large eggs on land or in vegetation, and guard them. Nests out of water are likewise the rule with the Old World *Rhacophorus* and related forms. Foam nests in leaves overhanging water are constructed by frogs both in the Old and New Worlds; from these the tadpoles, on hatching, drop into the water.

The male midwife toad, *Alytes obstetricans,* sits in a quiet retreat with the string of eggs around his legs, occasionally going to a nearby pool to moisten his charges; at the end of a month the tadpoles hatch and wriggle away in the water. Some females carry the eggs and developing young on their backs, as the Surinam toad, *Pipa pipa,* and the marsupial frog, *Gastrotheca,* as well as *Hyla goeldii, Protopippa,* and *Nototrema,* most of the young emerging as fully formed frogs. "The female of *Rhacophorus reticulatus,* in Ceylon, carries about a dozen young attached to her under-surface," while *Hylambates breviceps* "from the Cameroons, incubates her few but bulky eggs in her mouth" (Regan, 1936:309).

The males of the neotropical *Phyllobates* and *Dendrobates* transport the tadpoles from the place of laying to the pools, and from pool to pool, or from tree hole to tree hole, the young clinging to the parental back by their adhesive lips. The male *Rhinoderma darwinii* stays by the eggs and when the embryos start to move about inside the eggs, he

snaps them up and keeps them in his vocal pouch for some three weeks, when he spits them out as fully formed frogs (Pflaumer, 1934).

Fantastic forms of parental care in frogs throughout the world are described by Lutz (1947). In another paper (1948) she summarizes 14 placements of eggs out of water in Brazil, as well as stages at hatching that range all the way from rudimentary larva to adult form. Frogs that have adopted the latter method, i.e., direct development, as well as those tadpoles that subsist on yolk until transformation, are "sheltered embryos (or larvae)" in contrast to most tadpoles that have to rustle for their living in the midst of hungry predators.

To summarize: Many amphibians show no parental care. Others supply the embryos with a large amount of yolk, at the same time providing passive defense by a wide variety of devices. Two salamanders are known actively to defend their eggs, and some frogs "guide" their young by carrying them on their bodies to favorable environments.

3. Reptiles

With reptiles, internal fertilization is fully established, and, even when the adults are aquatic, reproduction takes place on land. Since eggs pass through their development within the mother's body, or, protected by a relatively impervious shell, in hidden places outside, reptiles lay comparatively few eggs, but these are well stocked with yolk. Lizards and snakes may be either oviparous or ovoviviparous, while the tuatara, turtles and crocodiles are oviparous. The development of a primitive kind of "placenta" has been noted in lizards and snakes.

Turtles show passive or indirect defense of their eggs in the selection of the location for their eggs and in their care in covering them.

Some lizards stay with their eggs. The glass snake, *Ophisaurus ventralis*, does not, however, defend them, but the skinks *Eumeces fasciatus* and *E. laticeps* in captivity "vigorously protect their eggs against small enemies including mice, lizards and snakes"; one female bit a king snake, *Lampropeltis getulus*, many times larger than she (Noble and Mason, 1933). Wild female *E. fasciatus*, despite the author's use of a heavy axe in finding the nests, remained with the eggs until touched; "if lightly touched she often attempted to bite the offending finger" (Cagle, 1940).

In nature, *E. fasciatus* excavates her nesting burrow and keeps it in proper condition for the eggs (Fitch, 1954). *E. obsoletus* turns her eggs daily and assists the young in hatching (Evans, 1955:227), while the yucca night lizard, *Xantusia vigilis*, helps her one or two fully formed young in their birth by nipping the fetal membranes (Cowles, 1944).

Noble and Mason believed that *E. fasciatus* supplied her eggs with a small amount of heat through her habit of sun-bathing and then returning to her eggs, but Fitch in his study of the species in the wild writes: "In the field, females were never observed to bask in the sun beside their nest burrows, and seemingly left them infrequently even to feed. When a female was caught in her nest burrow, her temperature nearly always approximated that of the surrounding earth with which she was in contact" (1954:63). "The female usually remains in the nest cavity for a day or two after the eggs hatch, showing affinity for the young by curling around them protectively. Family ties are broken as soon as the young leave the nest" (p. 146).

Females of many snakes have been found coiled around their eggs, and occasionally both parents are present. This habit usually seems to be a matter of passive defense, but male and female king cobras, *Ophiophagus,* and *Naja naja* actively defend their nests, and black mambas, *Dendroaspis,* are very aggressive during the pairing season (Lowe and Norris, 1950). The primitive sea serpent, *Laticauda colubrina,* "guards her eggs and snaps at intruders" (Noble and Mason, 1933). All of the more highly developed sea snakes are ovoviviparous and produce their young in the water.

Occasionally it has been reported that heat has been supplied to the eggs. A pair of pilot snakes, *Elaphe obsoleta,* with a clutch of eggs in a cold, damp sawdust pile would leave to sun themselves and then return to "incubate" the eggs (Noble and Mason). Benedict (1932) reports that in the case of a python in captivity quietly coiled about her eggs, the temperature within the coils rose some 4°-5° C. above that of the surrounding air, but this observation does not seem to have been confirmed.

"It is noteworthy that many snakes in the north, like the northern populations of the prairie rattlesnake, *Crotalus viridis,* and the common European viper, *Vipera berus,* require two seasons to mature the brood within the mother's body. The ability of the mother snake and lizard to keep in the sun seems to be clearly associated with the high incidence

of ovoviviparity in northern latitudes, reappearing in Patagonia. Temperature is quite closely controlled in most reptiles by moving from place to place, i.e., following the sun or avoiding it; burrowing to the correct depth or entering a burrow. The optimum temperature and the ranges of tolerated temperature vary from group to group" (Karl P. Schmidt, personal communication).

Parental care is rather highly developed in the Crocodilia. Some female crocodiles sleep on top of the nest; they dig out the newly hatched young and conduct them to the water. A mother caiman in Paraguay attacked men who were capturing her newly hatched young (Krieg, 1948:22). In Guiana the female caiman gathers wet vegetation, carries it in her mouth to a secluded spot and builds a heap two feet high. Several weeks later she tears it open and lays in it; she stays nearby, leaving only for feeding. Some females are timid, while others refuse to leave the nest upon the approach of hunters. The mother helps the young hatch and keeps them with her until the following spring, defending them from enemies (Beebe *et al.,* 1917:287).

All reptiles may be said to exhibit passive defense of the eggs; a few lizards and snakes show active defense of the eggs, while Crocodilia vigorously protect eggs and young, the latter for a long period. The eggs of caimans, alligators and some crocodiles are heated through fermentation of the nesting material. Crocodiles and alligators may guide their young.

4. Birds

With the advent of homeothermy (temperature maintenance) in warm-blooded animals parental care became universal. In some birds, it is the female that takes the major role in the care of eggs and young; in others, it is the male, but in the majority of species both parents share these activities.

Indirect defense of eggs and young is partly effected by the choice of nest site and by the cryptic coloring and behavior of many bird parents. Territorial behavior ensures protection of the brood from interference by fellow members of the species. Direct defense of the brood may consist in deflection (injury-feigning, distraction display), threat or attack (Nice, 1943:245; Simmons, 1955b). In many cases the male's chief parental function seems to lie in defense of the brood.

Avian eggs are well supplied with yolk, especially in precocial spe-

cies. Feeding by parents is all-important with altricial young; it is also important in early stages with some precocial chicks. Some parents of precocials show the young food with notes and gestures. Altricial and precocial young may learn preferred foods by association with the adults.

Development of the embryo in a cleidoic (closed box) egg demands "a definite type of metabolism in which protein breakdown is suppressed and uric acid takes the place of urea and ammonia as nitrogenous waste products" (Needham, 1931, I:432). Active sanitation is an essential element of parental care with many altricial birds where the parents remove the excreta. Parents of precocial birds remove broken eggs from the nest.

All truly precocial chicks except megapodes follow their parents; thus they are led to food, water and sleeping places, and are protected from enemies. Some altricial young, such as Corvidae, titmice and others, follow their parents after they have left the nest. Whether or not they follow, most young birds probably benefit from parental example and warning cries in learning to recognize enemies (Nice, 1943:255).

The regulation of temperature is essential for the development of eggs and young. Heat is provided for the eggs by all birds, even by megapodes, and for all young except by megapodes. Shade is furnished where necessary—for eggs by some birds in hot regions, and very generally for young in exposed situations.

All birds show defense of eggs, usually indirect, while many actively defend the young. Most birds feed their young. Some provide sanitation, and some guide the young. Regulation of temperature is provided by all birds for the eggs, and by most birds for the young. A comprehensive review of the relation of hormones to parental behavior in birds is presented by Erica Eisner (1960).

5. Mammals

With mammals the mother plays the essential role, first through carrying the embryos in the uterus or marsupial pouch (or in a nest in the case of the platypus), second through nourishing the young with milk. In a great many forms the male plays no part in the care of the young; in some he defends them, while occasionally the other parental functions are present. Horner (1947) describes a male deer mouse, *Peromyscus maniculatus,* in captivity that carried his young about,

while another washed his young, pulled covering over them, and tucked them under his body. Similar behavior has also been noted in *P. leucopus.* Although in the wild the male dormouse, *Glis glis,* apparently pays no attention to his offspring, in captivity he may help the female clean and defend the young (Koenig, 1957).

Passive defense is afforded first of all by the development of the young within the mother's body. It also operates through the maintenance of territory, digging of holes, building of nests, hiding of some precocial young by the mother, etc. Active defense of the young is highly developed in mammals. This is usually the function of the mother, but is prominent in some males, as yaks, bison, musk-oxen, banting, roe deer, African porcupine (Bourlière, 1951:134), baboons, gorillas, and other primates.

All mammals receive their first food after birth from the mammary glands of their mothers. Among the Carnivora, the mother later brings prey to the young. Fathers in some species are also active: ring-tail, *Bassariscus astutus,* a number of weasels, *Mustela frenata* and *M. erminea,* the mink, *M. vison,* and particularly various Canidae, among which many males—for instance, all the North American foxes and wolves—bring food both to the nursing mother and the pups (Palmer, 1954). Young rats depend on the adults to show them food (Lorenz, personal communication); young ungulates eat what they see the adults eating.

As to sanitation, mothers of some altricial mammals stimulate excretion by licking the genital and anal areas of the young, then swallow the excreta. A deer has been seen to induce urination by licking (Haugen *et al.,* 1957).

With very precocial mammals, such as ungulates, guiding is of the utmost importance. In less precocial mammals, the coypu, for example, babies follow their mother in the water like a brood of ducklings. Young raccoons, skunks, badgers, etc., follow their mothers closely on nightly expeditions. The precocial hare does not follow its mother, but the altricial rabbit does so to some extent. Some of the many different techniques employed by mammalian mothers to transport their young are mentioned by Bourlière (1951:135). Hamsters and rats depend on path habits—stereotyped like railroad tracks. Baby hamsters know their way about while still blind. The Galapagos sea-lion father drives back the pups that venture into deep water (Eibl-Eibesfeldt, 1955).

Altricial mammals are often born naked; they require a warm nest and brooding by the mother. Some precocial mammals, such as hares, need some warmth at first from the mother, while others, such as ungulates, have temperature control from the start.

In mammals it is the mother that provides defense and nourishment, heat, sanitation and guidance. A few males help defend the young, and a few bring them food.

C. Summary

Two patterns of ensuring the continuance of species have been evolved: increased number of offspring without parental care and reduced number of offspring with parental care.

Defense and provision of nourishment are the fundamental functions of parental care, while sanitation, guidance and provision of heat are supplementary. All of these may be provided passively or actively.

Some forms of parental care occur in all the main animal phyla; they are best developed in some of the insects, some fishes, some reptiles, and in all birds and mammals.

In general it is the mother that shows parental care, but in both invertebrates and vertebrates, in some species, the father assists or takes the major share.

CHAPTER II

Examples of Post-Embryonic Development of Behavior in Vertebrates

In pursuance of the closely related subjects of parental care and development of young among animals, it will be of interest to compare briefly the development of some representative species of vertebrates.

A. Observations on Embryonic Behavior

Detailed observations on the sequence of movements of the embryonic chick were made by Kuo (1932); his findings were confirmed in a general way by Orr and Windle (1934), but at somewhat later stages of development. This subject has been reviewed by Collias (1952) and Wood-Gush (1955). Smith and Daniel (1946) studied behavior development in fetal loggerhead turtles during the 45- to 50-day incubation period; earliest movements were seen at 12 to 14 days; coordinated swimming movements, avoidance activity, snapping, crawling, etc., appeared between the 26th and 32nd days. The authors decided that "behavioral maturation and integration in the turtles are not related to embryonic repetition or response." The turtles could perform all the basic reactions if taken from the shell eight to 12 days before term.

B. Some Aspects of Development in Seven Vertebrates

Let us compare some aspects of maturation and behavior development in five classes of vertebrates, taking for examples seven representative species, five that are precocial and two altricial. Three species were chosen because of my own experience with them, the others because more or less detailed studies on them have been published. The scientific names and the references to the papers are as follows: the mouth-breeding cichlid, *Haplichromis desfontainesii* (Kirchshofer, 1953), the leopard frog, *Rana pipiens* (Dickerson, 1913), the loggerhead turtle, *Caretta caretta* (Smith and Daniel, 1946), and the altricial mammal, the white mouse, *Mus musculus,* (Williams and Scott, 1953). The development of the hare, *Lepus americanus,* is analyzed in Nice,

Nice and Ewers (1956). We will consider the attainment of temperature control, the appearance of two senses, nutrition, comfort movements, locomotion, escape and social responses, and age of independence.

In the frog and turtle there is no parental care of the young, while in the fish the mother guards the brood for about six days. Parental care of the birds and mammals is prolonged and highly developed.

TABLE 1

SOME ASPECTS OF DEVELOPMENT IN VERTEBRATES

	Age in Days						
Class	*Fish*	*Amphibian*	*Reptile*	*Bird*		*Mammal*	
Stage at birth	*Precox*	*Precox*	*Precox*	*Precox*	*Altrix*	*Precox*	*Altrix*
Example	*Cichlid*	*Leopard frog*	*Logger-head turtle*	*Pintail*	*Song Sparrow*	*Snow-shoe Hare*	*White Mouse*
Temperature control	0	0	0	ca.14	ca.7	5?	18
Dermal covering	b	b	b	b	(6)10	b	(6)10
Hearing	b	?	b	b	b	b	5
Sight	b	7	b	b	5	b	12
Ingestion							
Yolk-sac	0	b	b	b	0	0	0
From parent	0	0	0	0	b-28	b-28	b-25
Independent	b	7	ca.5	1	(13)28	(8)20	(17)25
Excretion							
Parental assistance	0	0	0	0	b-10	b	b-12
Independent	b	b	b	b	10	?	13
Grooming or preening	0	0	0	b	(5)7	3	(8)12
Scratching the head	0	0	0	b	7	1	5
Stretching	?	0	0	b	(5)7	2	2
Locomotion							
In water	b	b	b	1	0	?	?
On land	0	90	b	1	10	b	(6)12
In air	0	0	0	45	(11)17	0	0
Crouching	0	0	0	1	6	b	?
Fleeing	b	?	5?	1	(8)10	2	(5)12
Bond to parents	b-6	0	0	b-45	b-28	b-28	b-25
Bond to brood mates	b-7	??	??	b-60?	b-10	b-14?	b-25
Aggression	21	0	0	5*	17	?	26
Independence	6	b	b	45	28	28	25

b = from birth; 0 = absent; ( ) = preliminary manifestations; ? = when does it occur? ?? = does it occur? * = to strangers.

Temperature control develops more or less slowly in the warm-blooded animals in the Table. This subject will be treated in Chapter XIV so far as it concerns birds. The reference for the mouse is Herter (1936). The tundra redback vole, *Clethrionomys rutilus dawsoni,* is able to regulate its temperature by the 18th day (Morrison *et al.,* 1954).

Hearing seems to be present at birth in all the animals but the mouse. Sight is present at birth in all the precocials but the leopard frog which hatches nine days after the egg is laid and for seven days remains clinging to water weeds while the eyes and mouth develop.

The yolk sac is the chief source of nourishment at first with the frog, turtle and duckling. The leopard frog first eats at seven days. Loggerhead turtles spend three to five days in the nest before they crawl to the ocean and feed (Daniel and Smith, 1947). Independent feeding develops gradually in the Song Sparrow* and the mammals. With the Song Sparrow, father and mother swallow or remove the fecal sacs for the first 10 days. The mother hare probably assists excretion in the young at first, while the mother mouse licks up the excreta of her offspring for the first two weeks.

As to comfort movements, it is only where the animal is covered with hair or feathers that grooming, preening, and scratching the head are regularly shown. These are stereotyped movements that may appear before there are any feathers or fur to be groomed. Stretching is a motor coordination present in fish, birds and mammals, but not in amphibians and reptiles, according to Heinroth (1930).

The precocial forms are able to move at birth or a few hours afterwards, although the Pintail duckling takes about 24 hours before it can walk well, and the hare a few days before it hops well. The duckling can run before it can walk, the hare can walk before it can hop. The tadpole has to change its form, developing from a "fish" into a frog before it can move about on land. The altricial Song Sparrow and mouse take some eight to 12 days before the muscular coordinations in their legs enable them to walk expertly. In the Song Sparrow first attempts at flying take place at 11 days, with skill established at 17 days. The duck can fly at six to seven weeks. The youngest age in vertebrates at which flying is attained is about one day in the megapodes.

The only flying mammals—the bats—are altricial. The pallid

* Scientific names of the birds mentioned will be found in the Index of Species.

bat, *Antrozous pallidus*, is blind, deaf and naked at birth; its eyes open at eight to 10 days; its ears are held erect at 10 days; fear is first shown by drawing back and the utterance of an "intimidation buzz" at 10 days. At 18 days it has grown a short, scanty pelage; at six weeks it will eat mealworms, although nursing for several more weeks; and at seven weeks it flies (Orr, 1954:225-28).

Crouching is shown early by birds and the hare. Active escape is not possible until locomotion is at least somewhat established; hence it occurs at birth or shortly after with the precocial forms, but not until later with the altricial animals.

With the majority of cold-blooded vertebrates there is no bond to the parent. The amphibian and reptile in the Table show none, but the cichlids stay near their mother and return to her mouth for protection for about six days. In birds and mammals the bond holds till the young are fully able to care for themselves—about 3½ weeks with the mouse, four weeks with the hare and Song Sparrow, and six weeks or sometimes longer with the Pintail.

The bond to brothers and sisters is strong at first in the cichlid, the birds and the mammals, but there is no clear information as to the frog and turtle. It seems to be lost in the fish rather soon after leaving the mother. With the Pintail it may persist longer than the bond to the parent. Song Sparrows appear to have a real sibling bond for the duration of nest life; a hand-raised brood frightened from the nest at nine days stood closely pressed together all that day, even though the weather was warm (Nice, 1943:20). With ground-nesting passerines there is often a definite tendency for the siblings to get away from each other as soon as they leave the nest. With some passerines, however, as Kingbirds, Phoebes, etc., young fledglings sit closely pressed together.

Aggression towards siblings appears at 21 days with the cichlids, 17 days with the Song Sparrows, and 26 days with the mice. Apparently it plays no part in the life of tadpoles or young turtles. Pintail ducklings at five days will attack a strange duckling, but I know of no observations on when quarreling appears within a brood under natural conditions. (With Mallards, members of a family are said never to fight one another [Weidmann, 1956].) Newborn hares show defense behavior towards enemies, but I have found no information as to when hostility arises in relation to a brother or sister.

Independence is attained by the frog and turtle at birth, by the

cichlid normally at six days. Three of the warm-blooded animals leave the parents at about four weeks, the Pintail at about six weeks or later. The cichlids may, however, leave the mother at birth, but they grow less well than the broods that take refuge in their mothers' mouths for the first six days.

As to very precocial mammals, Collias (1956) describes how lambs stood and walked 29 and 32 minutes after birth, while kids did so at 11 and 15 minutes. A white-tailed deer fawn nursed 8½ minutes after birth and got to its feet when 19 minutes old (Haugen *et al.*, 1957). Hediger (1955) describes behavior of newborn giraffes, gnu, nilgai and wild pigs. Agoutis can leave the nest when an hour old; they start to gnaw at four days (Roth-Kolar, 1957). In a detailed study of 11 newborn camelids of the Old and New World, Pilters (1954:298) states that "the movements of rolling on the ground, shaking, stretching, yawning, stamping and chewing appear spontaneously immediately after birth," but scratching and nibbling come later.

The most precocious of all precocial mammals of which I have heard is the Alaska fur seal *(Callorhinus ursinus)*. "Usually, 15 to 45 seconds elapse between the completion of delivery and the time the pups stand up and vocalize, although sometimes the interval is as long as three minutes. The pups are capable of shaky but effective locomotion a few minutes after birth and appear to be as well coordinated then as they are several days later. Even while they are still attached by the umbilical cord to the undelivered placenta, the pups perform many of the movements typical of the older pups and adults—shaking off water, snapping and biting at other animals, and scratching dog-fashion with one hind flipper. . . . The pups also frequently attempt to nurse before the placenta is extruded—sometimes within less than five minutes *post partum*" (Bartholomew, 1959).

C. Summary

Studies are cited on the development of behavior of chicks and turtles before hatching.

Some aspects of development in seven species of five classes of vertebrates are summarized. The subjects treated concern temperature control, senses, nutrition, comfort movements, locomotion, escape responses, social responses and independence.

References are given to descriptions of behavior of newborn mammals that are strikingly precocious.

CHAPTER III

Precox and Altrix in Birds

Two sets of terms are found in the literature: precocial and altricial; nidifugous and nidicolous. *Praecox* means ripened beforehand; *altrix* means a nurse, from *alere*, to nourish. The first word gives a generalized picture of the state at hatching, while the second refers to the necessity for parental feeding. *Nidus* means nest, *fugere*, to flee, *colere*, to dwell. These terms describe the activity of the hatchling; as Witschi (1956) graphically puts it, birds are nest-quitters or nest-sitters. Personally I prefer precocial and altricial because of their distinctiveness.

A. Maturity at Hatching in Birds

There is great variation in the stage and nature of maturity at the time of hatching. In Table 2 newly hatched birds are divided according to manner of getting food, activity, amount of down, and development of sight.

TABLE 2

Classification of Maturity at Hatching in Birds

Feed Selves
Precocials—eyes open, down covered, leave nest first day or two.
Precocials 1. Independent of parents—e.g., megapodes.
Precocials 2. Follow parents but find own food—e.g., ducks, shorebirds.
Precocials 3. Follow parents and are shown food—e.g., quail, chickens.
Fed by Parents
Precocials 4. Follow parents and are fed by them—e.g., grebes, rails.
Semi-precocials—eyes open, down covered, stay at nest though able to walk—e.g., gulls, terns.
Semi-altricials—down covered, unable to leave nest.
Semi-altricials 1. Eyes open—e.g., herons, hawks.
Semi-altricials 2. Eyes closed—e.g., owls.
Altricials—eyes closed, little or no down, unable to leave nest—e.g., passerines.

Precocial and semi-precocial birds are mobile, actually or potentially; altricial and semi-altricial birds are sedentary. The four categories of precocial birds are hatched with their eyes open; they are completely covered with down; they leave the nest during the first day or two. The most precocial are independent of their parents from

the start, while the others follow their parents. The first two categories feed themselves with no help; the third gets some help through the parents calling them to food; the next step is taking food from the parental bill.

Semi-precocial birds are physically well developed, but because of the feeding habits of the adults, they must stay on or near the nest until fledged.

Semi-altricial birds, on the contrary, are physically unable to leave the nest, but they are well provided with down from the start. Some are hatched with open eyes, others with eyes closed.

Altricial birds are hatched with closed eyes and little or no down; they are unable to leave the nest. At times it is not easy to decide whether to call a hatchling an altricial or a semi-altricial 2. (See Burkhardt [1954] for a detailed study of the down of altricials.)

Thus we have a progression from chicks so developed in every respect that they need no parental care to chicks so helpless that they demand prolonged and specialized care. Verheyen (1948) says that altricials are "born prematurely, like abortions"; Portmann (1938) compares them to larval forms. Parent and young constitute an entity, the instinctive reactions of both fitting each other and effecting the rapid, successful development of the young. The precocial state corresponds to the reptilian pattern and must have been the primitive one, yet there is no consistent evolution towards the altricial condition. Gofman (1955) concludes that the latter type developed quite independently in different classes of birds and at different times.

Most precocial birds subsist on food that can be procured by young birds—small invertebrates or, occasionally, seeds. Some precocials in Class 4, as grebes and loons, semi-precocials and many altricials live on food that must be captured with strength and skill, so growth, maturation and learning are necessary before the chick can feed itself. In general precocials nest on the ground, and altricials in trees. The Heinroths (1924-33, III:2) point out that in the Caprimulgiformes the species nesting on the ground are semi-precocial, those nesting above it are altricial.

B. Maturity at Hatching Throughout the Class Aves

Stage of development at hatching is usually consistent throughout an order, but not always. Relative precocity of hatchlings is listed in

Table 3 for all the orders of living birds recognized by Wetmore, and for most of the families in eight of the orders. The classification and nomenclature followed is that of Wetmore (1951).

TABLE 3

MATURITY AT HATCHING OF ORDERS OF BIRDS

Sphenisciformes: Penguins	Semi-altricial 2
Struthioniformes: Ostriches	Precocial 3
Rheiformes: Rheas	Precocial 3
Casuariiformes: Cassowaries, Emus	Precocial 3
Apterygiformes: Kiwis	Precocial 2
Tinamiformes: Tinamous	Precocial 2 or 3
Gaviiformes: Loons	Precocial 4
Podicipediformes: Grebes	Precocial 4
Procellariiformes: Albatrosses, Petrels	Semi-altricial 1, 2 Semi-precocial
Pelecaniformes:	
Phaëthontidae: Tropic-birds	Semi-altricial 2
Pelecanidae: Pelicans	Altricial
Sulidae: Boobies, Gannets	Altricial
Phalacrocoracidae: Cormorants	Altricial
Anhingidae: Anhingas	Altricial
Fregatidae: Frigate-birds	Altricial
Ciconiiformes:	
Ardeidae: Herons, Bitterns	Semi-altricial 1
Balaenicipitidae: Whale-headed Storks	Semi-altricial 1
Scopidae: Hammerheads	Semi-altricial 1
Ciconiidae: Storks, Jabirus	Semi-altricial 1
Threskiornithidae: Ibises, Spoonbills	Semi-altricial 1
Phoenicopteridae: Flamingos	Semi-precocial
Anseriformes: Swans, Geese, Ducks, Screamers	Precocial 2
Falconiformes: Hawks, Vultures, Secretary Birds	Semi-altricial 1
Galliformes:	
Megapodiidae: Megapodes	Precocial 1
Cracidae: Guans, Curassows	Precocial 4
Tetraonidae: Grouse	Precocial 2, 3
Phasianidae: Quails, Pheasants	Precocial 3, 4
Meleagrididae: Turkeys	Precocial 3
Opisthocomidae: Hoatzins	Semi-precocial ?
Gruiformes:	
Turnicidae: Button-quails	Precocial 4
Gruidae: Cranes	Precocial 4
Aramidae: Limpkins	Precocial 4
Rallidae: Rails, Coots, Gallinules	Precocial 4
Rhynochetidae: Kagus	Semi-precocial
Eurypygidae: Sun-bitterns	Semi-precocial
Cariamidae: Seriemas	Semi-altricial 1
Otididae: Bustards	Precocial 4

TABLE 3 (continued)

MATURITY AT HATCHING OF ORDERS OF BIRDS

Charadriiformes:	
Jacanidae: Jaçanas	Precocial 2
Haematopodidae: Oystercatchers	Precocial 3, 4
Charadriidae: Plovers, Turnstones	Precocial 2
Scolopacidae: Snipe, Woodcock, Sandpipers	Precocial 2, 4
Recurvirostridae: Avocets, Stilts	Precocial 2
Phalaropodidae: Phalaropes	Precocial 2
Dromadidae: Crab-plovers	Semi-altricial 1
Burhinidae: Thick-knees	Precocial 4
Glareolidae: Pratincoles, Coursers	Precocial 4
Stercorariidae: Skuas	Semi-precocial
Laridae: Gulls, Terns	Semi-precocial
Rhynchopidae: Skimmers	Semi-precocial
Alcidae: Auks, Auklets, Murres	Precocial 2 Semi-precocial
Columbiformes:	
Pteroclidae: Sand Grouse	Precocial 2
Columbidae: Pigeons	Altricial
Psittaciformes: Parrots	Altricial
Cuculiformes:	
Musophagidae: Touracos	Semi-altricial 1
Cuculidae: Cuckoos	Altricial
Strigiformes: Owls	Semi-altricial 2
Caprimulgiformes:	
Steatornithidae: Oilbirds	Altricial
Podargidae: Frogmouths	Semi-altricial 1
Nyctibiidae: Potoos	Semi-altricial 1
Caprimulgidae: Goatsuckers	Semi-precocial
Apodiformes: Swifts, Hummingbirds	Altricial
Coliiformes: Colies	Altricial
Trogoniformes: Trogons	Altricial
Coraciiformes: Kingfishers, Rollers, Hornbills	Altricial
Piciformes: Jacamars, Toucans, Woodpeckers	Altricial
Passeriformes: Perching Birds	Altricial

The status of the young of many birds is well known, but for others the lack of definite data has made it hard to decide in which category certain birds should be placed. Further observation may well make changes and particularly additions, i.e., greater variety than is now apparent may prove to be the case in some families and orders. It has been difficult to find out whether some parents of precocials call the chicks to food or give them food. Evidence will be presented for the classification of those birds on which statements have been contradictory or difficult to find.

Newly hatched Yellow-eyed (Richdale, 1957) and African Penguins (Wackernagel, 1952) are helpless things with closed eyes. At four days of age the eyes are open in the Yellow-eyed and Little Blue Penguins (Richdale, 1940).

In regard to ratites, Kenton C. Lint, Curator of Birds at the San Diego Zoo, writes me of his experience in raising chicks of Ostriches, Rheas, Emus and Cassowaries: "In all four species the male bird hatches the eggs and cares for the young." He also teaches the chicks to eat by picking up the food from the ground and calling. They pick the food from his beak and gradually come to pick it up themselves. When Kiwi chicks hatch, the father "blocks up the opening of the box and keeps it blocked until the sixth day." At four days the chick can stand and at six days it comes out of the nest. "The first food is worms, and right away it starts driving the bill into the ground looking for them. . . . The chick doesn't look for any food from the parent" (Robson, 1947).

In describing the breeding in captivity of the Tataupa Tinamou, Seth-Smith (1904) writes: "These chicks are extraordinarily strong on the leg from the time they leave the nest, and are much more independent than the young of the true gallinaceous birds, the parent seeming to take but a casual interest in his chicks." A more recent paper on the Great Tinamou in captivity (Taibel, 1939) tells of the excellent care given the chicks by the father, but unfortunately fails to give details. Most of the chicks were reared by bantams, whose "invitations" to food helped their charges to get started in feeding, so this behavior may well be shown by the tinamous.

In the Procellariiformes the hatchlings stay in the nest for protracted periods; many are physically unable to leave it. Some are hatched with open eyes, others with closed eyes. Lockley (1942) writes that Storm Petrels on Skokholm, Wales, "cannot hold up their heads at first, or open their eyes," but day-old Bulwer's Petrels near Madeira "had their eyes open and could move about and even try to climb rocks with hooking bill and wing stumps, if placed in the sunlight." So Bulwer's Petrel might be classified as semi-precocial. (See the discussion under Table 4 of the amount of yolk in the eggs of Antarctic petrels.)

All of the Pelecaniformes are hatched blind, and all are naked except the Phaëthontidae; Gross (1912) describes the chick of the Yellow-billed (White-tailed) Tropic-bird as a ball of down.

The Galliformes show every variety of precocity; also semi-precocity, while the chicks of one family (the Hoatzins) do not seem to fit well into any of the categories. Curassows, guans and chachalacas are fed by the parents for long periods, even up to 10 weeks in case of a captive female Heck's Curassow (Pocock, 1908; see also Heinroth, 1931; Taibel, 1940, 1953, 1954; Carpentier, 1956). The Hazel Hen (Pynnönen, 1954:85) and Capercaillie (Krätzig, 1939:19; Höglund and Borg, 1955) are said not to call the chicks to food, but the Ptarmigan (Krätzig, 1940:156) does so occasionally. When the hen Sage Grouse "signals the chicks that she is pointing out some article of food, she clucks rapidly, at a low pitch" (Girard, 1937:28). Most of the Phasianidae seem to call their young to food, as the North American quail, Marbled Wood-Quail (Skutch, 1947:226), Jungle Fowl, etc. (See Chapter VII.) The chicks, however, when brooder-raised, feed themselves from the ground with little difficulty. A few pheasants, as the Great Argus, Crested Argus, and Peacock Pheasant, feed entirely from the parental bill for the first few days, and small chicks will not pick up food from the ground (Delacour, 1951). Hoatzins are hatched with very scanty down (Beebe *et al.*, 1917). Within 48 hours after birth they "begin to crawl about, using the bill, the feet and wing claws to pull themselves from place to place" (Cherrie, 1909). In face of danger they dive into the water below the nest, swim expertly, then climb back to the nest. They are fed by regurgitation, the chick thrusting its head well down its parent's throat to obtain a brew of pimpler leaves (Beebe *et al.*, 1917). Despite their meager covering, their potential activity entitles them to be classed as aberrant semi-precocials.

As to the Gruiformes, of eight families on which I could find information, five have precocial young fed by parents. The Kagu appears to be semi-precocial; the young are "semi-active," usually squatting, but able to take short runs (Finn, 1930). A pair of Sun-Bitterns in the London Zoo hatched a chick, thickly covered with down and with open eyes; the parents fed it in the nest for 21 days and continued to feed it for a long time after it had left the nest (Bartlett, 1866). The Seriema is semi-altricial, hatched covered with down, with eyes open, but staying in the nest for 12 days (Heinroth, 1924).

A wide range of variety occurs among the Charadriiformes. The Jaçana father cares for the chicks but never shows or gives them food (Hoffman, 1949). Oystercatchers bring food to the chicks, drop

it in front of them and point to it with their great red bills; this is true of both European and Black Oystercatchers (Webster, 1941). European Oystercatchers may feed them from the bill as well as dropping morsels before the chicks (Dircksen, 1938). Sandpiper chicks as a rule find food for themselves, but Black-tailed Godwits, European Snipe and European Woodcock took food only from the forceps for the first few days (Heinroth, O. and M., III). A mother American Woodcock with small young was watched by Pettingill (1936:328); she inserted half her beak into the soil and the chicks crowded around; she dangled earthworms before them, whereupon they tilted their heads to one side and took the worms crosswise in their beaks.

As to European Avocets, "At first the young birds peck food directly from the ooze" (Turner, 1921). The Crab Plover chick lives in a burrow; it is very helpless and unable to run (Stresemann, 1927-34:776). Derek Goodwin writes me he has seen Stone Curlews carrying food from a distance to large young. Coursers also feed their chicks for a time.

Skuas, gulls and terns are typical semi-precocials. Most alcids are semi-precocial, but downy chicks of the Ancient and Xantus' Murrelets join their parents on the ocean when two to three days old (Bent, 1919:137, 151). In answer to my query, Charles J. Guiget, Biologist at the Provincial Museum, Victoria, British Columbia, wrote me: "I believe young Ancient Murrelets secure their own food in company with their parents. I've yet to see an Ancient Murrelet feeding its young at sea. Our pelagic waters, in areas frequented by these birds, are teeming with minute crustaceans and small fishes. It is apparently no trick at all for a newly hatched but nonetheless adept diver such as this to maintain itself."

Pin-tailed Sand-Grouse chicks, hatched by their parents in captivity, were very advanced, "dusting and foraging for themselves; they feed on the half-ripe seeds of various plants." At 10 days they refused to be brooded any longer by their parents, but roosted separately from each other among the stones (Meade-Waldo, 1897).

Touraco chicks are covered with down; they "can crawl about on their legs from the first, and have more activity in the nest than the young of pigeons" (Finn, 1905).

Thus, so far as I could determine, in 19 orders there seems to be uniformity in the stage of maturity at which the young are hatched,

while in eight orders there is diversity, sometimes very marked. Further observations will undoubtedly reveal more diversity.

C. Percentage of Yolk in Eggs of Precocials and Altricials

There is more yolk in the eggs of precocials than in eggs of altricials. Investigations on this subject by a number of authors are summarized in Table 4.

TABLE 4

Percentage of Yolk in Eggs

	Number Examined		*Percentage of Yolk*		
	Species	*Eggs*	*Range*	*Median*	*Reference*
Reptiles					
Turtles	5	?	33-50	40	Heinroth '22
Crocodilians	2	?	39-50	45	Heinroth '22
Birds					
Precocial 1					
Megapode	1	7	59-66	62	Meyer '30
Precocial 2, 3					
Fowls, ducks, shorebirds	28	many	25-50	33	Heinroth '22
	4	many	30-43	35	Meyer '30
	8	190	32-43	36	Grossfeld '38
	5	615	31-40	32	Asmundson '43
Precocial 4					
Grebes, coots, gallinules	7	many	21-31	27	Heinroth '22
Semi-precocial					
Gulls, terns	6	many	22-37	25	Heinroth '22
Common (Mew) Gull	1	27		26	Meyer '30
Gulls	1?	6	24-30	27	Grossfeld '38
Semi-altricial					
Hawks, owl, heron	4	6	18-22	19	Heinroth '22
Penguins, petrels	5	44	26-33	30	Etchécopar '54
Altricial					
Pigeons	2?	10	16-22	19	Grossfeld '38
Passerines, etc.	20	many	15-25	20	Heinroth '22
Passerines	4	30	18-27	20	Asmundson '43

The eggs of turtles and crocodilians show a somewhat larger percentage of yolk than those of any birds except the megapodes. The median value of seven eggs of *Megapodius freycinet eremita* was 62 per cent yolk; of eggs of 34 species of precocials of Classes 2 and 3.

about 34 per cent; of seven species of precocials of Class 4, 27 per cent; of seven species of semi-precocials about 26 per cent; of four species of semi-altricials in Europe 19 per cent, but of five species in Antarctica 30 per cent. The yolk in eggs of 24 species of altricials was 19 to 20 per cent.

Hence in the birds, with the exception of one group of semi-altricials, we have a consistently descending scale of amount of yolk in the eggs from the most precocial to the altricial. Etchécopar and Prévost (1954; reviewed in Nice, 1956) found the percentage of yolk averaged 25.5 per cent in 13 Emperor Penguin eggs and 28 to 33 per cent in 31 eggs of four species of Antarctic petrels—values nearly as high as those in eggs of precocial birds. These are the only data on this subject I have found for Sphenisciformes and Procellariiformes; we do not know whether the large amount of yolk is an adaptation to extreme cold or is characteristic of these orders throughout their range. It may indicate that penguins, albatrosses and petrels are really more semi-precocial than semi-altricial.

If we consider birds of the North Temperate Zone, we find that fresh eggs of precocials that feed themselves on hatching are provided with some 34 per cent of yolk; of precocials and semi-precocials that are fed by their parents with about 27 per cent of yolk, and of semi-altricials and altricials about 20 per cent.

The percentage of yolk in newly hatched birds came to 30 in an Ostrich (Brinkmann *et al.,* 1954), 24 in a Mute Swan, 14 in a Mallard, and 1.5 in a Great Cormorant (Heinroth, O. and M., 1924-33, II:122).

In a 12-hour chick of the domestic fowl, yolk made up 14 per cent of the total weight; in a 36-hour chick, 9 per cent; in a 3-day chick, 7 per cent; and in a 4-day chick, 2 per cent (Stresemann, 1927-34:295).

With the Red-winged Blackbird in Colorado, Daniel (1957:342 and personal communication) found the average weight of a fresh egg was 4.3 grams and of its yolk 0.8 grams, i.e., 19 per cent; at eight days of incubation yolk comprised 15 per cent; at 10 days, 10 per cent; and at hatching at 12 days it had disappeared.

D. Summary

Birds may be divided in respect to maturity at hatching into eight classes according to manner of getting food, amount of down, activity, and development of sight.

The first three classes feed themselves from the start, while the others are

fed for longer or shorter periods by the parents. Chicks of the first seven classes are covered with down; those in the last are hatched naked or nearly so. The first four—precocials—are active from the start, while semi-precocials are potentially active, but semi-altricials and altricials are physically unable to leave the nest. The first six classes are hatched with open eyes, the last two with closed eyes.

In Table 3 relative precocity of hatchlings is shown for all the orders of birds and for most of the families in eight of the orders.

The percentage of yolk in fresh eggs shows a decrease from the most precocial state with 60 per cent to the altricial state with 20 per cent. It is only Antarctic penguins and petrels that have been found to have a higher percentage than expected. In the North Temperate Zone, eggs of species which feed themselves from the start have about 34 per cent of yolk; eggs of precocial and semi-precocial species fed by their parents have about 27 per cent of yolk, while eggs of altricial and semi-altricial species have about 20 per cent.

CHAPTER IV

Stages of Development in Behavior

A number of studies have been made on various stages in the development of behavior in altricial birds and mammals.

A. Five Stages of Development in Altricial Birds

In 1909 Kuhlmann made a study from blinds of the nest life of a number of open-nesting passerine species—Chipping Sparrow, Rose-breasted Grosbeak, American Robin, Red-winged Blackbird and Brown Thrasher; he divided the 10 days spent in the nest into three stages. These were: the first four days when the "only coordinated movement present is the food reaction"; five and six days—"a stationary stage of development," the birds becoming "more active and vigorous, but otherwise the nature of their movements" not changing "noticeably"; from seven days on—a period of rapid progress in motor coordinations.

These stages fit well the development of Song Sparrows except that there may be more progress in the second stage than noted by Kuhlmann. After leaving the nest, the 18 days or so before independence may be divided into two further stages. The five stages may be briefly characterized as follows:

I. Post-embryonic: first four days. Coordinations mainly concerned with nutrition; hearing present, but not sight.

II. Preliminary: five and six days. Beginnings of comfort movements; eyes open.

III. Transition: seven, eight and nine days. Crouching; maturation of comfort movements.

IV. Locomotory: 10 to 16 days. Leaving the nest; start of self-feeding.

V. Socialization: 17 to 28 days. Aggression; flight; perfecting of self-feeding.

In Tables III and IV of my "Behavior of the Song Sparrow" (1943:34, 57) I summarized the maturation of activities according to these five stages in the Song Sparrow and four other passerine species. These tables clearly show the striking similarity and orderly sequence of the appearance of the different motor coordinations in these open-nesting altricial birds of different species.

Recently these stages have been described in the Red-eyed Vireo (Southern, 1958) as well as in two species that develop more slowly than Song Sparrows: a Piet-My-Vrou, an African cuckoo (Liversidge, 1955) and the semi-altricial California Condor (Koford, 1953; see Chapter X of this volume).

B. Comparison of an Altricial Bird and Mammal

It was with the greatest interest that in 1953 I read a detailed analysis of "The development of social behavior patterns in the mouse, in relation to natural periods," by Elizabeth Williams and J. P. Scott. These authors divide the development of the white mouse into four stages: neo-natal, 0 to 4 days; transition, 5 to 11 days; socialization, 12 to 25 days; and juvenile, 26 to 40 days. Their *transition* period seems to correspond fairly well with my *preliminary* and *transition,* and their *socialization* with my *locomotory* and *socialization.*

In Table 5 the stages of development of the Song Sparrow and white mouse are compared. Both species exhibit rapid development (see Nice *et al.,* 1956).

The course of development follows much the same lines in the bird and the mammal. Even the length of the five stages to independence corresponds. The senses develop earlier in the bird; certain comfort movements and locomotion earlier in the mammal. (A closely similar course of behavior development to this study of the white mouse was found by Eibl-Eibesfeldt both in its wild form, the house mouse, *Mus musculus* [1950b] and in the Persian desert mouse, *Meriones persicus* [1951].) The incubation period of the Song Sparrow is 12 to 13 days, the gestation period of the mouse 20 days. The newly hatched Song Sparrow weighs about 1.5 grams, the mouse about 1.4 (Gates, 1925). The adult Song Sparrow averages about 22 grams, the white mouse somewhat higher. At the age of 28 days the former weighs about 20 grams, the latter only 7 to 8. But the mouse reaches sexual maturity at 40 days; the bird not until 9 to 10 months. Mammals will breed when much below the weight ultimately attained, but this is not true of birds. This delayed sexual maturity of the Song Sparrow would seem to be an adaptation to climate. Miller (1955) found that in the constant equatorial environment in Colombia, South America, certain "young passerine birds are able to breed at ages of four to nine months." Steinbacher (1936) reviews the evidence of early

TABLE 5

Comparison of Development of an Altricial Bird and Mammal

Stage	Age in Days			
	Song Sparrow		*White Mouse*	
	Age	*Coordination*	*Age*	*Coordination*
I. Post-embryonic. Coordinations concerned mainly with nutrition	0-4	*Gaping;* hearing-E	0-4	*Nursing;* deaf
II. Preliminary. Beginnings of comfort movements	5-6	*Preening; standing;* sight-E	5-6	*Grooming; standing;* scratching head-E; hearing-L
III. Transition. Maturation of comfort movements; escape reactions	7-9	*Crouching;* scratching head-L; stretching	7-11	*Escape;* walking-E
IV. Locomotory. Leaving nest; start of self-feeding	10-16	*Leave nest; hopping;* walking-L; *flying;* picking up food; drinking-E	12-16	*Leave nest; hopping; running;* sight-L
V. Socialization. Aggression; perfecting of locomotion	17-28	*Aggression; flight perfected; feeding self;* play-fleeing-E	17-25	*Biting; climbing; long hops; eating solid food;* drinking-L
VI. Juvenile. Precocious sexual behavior	29-90	*Copulatory attempts;* nest molding	26-40	*Mounting;* playing-L; fighting

Similar and analogous coordinations appearing in the same stage are italicized. Those coordinations appearing in a stage which in one animal is earlier or later than in the other animal are designated by E or L respectively.

breeding in aviaries, reporting parakeets breeding at three to four months and Estrildine Finches from two to six months. Earliest of all, Japanese Quail in captivity start laying at 40 to 50 days (Meise, 1954).

That many resemblances occur in the development of behavior between a small altricial mammal and a small altricial bird is suggestive, but generalizations must be made with caution. A somewhat different picture of developmental stages is given in Scott's (1958) report on

puppies. Here the neo-natal period lasts two weeks and the transition one week, while the crucial "socialization" period lasts from four to seven weeks. During this period puppies establish their primary social relationships. Dogs, of course, are markedly social animals, far more so than mice or Song Sparrows. The three periods in puppies have been shown to be correlated with changes in anatomical development.

C. Comparison of an Altricial and a Precocial Bird

As I watched in 1938 my hand-raised Song Sparrows two days out of the nest I was struck with how much they resembled day-old Bobwhite chicks. It occurred to me that perhaps with the latter, Stages I, II and III were passed in the egg and the precocial bird hatched at the beginning of Stage IV (1943:73). It was primarily to test this idea that we first went to the Delta Waterfowl Research Station in 1951. Experience there with a large variety of precocial chicks showed me I was wrong: these precocials may be said to pass through Stage I in the egg; they hatch ready to pass through Stage II in a few hours, and Stage III in a few more hours or perhaps a day or two. Then at the age of 8 to 48 hours they reach Stage IV, and leave the nest, clothed in down, able to walk and run, and to some extent escape from enemies.

At the meeting of the American Ornithologists' Union at Montreal in October 1951, I gave a paper on "Appearance of motor coordinations in some precocial birds," showing a slide comparing development of a Song Sparrow and a Pintail, reckoning from the start of incubation (which lasts 12 to 13 days in the former, about 21 in the latter). In these two species Stage IV was reached at about 23 to 24 days, and Stage V, so far as aggression goes, at 30 to 31 days. Later observations showed that in many respects the Spotted Sandpiper was a better species for comparison with the Song Sparrow, partly due to less disparity in size, as shown in Table 6.

Assuming then that Stage I is passed in the egg by precocial birds and that the next two stages may be telescoped into hours instead of five days, the development of behavior in a Song Sparrow and a Spotted Sandpiper is closely parallel. The sandpiper is larger than the sparrow, adult females averaging about 50 grams, males 40 grams; the newly hatched chick weighs about 6.5 grams, a 25-day chick we raised weighed 33 grams. Scratching the head, exploratory pecking and independent feeding come earlier in the precocial than in the

TABLE 6

THE FIVE STAGES IN DEVELOPMENT OF BEHAVIOR IN AN ALTRICIAL AND A PRECOCIAL BIRD

Stage	*Song Sparrow*		*Spotted Sandpiper*	
	Duration	*Coordination*	*Duration*	*Coordination*
I. Post- or Late Embryonic. Coordinations concerned mainly with nutrition	4 days	Hatching-E; gaping	ca.9 days	
II. Preliminary. Beginnings of comfort movements	2 days	*Preening; yawning; standing; sight*	4 hours	Hatching-L; *preening; yawning;* scratching head-E; *standing; sight*
III. Transition. Maturation of comfort movements	3 days	*Stretching; crouching;* scratching head-L	8 hours	*Stretching; crouching;* exploratory pecking-E
IV. Locomotory. Leaving nest; start of self-feeding	7 days	*Leave nest; fleeing;* exploratory pecking-L	7 days	*Leave nest; fleeing;* feeding self-E
V. Socialization. Aggression; perfecting of flight	11 days	*Flight; aggression; play-fleeing; bathing;* feeding self-L	12-20 days	*Aggression; play-fleeing; bathing; flight*

Similar and analogous coordinations appearing in the same stage are italicized. Those coordinations appearing in a stage which in one bird is earlier or later than in the other bird are designated by E or L respectively.

altricial bird. The latter grows much faster, increasing in weight 13 times between hatching and independence in contrast to the sandpiper's five times. The Song Sparrow is clothed in feathers at 10 days, the sandpiper at two weeks. The Song Sparrow attains a fair degree of temperature control in Stage III, the sandpiper not until some time in Stage V.

These five stages comprise: a period of immobility—Stages I, II and III; a period of relative mobility—Stage IV; and of full activity—Stage V. This time of immobility—Stages I through III—is

the feature of the altricial state in birds and mammals. The undeveloped young lack muscular coordination, dermal covering, temperature control, sensory development; they are blind, and some are deaf. They also lack the fear response. They live in a nest which provides insulation and concealment. They have a strong bond to nest mates and parents, largely dependent on their need for warmth. Their first business is growth, and they have to work for their nourishment instead of receiving it passively as do precocials in the egg or uterus. The bird has to raise its head, open wide its mandibles and swallow; the mammal has to find the nipple and suck. They are absolutely dependent on their parents for food, disposal of waste products, heat, and defense from enemies.

With precocial birds and mammals most of this period of immobility is passed in the egg or uterus. During four hours after hatching —Stage II—the precocial bird is fairly helpless; and it takes another 8 to 20 or 44 hours—Stage III—for it to gain sufficient strength and muscular control to follow its parent adequately. Most precocial mammals also need a few hours or days of quiet before they can navigate successfully (Nice *et al.*, 1956; Collias, 1956). At the end of Stage II many precocial and altricial birds *can* leave the nest in case of emergency, but this usually spells disaster.

Stage IV may be a period of relative mobility. The Song Sparrow hides in the undergrowth and moves but little during the first week after leaving the nest. Hole-nesting passerines typically pass this stage in the nest, not leaving until they can fly to some extent at the age of 15 to 17 days or more (Nice, 1943:70). The first two stages in these birds are somewhat more prolonged than in open-nesters; in the European Redstarts I studied in Austria which left the nest at 14 days, Stage III started some four days later than in the Song Sparrows and other species nesting in the open. The same is true with Chaffinches which leave the nest at 13 to 14 days. "During the last four days in the nest the chicks, which have previously kept still while the parents were absent, begin to stretch, preen, and flap their wings." After leaving they keep hidden for three days (my Stage IV); during the next five days they are free-moving but dependent on parental feeding, then for 10 to 14 days they start to feed themselves and to chase each other (Marler, 1956).

Altricial mammals in Stage IV may make expeditions from the nest but return to it. Semi-precocial birds pass this stage largely in

or near the nest. Precocial birds follow their parents on foot or in the water; flight develops later.

In Stage V locomotion is perfected. This stage is conspicuous in Song Sparrows in the wild for then they come out of hiding, well able to fly. Aggression towards siblings may appear the same day. Most precocials do not attain the power of flight until the end of Stage V, hence with them it is less easy to decide when to date its start. We have used the first sign of aggression as the crucial point; on some species we obtained much evidence, but on others we had to base our decision on only a few individuals and wider experience might well have changed the picture.

It must be emphasized that there is nothing rigid about these stages; the change from one to the next is often gradual and ill-defined. This is especially true of Stages I, II and III in altricials, and II and III in precocials. In many cases Stage IV is sharply defined with the leaving of the nest, but in others Stages III and IV are merged, the bird not leaving the nest until some power of flight is attained, i.e., at the start of Stage V.

D. Summary

Five stages are described in the development of open-nesting passerines from hatching to independence.

These compare well with the development of a small altricial mammal—the white mouse.

These stages also compare well with the development of a precocial bird; here Stage I is passed in the egg, and Stages II and III are telescoped into hours instead of days.

The first three stages constitute a period of immobility; the fourth stage is typically a time of relative mobility, while in the fifth stage full activity develops.

CHAPTER V

Precocial Chicks Independent of Their Parents: Megapodes

The Megapodes, a family of gallinaceous birds widely distributed throughout Australia, Malaysia, Polynesia and Melanesia, are unique among birds in that, although not parasitic on other birds, they do not incubate their eggs with their own body heat, nor do they care for their young. They depend upon solar (or volcanic) heat, or fermentation heat, or a combination of solar and fermentation heat (Frith, 1956b). In some species no attention is paid to the eggs after they are laid, while in others a great deal of care is expended by one or both parents in constructing a mound and in regulating its temperature (Frith, 1956a, 1956b, 1957). Thus some species resemble the turtles in their lack of parental care, while others outdo the crocodilians in their concern for the eggs, but differ from them in their indifference or even hostility (Fleay, 1937) toward the young, as soon as the latter have emerged from the mound.

There is considerable information on the chicks of two of the nine species in the family. The Brush (or Scrub) Turkey *(Alectura lathami)* has been raised in aviaries in Australia, England, Germany and France, while the Mallee Fowl *(Leipoa ocellata)* has been intensively studied in the wild and in captivity by Harold J. Frith.

A. The Eggs and Their Incubation

The eggs are extremely large in proportion to the size of the female. Heinroth (1922:198,245) reports an egg of *Megapodius freycinet eremita* as weighing 17 per cent as much as the bird that laid it, and of *Alectura lathami* 12½ per cent. In the Mallee Fowl the egg averages 10 per cent of the weight of the mother (Frith, 1959a). She appears exhausted after laying (Frith, personal communication). As is shown in Table 4 in Chapter III, eggs of *Megapodius* contain almost twice as much yolk as eggs of those precocials that feed themselves but are cared for by their parents.

Eggs are usually laid at considerable intervals—about once a week in the case of the Mallee Fowl—whereas clutch size averaged 22.3 eggs (Frith, 1956b). The incubation temperature is low, averaging about 92° F. (33° C.) in *Leipoa*. Maintaining the proper temperature is an

absorbing occupation for the male *Alectura* and for the pair in *Leipoa,* and probably also in *Aepypodius* and *Tallegallus* (Mayr, 1930). The incubation period averages about 57 days in *Leipoa* (Lewis, 1940), but varies rather widely according to the time of the year and the mound temperature (Frith, 1956b:632). This subject will be discussed more fully in Chapter XIV.

A somewhat analogous case to megapode incubation is reported by Cottam *et al.* (1959). In mid-July 1957 in southern Texas a Common Gallinule's nest containing two eggs was appropriated by Coots that built a fairly compact nest on top of the Gallinule eggs. The 10 Coot eggs hatched between about August 8 and 17. On the 19th, Dr. Cottam heard a frantic peeping from inside the nest; three inches down he found and released a Gallinule chick "several hours old." It drank avidly, then "paddled off pecking at every small object in sight trying to get something to eat." The weather had been hot and humid during the full month that incubation must have lasted. "It is possible that some warmth from the body of the incubating bird might have aided in the incubation of this Gallinule egg yet the reduced temperature obviously slowed down incubation. It is certain that the egg had never been turned during its extended period of incubation." The normal incubation period is about three weeks.

B. The Chicks

Are the chicks covered with feathers or down at hatching? Pycraft (1905) writes of the young megapode as "passing through the downy stage during embryonic life, and emerging from the shell fully fledged and able to fly." According to Leake, as quoted by Ashby (1929), the Mallee Fowl is hatched "fully feathered." In 1931 Friedmann described a specimen, preserved in alcohol, of an embryo of *Megapodius pritchardi* that was "close to hatching"; it had "the pennaceous juvenal plumage well developed, although still encased in sheaths like the trichoptiles of cuculiform birds." Portmann (1938) insists on feathers versus down, and in 1955 states in regard to feather formation that megapodes show the type without down formation which he considers as the primary condition; he gives a cut of feather formation in *Megapodius,* but cites no authority. Becker's (1959) doctoral thesis at Basel University is devoted to an analysis of the "first feathers" of *Megapodius freycinet*; she is fully convinced that the first feathers of the two two-day specimens she studied are contour feathers.

On the other hand, so far as I can determine, all ornithologists (with the exception of Leake as quoted by Ashby) *who have raised megapodes* and reported their experiences *state that they are hatched covered with down.*

Alectura chicks are covered with down except for the wings and tail according to Bertling (1904), the Heinroths (1924-33, III:1), Delacour (1935), Coles (1937), and Fleay (1937). Bertling noted that at three weeks "the black feathers are distinctly visible through the down."

In regard to the Mallee Fowl, *Leipoa,* Mr. Frith writes me:

"The chick is covered with down, each down feather being encased in a sheath. These sheaths have sloughed off by the time the young reach ground level 2 hours after hatching. The wings have what are probably transition forms. . . . The small down feathers on the body immediately begin to 'grow out' and by 2 weeks early contour feathers are visible over the whole body with the down feathers attached to the top; by about 4 weeks they begin to break off and the contour feathers are left; by 6 weeks the young are fully feathered. Feather development is most rapid on the wings and crest and then down the breast. Ashby is quite wrong, I am afraid."

Hence it seems established that in *Alectura* and *Leipoa* the chicks at hatching are covered with down. Two species of *Megapodius,* however, are reported as starting out with feathers.

1. The Brush Turkey

The male *Alectura* is reported by Bertling, Delacour and Fleay as sometimes helping the chick as it scratches its way upward by excavating a hole and leaving it uncovered. (Eggs are laid at a depth of about 18 inches.) Once the chicks are out of the mound, however, the parents are "not kindly disposed" towards them (Fleay).

Fleay thinks it may take the chick "a day or two" to get to the surface; in the Melbourne Zoo where the climate is much colder than that of this bird's normal range some chicks died before they could get out and two died on reaching the surface. One chick peeped out and remained quiet for 10 minutes. "Then it fluttered and ran down the side of the mound and scampered for cover." For several days the chicks were extremely wary. "Furtively they come out to feed and as quickly hide again. Their food at first is almost entirely insectivorous and they spend much time scratching in the ground . . . with three or four raking movements of one foot and then a change over to the other." "Until well grown, they appear to be voiceless. At four weeks of age they are miniature adults. They are extremely playful and

interesting from the age of one week onwards and they are frequently seen spreading their wings suddenly, lowering their heads and darting away, to reverse just as suddenly and rush in another direction." This appears to be "frolicking" or, better, "play-fleeing."

A chick raised in the London Zoo remained in the mound about 24 hours after hatching; "an occasional small voice was heard from the young birds," but "this did not appear to excite any notice among them" (Bartlett, 1860).

Bertling believed a chick rested in the mound (in London) for 36 hours after hatching, for it could fly on emerging. The following day it threatened and attacked a much less advanced brother just hatched in the incubator, but later showed no hostility. Jean Delacour told me he found the chicks fearless, but indifferent to one another and to the adults. From the start they ate grain and grew rapidly.

2. The Mallee Fowl

Notes on behavior of newly hatched chicks of *Leipoa ocellata* are given by Lewis (1940) and Frith (1959a and b). About two hours elapsed between hatching and emerging, and there is no parental assistance. On opening a mound a completely hatched chick was found; it was damp and covered with "pin-feathers" (Lewis, 1940). Placed in the sun it soon dried; two hours later the pin feathers had expanded and the young bird was strong enough to run off and fend for itself. "Some of the young birds on arriving at the surface of the mound lie and bask in the sun for half an hour before moving off. Others, as soon as they reach the surface, stand up, shake themselves and run off at once into the Mallee scrub" (Lewis, 1940).

"The mallee chick hatches three feet beneath the soil; we have watched them do so behind glass. The egg bursts and the chick immediately begins his struggle, moving slowly and spasmodically upward. The journey can take 15 to 20 hours" (Frith, 1959b).

I am much indebted to Harold Frith for further details in answer to my inquiries. The chicks, he writes, "can survive 24 hours under 2 feet of soil after hatching. I have also incubated many eggs and raised the chicks. One egg was just pipping when I picked it up and it crumbled. The chick at its instant of 'birth' struggled vigorously in my hand and cheeped loudly. I put it down and it struggled manfully to cover. Another chick was lying on the half shell on a laboratory bench, pecking at bird seed one minute after emerging from the egg.

"In the bush, on hatching each feather is enclosed in a gelatinous sheath which needs an hour or so to dry up and peel off. The chick by then is coming out of the ground. Normally the head emerges and has a look around and then

with a struggle and a heave the chick pops out. It may then rest on the mound but more often moves at a staggering wobbly run to closest cover. Here it remains for an hour or so and idly feeds from where it sits. After this resting period the chick moves off. If chased it can run strongly and flutter a foot from the ground but not fly in the true sense. The next day they fly up to roost. Immediately after the rest period they scratch, feed and preen just like an adult."

Frith (1959a) states that the parents do not recognize the chicks and the chicks flee from the adults. "The chicks' general behaviour is also antisocial. When newly hatched chicks are placed in an aviary they mildly repel one another with miniature threat-displays and live completely separate lives. They feed, rest, and roost independently."

3. Comparison with Other Precocial Birds

The megapode chick does not have an egg tooth. Bertling writes that the shell of *Alectura* eggs is thin; the chicks do not chip around to emerge, "but appear to give a violent wriggle and shatter the whole shell." Hence hatching seems to entail less effort than with most birds, but climbing to the surface of the mound demands a great deal of effort. This might be compared to Stage II—the drying period—in other precocials, and the usual "resting period" to Stage III. Stage IV begins with leaving the mound.

As described in Chapter VII, some chicks of the domestic fowl are very precocious, starting to crawl about as soon as hatched, pecking at the floor when 9 to 15 minutes old, and preening, shaking themselves and fanning their wings during the first half hour. Scratching the ground, however, was not noted with these chicks before the age of about 36 hours.

Megapodes are the most precocious flyers of any birds, for they can flutter during their first day and fly well the next. The next most precocious in this regard appear to be Peacocks and Tragopans that flutter at three days (Heinroth, O. and M., 1924-33, III:236).

As to Stage V, a two-day Brush Turkey attacked a newly hatched sibling, while a five-day Mallee Fowl "ruffled its feathers, spread out its wings and would not go near" a fresh arrival (Ashby, 1929:300). Play-fleeing apparently appeared with the Brush Turkey at one week or shortly after. (See Chapters VII and XII for discussions of this activity.)

Precocial chicks that follow their parents are vocal, giving distress notes when cold or lost, and contentment notes when all is well, both

sets of calls serving to keep the brood in contact with each other and with the parents. Megapode chicks, with no need to advertise their location to anyone, are usually reported as voiceless, but exceptions are noted for *Alectura* by Bartlett and for *Leipoa* by Frith.

The megapode egg is very large with a percentage of yolk twice that of other Galliformes; its incubation period is long for a bird of this order, even when, under experimental conditions, similar temperatures are used (Chapter XIV). The chick hatches at a somewhat more advanced stage than that of other birds. With no parent ready to defend it or offer it warmth, its powers of locomotion develop extremely rapidly, and, unique among birds, it possesses temperature regulation from the start.

C. Summary

Megapodes do not incubate their eggs or care for their young. Some of them lay their eggs in sand and leave them to be hatched by solar or volcanic heat. Others construct nesting mounds of sand and leaves, and spend a great deal of time and energy attempting to keep the temperature of the mound around 92°F (33°C).

The eggs are very large; they are laid at about weekly intervals and hatch in about 57 days.

Some authors have insisted that megapodes in general, and *Megapodius* in particular, are covered with feathers at hatching. Ornithologists, however, who have raised *Alectura* and described the chick at hatching, say it is covered with down. H. J. Frith states the same in regard to *Leipoa*.

Early behavior of *Alectura* and *Leipoa* is described. Comparisons made between the development of these chicks and those precocials that follow their parents but find their own food, show that megapodes are somewhat more precocious, especially in motor coordinations. The unique characteristic that enables them to be independent of parent and sibling is the attainment of temperature regulation by the time they have hatched.

CHAPTER VI

Precocial Chicks That Follow Parents and Find Their Own Food: Ducks, Killdeer, Spotted Sandpiper

During four summers my daughter Constance and I studied the development of hatchlings at the Delta Waterfowl Research Station at Delta, Manitoba. Most of the eggs were hatched in an 18-compartment Jamesway hot-water incubator, but in 1954 we used an electric incubator in our laboratory. We were able to watch hatching behavior of over 100 individuals of 30 species. These included all the classes of birds in Table 2 except Precocials 1 (Megapodes) and Semi-altricials 2.

We kept the hatching eggs and baby birds under an electric lamp in the down of a Pintail nest in a basin set on a table. Thus the little birds received heat much as in a brooder, and in most cases they were in contact with other chicks. For the first night or two they were returned to the incubator. The situation was, of course, unnatural, and drying was evidently slower than it would have been in the wild, particularly in the incubator room where the humidity was held close to the saturation point. On the other hand, it was possible for us to note the exact age at which the various motor coordinations appeared, something that could not have been done while watching from a blind a parent brooding newly hatched young. Although drying was retarded, some of our subjects were probably more active than they would have been in the dark, feathery environment in nature. Ideally our laboratory studies should have been paralleled by observations of families hatching in the wild, but unfortunately this was not possible because of limitations of time and strength.

Hatching was often a prolonged process. We fixed the point of "hatching" at the moment the chick was entirely out of the shell. When, as occasionally happened, a chick yawned or preened while only part way out of the shell, we recorded this as happening at —1m or —11m, according to the number of minutes before the bird was completely free.

Chicks of the same species varied in precocity. Often the earliest to hatch of a set of ducklings proved the most active; perhaps they were less exhausted from their labors in getting out of the shell; perhaps also their activity reflected lack of sufficient contact with parent and nest mates. As chicks accumulated in the Pintail nest, many were prone to spend most of their time sleeping, closely cuddled to their companions.

When the birds were kept after the first day, the absence of the rightful parent and proper environment made the situation progressively more abnormal. There were no parental signals for being hovered or for escape. Although the chicks spent part of each day out-of-doors,

still they had insufficient opportunities for procuring natural food, and for swimming, bathing, and diving.

We fed our charges on a variety of foods: insects, dog meal, canned dog food, turkey-starter, pablum, fish, hard-boiled egg, and custard (one tablespoon of milk to each egg, enriched with three multi-vitamin drops, baked in a slow oven until set).

We were able to study chicks of two orders—Anseriformes and Charadriiformes—as examples of the second class of precocials.

A. Ducks

Next to the megapodes, ducklings are the most highly developed precocial birds (Heinroth, O. and M., 1924-1933, III; Veselovsky, 1953). They are hatched with the thickest and most complete down plumage and hence need little warming. Indeed, Ruddy ducklings set free at the age of a day or two at Delta have raised themselves, as did a few broods of Tufted Ducks deserted by their mother when a few days old (Gillham, 1957, 1958). The eggs are large but the incubation period is not long. The ducklings swim, dive, and hunt for insects with no assistance from the mother. Interestingly enough, Red-crested Pochard ducks have been recorded as diving and bringing up algae for their young "aged four weeks or over" (Gillham, 1955).

Derek Goodwin writes me he has also seen this: "The young [pochard] forage about for themselves otherwise just like any other ducklings, but they seem to consume more algae than other species." Heinroth (1910) writes that Wood Duck and Mallard mothers nesting at liberty near the Berlin Zoo took their newly hatched broods to their own favorite ponds no matter how unsuitable they were to the needs of the ducklings. "The adult duck apparently has no idea that her young wish to eat nor on what they nourish themselves." It is a common experience in parks to throw bread to little Mallards and see the mother gobble all she can without the slightest concern for her offspring.

1. Numbers and Species Watched

Our original purpose in going to Delta was to study the behavior of newly hatched ducklings. We watched 19 individuals of surface-feeding ducks—six species of river ducks (Anatini) and one perching duck (Cairinini)—and 20 individuals of diving ducks—three species

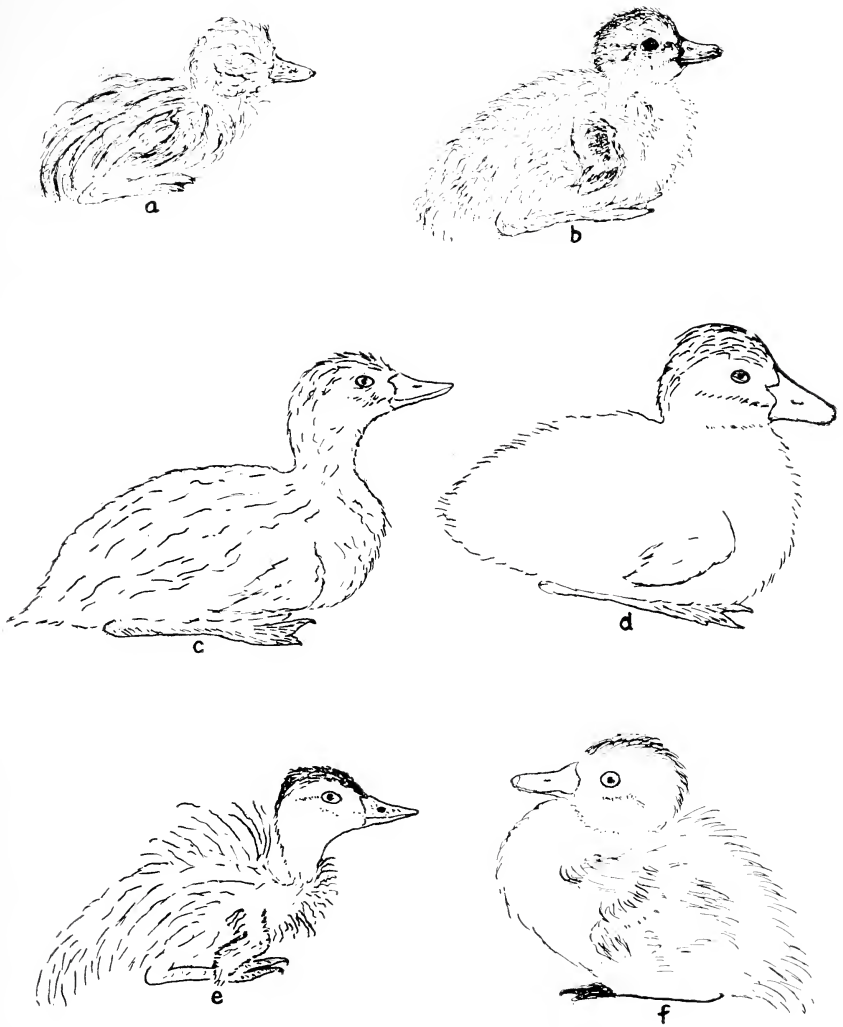

Figure 1. DUCKLINGS. *a*, American Widgeon, 40 minutes; *b*, 18 hours. *c*, Ruddy Duck E, 30 minutes; *d*, 2½ hours. *e*, Wood Duck A, about 1 hour. *f*, Canvasback, 2 days.

of pochards (Aythyini), one sea duck (Mergini), and one stiff-tailed duck (Oxyurini). (The classification of Delacour and Mayr (1945) is followed.) The species and length of observation periods are shown in Table 7.

TABLE 7

Ducklings Watched Continuously from Hatching

Surface-feeding Ducks				*Diving Ducks*			
		Hours Watched				*Hours Watched*	
Species	*No. of Birds*	*Range*	*Total*	*Species*	*No. of Birds*	*Range*	*Total*
Pintail	3	2-3	7	Canvasback	5	2-12	30½
Mallard	5	1¼-9	31¼	Redhead	5	1¾-4½	16¼
Gadwall	3	2½-3	8½	Lesser Scaup	1	1	1
American Widgeon	2	1-3	4	Goldeneye	4	1-8	14½
Blue-winged Teal	2	3-7½	10½	Ruddy Duck	5	3-6	26
Shoveler	2	1½-3	4½				
Wood Duck	2	1-3	4				
7 species	19	1-9	69¾	5 species	20	1-12	88¼

The number of individuals happened to be nearly evenly divided between surface-feeding and diving ducks; the length of observation was much the same for both groups in Stage II, but in Stage III more divers than surface-feeders were watched.

Most of our ducklings were soon returned to the incubator and to the care of the Station personnel. A group of Pintails was watched in the brooder for a few days in 1951, and three Gadwalls were kept for a week in 1952 with our Franklin's Gulls and Coots. In 1954 we saw something of Helen Hays' Ruddy ducklings, and N. E. Collias' Mallards raised with a domestic hen. Our observations are rather full for the time the ducklings would have stayed in the nest but only fragmentary after that.

Recently two important papers have appeared on innate and learned behavior in Eider and other ducklings. Peter M. Driver (1960a) describes the "brooding reflex" of the newly hatched duckling—"an active search . . . for a feeling of enclosure around the head." Six different vocalizations of the Eider ducklings are described and their significance given (1960b). These two papers are preliminary notes to the full publication of the results of his intensive studies on sea-ducklings.

With birds where both parents care for the brood, hatching may extend over several days, but with only one parent, hatching of the clutch must be fairly simultaneous. Sowls (1955:143) reports that in six nests of Pintail and Blue-winged Teal in the wild "all eggs of each clutch began pipping at the same time, and all young emerged within an hour of each other." With Velvet Scoters all eggs in a clutch generally hatch on the same day (Koskimies and Routamo, 1953:89).

2. Examples of Post-hatching Behavior

Examples of behavior during the first few hours after hatching will be given for two of our ducklings.

Mallard G: June 12, 1952.
0—Hatches. *Shakes wings.* Eyes open.
1m—*Preens.* Sits up and preens under belly; continues to preen.
3m—Has moved 10 inches from the egg. Distress note; I say *kom kom kom* and hold my hand over him.
5m—*Nibbles* my fingers. Preens and preens.
9m—Quiet in my hand. Nibbles at it. I put him in the nest with baby Coots and Teal; he sits up and preens. Distress note; I say *kom kom kom.*
12m—Preens. Very alert. Head up. Shakes wings. Now burrowing under my hand.
17m—Shakes wings and preens steadily.
24m—*Shakes tail;* preens; crawls forward. Nibbles.
27m—Distress notes. I say nothing. Stops.
35m—*Scratches head.* Scratches again.
39m-50m—Preens.
54m—*Pecks at baby Coots* and at straws; nibbles Teal.
1h1m—*Yawns.* Preens.
1h6m—*Stands on feet;* preens and shakes wings.
1h7m—Dry around the head.
1h12m—Pecks at straws.
1h17-37m—Preens much of the time. Nibbles at down in the nest.
1h47-49m—Scratches head, yawns, scratches head.
1h59m—*Rubs head on shoulders.*
2h27m—*Pecks at end of green pencil and at my ring.* Nearly dry now.
2h37m—*Stands up on tarsi.*
2h41m—Put him on the shelf; pecks at specks. Crawls toward me with soft conversational notes. Nibbles at my hand and ring; scratches head and preens.
3h4m—Stretches one leg back. Repeats. Yawns.
3h19m—Asleep. Breathes 36 times a minute. Stretches leg back again. Opens eyes. Yawns.
3h37m—Scratches head.

At 6½ hours he occasionally stood on his tarsi. The next morning at the age of 16 hours he stood well; for the most part he walked on his feet, but occasionally on his tarsi. He ate duckweed *(Lemna)* eagerly. (See Nice, 1953: 34-35 for later activities of this duckling.)

Ruddy E: June 26, 1953.
–8m—Cracking shell, calls 100 times in minute.
–3m—Head out. *Yawns. Nibbles. Preens.*
0—Hatches. Gives one note.
5m—Rises, struggles about in duck nest. Weigh him; he gives contentment notes.
7m—Nibbles and nibbles.
17m—Preens. Contentment notes.
37m—Nearly dry. Cuddles against other small birds. Nibbles at Coot and at Sora.
49m—Quiet. Nibbling the Coots.
52m—Preens; four-day Coot attacks him. He nibbles two-day Coot, who evidently enjoys it: staying very still with head hanging down.
53m—Preens self; *scratches face.* Preens self a little, but mostly the two-day Coots.
1h—Now nibbles the four-day Coots. Preens own breast, then under wing. Mostly preens Coots.
1h6-13m—Preens self and Coots.
1h14m—*Hops like a toad.* Hasn't slept a wink. Preens breast, then back. Preens almost at oil gland, then in front. *Shakes self* a bit. Seems perfectly dry.
1h20m—Takes two steps on tarsi. Preens over his leg.
1h43m—Take all birds out to the water. Ruddy gives distress call when all the rest are in the grass. Nibbles at grass. Crawls up the bank.
2h—Preens breast.
2h17m—Napping at last, the first time since hatching.
2h25m—Preens at oil gland.
2h50m—More preening, of self and Coots. Scratching his face. Followed me, crawling, when I called.

At five hours he scratched his face with one foot, stretching out other to balance himself; stretched one leg back. Still preening Coots.

At seven hours he flapped his wings.

3. Development of Behavior in Ducklings

The ages at which the coordinations in Stages II and III were first observed in our ducklings are shown in Table 8.

There was a great difference in individual precocity between strikingly active ducklings and others that slept most of the time. The earliest to hatch in the day were usually more enterprising than the later ones; probably a comparatively empty nest was more conducive to action than a crowded one. The most precocious individuals were Mallard G, Gadwalls A and B, Blue-winged Teal B, Redhead D, and Ruddy E.

4. Stage II—Preliminary

Ducklings were by far the most active preeners of any of the birds watched by us. This is understandable in view of the necessity of

TABLE 8

Development of Behavior in Ducklings

m = minutes, h = hours, d = days

Coordination	*19 River Ducks*			*20 Diving Ducks*		
	Number showing behavior	*Age at first appearance*		*Number showing behavior*	*Age at first appearance*	
		Range	*Median*		*Range*	*Median*
Stage II						
Nibbling	9	–5m-55m	19m	7	–7m-46m	3m
Preening	19	–4m-1h15m	36m	19	–3m-2h18m	15m
Scratching head	17	3m-2h36m	45m	15	2m-3h52m	1h8m
Yawning	15	–7m-2h5m	1h	14	–3m-4h19m	1h17m
Random pecking	8	54m-2h6m	1h40m	8	22m-2h45m	1h50m
Escape reaction	3	1h23m-5h50m	2h36m	4	53m-1h41m	1h11m
Rubbing head on back	3	1h26m-3h27m	2h	3	2h30m-4h10m	2h30m
Shaking self	5	1h11m-7h	2h10m	8	1h14m-7h	3h
Stage III						
Exploratory pecking	10	1h12m-4h14m	2h30m	9	1h8m-5h	2h58m
Wagging tail	4	2h47m-7h19m	5h	2	1h5m-3h7m	2h6m
Fanning wings	3	3h17m-6h	4h50m	7	1h53m-6h32m	2h50m
Stretching leg back	5	2h52m-7h19m	3h34m	7	2h4m-6h38m	3h47m
Stretching wings back	2	3h4m-6h45m	4h25m			
Jumping	4	40m-8h	4h	6	1h53m-8h35m	4h24m
Running	4	5h-8h10m	6h30m			
Walking on feet	2	6h30m-7h32m	7h	2	6h37m-7h	6h49m
Picking up food	4	2h33m-8h20m	3h17m	2	7h30m-9h19m	8h25m

early and continued waterproofing which has been shown by Fabricius (1959) to depend on the maintenance of a "large amount of finely distributed air among the ramifications of the feathers," kept there by intense and elaborate preening. The belief of Hou (1928) that the preen gland contains ergosterol has been convincingly disproved by Rosenberg (1953) who found no provitamin D in any tissues of fowls except in the sterols of the feet, and here it was present in high concentration.

Ducklings were also the most zealous of our subjects in scratching the head. Little stretching of wings and legs was seen. Little consistent difference was found between the two groups of ducks. On the average, surface-feeding ducks yawned and scratched their heads earlier, while diving ducks preened earlier. While drying, the ducklings crawl on their tarsi.

Although several coordinations that would seem normally to belong to the waiting period did occur with our more lively subjects before they were dry, it seems probable that under natural conditions development would have been less accelerated.

5. Stage III—Transition

Ducklings as a rule stay in the nest longer than many other precocials. They need to gather strength from absorption of the yolk sac, so as to be able to follow their mother as a brood on what is often a considerable expedition to the water. Many other precocial birds are raised in the vicinity of the nest and their actions do not need to be as closely coordinated with those of their parents and brood mates as do those of ducklings.

How long do ducklings stay in the nest? Frank McKinney watched a nest of Eider and tells me the brood was led away approximately 26 hours after the first duckling was dry. Nordberg (1950) noted in four cases that broods of this species stayed in the nest two days. Helen Hays writes me that a brood of Ruddy Ducks at Delta left 19 hours after hatching; the Colliases (1956) report Blue-winged Teal leaving at 18 hours; a Canvasback brood at 24 hours of age. Goldeneyes leave at one to one-and-a-half days (Sirén, 1952); Velvet Scoters at about 24 hours (Koskimies and Routamo, 1953). With Wood Ducks, "the exodus takes place the day following hatching," early on pleasant mornings, perhaps not before noon on rainy or chilly days (Leopold, 1951). In experiments on incubator-hatched Mallards, Ramsay and Hess (1954) found the critical age for imprinting lay between 13 and 16 hours. Our Gadwalls became very restless at 24 hours, but were content after I had conducted them on a 100-yard walk.

If Stage III is artificially prolonged, the effects may be bad. Ducklings kept in the incubator for more than 48 hours usually started to jump, and it sometimes was difficult for them to settle down to eat.

In Stage III the ducklings showed new comfort movements; sometimes they climbed or jumped out of the nest; some started to walk and run; they practiced exploratory pecking and a few even picked up food. Many of our birds were more active under the abnormal conditions of light and freedom than they could have been if closely brooded by the mother. Some mother ducks have been seen to leave the brood in the nest for a short period—Wood Duck (Leopold), Canvasback (Collias,

N. E. and E. C., 1956), Mallard (Frank McKinney, letter), Ruddy Duck for a half hour after the ducklings were dry (Helen Hays, letter). In two cases of nests over water, ducklings followed their mothers for short excursions onto the water then back to the nest—the Colliases' Canvasbacks, and a Redhead brood (Weller, 1956).

We noted walking as a temporary achievement for the first time at five to seven hours. Fabricius (1951) found it established at 16 to 28 hours. Ramsay and Hess state that their Mallards "were running normally at three to four hours," but apparently they did not realize that under stress Anatidae and many gallinaceous birds can run before they can walk or stand (Lorenz, 1949:144).

6. Stage IV—Locomotory

Before calling the young off the nest, the mother duck has been observed carefully inspecting the surroundings. The Goldeneye also makes reconnaissance flights (Sirén, 1952). If the coast is clear, the mother in hole-nesting species flies to the ground or water and gives a call that induces the ducklings to scramble up the side of the hole and jump out—Wood Duck (Leopold, 1951); Goldeneye (Sirén), (Fabricius, 1951:47); Goosander (Wilhjelm, 1938). A Blue-winged Teal looked about in an alert, cautious fashion for three minutes before leading off her brood, a Canvasback did so for 10 minutes (Collias, N. E. and E. C., 1956). The mother's call has been described as a soft *kuk, kuk, kuk* in the Wood Duck (Leopold), much the same sound given six times a second by a Canvasback, and a louder *kunk! kunk! kunk!* three times a second by a Blue-winged Teal (Colliases). A series of light taps with a tack hammer stimulated a brood of Wood Ducks to leave the nest box (Leopold, 1951:217).

Leopold tells of the long and dangerous trip of the baby Wood Ducks from the place of hatching down a steep bluff and along the railroad track to the Mississippi River, which they swam across in about 20 minutes, although the distance must be close to a mile. A mother Goldeneye led a newly hatched brood 1½ km. through trailless country from one pond to another, while another brood swam 2140 meters in 67 minutes. On the ground they traveled from one-half to one km. an hour, on the water up to 4.5 km. per hour (Sirén).

Very young ducklings, despite their short legs, show an astonishing agility in running, jumping, and catching insects. Day-old Wood

Ducks, "when pressed immediately on leaving the nest," dived and swam under water, staying under from seven to 13 seconds; one swam 16 feet in 7.5 seconds (Stewart, 1958).

a. *Eating.* That ducklings may feed before they leave the nest permanently is shown by Milton Weller's discovery of small insects and vegetation, probably *Lemna,* in the stomachs of very young ducklings killed on the nest by a mink. He has seen ducklings snap at flying insects during their first day of life while still in the nest (letter). The Colliases (1956) watched Canvasbacks and Redheads when less than 24 hours old, make two expeditions out in the water and feed in the absence of their mother.

"Eating movements are innate," writes Hochbaum (1955:16), "but the object toward which those actions are directed—food—is learned. A duck learns what to eat and what not to eat," starting by nibbling objects when very young, but discovering (in captivity) on the second day that chopped egg is edible.

As shown in the examples of post-hatching behavior and in Table 8, nibbling often started before the duckling was out of the egg. Random pecking was seen in the second hour, and exploratory pecking in the third. The inexperienced duckling pecks at small objects that contrast with the surroundings—a conspicuous spot, something shiny, or bumps on a smooth surface. Day-old White Pekin ducklings preferred green and yellowish-green objects to those of other colors (Hess, 1956b). The earliest records of picking up food were as follows: Gadwalls at 2 hours 33 minutes and 2 hours 38 minutes; Mallards at 4 hours 1 minute and 8 hours 20 minutes; Canvasbacks at 7 hours 30 minutes and 9 hours 19 minutes. Our Gadwalls were eating well at 18 hours of age.

Veselovsky's (1951) Tufted Ducks did not eat for two or three days, only drank. "At first they collect food only from the surface of the water." "At the tenderest age the young Tufted Duck lives mostly on insects and molluscs, and seizes the food by simply catching it in the beak, without any sieving movements with the beak." In both river and diving ducks Veselovsky (1953) found that the lamellae on the edges of the bill appeared at six to seven days.

7. Stage V—Socialization

In Stage V aggression may develop early; the adult technique of bathing comes later, and last of all, flight.

a. *Aggression.* We saw no aggression in the Gadwalls we kept for a week. At seven days the Pintails attacked a stranger (a six-day Mallard) and the next day one pecked a brother. Weidmann (1956) reports that Mallards may attack strangers at three days and the Colliases (1956) report the same in mixed broods under crowded conditions. The Ruddy Ducks were peaceable in familiar surroundings, but sometimes belligerent in new situations.

When Ruddy E was 29 hours old we put him with a group of three- and four-day-old Mallards and Redheads and watched through a window; he opened his bill at each bird that approached and bit it. When many crowded by him, he made no move, but later attacked individuals. A few attacked him. I went into the room and called; he paddled straight to me and settled down placidly with our group of Coots and grebes. Although he had been aggressive when suddenly confronted with a horde of ducklings of other species, he was peaceable with a newly hatched Ruddy and young Western Grebes brought in from the marsh. Helen Hays found she could add Ruddy ducklings indefinitely to her flock with no show of hostility on the part of the older birds.

Frank McKinney writes me that he and a friend had a Ruddy duckling threaten them in the nest. One three-day-old Ruddy at the Station was chasing after a brood of two-week-old Mallards being raised by a domestic hen. They attacked him; he threatened and bit them. The Mallards rushed at young Franklin's Gulls and drove a group of younger Mallards ruthlessly.

The Colliases (1956) found at Delta that, "When reinforced by the aid or presence of the mother, ducklings of the brood readily attack much older and larger ducklings." In mixed broods of like age reared together in confinement, they reported that Mallards dominated Pintails; Redheads and Canvasbacks dominated Mallards and Pintails; while Redheads dominated Canvasbacks. "The dominance order, regardless of species, showed no consistent parallel to differences in sex or weight." "In general, aggression did not occur in relation to food competition but was often observed when one bird was moving about and disturbing resting birds, and aggression could readily be provoked by moderately crowding the birds" (p. 398).

Under natural conditions Weidmann (1956) found that with Mallards, members of a family never fight each other and do not flee from one another; no peck order exists among the young.

b. *Bathing.* Simple bathing appears at two and three days with Ruddy ducklings. This consists of crouching, and dipping the head, usually vibrating the wings simultaneously (see Nice, 1943:47, for description of bathing in passerines.) Such bathing was noted with Mallards up to three weeks of age. "This is the commonest bathing

movement of adults; 'dipping' must occur daily after first appearance in ducklings" (Frank McKinney, letter).

The first appearance of the alternate movement was seen with a brood of Pintails in their third week. McKinney (1953) calls this "wing-thrashing" and describes it as follows: the duck "half rises from the water, leans to one side and rapidly beats the partly opened wing on the water. Leans to other side and flails water with other wing. Thrashes with one wing, pauses, then with other."

He describes two further movements in bathing by ducks: "somersaulting" and "dashing-and-diving." In the former the bird "dips breast and neck forwards into water and kicks vigorously, thus immersing the fore part of the body. Turns over and faces in opposite direction." Vigorous wing-thrashing follows. This coordination is incomplete in diving ducks and mergansers. In "dashing-and-diving," "diving with the wings open is usually the basic movement." This is clearly derived from escape-behavior patterns, now largely under control of the "bathing instinct." (Facing in opposite direction might correspond to rapid turns practiced by other species in play-fleeing.)

Lebret (1948) describes the "diving-play" of surface-feeding ducks: (1) the rising and headlong plunge, alternating with (2) the splashing rush over the surface of the water, and interprets them as "escape reactions carried out in the absence of a bird-of-prey." The first component is "quite similar to the escape reaction of a duck harassed by a falcon," while the second "closely resembles the escape reaction of a moulting duck." Thus the dashing-and-diving is analogous to play-fleeing. Ducks may perform these motions on dry land, Konrad Lorenz informs me. If reared without water, then given a dish of water, they may go through escape diving on a carpet. Hochbaum (1955:78) gives a wonderfully vivid description of the "morning bath of waterfowl," particularly of large geese and swans.

c. *Flight.* The attainment of flight marks the end of Stage V. Weller (1957) summarizes records of the age when this occurred with 12 North American species; with the river ducks it averaged from 38 to 70 days, with the divers from 49 to 84. Redheads flew at 8½ to 9 weeks, although the primaries were not fully hardened until 10 to 11 weeks of age. With captive-reared young in Czechoslovakia Veselovsky (1953:73) found the age of flight varied from 36 days with European Teal to 60 days with Mallard. Fabricius (1951:144) gives notes on first flights of three of his hand-raised birds. Two Tufted Ducks flew

some 10 meters over the surface of the water each day from the age of 58 to 67 days, at which time they disappeared. His Shoveler made small flights for a week before it attained full flight at 52 days. Hochbaum (1955:17,46) describes how a duck flies instinctively but must learn the fine art of alighting. He believes it takes three to four weeks after fledging for the young ducks to perfect their muscles sufficiently for the fall migration.

8. Escape Reactions

From the age of one hour our ducklings responded to sudden noises, as the grinding of a truck, or slamming of a door. Sometimes they lowered the down on their heads; sometimes they gave a small jump.

As to visual impressions, Sowls (1955:146) saw no fear reactions with ducklings until after they had dried; then "they showed an awareness of intrusion and attempted to scurry out of the nest to hide in the grass." Fabricius (1951:62) found in incubator-hatched ducklings that the tendency to react with escape upon first confronting a human being increased with age; none of the four birds under six hours showed this behavior, 10 out of 16 showed it between six and 24 hours, and all did so between 24 and 48 hours. Ramsay and Hess (1954) found alarm in only three of more than 100 Mallards under 24 hours of age (at 16, 16 and 20 hours), but in 11 of 14 at 24 hours.

Goslings respond to a warning call much earlier than to sight of a strange object; Lorenz has a film showing a Greylag not yet dry running at a warning cry. He told me: "You cannot frighten a gosling except by a warning call."

Tufted Ducks from an early age reacted with cowering and an alarm note to the sight of large gulls flying overhead, but not to Blackheaded or Common Gulls, nor to Hobbies or Sparrow Hawks, but Eider and Shoveler ducklings showed no concern under these conditions (Fabricius, 1951:140).

Weidmann (1956:228) experimented on 3-, 11-, and 24-day incubator-hatched Mallards with cardboard models of different sizes and shapes, drawn at different speeds at a height of four meters. The ducklings crouched, elongated their necks, then ran with an alarm cry to the experimenter (their parent-companion); here they stayed crouched for 20 to 60 seconds. Each model began to lose its effect after three to five trials.

9. Bond to Parent

Mother ducks, as a rule, are devoted to their broods, leading them, brooding them, warning them of danger, and defending them by threat and distraction display. In some species, as Mallards, the mother is intolerant of other young, and this has also been reported for Canvasbacks and Redheads (Hochbaum, 1944:98), as well as for Velvet Scoters (Koskimies, 1957). In other species families may join forces. "Lesser Scaups are commonly seen with broods of 20 or more, sometimes with two or more hens attending such combined families" (Hochbaum, 1944). One mother Greater Scaup puts on a great display at the approach of a canoe, while "the other female, or females, leads the brood to another part of the lake" (Munro, 1941b). Eider ducks nesting on a Finnish island sanctuary often join forces after the young are hatched, from two to 20 hens having been recorded leading groups of ducklings, while at times a few drakes also join. The adults defend the young from Great Black-backed Gulls by coming close together and kicking up the water and biting at the gulls. It is only when ducklings are with a single mother that the gulls are able to capture any (Ruthke, 1939a). Combined broods are also common in King Eiders and Oldsquaws (Witherby *et al.*, 1938-41).

The Velvet Scoter normally nests on small inland lakes and here, with well-defined boundaries and equable water temperatures, a strong mother-young bond is not essential. With the population, however, that recently has moved to the outermost archipelago off the south coast of Finland the weakness of this bond spells disaster to the ducklings. They easily become lost and fall victims to bad weather and to Lesser Black-backed Gulls (Koskimies, 1955).

In his detailed study on mother-young relationships in the Velvet Scoter, Koskimies (1957) stresses the importance of the mother duck not only as guide, defender and dispenser of heat, but also in her role of setting the rhythm of activity of the brood—of feeding, preening and resting. He describes the signals given by the mother to the young and their signals to her.

River ducks customarily stay with the young until they can fly, and occasionally longer, but diving ducks usually leave much earlier, especially in cases of late-hatched broods. Young Canvasback broods band together, sometimes "two- or three-week-old birds tagging along behind a four- or five-week-old duckling. . . . Such birds are much

less wary than those attended by a mother" (Hochbaum, 1944:100). The Ring-necked Duck, in contrast to many other diving ducks, is a devoted mother; she stays with her young until they can fly (Mendall, 1958).

10. Bond to Brood Mates

Little ducklings have a very strong bond to one another—a great need for companionship of their fellows. This helps keep them in a compact body behind the mother.

How strong this need is was shown by an experiment made by the Colliases (1956:391): "One downy Mallard duckling, removed from the company of other ducklings in the incubator and introduced on the day of hatching into a box containing two five-day-old Redhead ducklings, was attacked persistently by the Redheads; but every time it was rescued by the observer and isolated, it gave distress calls until it was returned to the company of its tormenters."

A small Velvet Scoter, lost from its mother and brothers and sisters, keeps constantly in motion and cannot stop to feed or preen or rest. The finding of another lost duckling is a great help to both; together they are able to carry on a fairly normal routine (Koskimies, 1957:32).

The attachment between members of the brood must often outlast the parental bond in the diving ducks where the mothers customarily desert before the young can fly.

B. Killdeer

Plover (Charadriidae) have short bills and relatively large eyes. With no functional hind toe and short front toes the birds are not suited for running through vegetation or on very soft ground. They run in spurts, then stand still with their heads motionless; they look all around, then dash onto their prey (Heinroth, O. and M., 1924-33, III). They typically scratch their heads *over* the wing like most passerines.

The Killdeer is a hardy, conspicuous, noisy, adaptable, successful plover nesting over most of North America from northern British Columbia to northern Ontario and southern Quebec south to central Mexico. "The nesting-site may be anywhere on gravelly bars and beaches, in pastures, cornfields, or gardens, or among the stumps of a

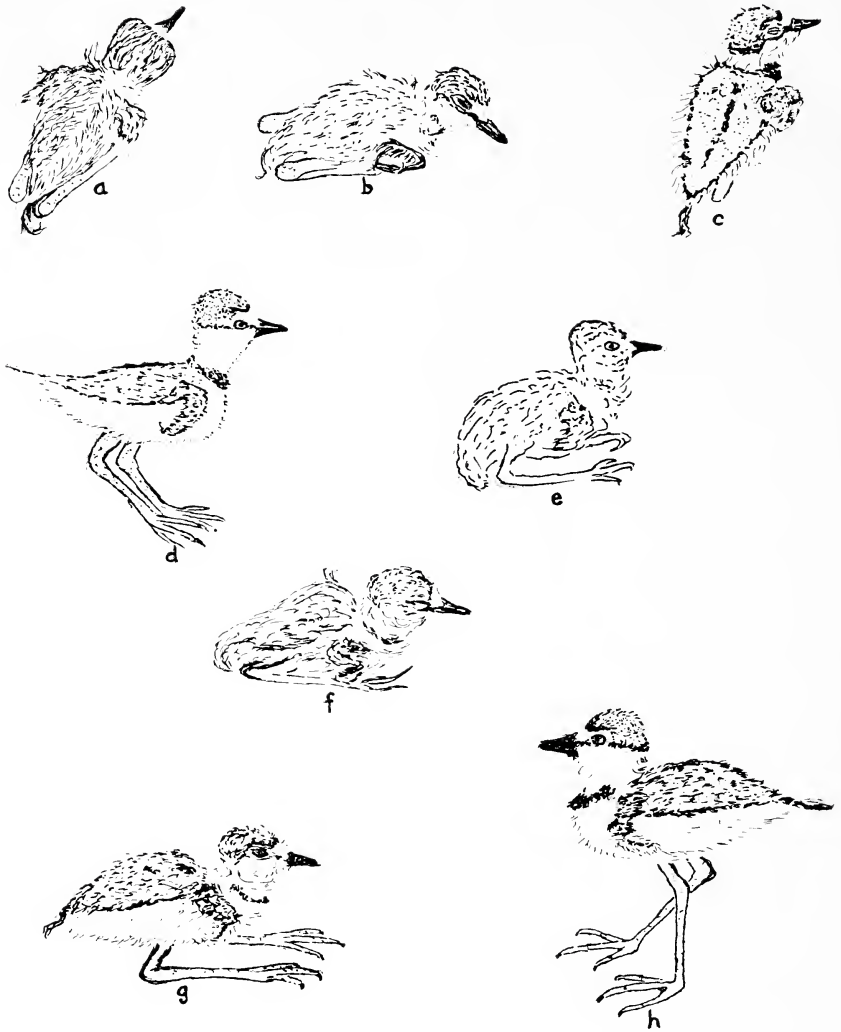

Figure 2. KILLDEER. *a*, K3, 17 minutes. *b-c*, K2: b, 30 minutes; c, 2 hours. *d*, K4, 4 hours. *e-h*, K1: e, 16 minutes; f, 30 minutes; *g*, 3 hours; *h*, 5 hours.

woodland clearing" (Roberts, 1932), or in the middle of roads through fields and occasionally on roof tops. Incubation lasts 25 to 26 days (Davis, 1943; Nickell, 1943), rarely as long as 28 and 29 days (Sherman, 1916; Ganier, 1934). The male Killdeer has been shown to take the more active part in brood care; Davis found that it was he that made the nest scrape; did most of the incubating (as Pickwell [1930] reported about two pairs in the wild), and the major part of the care of the young.

In 1953 two pairs of Killdeer nested near the Station. We brought four of the eggs into the laboratory and watched the chicks from 3¼ to 9 hours after hatching, then returned them to their parents. In 1954, a year of high water, there were no nests of this species nearby. Three eggs were brought to us and 25 days later one "hatched" with our help; we kept this chick to the age of seven weeks. His companions in the laboratory were three Spotted Sandpipers, one his age, the others two days younger.

1. Examples of Post-hatching Behavior

The first Killdeer proved to be the most precocious bird we ever watched. K1 hatched in my hand at 5:52 a.m., July 1.

2m—Opens eyes. Calls with single notes, 14 to a minute.
9m—*Sits up in my hand* as if ready to run.
18m—Up on tarsi calling 17 times a minute; at times these were content notes, at other times distress.
28m—Cuddles down with closed eyes; soft notes.
43m—*Wags tail.*
47m—*Yawns.*
51m—*Bobs.*
52m—*Picks at spot; walks about on tarsi;* bobs; wags tail.
1h3m—*Preening intention;* reaches part way under wing. Went *pat-pat-pat* on tarsi, a foreshadowing of the run and stop plover technique of progress.
1h6m—*Up on his feet* an instant, then cuddled down by the Eared Grebe.
1h8m—*Stretches a leg back* momentarily; turned to preen his side, but did not quite touch it; wagged his tail; bobbed.
1h22m—*Holds wings straight out* momentarily.
1h25m—Actually *touches side in preening* for an instant.
1h28m—Pecks at foot; looks intently at spots on table; pecks back of Western Grebe.
1h30m—*Walks on feet* with little nervous steps. *Crouches* when bumped into by Eared Grebe.
1h36m—Bobs as he sits on tarsi; runs seven inches on feet.
1h53m—Drinks a drop of water from my finger.
1h55-59m—Naps; preens under wing and falls over; preens twice near his leg; works at paper napkin; nearly dry.

2h2m—Pecks at tiny spots on the table; picks up tiny piece of fish, drops it; pecks at end of Eared Grebe's bill.

2h6m—Picks up a bit of fish and *eats* it. Eats another bit of fish; wags tail.

During this third hour of his life K1 pecked at objects 13 times; during the next hour 18 times. He yawned, bobbed, wagged his tail, rested, ran around on his feet and gave many notes. New coordinations appeared:

3h33m—*Stretches both legs back* while lying flat on the floor; rises and *stretches legs up.*

3h48m—Offer him a small snail on the forceps; he tastes it but evidently dislikes it, for he *scratches his bill from under his wing.*

4h49m—*Stretches wing and leg sidewise.*

5h—We offer him a mosquito; he looks at it, takes it into his mouth, then scratches it out.

7h40m—Puts bill into water dish and *drinks.* We then took him to nest site. Here he crouched as his parents shrieked. We withdrew. Soon one parent brooded him and his day-old brother; 10 minutes later both chicks emerged and started to forage.

Killdeers 2, 3 and 4 from the other nest were much less active than K1, yet as shown in Table 9, yawning, tail-wagging and preening appeared earlier with some of them than with K1.

In 1954 two of the three eggs began to show activity after 23 days in the incubator; two days later one chick had died and the other had become very quiet. We opened this egg, finding the yolk not entirely absorbed. This bird, K5, remained in the embryonic position and we put him in the incubator. A half hour later the yolk was absorbed, the little bird turned on his tarsi and called. Two hours after 'hatching' he had yawned, stretched his legs back, wagged his tail, bobbed, and pecked at straws.

2. Development of Behavior in Killdeer

The first appearance of motor coordinations is shown in Table 9. The data on Stages II and III except "shaking" are based on Killdeers 1 to 4, all the rest on K5.

3. Stage II—Preliminary

The newly hatched Killdeer preened far less than the ducklings and did not scratch their heads at all. Two characteristic coordinations came very early. Bobbing appeared in all five chicks from 51 minutes to 3 hours 6 minutes. Three birds went through a *pat-pat-pat* movement while still on their tarsi (from 1 hour 3 minutes to 2 hours 44 minutes) —evidently a foreshadowing of the family run-and-stop method of progress. All the chicks did considerable pecking at small objects.

TABLE 9

DEVELOPMENT OF BEHAVIOR IN KILLDEER

Five individuals (four watched from hatching)

m = minutes, h = hours, d = days

K1's record in italics

Stage	*Coordination*	*Age at first appearance*
II	Wagging tail	2m, 25m, *43m*
	Yawning	3m, 9m, *47m*, 1h50m
	Bobbing	*51m*, 1h20m, 1h29m, 3h6m
	Random pecking	*52m*, 1h37m
	Preening	31m, *1h25m*, 2h12m
	Walking on tarsi	*52m*
	Pat-pat-pat on tarsi	*1h3m*, 1h25m, 2h44m
	Standing on feet	*1h6m*, 3h50m
	Stretching one leg back	*1h8m*, 3h10m
III	Walking on feet	*1h30m*, 4h34m
	Crouching	*1h30m*, 1h39m, 4h30m
	Exploratory pecking	*2h2m*, 3h4m, 3h6m, 3h12m
	Eating	*2h6m*
	Stretching wings up	*1h22m*, 4h15m
	Stretching both legs back	2h23m, 3h22m, *3h33m*
	Scratching head under wing	*3h48m*
	Stretching sidewise	*4h49m*
	Drinking	*7h40m*
	Shaking self	10h±
IV	Play-fleeing	2d
	Catching insects	2d
	Running away with insect	3d
	Beating insect	3d
	Jumping-and-flapping	7d
	Scratching head over wing	8d
V	Aggression	9d
	Bathing	10d
	Standing on one leg	10d
	Thrashing in bath	14d
	Probing	17d
	Foot-patting	18d
	Raising crest	18d
	Flying a little	21d
	Hopping on one foot	23d
	Flying well	31d

In nature many of the coordinations listed in the Table would probably not have appeared before the chicks were dry.

4. Stage III—Transition

Young Killdeer may stay in the nest from about eight (Spurrell, 1917; our observations) to 24 hours (Ganier) or even longer (Nickell), but in this last instance where hatching extended over three days the older young must have returned to the nest for brooding after excursions. Shorebirds do not need to "rest" in the nest so long after hatching as do ducklings, for demands on their energies are much less because they customarily remain in the vicinity of the hatching place until independence.

At a nest of Ringed Plover the chicks were dry at two hours, and soon after crept out on their tarsi, but were gathered back by the brooding parent. Bobbing first appeared at 30 minutes of age. At a disturbance one chick aged 1 hour 37 minutes ran out and crouched. It followed an insect at 3½ hours, and caught and ate a fly at 7 hours 11 minutes. The chicks walked well at 4 to 5 hours. The eldest left the nest permanently at 8 hours 50 minutes after a disturbance (Laven, 1940).

5. Stage IV—Locomotory

K1 was strong on his feet at five hours, but the other three watched from hatching were slower in their development.

Killdeer chicks find their own food by trial and error with no assistance from their parents, who lead, brood and warn their offspring. When K5 was three days old we were giving him and the Spotted Sandpipers insects caught by sweeping the grass; all the little birds took these eagerly, beating and beating them. K5 rushed away with a damsel fly.

a. *Play-fleeing.* When two days old K5 raised his wings and ran about with sharp turns—a very early appearance of "play-fleeing." This was seen again at four days and was frequent after 17 days, as long as we kept him. He first crouched, then dashed about making sharp turns.

b. *Jump-and-flap.* The bird gives a little jump and flaps its wings. This is so characteristic of young gulls that we called it the "gull-act." We saw it occasionally in our Killdeer and Spotted Sand-

pipers, and in our rails and Coots. Seitz noted it in the Eurasian Curlew (1949).

c. *Scratching the head.* There are two main ways in which birds scratch their heads. One consists in bringing the foot directly up to the head; this was called *vornherum*—"under the wing" by Heinroth (1930), "directly" by Simmons (1957, 1961). In the other method the bird lowers a wing and brings its foot up over the shoulder—*hinterherum*, "over the wing," or "indirectly." Of the precocials we studied all scratch directly except the Killdeer.

At first K5 scratched directly, as K1 had done at the age of 3 hours 48 minutes. This was first noted with K5 at about 12 hours. I watched closely to see when the characteristic plover coordination of indirect scratching would appear. At four days K5 scratched directly several times. At eight days he did this once in the morning, but seemed to drop his wing slightly as he did so. At 4:30 p.m. he scratched his head indirectly and this was his invariable practice from then on.

Little Ringed Plover chicks scratched directly for the first two days, then indirectly; Avocet chicks used both methods during the first three days (von Frisch, 1959b). Lapwings scratched indirectly from the age of four or five hours (Laven, 1941:51). Von Frisch reports that his Lapwing chicks did likewise from the start; at the age of six days he lightly bound the wings with adhesive tape so the birds had to scratch directly, but when the tape was removed at 14 days, they immediately resumed their instinctive method of scratching.

Direct scratching of the head has been reported for tinamous, grebes, a petrel, cormorants, herons, storks, flamingos, ducks, geese, swans, hawks, gallinaceous birds, rails, seriema, jaçana, sandpipers, turnstone, gulls, terns, pigeons, some parrots, cuckoos, puffbirds, barbets, toucans, woodpeckers, and for a few passerines (including Timaliinae, wrentits and a few American wood warblers).

Indirect scratching has been reported for Laysan Albatross (Eisenmann, personal communication), frigate-birds, oystercatchers, plovers, stilts, avocets, sand-grouse, some parrots, touracos, goatsuckers, swifts, hummingbirds, kingfishers, bee-eaters, hoopoes, rollers, hornbills, and most passerines.

The chief authorities for these observations are Heinroth (1930), Kilham (1959), Nice and Schantz (1959b), Simmons (1957, 1961). The last three papers give detailed discussions of the subject.

Recent observations on North American wood warblers (Parulidae) have shown variations in head scratching in this family. The Fickens (1958) found that of three species of one genus *(Seiurus)* the Ovenbird *(S. aurocapillus)*, scratches directly both as nestling and adult, but that the Northern and Louisiana Waterthrushes *(S. noveboracensis* and *S. motacilla)* scratch directly while in the nest, but indirectly afterwards. W. E. Schantz (Nice and Schantz, 1959a, 1959b) carried out extensive experiments on 122 individuals of 19 species of this family by sticking a piece of gummed paper to the head of the bird, then watching and

photographing the subject's behavior. He found direct scratching consistently used by 27 individuals of three *Vermivora* species, by two Ovenbirds, a Yellow-breasted Chat, *Icteria virens,* and two Canada Warblers, *Wilsonia canadensis.* Fourteen species scratched indirectly, but four individuals of three species sometimes brought the foot directly to the head, apparently when particularly annoyed.

6. Stage V—Socialization

a. *Aggression.* At nine days K5 started pecking his Spotted Sandpiper companions severely when they tried to share the insects that had just been put into the cage. We removed him to a separate brooder where he called continually, but when we reunited the birds he renewed his attacks, so he had to be banished again. Five days later I put him in the brooder with the Spotted Sandpipers and a baby American Coot; this chick begged extravagantly to K5 who stood for three minutes, then dashed at it and jabbed it fiercely in the back. Again he jabbed; Coot squawked and fled. Later that day we put K5, the three sandpipers and some baby coots during the daytime into a roomy outdoor "Piper Pen" containing shallow water, dry land, weeds and rose-bushes. In this natural environment with plenty of room, peace reigned. At 16 days he attacked a five-week-old Virginia Rail introduced into the pen, shouting *killdee* after the jab. The Virginia Rail weighed 65 grams, K5 40. Three days later a wild Least Sandpiper with an injured wing was put into the pen; K5 spread his wings slightly, hunched his shoulders, uttered *killdee, killdee* softly and dashed at the stranger, which we removed.

In a brood of hand-raised Lapwings, antagonism was first seen at 24 days at which time quarrels arose over the food dish and "territories" (Noll, 1954:226). With another hand-raised brood, aggression towards members of other species started at about 15 days (von Frisch, 1959b).

b. *Bathing.* For his first 10 days K5 made no response to opportunities for bathing. I then put him into a basin of water and stirred it with my finger to no avail. Then I dropped a little water on his back, whereupon he dipped his bill several times in the water, squatted, dipped his head and breast again and again, but without any wing movement. He scratched over his wing several times, stepped out, wagged his tail, shook himself, preened under his tail and shook his tail and wings. Later he preened thoroughly. Four days later he bathed thoroughly, using his wings together and alternately. After

this he seldom used his wings together, but customarily thrashed three, four, or five times with each wing.

c. *Foot-patting.* This characteristic coordination of plovers was not seen until K5 was 18 days old.

> Standing on his right foot in a half inch of water he started trembling throughout his body and left leg. He started to pat the mud a bit with his left foot, *but did not look to see what he was stirring up.* Then, moving to dry land, he patted with his right foot, then with the left. Later in the day he was noted patting in one inch of water. The next day at 4:58 p.m. I noted: "Pats with left foot on wet ground. Trembles his right foot. Runs a bit. Pats with left in water. Hunts for food. Every few steps a probe in the earth or a snatch in the water." At 5:03: "Trembling his body, patting with right foot, then pecking in front. Trembling and patting steadily. A wet place." At 21 days in the laboratory: "Pats with right foot, then with left foot on newspaper. After patting several times, *bends down to look for prey.*" At 25 days a count showed 10 pats with the left leg, four with the right, five with the left and five with the right. A week later he patted for 20 minutes at one session, but he never looked to see what he had stirred up. When seven weeks old he was standing on a Persian rug in our living room; he patted with one foot, then probed the rug, patted with the other and probed again.

Davis (1943) noted patting from the age of four weeks with the offspring of her hand-raised Killdeer. "The foot that is patting is extended in advance of the other. Meanwhile the bird watches the mud closely." The Heinroths (1924-33, III:10) reported it with the Little Ringed Plover at nine days; these chicks and young Lapwings trampled on sand, linoleum and the wooden floor. Noll (1954) describes the success of this technique with Lapwings in hunting earthworms. Boyle (1956) records chicks of this species "pattering" when "less than a fortnight old"; von Frisch (1959b) noted it from the fifth day on.

Five species of *Charadrius* are mentioned by Meinertzhagen as patting in the wild; "Sometimes the pattering occurs without any apparent observation on the part of the bird to watch for results" (1954:477). Milon (1951) describes how several *Charadrius* species in Madagascar pat to cover their eggs when leaving them; the parents pat for four seconds whatever the nature of the soil, hence some nests become completely covered, others partially covered, and some not at all. The Ringed Plover uncovers buried eggs with this movement (Goethe, 1955:426). We have noted wild Killdeer and Golden Plover patting in shallow water. There are two records for the family Scolopacidae—the Solitary (Forbush, 1912:308) and Semipalmated Sandpipers (Meyerriecks, 1959b).

"Foot-stirring," "paddling," or "pattering" has been noted in two

other families in the Charadriiformes—Dromadidae (Meinertzhagen) and Laridae—and in seven families in four other orders.

In connection with a detailed description of the foot-stirring of the Wood Ibis, Rand (1956) discusses six different methods whereby birds use their feet in water on wet ground as an aid in getting food. He cites Snowy Egrets and Louisiana Herons (although American Egrets and Little Blue Herons do not have this habit), the Hammerhead Stork, Flamingos, and Gulls. "Foot-stirring feeding behavior" is analyzed by Meyerriecks (1959a) in the Snowy and Reddish Egrets and Louisiana Heron, and references are given to this habit in some European and Australian Herons. Burkhardt (1944) gives photographs of Black-headed and Common Gulls "trampling" in water. Goethe (1955:425) tells that it occurred with only one of his hand-raised Herring Gulls, being seen from the thirteenth to the twenty-fifth day; with wild birds of this species he concludes it is especially adapted to the hunting of cockles. Tinbergen (1953a:33) believes it is directed chiefly at earthworms in meadows.

This behavior is practiced by Anatidae: Swans and Bar-headed Goose (Tinbergen); Shelduck (Rickman, 1949); domestic ducks (Burkhardt). I saw a pair of Whooper Swans paddling at the Kellogg Bird Sanctuary, as they were leading their cygnets from the nest.

Foot-patting has been recorded in three passerines. Meinertzhagen (1954: 480) has seen the "bifasciated lark *Certhilauda* and the blackbird *T. merula* doing short patters on dry soil." Hermit Thrushes in late April on a freshly watered lawn in Iowa, "beat the ground very rapidly with one foot, then suddenly reached down and pulled up an angleworm" (Youngworth, 1956).

d. *Flying.* At 21 days K5 fluttered across a three-foot ditch; at 23 days he flew 18 inches up and three feet horizontally. At 31 days he was flying freely. Almost always he cried *killdee* as he took off.

e. *Other coordinations.* At 10 days K5 stood on one foot, at 23 days he hopped on one foot. He was accustomed to sit on his tarsi almost from hatching. Davis says her Killdeer chicks "sunned" sitting upright on their tarsi until the age of 19 days. K5 was still doing this occasionally at seven weeks. He often sat or stood in the sun, slightly drooping the wing towards the sun.

When given the chance, he enjoyed probing for insects. He also ate ants. When we put grasshoppers in his cage in Chicago he chased them, caught and beat them. One grasshopper was too large for him to manage; he shook and shook it holding it in his bill by one wing. When I tried to get it from him he kept running away with his prize. If a grasshopper hopped up on the cage just outside his reach, he showed no impulse to jump up to get it.

7. Escape Reactions

Crouching was seen early: at 90 minutes when K1 was bumped into by the Eared Grebe, at 4½ and six hours with K4 and K3 when

parental warnings were heard through the laboratory windows. (At 17 days K5 paid no attention to the cry of a wild Killdeer.) When we took K5, aged two and three days, into the Rail Pen, he immediately crouched at the shrieking of the young Herring, Ring-billed and Franklin's Gulls and stayed crouched as long as we kept him out there —one hour and 20 minutes on the first occasion. At nine days when we took him there he crouched most of the time in response to the gulls' clamor, but ran about to some extent. (With newly hatched Lapwings "crouching and neck-shrinking" occur "within four to five hours, and the escape reaction, leaving the nest and crouching outside it, may occur within eight hours" [Nethersole-Thompson, 1951:193].)

At all times K5's calm, confident demeanor was in marked contrast to the nervous, shy actions of his Spotted Sandpiper companions. It seemed as if he left all responsibility in regard to danger to his parents, and as long as no screams were heard, took it for granted that all was well.

In the Piper Pen he would crouch or run to cover on hearing loud shouts or when men walked quickly past. On the sun porch in Chicago, he, like our hand-raised Meadowlark, was frightened when people appeared higher than he, either neighbors on their porch 10 feet distant, or workmen climbing ladders against our porch or the neighbor's house. On such occasions he would give loud cries of distress; I would take him in my hand and pet and soothe him.

8. Bond to Parents

Having been hatched in an incubator, K5 apparently treated me as parent. At one day of age K5 came to me in answer to my call. He liked to nestle in our hands when he felt the need to be brooded, but he invariably protested with a high-pitched *dee* when he was carried about in our hands; perhaps it seemed to him that he was caught. At Delta he called loudly from the brooder each morning until I appeared, whereupon he became silent or gave soft, contented *dees*. He paid no attention to my calling to him as soon as I entered the entrance hall; he had to see me in order to be reassured. (Seitz's [1950] Curlews, raised alone, called for hours, especially in the early morning; as soon as a person appeared, they greeted him with soft notes.)

In Chicago, K5 did not call in the mornings until he heard us coming downstairs. Perhaps at this stage—from three weeks on—we

no longer represented parents so much as social companions. Davis' (1943) male Killdeer brooded the chicks till they were 23 days old. At Delta three young of the K2, K3 and K4 family were still with a parent at 22 days, while K1 or his brother was with a parent at 29 to 30 days. In southern Michigan Nickell (1943:28) found young still with the parents after "39 and (about) 42 days"; in these cases the parents were raising second broods.

At Delta from the age of 12 days K5 had the company in the daytime of the Spotted Sandpipers and small Coots, but in Chicago he had only us. He was contented when we were on the porch, but called when left alone. How much personal recognition he had of individuals is difficult to say. At Delta we customarily wore slacks; when Constance appeared in shorts or in a dress, K5 looked upon her with suspicion. In Chicago everyone was accepted except the colored cleaning woman.

At seven weeks of age K5 was placed in the large sun cage at the Brookfield Zoo where his companions were other shorebirds, ibises and others. Unfortunately we were not able to visit him and see how he had adapted himself before he died of enteritis some three weeks later. An autopsy proved he was a male. Karl Plath, Curator of Birds, told us he had always remained tame, following the keepers about and eating from their hands.

If K5's brood mates had not died in the shell and he been raised with companions of his own species, conditions would have been less unnatural. His social needs would have been satisfied by his nest mates, and his bond to people would have been less strong.

C. Spotted Sandpiper

The Spotted Sandpiper is widely distributed over North America from the northern limit of trees to southern United States. "Any variety of shore-line or water-margin seems to be acceptable. . . . It is rare that more than a pair, or at most a family, are seen together, as they do not flock even in migration" (Roberts, 1932).

From 1908 to 1949 the incubation period of this species was reported in books as 15 days (see Nice, 1954a:183). In reality it lasts 20 to 22 days (Nelson, 1930; Mousley, 1937; Knowles, 1942; Miller, J. R. and J. T., 1948). Van Rossem (1925), Nelson, and Mousley found it was the male that incubates the eggs and cares for the young. Occasionally, however, a female may share incubation for a few days;

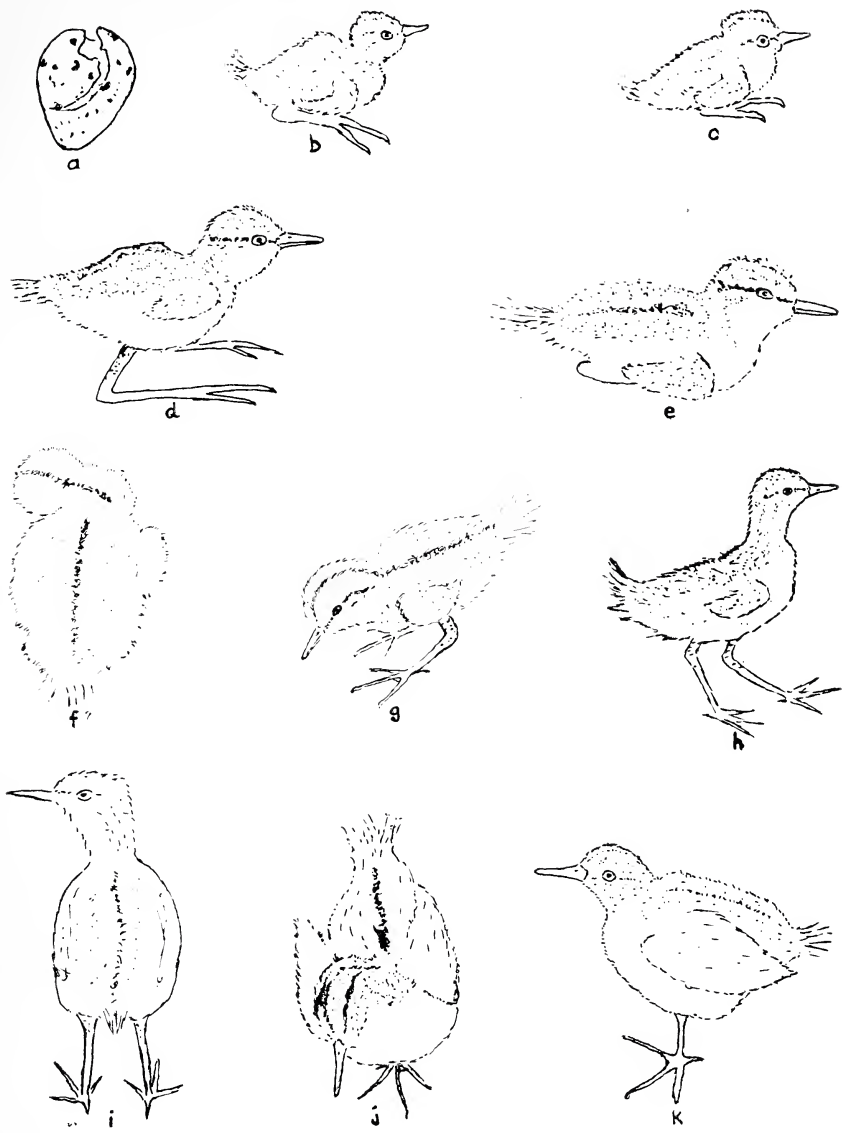

Figure 3. SPOTTED SANDPIPER. *a*, hatched egg. *b-c*, Spotty 2: *b*, about 1½ hours; *c*, about 5 hours. *d-k*, Spotty 1: *d*, 2 days; *e,f,g*, 3 days; *h*, 4 days; *i*, 5 days; *j*, 10 days, napping; *k*, 10 days, standing on right foot.

Theodora Nelson (1938) reported a female as doing so for the first four days, and Van Tyne (1948) collected an incubating female.

We studied five Spotted Sandpipers. Spotty 1 was raised in 1953 along with two Soras of like age and a Coot one day younger. These companions were completely tame and placid, and Spotty 1 remained comparatively confident. We judged her to be a female by her weights and heavy spotting after she became adult. We kept her for five weeks, then gave her to the Philadelphia Zoo. In 1954 Spotty 2 was brought up with nine Sora and Virginia Rails from two to eight days older than she; although the Rails showed a strong bond to us, Spotty 2 became wild after 10 days. Our last three birds were raised together with a Killdeer of like age, but had to be separated from him at 10 days because of his persecution of them. (They had become wild when four and six days old.) Spotty 4 escaped at the age of eight days. The next day we gave Spotty 3 and Spotty 5 the companionship of a family of five baby Coots, and these fat and tranquil little birds exerted a calming influence.

1. Example of Post-hatching Behavior

We watched two Spotted Sandpipers hatch. Their records were very similar.

Spotty 4: July 20.
0—Hatched at 7:25 a.m.
1m—*Yawns.*
10m—Moves to be covered by my hand.
25m—Progresses by jumps. Yawns. Preening intention.
31m—*Teeters.*
35m—*Pecked* at Killdeer's head.
40m—*Preens.*
47m—Yawns; rises on tarsi.
1h42m—Rises, teeters, tries to preen breast.
1h43m—*Walks unsteadily on tarsi;* teeters and teeters.
1h57m—*Stretches both legs out.*
2h—Tried to *scratch face.* Nearly dry. Pecks. *Eats* a bit of custard.
2h11m—Walks on tarsi.
2h50m—*Rubs head on shoulders.*
3h30m—Partly on tarsi, partly on feet.
6h—Stretches one leg out while lying down, then both legs. Preens near tail.
10h—Very strong on feet.

2. Development of Behavior in Spotted Sandpipers

The first appearance of motor coordinations is shown in Table 10.

TABLE 10

DEVELOPMENT OF BEHAVIOR IN SPOTTED SANDPIPERS

Five individuals, two watched from hatching

m = minutes, h = hours, d = days

Stage	*Coordination*	*Age at first appearance*
II	Yawning	1m, 1m
	Teetering	29m, 31m
	Pecking	35m, 38m
	Preening	40m
	Stretching one leg	29m
	Stretching both legs	54m, 1h57m
	Walking on tarsi	1h43m
	Scratching head	2h
	Eating	1h19m, 2h
III	Stretching wings up	3h
	Crouching	3h20m
	Walking on feet	3h30m
	Fanning wings	6h
IV	Strong on feet	10h, 11h
	Shaking self	18h
	Stretching sidewise	1d4h
	Catching insects	1d, 2d
	Beating insects	3d
	Stalking prey	3d, 3d, 4d
	Bathing	3d, 4d, 5d
	Play-fleeing	5d, 6d
	Jumping-and-flapping	5d
V	Aggression	7d
	Standing on one foot	10d
	Thrashing	11d
	Bill in scapulars	12d, 13d
	Flying a little	13d, 14d, 16d
	Flying out of pen	16d, 18d, 19d
	Probing	19d

3. Stage II—Preliminary

The data on Stages II and III are based on Spotted Sandpipers 3 and 4. These proved about as precocious as the Killdeer. Teetering appeared at 29 and 31 minutes in the birds we saw hatch and very early in the others. Teetering at times is a sign of nervousness, like flipping

the tail in rails and some passerines. It also must serve as a recognition mark. Nelson (1938) found that adult Spotted Sandpipers on their breeding grounds ignored a mounted model as long as it was stationary, but quickly responded to an animated decoy provided with curtain springs for legs.

4. Stage III—Transition

In nature chicks are reported as leaving "a few hours after hatching" (Knowles, 1942), and "by breakfast time" after hatching in the night (Nelson, 1930).

5. Stage IV—Locomotory

Three of our chicks were strong on their feet when 10 and 11 hours old. Theodora Nelson writes me: "Spotty chicks can swim as soon as they are able to run but it is not their usual means of escape for the first three days or so. Hiding in the vegetation, near the parent, is much more usual."

Spotty 2 at about 18 hours of age was in the pie pan with insects scattered on the water. "Picks about, mostly drinking. Picks at green grass spikes; tries for a daphnia, eats a mustard petal and two tiny pieces of plants. 20h—Waves wings and runs. Ate a few tiny insects, but prefers custard. 28h—Stretched wing and leg. Ate grass spikelets."

At one and two days the Spotties caught insects; at three days they beat them. At five days Spotty 2 jumped for insects. At six days Spotty 1 caught minnows in a shallow bowl and beat them before swallowing them.

a. *Stalking prey.* When Spotty 3 was three days old I noted: "She sees a fly, aims her bill at it, then darts out her neck, but misses it." Spotty 5 at three days "sneaks up on a fly, then gives up." At four days Spotty 2 successfully stalked prey.

Spalding (1873) described the first intimations of this behavior in a turkey. "When not a day and a half old I observed the young turkey . . . slowly pointing its beak at flies and other small insects without actually pecking at them. In doing this, its head could be seen to shake like a hand that is attempted to be held steady by a visible effort. . . . I found it to be the invariable habit of the turkey, when it sees a fly settled on any object, to steal on the unwary insect with slow and measured step until sufficiently near, when it advances its head very slowly and steadily till within an inch or so of its prey, which is then seized with a sudden dart." He placed a newly hatched chicken with the 11 day turkey, but although they were the closest of companions, "the chicken never caught the

knowing trick of its companion—seemed, indeed, wholly blind to the useful art that was for months practiced before its eyes."

b. *Play-fleeing.* Jumping, waving wings, and sudden turns were noted with Spotty 1 at five days and Spotty 2 at six days. European Snipe at four days began to wave their wings, make little jumps and run zigzag here and there with raised rumps. "This is an expression of well-being somewhat as dogs suddenly run wildly in a circle" (von Frisch, 1959b:553).

6. Stage V—Socialization

a. *Aggression.* It was only with Spotty 1 that we noted aggression. When seven days old she and Sora 4 were having a tussle over a moth; she gave her opponent several pecks on the head. From the age of 25 to 35 days the two occasionally exchanged pecks, sparring together, pecking each other's bills, but at other times she pecked at his foot or wing. At 30 days she defied him with outspread wings. Two days later she gave a threat note, *tree-tree,* when the Sora was chasing her. (See p. 163 for her behavior towards S4 two years later.)

Hand-raised Curlews showed little bond to each other; they threatened one another from the end of the third week (von Frisch, 1956). Avocets at 10 days drove off chicks of other species (von Frisch, 1959b).

At 10 days Spotty 1 stood on one foot. At 13 days she hopped on top of the water can and stood there. From three to five weeks she usually roosted on a perch in her cage. At 12 days she slept with her head in her scapulars; this was true of Spotty 2 at 13 days. Thrashing in the bath appeared at 11 days.

b. *Flight.* First flights were seen at 13, 13, 14, and 16 days. The sandpipers flew out of the outdoor pens at 16 (Spotty 2), 18, 18, and 19 (Spotty 1) days. Spotty 2 returned to the Rail Pen the first night, and Spotty 1 came back for two nights after which we took her to Chicago. From the ages of 11 and 13 days Spotty 3 and Spotty 5 passed the daylight hours in the Piper Pen; after a few days, despite the favorable environment, they became restless and began to spend much time running up and down looking up at the wall board. This activity was confined to a space about two feet wide. About a foot to the south a rosebush offered an easy pathway for escape, but the little birds never noticed this, sticking to their chosen spot until they were able to fly unassisted from the enclosure.

7. Stage VI—Independence

At the Philadelphia Zoo, Spotty 1, five weeks old, was placed in a cage with sand floor and a little stream; her companions were small passerines and a pair of Harlequin Quail. She ignored the former, but tended to seek the company of the quail.

a. *Food-washing.* In the winter it was noted by my daughter that Spotty 1 customarily picked out pieces of the prepared food at the Zoo and dropped them onto the ground, where they became covered with sand. She then dropped them into the little stream, caught them and ate them.

Food-washing has been reported in 10 other species of Scolopacidae, three species of Charadriidae, and the Oystercatcher (Beven, 1946; Tebbutt, 1946; Harber, 1947); in Caspian Terns and other Laridae (Bergman, 1953:33); Buff-backed Heron or Cattle Egret (Goodwin, 1948a); Dipper (Evenden, 1943); and Clapper Rail (Williams, 1929).

8. Escape Reactions

Spotties were the only birds we raised that showed a marked tendency to become shy at an early age. The first two had as companions tame and placid birds, which much of the time uttered a series of soft notes. For the first 10 days Spotty 1 and the two Soras were about the same size, starting at about 6 grams and reaching 14 grams at one week; at two weeks, however, their weights were 25 and 36 grams, and at three weeks 31 and 57 grams respectively. The Coot, on the other hand, started at 19 grams, and its weights at one, two and three weeks were 47, 107 and 190 grams. It may be that the Soras served as brood mates, the Coot as a parent substitute. Spotty 2, being younger than the Soras, weighed about half as much as they throughout her stay with us. She often rested in the midst of them.

With Spotties 3, 4 and 5 the only companion we could offer at first was the Killdeer that weighed 9.8 grams at hatching in comparison to their 6.3; at one week he weighed 17 grams, they averaged 11; at two weeks he weighed 35 and they averaged 23 grams. The three spotties customarily rested separately from one another and they did not seek the Killdeer, which usually stood upright. But whenever during the first week a duckling was introduced, they eagerly nestled next to it. The sandpipers did not reassure each other, but stirred each other

up to flee. The addition of the newly hatched Coots when the Spotties were nine and 11 days old gave them confidence. I noted: "Spotties calm. Lie down on each side of Coot. Spotty 5 takes custard from my fingers." This Coot weighed no more than Spotty 5 and less than Spotty 3, so size was not involved in the calming influence. Shape, however, may have played a part; the low-slung, puffed-out body might well have suggested a brooding parent and this impression might have been reinforced by the Coot's soft little songs. Morris (1956:84) describes how Estrildine Finches respond to a bird in fluffed, spheroid position by "clumping" beside it.

The beneficial effect of the Coots is reflected in the weights of the Sandpipers; at one week these Spotties weighed only 75 per cent as much as Spotties 1 and 2, but at two weeks they averaged 90 per cent as much.

The earliest instance of crouching that we noted came at about 3 hours and 20 minutes in Spotty 5; it crouched as my hand moved past the Pintail nest. At 15 hours Spotty 3 when taken outdoors crouched at the screams of the Franklin's Gulls. This happened at various ages, but the Sandpipers were much less affected than was the Killdeer. When the one- and three-day-old sandpipers were out in the Rail Pen for a visit they kept poking their heads through the wire despite the attacks of the gulls.

When taken out alone to forage at the age of two days, Spotty 1 fled at the approach of a man and hid under a board; the next day she took refuge in a forest of nettles, so after that she was let out only in a small outdoor pen (Nice, C., 1954).

When Spotty 1 was 15 days old we introduced a little Blue-winged Teal duckling. The Sora (one had died) begged at, then pecked it. The Coot elongated her neck, then rushed away; Spotty gave a strange cry, then fluttered frantically up on the wire. Four days later we put a fledgling House Sparrow into the box. The Coot and Sora at once attacked it, but Spotty opened her bill and gave high notes and flew about the cage.

Young Greenshanks show no fear during the first four hours, according to Nethersole-Thompson (1951:193). "From four hours onward, however, the little ones may respond to the parents' alarm by a slight contraction of the neck and by cringing in the nest; and within six hours, on hearing the alarm calls of the parent, the chick may quit the scoop and crouch on the ground outside." Baby Curlews crouch instinctively on sight of an enemy in the air or on the ground. They have an inborn response to the parents' warning call, but at first it may only alert them until they themselves see the cause for alarm. Later they take

cover immediately on hearing the call (von Frisch, 1958). It took seven hours for Redshanks hatched under Lapwings to respond to their foster mother's call note and a full day before they reacted to her alarm note (von Frisch, 1959a).

9. Bond to Parent and Brood Mates

The father Spotted Sandpiper warns the chicks with a "strong *pett-wheet* which invokes immediate hiding and freezing, while a softer *wheet,* often repeated, brings the chicks together" (Knowles, 1942). The fluffed-out attitude of the father also serves as a stimulus to the chicks to join him. We were unable to give any of the proper signals and soon ceased to play the role of parent-companion.

When the 1954 Spotties were two and four days old and weighed from 5 to 7 grams, we put a three-week-old Virginia Rail weighing 43 grams into their brooder; they started to follow her, but she pecked them. In our experience baby Coots seemed to offer the best parental substitutes; their appearance was somewhat like that of a brooding sandpiper and their oft-repeated location notes correspond to the attraction-notes of the mother domestic fowl in their brevity, repetitiveness, and low pitch (Collias and Joos, 1953).

The bond between brothers and sisters was not especially strong with our brood; ordinarily they rested separately, in contrast to our ducklings, rails, gulls, and other species. This lack of bond between siblings was found by von Frisch (1959b) in five species of hand-raised sandpipers and four species of plover. It was strong, however, in four other shorebird species: European Oystercatchers, Snipe, Avocets, and Stone Curlews.

D. Summary

During four summers my daughter and I watched hatching behavior of over 100 birds of 30 species at Delta, Manitoba. Many of the birds were kept until they flew.

As examples of precocial chicks that find their own food, ducklings, Killdeer and Spotted Sandpipers are discussed.

We watched 19 individuals of surface-feeding ducks and 20 of diving ducks. Post-hatching behavior of a Mallard and a Ruddy Duck is described. The ages at which 17 coordinations appeared during the first nine hours of life of the ducklings are shown in Table 8. Behavior in the wild of hen and ducklings on leaving the nest is described and observations given on development of behavior till attainment of flight.

Four Killdeer were watched from 3½ to nine hours after hatching, while a fifth was kept till the age of seven weeks. Bobbing appeared from the age of 51

to 186 minutes. The first evidence of the plover run-and-stop rhythm of locomotion came with three chicks still on their tarsi, aged 63 to 164 minutes. Development of behavior of a very precocious individual is related during its first nine hours. The ages of attainment of 35 coordinations are shown in Table 9. The hand-raised Killdeer scratched his head under the wing at first, but from eight days on scratched over the wing. The occurrence of these two methods of scratching the head is described in other birds. Foot-patting was first seen at 18 days; the occurrence of this behaviorism in other species is discussed. Our hand-raised Killdeer was a placid individual and showed a strong bond to us, his foster-parents.

Five Spotted Sandpipers were raised. The first hour of one of these is described. The ages of attainment of 29 coordinations are given in Table 10. Teetering was first seen at 29 and 31 minutes. Stalking prey was noted at three days. Washing food was not seen until Spotty 1's first winter. These sandpipers were about as precocious as the Killdeer, but they soon became shy and after a few days showed very little bond to us and not much attachment to each other.

CHAPTER VII

Precocial Chicks That Follow Parents and Are Shown Food: Domestic Chicken

The most conspicuous examples of parents showing food to chicks occur among gallinaceous birds.

That calling to food can lead to feeding from the bill is shown by Goodwin's (1953:599) description of the process in the Red-legged Partridge. "The parent calls the chicks to food (although from the first they find much for themselves), either dropping the morsel onto the ground in front of them, or pointing its bill to it. Sometimes the chick takes the food direct from the parent's bill. This happens more often with older chicks and takes place when the bird's impulse to feed the chicks is to some extent inhibited by its impulse to feed itself."

Galliformes in general have short incubation periods in keeping with their predominantly ground-nesting habits. The young are precocious and lively, but very dependent on parental brooding (see Ryser and Morrison, 1954). For the first week Attwater's Prairie Chickens in Texas were brooded about 50 per cent of the time (Lehmann, 1941), and this seems to be the case with Hazel Hens in Finland (Pynnönen, 1954). The Heinroths (1924-33, III:230) point out that all Galliformes are characterized by remarkably early development of flight, particularly in those forms that live in the woods.

The best studies I have found on the behavior of gallinaceous chicks are Krätzig's papers on the Hazel Hen (1939) and Ptarmigan (1940), and Goodwin's on the Red-legged Partridge (1953). In 1908 when studying with Clifton F. Hodge at Clark University, Worcester, Massachusetts, I raised Bobwhites and have scattered notes on their development (Nice, 1939:135-144). Collias (1952) discusses the development of social behavior in domestic chickens, while Wood-Gush (1955) gives a general review of the literature on the behavior of this species.

A. Domestic Chickens

We had no success at Delta in watching gallinaceous young. A set of Sharp-tailed Grouse chicks hatched with weak legs. Domestic hen eggs placed in the incubator failed to develop.

Under some difficulties I was able to watch White Rock Chickens at the Museum of Science and Industry in Chicago in the fall of 1954. Swift and Company presented two exhibits of about 100 chicks each,

one of hatching chicks, the other of chicks in a brooder kept until three or four weeks old. I watched five chicks from hatching for one, one, two, two and three hours respectively. Observations on the brooder chicks were made one-half hour daily. The first set was visited every day for the first three weeks except on the days they were 13 and 19 days old; after that they were watched at 21, 25 and 28 days of age. The second set was visited four times during the first three days, and at 6, 10, 11, 14 and 17 days. The third set was seen only once when six to eight days of age. With the first set two older chicks were present—BC some six to seven weeks old at the start, MC about three weeks old.

Owing to the confusion of so many hatching chicks and the impossibility of marking them, I could not keep any one bird under observation for longer than three hours. Hence I have no records on exactly aged chicks in Stages III and IV. The chicks of the second set were younger than the first set when first put in the brooder; many were definitely in Stage III.

The brooder was a glass-enclosed hexagonal structure some 10 feet in diameter. It contained a heap of gravel in the center, feeding troughs containing mash at four sides, drinking bottles, and a perch about 10 inches from the ground. In the center hung a radiant lamp. The environment was a particularly impoverished one, with no chance for the chicks to meet an insect, nor even a blade of grass; no opportunity to respond to people, nor to encounter birds of other species and ages as with our subjects at Delta.

No attempt was made to follow individual chicks in the brooder. Instead, I tried to record the number of times various coordinations appeared in each observation period. It was impossible to get a complete record, partly because from no point was the entire field visible, and partly because when intently watching one trough, activities at another were missed. Yet a general picture was obtained of the first appearance of many coordinations and the frequency with which they occurred thereafter.

The frequency of some coordinations, such as stretching, shaking, scratching the face, etc., was easy to record because they were so momentary; others were easy because so conspicuous, as play-fighting and dust-bathing, but preening was difficult since each chick preened for several minutes. Since only two days were missed with the first set during the first three weeks, a good picture was obtained of the course of

development. Observations on the second set furnished valuable information on Stage III and the start of Stage IV, and corroborated the dates of appearance of play-fighting, dust-bathing, flying and play-fleeing found with the first set. On the one visit to the third set play-fighting and dust-bathing were seen.

1. Example of Post-hatching Behavior

The newly hatched chicks were precocious and active, but did a great deal of resting.

The chief activities of one chick during its first two hours were as follows:

White Rock Chick C.
0—Hatches. Crawls right out on platform. Very alert.
9m—*Pecks* at floor. Pushes back, a kind of jump over the eggs. A wonderful baby.
11m—Pecks and pecks at floor. Tries to climb over eggs.
15m—Jumps over on lower platform, three inches down. Alert, climbs back.
18m—*Pecks at another chick's bill.* Climbs down and back.
21m—Preening intention. Turns about; rests. Crawls to lower platform; up again.
22m—Shakes wings. Pecks at neighbor's bill. Climbs down and back.
26m—*Preens.*
31m—For first time *stands on feet* unsteadily. Pecks at wire.
34m—Stands on feet.
38m—Preens at breast. Struggles about on feet; rests.
41m—Pecks at wire; preens at wings; stands on feet.
49m—Rests; pecks at eggs; walks unsteadily on feet for two steps. Pecks at shell.
53m—*Shakes self* when standing, especially wings.
54m—Walks two steps on tarsi. During the second hour this chick rested much of the time.
1h46m—Still progressed for the most part on its tarsi.

This chick was the most active of all five during its first hour, but slept practically all of its second hour. D and E, watched for one hour each, were nearly as active as C. A was moderately active for the first two hours, but slept most of the third. B, however, was very inactive during its first two hours; 14 minutes after hatching it pecked at the floor, and at 60 minutes it pecked at an egg shell; otherwise it merely rested in the spot where it first came out of the egg.

2. Development of Behavior in Chickens

Drying takes some three to four hours. The waiting period—Stage III—may be very brief, or may last 15 or even 20 hours.

Bobwhites if hatched in the forenoon may stay in the nest only four or five hours, but if hatched in the afternoon do not leave until the dew has dried the following morning (Stoddard, 1931:38). The same is true of Ring-necked Pheasants (Delacour, 1951:238), and both the Greater (Bent, 1932:252) and Attwater's Prairie Chickens (Lehmann, 1941:16). Red-legged Partridges were led from the nest at about 24 hours of age (Goodwin, 1953:601). I have considered Stage IV as including from leaving the nest (with wild birds) to the start of play-fighting with the birds I watched.

Table 11 summarizes the observations on the White Rock chickens in Chicago.

TABLE 11

DEVELOPMENT OF BEHAVIOR IN WHITE ROCK CHICKENS

Five chicks watched from hatching for 1 to 3 hours; 300 chicks observed in later stages

m = minutes, h = hours, d = days

( ) = chicks not watched the previous day

		Coordination	*Age at First Appearance*		
Stage	II	Random pecking	9m, 13m, 14m, 14m, 15m		
		Exploratory pecking	18m, 20m, 22m, 38m		
		Crawling on tarsi	15m, 16m, 22m, 31m		
		Preening	20m, 26m		
		Yawning	27m, 42m		
		Shaking selves	27m, 53m, 59m		
		Fanning wings	27m		
		Stretching out leg	60m, 1h56m		
Stage	III	Scratching head, walking on feet			
Stage	IV	Eating, drinking, wiping bills, running, stretching wings up and sidewise			
		Scratching ground	1½ to 2d		
Stage	V		*1st set*	*2nd set*	*3rd set*
		Play-fighting	6-7d	(6-7d)	(6-8d)
		Dust-bathing	9-10d	(10-11d)	(6-8d)
		Flying	10-11d	11-12d	
		Play-fleeing	14-15d	(14-15d)	
		Pecking each other	25-26d	(17-18d)	

3. Stage II—Preliminary

The drive to be hovered is very strong in newly hatched gallinaceous birds (except of course Megapodes). "When the chick wants to be brooded it creeps under the parent, then stands up and pushes upward to bring its head and upper-parts into contact with the parent's body" (Goodwin, 1953:604). This pushing upward and against our hands was pronounced in our Sharp-tailed Grouse and Bobwhites as well as in Soras and other precocials.

The five White Rocks watched from hatching, showed eight main coordinations. (Breed [1911] mentions all but two of these—yawning and shaking—as appearing before the chicks are dry.)

4. Stage III—Transition

While waiting to leave the nest, the chicks become strong on their feet.

a. *Exploratory pecking.* This was the earliest and most striking activity of these baby chicks. Much study has been devoted to observations on this subject in domestic chickens to try to determine whether improvement in accuracy is a matter of maturation or of learning (Spalding, 1873; Breed, 1911; see Wood-Gush [1955]).

Hess (1953) fitted newly hatched chicks with plastic lenses, some of which caused 7° displacement of the visual field to the right or left; he found no adjustment was made to the actual position of food objects, and concluded: "Improvement of pecking accuracy is independent of learning in the strict sense and can probably be interpreted in terms of maturation of the motor response." In a more detailed paper (1956a) he states that the "chicks' visual apparatus for locating objects in space is innate and not learned." An innate preference for appropriate size of food particles was established by Curtius (1954) in three species of newly hatched chicks: turkeys preferred objects 5 mm. in diameter, domestic chickens those of 2.5 mm. and Lapwings 1 mm. In an investigation of color preferences, day-old White Rocks pecked most frequently at orange and at blue color chips, while White Pekin ducklings favored green and yellowish-green chips (Hess, 1956b). As to innate preferences for visual properties of water, the first choice of three-day White Rock chicks without experience of food and water was mercury, followed by plastic, blue water, water, metal, and red water. Four days later, despite experience with food and water, mercury was

still the most attractive choice and water still fourth choice (Rheingold and Hess, 1957).

Hazel Hen chicks for the most part peck *above* their heads, not on the ground (Krätzig, 1939; Pynnönen, 1954:53).

b. *Scratching the head.* I saw this four times in a group of the "hatching" chicks, but it was impossible to find out the ages of the birds concerned. The second set was put in the brooder on November 18 when less than a day old; this coordination was noted once in the morning session and twice in the afternoon; three times on November 19, five times on November 20, 17 times on November 25, and after that varying between five and 12 times. With the first set it also increased in frequency, being seen one, two, three, nine and six times during the first five days, reaching 17 on the seventh day, after that fluctuating between five and 20 times.

5. Stage IV—Locomotory

Running, eating, drinking, wiping bills, stretching wings up, and wing and leg sidewise—all these are established early.

a. *Comfort movements.* The two ways of stretching were about equally frequent throughout the observations, averaging from seven to 11 times per period in the two sets. Shaking selves averaged nine times per half hour with the first set, 14 with the second.

Breed (1911) records bill-wiping as first seen on the second day. It was noted 10 times in the first session with the second set and reached its peak with 35 times 12 days later. Under the museum conditions it seemed to have little to do with eating, but often occurred as a displacement-movement after a fight. Goodwin (1953:607) writes of the Red-legged Partridge: "Bill-cleaning is—as with passerines—also used as a displacement-movement when the bird is in a state of nervous tension."

b. *Scratching the ground.* This appears on the second day according to Spalding and Breed, as well as in my experience. It was not seen at all with the second set during their first day in the brooder, but was noted 11 times the next day, and at least 65 times the third day; from then on it was recorded from 67 to 90 times a session. With the first set scratching was noted four times during the first day when some of the chicks were two days old; it was recorded 15 times the next day and 40 times the third. It was pursued even more frequently

after that, but decreased somewhat when the chicks were nearly four weeks old. The chicks usually scratched twice (occasionally three times) with one leg, then once or twice with the other. Most of the scratching was done in the food troughs; some in the gravel. The chicks evidently derived satisfaction from the performance of this instinctive activity, even though in this situation it could have helped little with the unearthing of food.

A group of 18-day-old Bobwhites when first brought into the laboratory at Clark University scratched with great zeal in new hay although they found no food. I scattered grain in the hay. After a rest, they felt hungry. I tried to show them the grain by stirring up the hay, but it never occurred to them to scratch to get it; they merely ran around calling.

Sumner (1935:187) describes the behavior of California Quail when they have discovered a patch of ground covered with bait. "In spite of the fact that the birds have only to stand still and eat, they pick up a little here and there, then run a few steps forward and pick up a dozen more seeds, often stopping to scratch the ground vigorously, although such scratching is not only unnecessary under these conditions, but actually scatters the seeds far and wide so that many are lost. Presently, as a result of this aimless feeding, the birds have wandered entirely away from the site of food abundance, in which case they usually do not return, at least not for several hours and often for days."

Many of the Emberizinae, as well as Viduinae (Poulsen, 1953: 38), scratch with both feet at once, making a little jump forwards and a larger jump backwards. With the hand-raised Song Sparrows "scratching did not seem to be stimulated so much by the situation of a supply of weed stalks and seeds as by the feel of various substances"—such as balls of yarn or steel wool, or a sweater (Nice, 1943: 42).

Scratching, however, is not a universal trait in Galliformes, being absent in the Cracidae (Poulsen, 1953) and Opisthocomidae. It is present in the other families. Poulsen (1953:36) gives a long list of species in which it does occur. Among the Phasianidae some scratch a great deal, others seldom. Delacour (1951:187) says the Eared Pheasants dig with their powerful beaks and "never, or very seldom, used their legs for scratching." As to the Tetraonidae, scratching occurs rarely in the Ptarmigan (Krätzig, 1940), Prairie Chicken (Frances Hamerstrom, letter), Capercaillie and Black Grouse (Poulsen). Thus this subfamily "possesses the scratching movements and they also

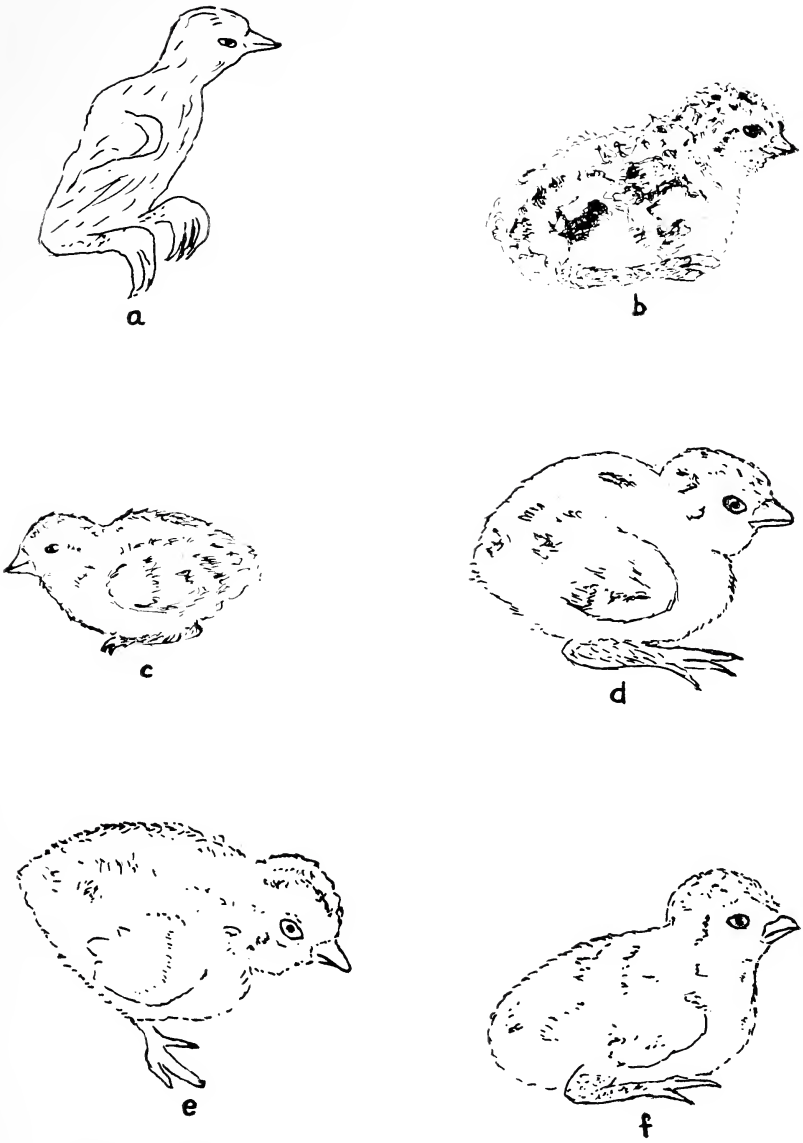

Figure 4. SHARP-TAILED GROUSE. *a*, 5 minutes. *b-f*, first to second day.

peck, but these movements are seldom performed because they seek their food on the ground or above the ground and seldom in the ground. They scratch and peck like other gallinaceous birds when bathing in the dust" (Poulsen, 1953:37).

c. *Sun-bathing.* This appears very early with chicks; they may lie flat on the ground with wings outspread, or lie on one side with legs stretched out and wings sometimes spread. Goodwin (1953:606) describes these postures in Red-legged Partridge chicks. The Heinroths (1924-33, III:234) mention the second posture as characteristic of Galliformes.

d. *Rushing away with food.* Many precocial chicks have a strong instinctive urge to rush away from the family when they find a sizable morsel. This behavior was seen only twice with the brooder chicks due to the lack of suitable objects. In each case a chick was running in a determined manner with its head held down instead of up as ordinarily; this attitude evidently served as a signal to its companions who at once pursued it.

Spalding (1873) points out that chicks, even those raised alone, "when they get something larger than can be swallowed at once, turn round and run off with it."

Brückner's (1933:75) "Kaspar Hauser" domestic chicks (i.e., those raised in solitary confinement) would rush away with the first three angle worms given them by hand, but not the rest. When my pet Bobwhite, alone since his tenth day, was presented with a can full of grasshoppers, he would seize one, hop down from my lap and run away to eat it. Not until the seventh or eighth insect would he eat on the spot. When he was eight weeks old, however, he gave the food call, used by adults to call the young, whenever he found his favorite, yellow wood sorrel, *Oxalys stricta,* and crabgrass, *Digitaria sanguinalis.* Hazel Hen chicks ran away with grasshoppers from the fifth day on, but when one found a supply of food, it gave an excited *pit pit pit pit,* whereupon the others hurried to it and uttered the same note as they ate. No age is indicated for this behavior (Krätzig, 1939:20).

Rushing away with food is seen with many species. Young green lizards *(Lacerta viridis),* raised in isolation, ran away with prey, but adults only did so when another lizard was present; "apparently they learned not to do it when it was not necessary" (Weber, 1957:461). It is also characteristic of small pigs (L. B. Nice, personal communica-

tion). It is seen with chicks of many species, such as ducks, pheasants, Soras, Eared Grebes (Van Ijzendoorn, 1944), etc., and is prominent with adult gulls. With the highly socialized Marbled Wood-Quail, however, large pieces of food are shared amicably among the members of the covey (Skutch, 1947:218). Goodwin (1953:594) discusses the rushing away and food calling in the Red-legged Partridge and points out how these seemingly contradictory activities might prove beneficial to a species—both the hiding of a large single piece from a bird's comrades and the sharing of an ample supply of small objects.

6. Stage V—Socialization

Play-fighting, dust-bathing, flying, play-fleeing, and pecking each other all appear during Stage V.

a. *Play-fighting.* Thorndike (1899) wrote that at six days two chicks will rush at each other; face each other, then separate—the start of fighting behavior. With my first set the development of play-fighting was clearly shown. The first intimation came at five days when one chick suddenly stopped in his running upon confronting a companion. The first play-fight came with a six- to seven-day chick in response to a challenge from BC, six to seven weeks older than the group. The next day BC made rushes at five of the chicks, but they did not respond. The following day MC, about three weeks older than the group, challenged two chicks and they responded. The next day a brief play-fight was observed between two chicks 9 to 10 days old. (With the second set two play-fights were seen at six to seven days; with the third set there were four suggestions of play-fights and one real one at six to eight days.) At 10 to 11 days the simple play-fight was well established. This consisted of (1) a rushing together; (2) the challenge when both chicks stood erect facing each other; (3) hopping up and down; (4) pecking each other. At 16 to 17 days a new development took place—sometimes the opponents raised their hackles. The next day two fights ended with one chick trying to trample the other. "One circles around after jumping up. *Real* pecks afterwards." (With the second set this attempt to jump on the other was seen at 14 to 15 days.) At 25 to 26 days "necks extended after one fight; try to jump on opponent." The next day, "some fights quite furious." The incidence of play-fighting with the first set increased almost consistently from 15 fights during the half hour at the age of 10 to 11 days to 70 at 18 to 19 days. During the last four days of observation the incidence was as follows: 50, 33, 67

and 39. With the second set this activity was noted 29 times at 11 to 12 days, 41 times at 14 to 15 days, and 34 times at 17 to 18 days.

Play-fighting was undoubtedly practiced to an exaggerated degree by these chicks living under crowded conditions in monotonous surroundings.

Play-fights among members of a brood of chicks serve to establish the dominance hierarchy, according to Baeumer (1955:389); he noted such contests from the age of three weeks. He gives photographs of the upsurge of fighting that may occur about the seventh week and that definitely settles questions of rank. In a later paper (1959) he describes in detail and illustrates the technique of fighting between adult cocks, between hens, and between cockerels and adult hens.

Young turkeys in a brood may fight each other fiercely. Adult Reeve's Pheasants are quarrelsome and their chicks "begin to fight among themselves at the age of a week or ten days" (Delacour, 1951: 228). Derek Goodwin writes me that his young Red-legged Partridges fought each other when a few weeks old.

b. *Dust-bathing.* This was first seen at nine to 10 days with the first set (one bird); was well established (five instances) at 10 to 11 days with the second set, and noted as early as six to eight days with the third set (one bird). Dust-bathing consists of four movements. (1) Scraping dirt towards the breast with a hoe-like movement of the bill; (2) scratching dirt into the plumage with the feet, the bird usually lying on its side; (3) throwing dirt over itself by shivering the wings, either together or alternately; (4) stretching the neck and rubbing it in the dirt. (All these were seen on the first occasion of dust-bathing except hoeing with the beak and the alternate wing movement.) Dust-bathing was seen each session from zero to 11 times with the first set after the first instance, from one to five times with the second set. Often when one chick started dust-bathing, others joined it, all working crowded together.

Hand-raised Hazel Hens and Ptarmigans were first seen to take sand baths at the age of seven days (Krätzig, 1939, 1940). Goodwin (1953:605) well describes the technique of dust-bathing as he has watched it in the Red-legged Partridge, "the ruffed and common pheasants *Chrysolophus* and *Phasianus* and the fowls *Gallus*." He does not state when it is established in any of these species, but he describes how when a Red-leg chick about three hours old, taken from the nest and released, "happened to pass over some fine dry earth, it at once stopped and commenced to dust-bathe, making all the characteristic movements, though in a rather fumbling manner." A second chick, treated in the same way "'automatically' made dusting movements . . . the moment it found itself on the dusty soil."

c. *Flying.* The earliest observation was on a chick of the second set six to 7½ days old that flew about three inches. When 11 to 12 days old eleven chicks flew to the perch about 10 inches from the ground during the half hour. The first set were noted as flying about four inches when 10 to 11 days old, many of them reaching the perch when 11 to 12 days of age. When 18 to 19 days old one flew to the top of the water can some 15 inches above the ground.

Observations on other Galliformes show the beginning of flight at three days with Tragopans and Peacocks (Heinroth, O. and M., 1924-33, III:236), 10 days with Hazel Hen (Pynnönen, 1954:55), Black Grouse and Jungle Fowl, 11 days with Gray Partridge and European Quail, and 14 days with Capercaillie (Heinroth, O. and M., 1924-33, III:236-251), Bobwhite (Stoddard, 1931:43) and Attwater's Prairie Chicken (Lehmann, 1941:17).

d. *Play-fleeing.* At 12 to 13 days some chicks of the first set made sudden turns—"almost 'frolicking.'" Two days later: "One dashed about, 'frolicking.' Another, then another. A fourth turned around and about quickly." The next day only one chick performed, but after that from five to 15 were recorded play-fleeing during each session. In the second set, play-fleeing was not noted at the age of 11 to 12 days, but at 14 to 15 days three chicks performed and three days later five did so.

What I called "frolicking" (1943:51, 67) has been characterized by Lorenz as "emotion-dissociated fleeing movements." It was often practiced by my hand-raised Bobwhite. McCabe and Hawkins (1946:63) describe it as frequent in six- to eight-week-old brooder-raised Hungarian (Gray) Partridges and occasionally seen at 17 weeks. This "peculiar kind of behavior always accompanied the release of the birds from the brooder to the pen." It consisted of a hop, a run, a half turn, ending in a tilted position with the head and shoulders on the ground and the tail continually flicked up and down.

Goodwin (1953:608) well describes this activity as it occurs in the Phasianidae: "The partridges ran about at full speed within a relatively small area, frequently taking a sudden short flight, and when running check and change direction with great suddenness after running only a few yards. As the bird swings round, its head and body are jerked low to earth and the outspread tail lifted high. This movement—the only one I know in which the tail is so raised—is no doubt fundamentally a mechanical necessity in order to maintain balance and achieve a rapid change of direction. It may, however, also be of use in presenting the easily spared tail feathers to the talons of a stooping raptor. . . . The 'play' movements of *Perdix, Phasianus* and *Chrysolophus* are similar to those of *Alectoris* and in each case they almost certainly represent the instinctive movements used for escape when surprised in the open by a bird of prey."

For further discussion of play-fleeing see Chapter XII.

e. *Pecking each other.* Pecking each other in connection with play fights appeared at 10 to 11 days. Pecking unconnected with play-fighting was first seen at 17 to 18 days in the second set of chicks but not until 25 to 26 days in the first set.

7. Escape Reactions

Collias (1952:134) states that "Any loud, harsh sound, such as the warning scream to 'aerial predators' of an adult chicken, the scraping of a chair over the floor, a sneeze, or the blaring of an automobile horn, often resulted in escape reactions" in baby chicks. At the Museum the whistle of the coal mine exhibit was unpleasant to chicks of all ages; whenever it sounded they invariably raised and shook their heads.

Hazel Hens were found by Krätzig to show no signs of fear during the first 10 days except in response to a whistle in imitation of the parental alarm cry. After that the chicks started to give the alarm cry themselves and at the same time became very sensitive to loud noises which sent them scurrying to cover. Both they and the hand-raised Ptarmigan recognized instinctively an *Accipiter* hawk as an enemy.

8. Responses to Parents

Innate responses to the parent-companion (Lorenz, 1935) appear to be largely based on auditory signals. Collias (1952:132) states: "Occasionally there is found a pipped egg containing a chick which will respond consistently to clucks by cessation of distress calls."

Spectrographic analyses of the sounds of the domestic fowl are presented by Collias and Joos (1953). The following common elements were found "in sounds that attract chicks: (1) repetitiveness or segmentation, (2) brief duration of the component notes, and (3) the presence of relatively low frequencies. Warning signals as a group have in common features that are the opposite: (1) relatively long duration, (2) relatively little segmentation or repetitiveness, and (3) absence of very low frequencies." These characteristics probably hold in general for many other birds.

Red-legged Partridge "chicks appear to have some innate recognition of the notes of the parent, but this is undoubtedly reinforced by imprinting which occurs when the parent is 'talking' to the hatching

or newly-hatched young." "Young Red-legs hatched and reared under domestic fowls . . . responded to her clucking when first led from the nest (doubtless through imprinting since this bird, like *Alectoris,* 'talks' to hatching chicks) and to her alarm notes. . . . They did not at first show any reaction to the domestic hen's food-call, but within 24 hours had learned to respond 'instantly' " (Goodwin, 1953:602-3).

My Bobwhites hatched under a bantam paid no attention the first day to her food-call; the second day they were removed to a brooder. Could it be that the guiding and alarm notes, present in practically all birds with precocial young, belong to a more fundamental pattern than the food-call, which appears in only a few species?

The Museum chicks heard no parental calls. The warmth of the mother was supplied by the always-burning lamp; guidance and protection were unnecessary in the confinement of the brooder; the ever-present troughs of mash were soon discovered by the chicks through their exploratory pecking.

The brooding mother gives a complex of signals: posture, special notes, and in a general sense size, i.e., she is larger than the chicks, but not so large as to have the meaning of an enemy. Collias' (1952:132 and personal communication) hen, mounted in the brooding position, was ignored by chicks fresh from the incubator in favor of the heating pad a few inches away. The chicks of my first set were never seen trying to creep under BC and MC, who offered only size as a signal for brooding. The Soras, on the contrary did try to push under a young Yellow-headed Blackbird, a baby Snowshoe Hare and young bittern. Their environment was less warm than that of the Museum chicks and they had come into bodily contact with warmth-companions somewhat larger than themselves, such as ducklings, Franklin's Gull chicks, and our hands. Goodwin (1953:614) concluded that the Red-leg chicks "respond primarily to the appropriate calls and parental behaviour of the adult, rather than to its visual image."

The guiding mother clucks and moves. Collias (1952:133) found that "by one hour after hatching, sight of an object moving nearby usually causes a chick to stop its distress calls." The Museum chicks showed a slight tendency to follow BC during their first day in the brooder, but not thereafter. If BC had been present while the chicks hatched, they might have become imprinted on him.

The feeding parent lifts food up, drops it and picks it up again, at the same time giving the loud, excited food-call. Goodwin says the

Red-legged Partridge chicks "appeared to recognize" the food-offering gestures of the domestic hen "(not surprisingly as these are in effect a burlesque exaggeration of those of the Red-leg)" (1953:603). From October 20 to November 4 whenever BC wiped his bill or pecked on the ground, chicks gathered around, although they never were rewarded by food. With both the Red-legs and White Rocks there appeared to be instinctive recognition of food-calling gestures, although in the latter the gesture was at its lowest denominator.

Of the different techniques parents of precocial young employ to protect their young from enemies—notes, distraction display, threat and attack—we will discuss only the notes, for to these the young show an inborn response.

"The alarm call [of the domestic fowl] to aerial predators is a loud, sustained and raucous scream, which causes chicks at once to run and hide under the nearest shelter" (Collias and Joos, 1953). This alarm call even induced hatching chicks to fall silent "for a good 15 seconds" (Baeumer, 1955:387); the experiment was often repeated. With the Red-legged Partridge the hawk-alarm note is a "rather high-pitched disyllabic" *Kwerrek!* which causes the chicks at once to "dash into the nearest cover and hide"; coming out again in "half a minute or less" (Goodwin, 1953:587, 603). Pynnönen (1954:51) followed newly hatched broods of Hazel Hens, waiting after the initial hiding of the young to see whether the mother would be fearless enough to gather her brood while he remained within five to 10 meters. In 12 cases he was successful, in six not. In the first category, chicks began to peep 1, 5, 5, 18 and 35 minutes after the first fright; in the second category they started to call 27, 27 and 40 minutes afterward.

Goodwin notes (1953:602) in regard to the Red-legged Partridge: "The immediate 'obedience' the chicks show to alarm notes contrasts strongly with their response to the cooing call and the rally call of the parent. If they are busy feeding, preening, dust- or sun-bathing, they pay little or no heed to these calls, to which the lost or anxious chick responds instantly."

Brückner found that chicks stay rather close to the mother hen for the first 10 to 12 days, but afterwards come to her chiefly for warmth. The family usually breaks up at six to eight weeks, the initiative coming from the hen.

9. Bond to Brood Mates

A definite bond exists between the chicks. In some experiments on domestic chicks' responses to light and shade cues, Hess (1950) reported that two to four subjects had to be used for each trial, for they "remained immobile when placed singly in the testing machine."

Most activities are done together—scratching, preening, dust bathing, eating, resting. Krätzig found this pronounced in young Hazel Hens until adult plumage was acquired at the age of 80 to 90 days. Two days after I had brought into the laboratory a brood of eight Bobwhites 18 days old, I returned four to Dr. Hodge's home; the others gave the lonely call almost all the afternoon.

Two domestic chicks raised in solitude were introduced at the age of seven weeks to 250 other chicks of like age; they were greatly confused, attacked the new chicks and turned for assurance to the caretaker with whom they had associated handouts of angleworms; this attachment had disappeared the following day. One "Kasper Hauser" became assimilated into the flock in three days, the other not for 12 days (Brückner, 1933:77).

Pullets from the same brood may show a bond to one another for over a year (Baeumer, 1955:394).

B. Summary

In some of the Galliformes, parental calling to food is conspicuous.

Groups of White Rock chickens were watched in Chicago from hatching to the age of four weeks. The activities of a chick during its first two hours are described. The ages at which 22 coordinations were first seen are shown in Table 11.

Accuracy of pecking has been shown to be a matter of maturation and not of learning.

Scratching on the ground appears on the second day. The instinctive nature of this coordination, as well as its occurrence in other species, is discussed. Rushing away with large morsels is an instinctive action which is also present in many other species. The development of play-fighting is described. Dust-bathing in domestic chickens and some other Phasianidae consists of four movements. Play-fleeing appeared at about two weeks of age; this behavior has been characterized by Lorenz as "emotion-dissociated fleeing movements."

Chicks react to certain sounds with escape reactions. Hazel Hens and Ptarmigan recognize *Accipiter* hawks instinctively. Notes and movements of the parents serve as signals to their offspring.

A fairly strong bond exists between the young in a brood.

CHAPTER VIII

Precocial Chicks That Follow Parents and Are Fed by Them: Grebes, Virginia Rail, Sora, Coot

Representatives of Precocial Category 4 are grebes, loons, a few pheasants, some of the shorebirds and the majority of the cranes and rails. The period of full dependence on parental feeding may be long or rather short, partly depending on the nature and availability of the food.

At Delta we were able to watch three species of grebes, as well as American Coots, Soras and Virginia Rails.

A. Grebes

Grebes are foot-propelled diving birds; they do not use their wings under water. They swim with the feet behind the body, and are so highly developed for swimming that they can hardly walk. They spend much time in preening and oiling themselves; this they do by lying on one side in the water. To warm a foot they lift it sidewise out of the water and put it in a wing pocket. They scratch their heads from under the wing (Woolfenden, 1956; Simmons, 1955a:100).

Adult grebes eat their own feathers that become detached during preening, and give feathers to the young from the first day on, sometimes from the first meal (Simmons, 1956; Hachler, 1958). Young Red-necked Grebes pick off and swallow their own down (Munro, 1941a). "The chicks soon learn to pick up floating feathers for themselves and occasionally pluck them from the adults. . . . thus the grebe is 'capturing' and eating feathers long before it gets true food for itself" (Simmons, 1956). Simmons suggests that feathers may assist in forming "ejectable pellets," although no such pellet has been observed. The prevailing opinion, however, is the one corroborated by Lawrence (1950) after a study of the feeding habits of the Western Grebe which involved the examination of 27 stomachs: "The feather mass which completely fills the stomachs of Western Grebes appears to function to protect the inner lining of the stomach from the sharp bones of fish; it also prevents undigested bones from passing into the lower alimentary tract. . . . The Western Grebe does not regurgitate undigested bones, scales and chitinous parts."

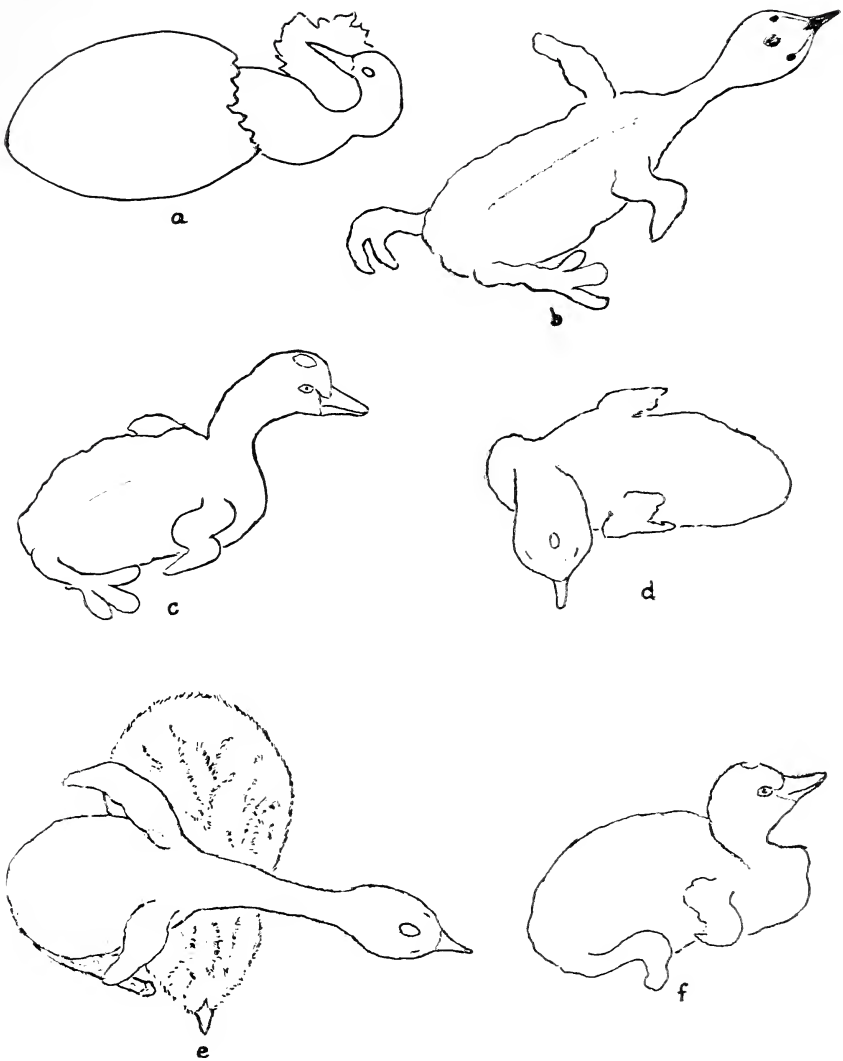

Figure 5. WESTERN GREBE. *a*, hatching. *b-f*, 2-3 hours; *e*, draped over Franklin's Gull.

According to the Heinroths (1924-33, III) grebe eggs are small with only 22 per cent of yolk in eggs of the large forms, but 29 to 31 per cent in those of the Little Grebe. Since the eggs are incubated as laid, chicks hatch at intervals; they do not pip the egg until shortly before hatching—a protection against drowning in the waterlogged nest—but they call loudly for two days before this, which is a warning to the parents not to desert.

The chicks have very short down and cannot follow their parents like ducklings, but for the sake of warmth must live in the parents' feathers somewhat like marsupials. Simmons (1955a) points out how this carrying of the young also serves to protect them from underwater predation, particularly by large pike.

In his paper on North American grebes, Munro (1941a) writes: "For the first few days of life young grebes are weak swimmers. . . . In comparison with young ducks of the same age they are relatively helpless and much less able to overcome the normal hazards of the nesting ground. Parent grebes carry the young on their backs but in other ways exhibit little evidence of care for them, so different from the energy with which female ducks of some species defend their broods." Mr. Simmons, however, writes me: "Larger grebes (the Great Crested certainly) surely will attack certain predators that show signs of molesting the young, and the smaller species (certainly our Dabchick and your Pied-billed) have special behavior, diving with splash and special call, which warns the young and causes them to dive, and also probably diverts the predator."

We watched grebes of three species hatch, but like the Heinroths' birds, they did not live more than a few days. The hatchling Pied-billed, Red-necked and Eared (Black-necked) Grebes are strikingly marked on head and body with stripes and spots, but the Westerns are a uniform silvery grey except for the bare red spot on the forehead.

1. Examples of Post-hatching Behavior

Eared Grebe: June 21, 1951.
0—Hatched at 12: 57 p.m.
2m—*Stands up.*
12m—*Yawns. Snaps* and pecks at random.
15m—Nipped my finger.
17m—Yawns, yawns.
18m—Rises on tarsi, snaps, yawns.
21m—*Preens* under right wing.

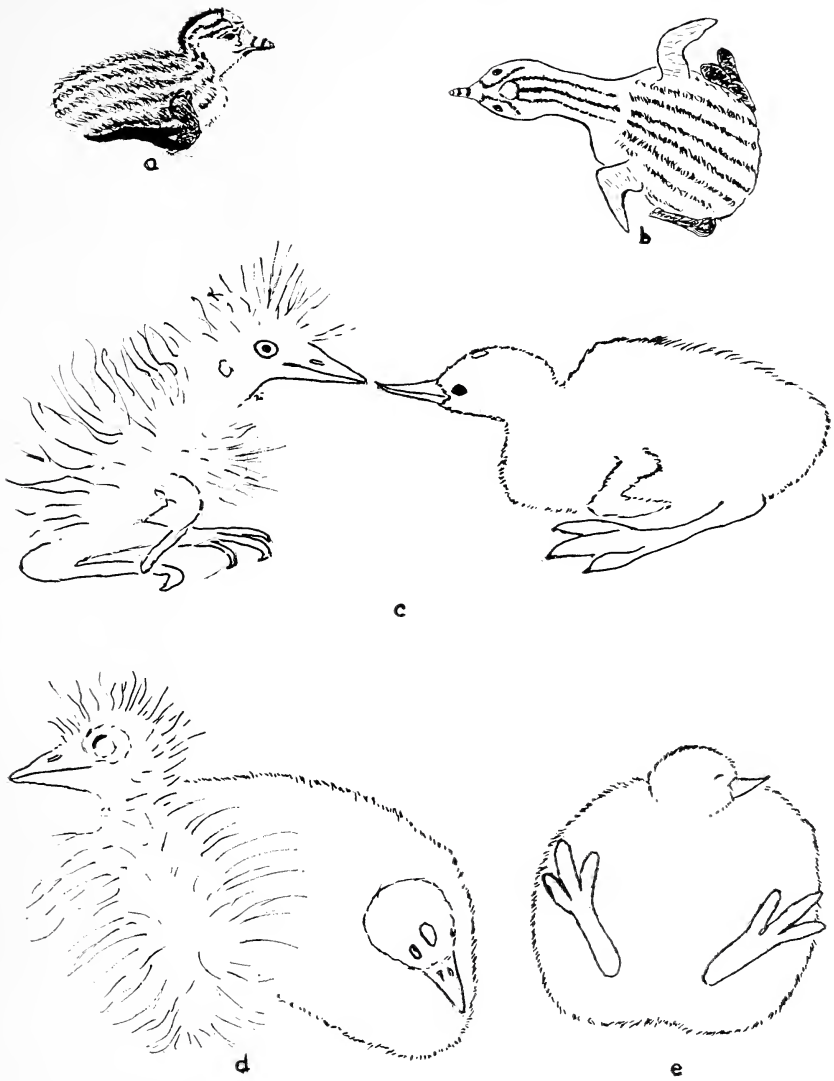

Figure 6. EARED GREBE, a, 1 hour; b, a few hours. c,d, grebe, about 2 weeks and bittern, 2 days. e, about 4 weeks.

23m—Yawns, pecks my hand.
36m—Seems dry.

By end of first hour seven more yawns, five more pecks. Completely dry. Trying to crawl out of the nest. In second hour struggled to get under the Canvasback; got between it and the Coot, then tried to burrow into Canvasback's down. Finally gets on top of duckling, neck stretched to the utmost.

2h30m—*Eats egg from the forceps.* Snatches at it and swallows it.

The Western Grebes were especially lively, as is evident from the following record.

W5. June 25, 1951, 8 a.m., shouting in egg; June 26, still shouting and egg unpipped at 11 a.m.; at 1:35, a hole; 4:05, coming out; 4:07, *kicks out.* At once tries to climb on top of bittern. Gulls 1 and 2 dash at it. With head up it crawls and struggles, saying *eek, eek. Can do everything right away.* 4:09, give it a chance to swim; sinks, then swims and comes to shore. Dry it and put it in hatching tray. 4:22, return it to nest, where it drapes itself over the Coots.

2. Development of Behavior in Grebes

Table 12 shows the first appearance of various motor coordinations in the seven grebes we watched hatch, as well as in one Western Grebe (W1) whose age we know only approximately.

TABLE 12

DEVELOPMENT OF BEHAVIOR IN GREBES

Eight individuals (seven watched from hatching)

m = age in minutes, h in hours

	Western					*Pied-bill*		*Eared*
	W1	*W2*	*W3*	*W4*	*W5*	*P1*	*P2*	*E1*
Yawning		−11m	2m	2m		27m	3m	12m
Preening	3h±						2h48m	21m
Snapping	4h±	39m				40m		12m
Climbing		4m	1m	2m	1m	37m	46m	57m
Eating		2h20m				42m	46m	2h30m
Stretching one leg	3h±					2h45m	36m	
Stretching both legs						1h24m	3h	

All the young grebes were very active from the first, and their short down was dry by the end of the first hour. The sogginess of their nests in nature would not encourage any dalliance there. Their

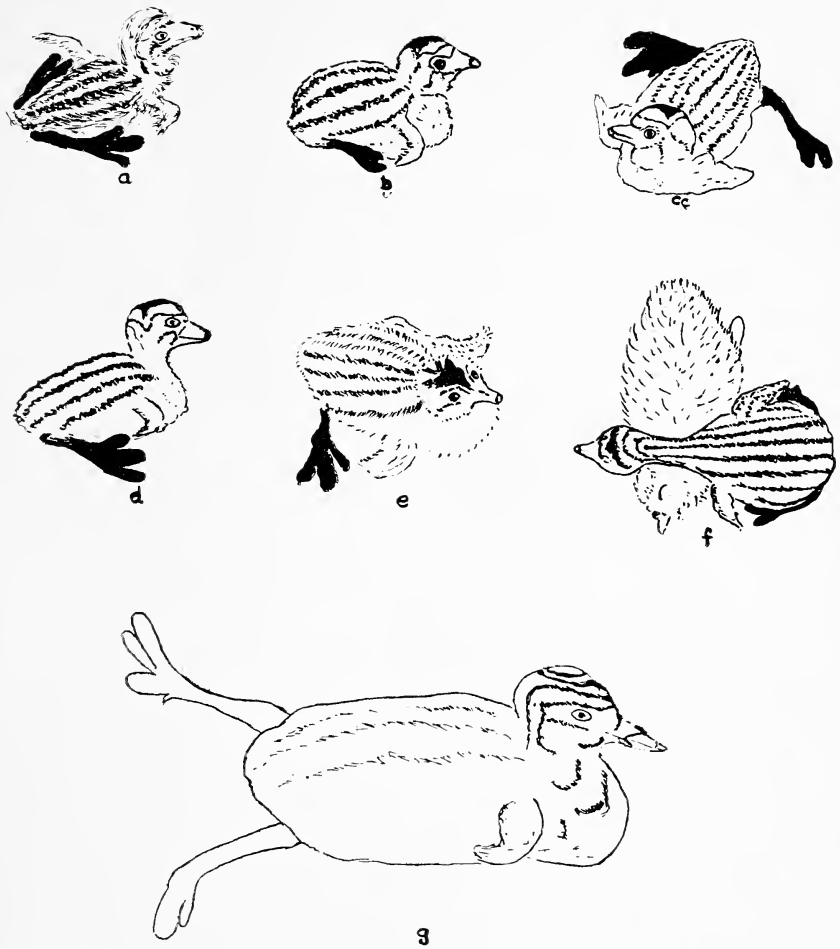

Figure 7. PIED-BILLED and RED-NECKED GREBES. *a*, Pied-billed Grebe, just hatched; *b-e*, a few hours; *f*, 40 minutes, draped over Coot. *g*, Red-necked Grebe, followed canoe; weighed 86.4 grams.

main endeavor was to climb on the top of the other little birds and drape their necks over the necks and backs of their companions.

They showed one coordination which had not been seen in the precocial chicks which feed themselves, namely, a random "snapping" directed upwards. This seems to be analogous to "gaping" in altricial hatchlings, but was of shorter duration. It was shown in Stage II by all the species in the Precocial 4 group, and by the semi-precocials and semi-altricials.

The young grebes progressed by crawling and by little jumps. Baby Pied-bills stood up on their legs and went through a little dance while backing a few inches before defecating. Such behavior must serve as a signal to the parent to lift its wings and let the chick drop into the water so as to prevent soiling of the plumage. An adult Horned Grebe while resting on a platform in a bathtub backed a few steps before defecating (Woolfenden, 1956).

Grebes, with their specialized mode of life, are somewhat aberrant precocials. The chief skill they need at hatching is to be able to climb up on the parental back into the warm, dry, feathery nursery. Fear does not seem to develop early. Young of all four species that nested at Delta at one time or another followed canoes; these chicks ranged from newly hatched to perhaps two weeks of age. Such behavior illustrates their strong instinctual urge to follow a moving object; in the absence of their parents they accepted a substitute. It also shows their great need for a haven from the cold water.

On June 30, 1953, an Eared Grebe was brought in. Judging from her weight of 19.6 grams, she might have been four to five days old. She stood up, waved her wings, stretched a leg out, preened and scratched her face. Her note was harsh and often repeated. On July 6 she preened energetically, rubbing her face on the oil gland. She also shook herself. On July 7 she fed herself well. On July 8 she stretched back wings and legs. Two days later we introduced a three-day-old bittern into the same brooder; the grebe attacked it, so they were separated. Afterwards they seemed amicable, but on July 17 the bittern died unexpectedly and we suspected it had been injured by the grebe.

On August 2 we took her to Chicago; she cried almost constantly in her traveling box, averaging 42 notes a minute. On August 15 at the age of seven weeks, and weighing 133 grams, she was taken to the Philadelphia Zoo; three weeks later she died of hepatitis; an autopsy showed her to be a female. It was

a very unnatural life she led with us, out of her proper element and without normal food.

3. Observations on Young Grebes in the Wild

An interesting description of parental and juvenile behavior in the Least Grebe is given by Gross (1949). A nesting pair in Cuba was watched on December 22, 1947, with a brood of young about three weeks old that captured dragonflies by themselves, but were fed crayfish by the parents, snatching them "from the parents' beaks and then from the beaks of successive young." "On December 27 the first young of the next brood hatched; it fell from its mother's back into the water." "Immediately it swam to the rear of its parent and apparently with little effort hopped onto her back and completely disappeared." During the day another young hatched and was carried by its parents. The older young were fed crayfish and vegetable matter, but no food was seen delivered to the newly hatched young. At 4:45 p.m. the mother with the two young on her back settled down on the nest to incubate, the young remaining on her back. The next day the male fed the three small chicks on the mother's back eight times during 30 minutes. This was the procedure for the first three or four days; "after that they were fed floating on the water," a procedure which would come later in the cold water of northern latitudes.

Rockwell (1910) describes how parent Eared and Pied-billed Grebes "would swim close alongside the young bird and by raising the fore part of the body out of the water would submerge the posterior portion, upon which the youngsters would scramble with alacrity. The wings of the parent were then raised something after the fashion of a brooding hen, and often several babies would be cuddled comfortably beneath them."

Western Grebe parents occasionally pick up food from the surface of the water and reaching back feed the babies on their backs (Finley, 1907). Deusing (1939) watched a Pied-billed Grebe with a baby under its wing. "The old grebe sank out of sight, but within a few seconds rose to the surface again with its back covered with the lace-like stems of the bladderwort. The young one pushed its head out of the back, and then the old grebe, turning its head backward, began to pick small insects out of the mass of bladderwort and feed them to the young."

Black-necked (Eared) Grebe chicks were noted by Van Ijzendoorn (1944) as rushing away with food immediately after receiving it from

the parent; he calls it "instinctive flight," as he "often saw it take place when there was no danger at all that the food would be taken by some enemy." Great Crested Grebes from a month onward according to Simmons (1955a:308) may adopt an "appeasing" attitude when approaching the parent for food; "the body is mainly submerged with the head and neck sticking sharply out of the water, bill open showing the red interior; and legs kicking out laterally to make a very noticeable disturbance on the surface," the chick meanwhile "peeping vociferously. It may snatch food very quickly from the adult, turning away to make off at almost the same instance." At this period the parents sometimes show aggressive behavior towards the young.

Young Black-necked Grebes in Holland dive for food at two weeks, and at about three weeks are "fully independent" (Van Ijzendoorn). Little Grebes, on the contrary, are still violently begging for food when three-quarters grown; they still mob their parents when the latter are incubating the second clutch. They rush at the parent as it comes from the nest, whereupon it starts fishing energetically (Konrad Lorenz, personal communication).

4. Notes on Loon Chicks

Newly hatched loons are covered with much thicker down than are grebes. Of two Common Loon chicks hatched in captivity Beebe (1907) writes: "In appearance the down is remarkably like the fur of a beaver or otter, when wet as when dry." From the first the birds took fish direct from the forceps. At two days one dove at a sudden movement of the observer's hand overhead, but would follow the slow movements of a hand all around the tank. At two and four days, although sleeping side by side, when awakened they attacked each other "like game cocks, rolling over and over in a frenzy of pecking," so they had to be separated when not under observation. At three days they bathed, and at seven days they caught fish for themselves. Although indifferent to most loud calls from the Bird House in the New York Zoological Park, they became greatly excited whenever they heard the loud, rolling cry of a Kookaboora; they tried to stand upright and piped their loudest. They also responded to an imitation of the loon's call.

B. Rails

The family Rallidae must be very old according to the Heinroths (1924-33, III) for it is widespread throughout the world, including islands. Rails possess great mobility of the spinal column, which in most birds is rigid; thus they are enabled to thread their way through dense reeds. They are noisy, since it is difficult for them to see each other in the thick marshy vegetation which most prefer.

We were able at Delta to study three species of rails of three genera: five Virginia Rails during one season, 11 Soras during three seasons, and 23 Coots during four seasons. Observations were also made for an hour, September 20, 1954, on five hand-raised King Rails, *Rallus elegans*, at the Trailside Museum in River Forest, Illinois.

In reiterated erroneous statements as to length of incubation, the Sora and American Coot have fared badly (Nice, 1954a:183). In the former it seems to be at least 19 days; in the latter probably at least 21.

In 1915 both were stated to hatch their eggs in 14 days. This figure was quoted for the Sora up to 1949; the correct period of 19 days for five nests and 20 days for one nest was given me by Ward D. Tanner who made a special study of this species in Iowa. As to the Coot, the 14-day period was quoted up to 1931, although Heinroth in 1922 had pointed out its absurdity. But two authors (in 1925 and 1949) favored 27 days. Gullion (1954: 384) found in four nests in the San Francisco Bay that incubation lasted about 23 days, but he cites records in the warmer summer climate of Iowa as 21 days. As to the Virginia Rail, Gentry (1882) gave it a period of 15 days, but no one seems to have copied him. Walkinshaw (1937: 468) established in two nests that the period was 20 days.

Strangely enough, Pospichal and Marshall (1954: 15) in their otherwise admirable report on the Sora and Virginia Rail state that incubation "from the laying of the last egg of the clutch to hatching of the last egg of the clutch" lasted from 11 to 22 days with the Sora and 13 to 20 days with the Virginia Rail. It is a biological impossibility for a precocial rail to develop in 11 or 13 days. An incubation period as short as 11 days is exceptional even for an altricial bird.

A'. Virginia Rails

Our five Virginia Rails, *Rallus limicola*, were hatched July 1 and 2, 1954. Three of these we watched hatch, keeping them under continuous observation for three to four hours. We released them at the age of 38 and 39 days on the day we left Delta. The Virginias were raised with a group of Soras averaging four days older than they were. They did not thrive as well as the latter; that their growth was somewhat retarded is evident in their bill lengths at 10 days and two and three weeks in comparison with wild birds (Pospichal and Marshall, 1954:23).

1. Development of Behavior in Virginia Rails

The development of motor coordinations in the Virginia Rails is shown in Table 13.

TABLE 13

DEVELOPMENT OF BEHAVIOR IN VIRGINIA RAILS

Five individuals (three watched from hatching)

m = minutes, h = hours, d = days

Stage	*Coordination*	*Age at first appearance*
II	Yawning	2m, 1h22m
	Snapping	1h2m, 1h40m
	Preening	1h34m, 2h30m, 3h47m
	Eating	1h42m, 2h15m
	Scratching head	4h4m
III	Crouching	3h34m
IV	Strong on feet	11h
	Bathing	1d13h, 1d19h, 2d
	Play-fleeing	5d, 5d, 6d
	Preening on haunches	6d, 6d, 6d, 7d
	Begging	10d, 10d, 10d, 11d, 11d
	Stretching wings up	11d, 14d
	Stretching wings back	14d
	Probing	14d, 16d
	Bill in scapulars	15d
	Standing on one foot	15d, 16d, 17d
	Social preening	15d, 16d
V	Aggression	16d, 19d, 20d, 22d
	Stretching sidewise	16d
	Stretching both wings and one leg back	16d
	Thrashing	18d, 19d
	Hopping on one foot	22d
	Nest building	23d
	Washing food	28d, 28d
	Sunning	30d, 35d
	Play fighting	31d, 31d

2. Stage II—Preliminary

Yawning, snapping, preening, eating and, in one instance, scratching the head were all seen while the baby rails were drying.

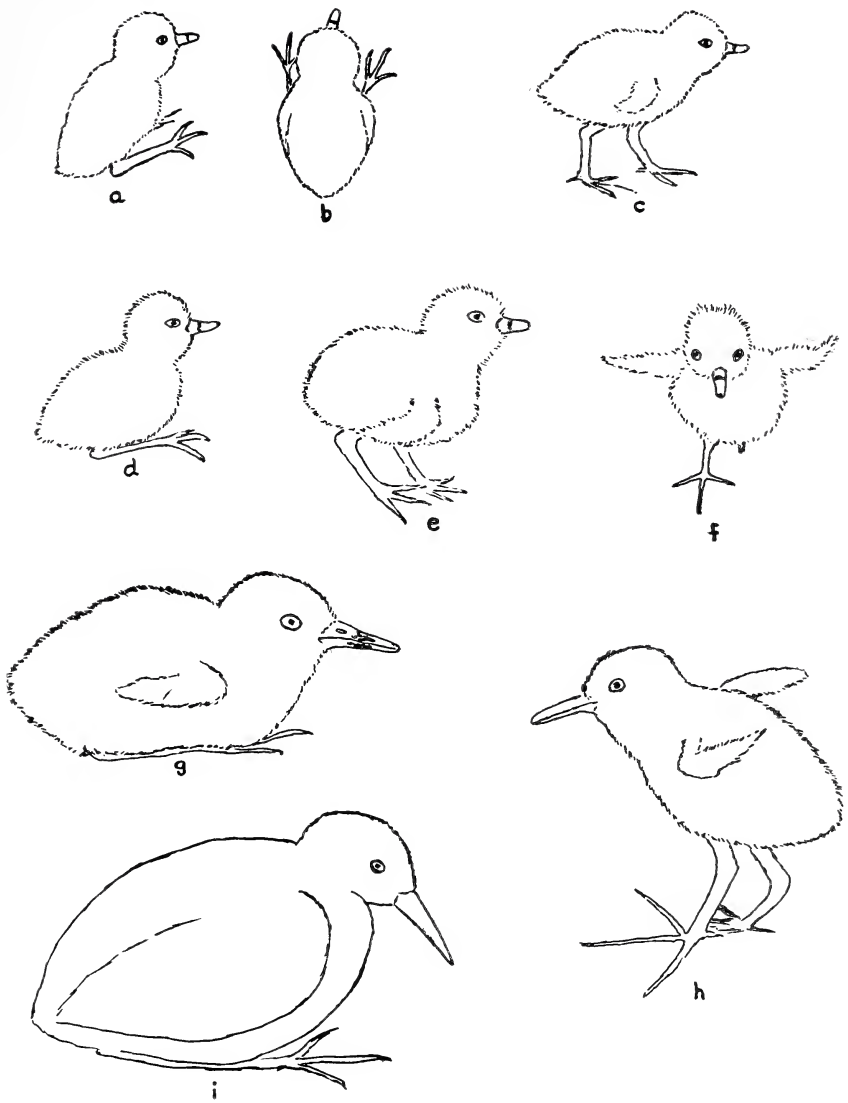

Figure 8. VIRGINIA RAIL. *a,b*, first day. *c,d*, 2 days. *e,f*, 3-4 days. *g-i*, V3: *g*, 15 days, *h*, 15 days, begging; *i*, 31 days.

3. Stage III—Transition

The sound of tearing paper induced a sudden response in the little rails; they rushed about as if seeking a place of safety. This was first seen at the age of 3 hours 34 minutes. That chicks in nature can swim as soon as dry is evident from Walkinshaw's (1937:470) experience: "As one approaches the nest during hatching time, the young leave soon after the adult flushes, clambering over the edge and either swimming away with jerky strokes through the neighboring rushes or hiding in some clump in the vicinity of the nest."

4. Stage IV—Locomotory

The Virginias walked well at about 11 hours; they were stronger on their feet at first than the Soras. At the age of two and three days they snatched continually at the Soras' bills. At this time the Soras weighed about twice as much as the Virginias. The two-day V3 was noted closely attending the largest Sora, aged seven days, watching it intently and snatching at its bill whenever it seemed to get something. When two and three days old they chased after a small stick that Peter Ward's little daughter was jabbing into the ground; possibly it resembled the long bill of a probing parent.

At this age they were more enterprising than the Soras, climbing into our laps, and dashing hither and yon out of doors. We put two of them into a box with the little Spotted Sandpiper, but they called back and forth to their fellows in the nearby brooder, jumping and jumping until we returned them. They took their first baths at the amazingly early age of 37 and 43 hours, becoming very wet during the process. Noll's (1924) Water Rails bathed "from the first day on." At five and six days the Virginias dashed about making sharp turns. Play-fleeing was not often seen; it was last recorded at the age of 37 days.

Begging behavior was not pronounced. At 10 days they would come running to meet us with outspread wings, then slightly flex their legs and gently flip their wings. This behavior was mainly directed to us, but was occasionally seen directed towards a brother or a Sora.

Probing probably appears early, but no mud was available to the birds until they were 22 days old at which time they at once probed. At the ages of 14 and 16 days, however, two of the Virginias had vigorously pounded on our fingers. At 15 days they started to preen

our hands and arms. Preening of other birds was first seen at 16 days when V3 gently nibbled the 10-hour-old Killdeer beside it. V5 at 20 days preened a baby Ruddy Duck. This activity became more pronounced as time went on, being especially noticeable late in the afternoon. Some preening was directed towards the Soras, but most of it was carried out on other Virginias.

5. Stage V—Socialization

The first sign of aggression with the Virginia Rails was seen at 16 days when V3 chased and pecked the 14-day Spotted Sandpiper; this bird had been raised with the rails but on this occasion was making itself conspicuous by new behavior—flapping its wings and rising some two feet into the air. From 19 days on they pecked strange birds that were introduced—the Killdeer, baby Spotted Sandpipers, a Purple Martin and a little Coot. No pecking of other Virginias or the Soras was ever noted, but at the age of 31 days V3 and V4 were seen play-fighting; they dashed about and sparred, clashing their bills.

When 28 days old two of the birds took large pieces of custard and dropped them into the water dish. Afterwards one picked up the bigger piece and ran away with it. Probing for clams and rinsing prey is described and photographed in Clapper Rails by Williams (1929).

Washing of food has been recorded in a number of species—shorebirds, gulls and terns, and herons, as mentioned in Chapter VI under the Spotted Sandpiper.

At 23 days V3 was seen nest building; as it sat in a tuft of grass it pulled grass heads down on its back.

A close bond to us, their foster-parents, continued as long as we kept them; whenever we sat on the ground in their pen some of them would climb into our laps. They enjoyed being stroked.

There was a strong bond between the brothers and sisters. When all the rails were about a month old they were allowed to sleep out in a cardboard box in their pen; on three nights we noted that the Virginias retired before the Soras. On the clear evening of July 31 the former were all in the box at 8:15, while all the Soras were still out at 8:26, and one was wandering around as late as 8:37.

Other coordinations will be discussed in the section on comparisons between the rails.

B'. Soras

Of our 11 Soras, *Porzana carolina,* we saw five hatch, watching them from one to three hours thereafter. In 1952 S1 died at the age of four days because of inadequate diet. Our other Soras, however, throve. In 1953 S2 died through an accident at the age of 20 days; S3 was killed at 12 days because he was hopelessly crippled in his legs; S4 we gave to the Philadelphia Zoo at the age of five weeks. In 1954 we raised four individuals to flight at five weeks, keeping track of them for another week, after which we left Delta. All these birds remained tame and confiding, except for S4 who became rather shy at the age of 24 days. S2 was raised with five Coots two to five days younger than he. S4 was raised with a Spotted Sandpiper his own age and a Coot a day younger. In 1954 the Soras were raised with five Virginias about four days younger than they. Weight of the Soras at hatching ranged from 4.8 to 6.8 grams, of the Spotted Sandpipers from 4.8 to 6.5 grams and of the Coots from 16 to 21 grams.

1. Example of Post-hatching Behavior

The Soras were very precocious. The high points in the first hour of S5 June 26, 1954 were as follows:

0—Hatches in my hand at 10:12 p.m. *Seep, seep.* Preening movements under breast. *Seep.* Lifts up head. Very alert.
7m—13 notes in minute. Opens bill and snaps.
9m—I kill a mosquito and offer it. Snaps and snaps and snaps and *eats it!!*
21m—Cuddled in my hand. Shuts its eyes.
26 and 28m—Tries to preen.
40m—Got second mosquito after many lunges at it. A few gentle peeps.
43m—Put it in a grass "nest" in a bowl. Yeeps loudly. Pecks at grass.
53m—Preened at neck.
58m—Yawned.

At 6:30 a.m. the next day I gave it bits of mealworm. It worked the insect from crosswise to lengthwise and swallowed expertly.

2. Baby Soras and the Bittern

For their first days—from June 27 to July 1—the Sora family had a young bittern as "nursemaid." It was five days old at the start, weighing 25 grams, four times as much as the newly hatched Soras. The Soras cuddled against and under the bittern and also continually begged from it.

At 6:40 a.m. on June 28, "S6 (19 hrs. old) buffets B in his determination to nestle under 'her.' Pushes with his head, burrows, presses back against her on his legs. B is very patient. Finally nips him. *See-See-See*—a loud cry of distress.
6:45 a.m. Back comes S6 and cuddles under her.
2:00 p.m. Put B in; three Soras crowd under her. S6 and S7 pecking at her bill; cuddle under her neck.
5:00 p.m. Put in a six-day-old snowshoe hare; babies cuddle against him. Later S7 is cuddling up to bunny who is busily licking him. S7 suddenly jumps away.
June 29, 7:00 a.m. The Soras peck and peck at bittern's bill. S6 pecks 12 times; stops, then 10 times. Then begs vigorously to bittern.
11:05 a.m. S7 begging to bittern's bill. Begs to a Ruddy duckling who rushes away.
4:45 p.m. All beg from B as she sits up tall.
June 30 All four Soras struggle desperately to be brooded by bittern."

3. Development of Behavior in Soras

The first appearance of motor coordinations is shown in Table 14.

4. Stage II—Preliminary

The early appearance of 'snapping' or lunging *in vacuo* is striking, as is the early appearance of eating. These are correlated with receiving food from the parents in contrast to the ducklings, shorebirds and chickens, which feed themselves.

5. Stage III—Transition

a. *Begging.* Begging was much more pronounced with Soras than with the Virginias.

The little Sora lies down, elongates its neck and waves its head and wings, sometimes together, sometimes alternately. First intimations were seen at 8½ hours with S5 just after I had rescued it from the bittern's bill. S6 and S7 showed this behavior in rudimentary form at about 20 hours. At two days it was well established with the 1954 group, directed primarily to their "nursemaid," the week-old, 29 gram, bittern. At this age S6 begged to a Ruddy duckling. From the age of three to 22 days they begged to our hands. S2 still begged to us at 19 days, S4 occasionally from four to 15 days.

S4 at 14 days begged to a newly introduced Blue-winged Teal, then attacked it. He never begged to his Spotty companion, and only twice to his Coot "nursemaid"—at 15 days when suddenly confronted by her after an absence, and momentarily at 18 days.

Some Soras begged much more than others. S6 was our most enthusiastic example in this regard. He was the most determined

TABLE 14

DEVELOPMENT OF BEHAVIOR IN SORAS

Eleven individuals (five watched from hatching)

m = minutes, h = hours, d = days

Stage	*Coordination*	*Age at first appearance*
II	Yawning	1m, 3m, 48m, 58m
	Snapping	6m, 7m, 7m, 12m, 15m
	Exploratory pecking	38m, 43m
	Preening	28m, 41m, 45m
	Stretching leg back	51m, 3h
	Walking on tarsi	44m, 57m, 60m
	Stretching wings back	51m
	Scratching head	3h
	Eating	9m, 17m, 1h, 1h20m
III	Begging	8h30m, 18h, 20h
	Shaking self	8h30m
	Crouching	9h, 18h
	Stretching wings forward	11h46m
IV	Walking on feet	18h, 19h, 21h, 24h
	Picking up food	1d3h, 1d4h, 1d11h, 1d16h
	Pursuing insect	24h
	Catching prey	1d8h, 1d8h, 1d21h, 3d
	Play-fleeing	1d8h, 1d17h, 3d, 4d
	Preening on haunches	1d21h, 4d, 5d, 6d
	Bathing	6d, 7d, 8d
	Stretching both wing and leg back	6d, 16d, 19d, 25d
	Stretching sidewise	9d, 19d, 26d
	Bill in scapulars	12d
V	Aggression	14d, 19d, 20d, 25d
	Social preening	17d, 17d, 17d
	Nest molding	17d, 27d
	Play-fighting	18d, 19d, 20d, 20d, 32d
	Stretching wings up	19d, 20d
	Thrashing in bath	19d, 26d, 28d, 29d
	Scooting	19d, 20d, 31d, 32d
	Standing on one foot	20d, 20d, 20d, 21d
	Hopping on one foot	20d, 31d, 32d
	Nest building	21d
	Sunning	23d, 29d, 30d, 32d
	Attempting copulation	28d, 33d
	Flying	35d, 36d, 36d, 36d

suppliant to the bittern. At two days he begged at a glass jar. At seven days he begged to the newly hatched Spotted Sandpiper, and repeated this behavior on the two following days. On the first two occasions Spotty 2 was lying down, on the last she was standing. At 12 days he was put in with a group of Ruddy ducklings 12 hours old. He went into the most extreme begging posture I ever saw, elongating himself and pecking gently at their bills.

This begging gradually developed into what seemed to be a greeting ceremony. After we released the Soras on August 3, S7 and S8 came to us flexing their legs, flicking their wings and giving series of contact notes.

6. Stage IV—Locomotory

Play-fleeing appeared very early—on the second, fourth and fifth days. It was seen occasionally until 33 days with the 1954 birds and at 45 days with S4 at the Philadelphia Zoo. Bathing was not seen before six days, but in a more natural environment would probably have appeared earlier. The Heinroths' (1924-33, IV:63) Little Crake, *Porzana parva,* bathed at two days.

7. Stage V—Socialization

Of the five Soras that we kept till fledging, S4, S6, S7 and S8 with wing measurements of 93 mm. at five weeks and weights from 75 to 77 grams appeared to be males, while S9 with a wing measurement of 90 mm. and weight of 68 grams at the same age we judged to be a female.

a. *Aggression.* Aggression towards other species was first seen at 14 days.

S4 was standing on top of a jar; Spotty 1 hopped up beside him; he gave her little pecks. At this time he weighed 36 grams, Spotty 1 weighed 27 grams and the Coot 95 grams. A baby Blue-winged Teal weighing 24 grams was introduced; S4 begged to it, then pecked it. At 18 days he pecked a fledgling House Sparrow. He never pecked his Coot companion, but he continued to chase and peck Spotty to some extent, especially when she looked bedraggled after a bath. When he and Spotty 1 were 25 days old and weighed 69 and 34 grams respectively, she pecked back, and this situation lasted until they were taken to the Philadelphia Zoo at the age of 34 days. Their sparrings consisted of pecking the ends of each other's bills. At the Zoo he was at first afraid of the Ruffs, but when 65 days old he was pecking them. He then weighed 92 grams; male Ruffs weigh about 200 grams (Niethammer, 1942:182). He was chased by two larger species—Black Oystercatcher and Lapwing. (See p. 163 for his behavior two years later with Ruffs and Spotty 1.)

Figure 9. SORA. a-d, S1: a, 3½ hours; b, 21 hours; c, 2 days, pressing against my hand; d, 2 days. e-i, S2: e, 2 days; f,g, begging; h,i, 4 days. j, S4, 9 days. k, Soras, 1 and 2 days, with 5-day American Bittern. l, S2: 18 days, begging; m, 18 days.

With the Soras in 1954 aggression was first noted in respect to Spotty 2 raised with them; at the age of 19, 20 and 21 days S8 and S6 chased the 14- to 16-day sandpiper that was acting strangely by jumping up, flapping its wings and making its first flights. S9 at 22 days pecked at a three-day Spotted Sandpiper. At four weeks several Soras rushed at a young Purple Martin that landed in their pen. At 20 days the oldest Sora, S6, started to peck the other Soras and Virginias in the evening in the brooder, so we put him elsewhere for the night. The only other pecking between the Soras that we noted came six days later: S6 was hard to catch that evening; when he was added to the flock in the brooder he received a peck from the 25-day-old S7.

When the Soras were 18 and 19 days old their outdoor pen was much enlarged. This had a stimulating effect on the birds; they began play-fleeing, chased Spotty 2, and started to play-fight. S7 and S9 ran at each other; stopped suddenly as if threatening each other like young cockerels, then separated. At 33 and 34 days S7 and S8 were sparring and threatening each other while standing in the wash basin.

b. *Bathing.* Thrashing was first noted July 17 with S8, then 19 days old. The same day he and S6 were seen trying to get under each other in the bath. On July 26, S9 was bathing by merely dipping; S7 gave her a peck and she left, but returned and continued the dipping. S7 then slipped under S9—diving behavior which I called "scooting." Then they threatened each other momentarily. On July 29 I described it thus: "Soras slink in bath; in crouched position with bill on bottom of pan run around the pan." On July 30 I described S9 as performing "under-water swimming around and around and around in wash basin." July 31, S7 was "scooting and scooting about in wash basin; later starts to bathe." This "scooting" would seem to correspond to the diving in connection with bathing exhibited by ducks.

c. *Social preening.* This was seen from 17 days on. The Soras in 1954 nibbled our fingers and our arms and each other's plumage. S4 at 17 days performed a kind of egg rolling movement with the ends of my fingers. From 29 to 31 days he was noted preening the Eared Grebe's head. (When Spotty 1 and S4 were taken to Chicago at the age of three weeks, their Coot companion was left behind and a six-week-old Eared Grebe substituted.)

d. *Premature breeding behavior.* This was shown chiefly by S8. On July 15, at the age of 17 days he "scrabbled," as if nest molding, on the back of my hand, which was resting on the ground. This hap-

pened nearly every day for the next 11 days, usually in my lap. On July 17 I noted him scrabbling on my notebook and on my hand; "pushes hard with breast and legs, a vibrating movement. It seemed a *body* movement, not really scratching with legs." I described it in the same way on July 18 when he scrabbled twice in my lap. On the 21st he scrabbled against my back as I sat on the ground, pushing back with both feet at once. S6 was noted scrabbling at the age of 27 days. The only signs of nest building were seen in S8; at 21 days he picked up and carried pieces of dead grass, then dropped them. This occurred five times. One piece was carried 18 inches. Two days later he picked up a dead leaf, carried it toward me, then dropped it. He lay in my lap working on the buttons of my jeans. He then brought a piece of phragmites and dropped it on me. Soon he got a piece of dead grass, carried it a foot and dropped it.

S4 at the age of 33 days was seen "pecking and pulling at Eared Grebe's back and sides and head as if trying to get nest material out of this fluffy mass! Now preens her head. Now cuddling beside her in the sun. *Now on top of grebe, holding her by feathers on top of head, trying to copulate with her*—Grebe complaining." Later he started to climb on her back, pecking her on the head. The grebe at this time weighed 133 grams, and S4 75 grams. The next day they traveled to Philadelphia where they were put in different cages in the Zoo.

e. *Flight.* The Soras were more crepuscular than their companions, the Virginia Rails. When 32 to 33 days old they started getting out of their pen, perhaps by climbing up on the weeds. S6 at 36 days flew over the five-foot fence of the gull yard in which their pen was located. The next day, August 3, we released the four Soras just north of the hatchery. We put out food for them and saw S7, S8 and S9 each day until we left on August 8th. On August 4 and 6 I was able to pick up S7 and S8 and take them to the laboratory for weighing.

C'. Coots

Of our 23 American Coots, *Fulica americana,* we watched 11 individuals from hatching for one to 12 hours. In 1951 we had five Coots; two of these, C3 and C4, we took to Chicago at the age of five and four days and raised them with two Franklin's Gulls until the age of 5½ weeks when we gave them to the Brookfield Zoo (Nice, C., 1956). Here they lived for one and two years until their deaths from

Figure 10. Baby AMERICAN COOTS. *a*, C7, newly hatched. *b*, C4, 15 minutes. *c*, C17, 1 hour. *d*, C10, 2 hours. *e,f,g*, C1, 1½ days, begging. *h,i*, C4, 10 days.

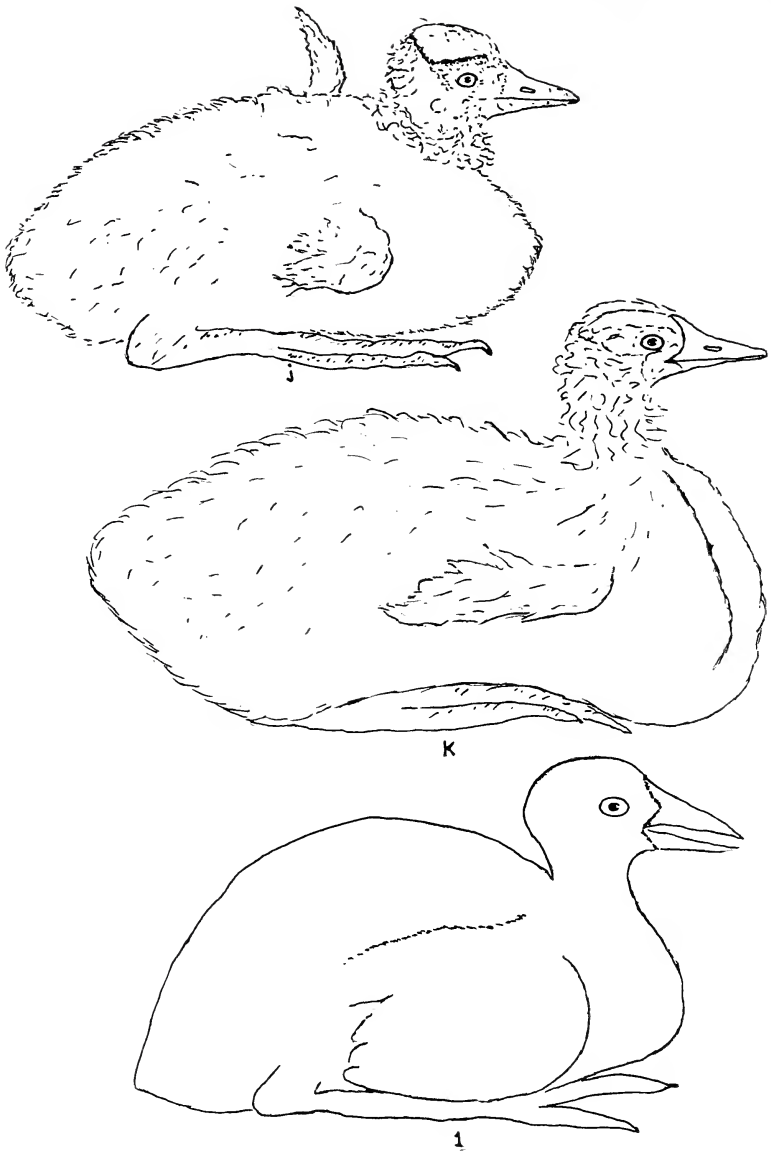

Figure 11. Older AMERICAN COOTS. *j*, C4, 23 days. *k*, C3, 26 days. *l*, C3, 38 days.

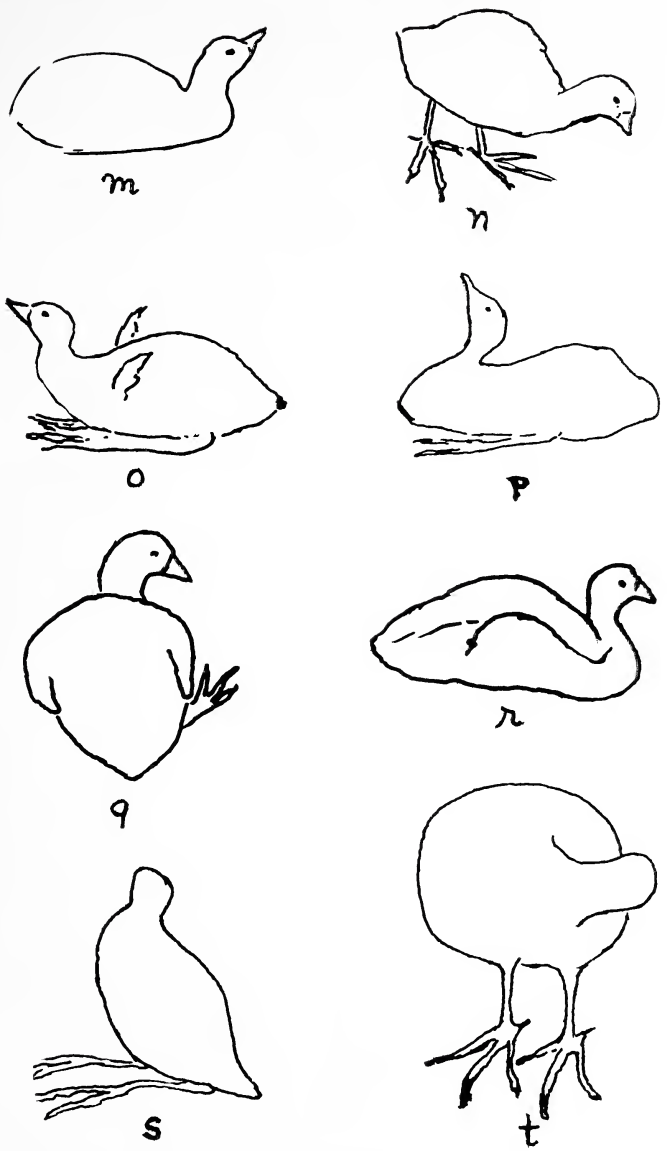

Figure 12. AMERICAN COOTS 2 to 7½ weeks. C3 and C4. *m*, 2 weeks, begging. *n*, 3 weeks. *o,p*, 3 weeks, begging. *q,r*, 5 weeks. *s,t*, 7½ weeks.

aspergillosis. Both proved to be females. In 1952, six Coots were watched for three weeks. In 1953 Coots 12 to 17 were cared for by us to the age of three weeks; later they were kept over winter in the hatchery. The next season C15 mated with her brother C17 and made three unsuccessful attempts at nesting. Two other brothers, C12 and C13, formed a homosexual pair, trying to nest on a platform in "Exhibition Pond." The following winter they migrated; C12 returned and nested two miles south of the Station. C18 was reared in 1953 with Spotty 1 and Sora 4, but was left at the hatchery at the age of three weeks. The final year we had no Coots until the end of our stay at Delta; then we obtained excellent observations on the first five to 10 days with Coots 19 to 23, keeping them during the day with the Killdeer and Spotties 3, 4, and 5, in a marshy outdoor pen.

Coots were a little less precocious than the Virginia Rails and Soras. They weighed at hatching about three times as much as these other rails; they were always fat, heavy birds, comparatively clumsy on land.

1. Examples of Post-hatching Behavior

Two examples will be given of behavior for the first two and four hours after hatching.

C15, a female, hatched June 24, 1953. (C12 two days old, C14 three hours old.)
–1m—Head out, body half out. *Quonk. Yawns.*
0—Entirely out. *Wheep, wheep.*
9m—Yawns again.
10m—Lifts head.
13m—Struggles about a bit.
18m—*Snaps* spontaneously. Yawns.
32m—Snaps at forceps holding egg. Struggles around to get to brothers.
33m—*Eats* custard. Tries to eat more.
1h—"Robin" call for first time.
1h20m—Yawns. Pecks at newsprint.
1h25m—*Preens,* one try at its neck. Now asleep.
1h55m—Stands up tall and snaps.
2h2m—Pecks at Sora's down and at C12's wing. Getting dry.
2h6m—Preens behind.
2h15m—Eats a small snail we offer. Pecks at Sora's yellowish bill tip.
2h20m—C15 and C14 pecking at each other's red bills.
2h37m—Pecks at yellow mouth of fledgling House Sparrow. Fluffing out.
2h43m—Preens breast. Yawns.
3h—Preens left shoulder four times. Dried out.
3h1m—Eats mashed potato. Gives a little jump.
3h25m—*Picks up food* from floor. Preens under left breast, pecks foot. Preens again.

3h27m—Yawns. Naps.
3h30m—Stands on feet a moment; wobbly. Yawns. Walks a bit on tarsi.
4h—All birds resting.

C21: July 31, 1954. (C19 two days old, C20 about two hours old).
0—Hatches. Lies on belly; calls with loud notes. Cuddles with C19 and C20.
18m—No reaction to scraping of chair.
21m—*Sits up on tarsi.*
27m—Struggles about.
37m—*Scratches head.*
40m—Does it again.
46m—*Snaps.*
58m—Turns to preen. No response to scraping of chair.
1h2m—*Preens on breast.*
1h5m—*Walks on tarsi* to Coot 19—directed locomotion.
1h13m—Offer him custard; snaps at it, but doesn't eat it.
1h25m—At loud scrapings C20 and C21 try to get away, but C19 indifferent.
1h32m—Scratches head vigorously. Preens.
1h55m—*Shakes self.* All are in a huddle now.
2h3m—Eats a bit of mealworm. He and C20 peck at each other's bills. C20 gets hold of a bit of C21's fuzz on the crown and pulls.

2. Development of Behavior in Coots

The first appearance of motor coordinations is summarized in Table 15.

3. Stage II—Preliminary

The earliest coordinations, as shown in the examples of C15 and C21, do not differ particularly from those exhibited by Soras except that they did not appear quite so early. They yawned, snapped, pecked, etc., preened, and scratched their heads.

4. Stage III—Transition

The best description of the behavior of baby Coots in nature is given by Gullion (1954:389):

"By the time the young coot is six hours old it has dried out. . . . It is quite buoyant and can climb in and out of the nest and swim to cover once it is on the water. However, in undisturbed nests, it is probable that young coots do not leave the shelter of the incubating parent for many hours after hatching, perhaps even for a day or two. When nests are disturbed every young goes over the side, except those that are less than 15 to 20 minutes old. Those young that go out of the nest before they are dry and fluffy generally drown."

TABLE 15

DEVELOPMENT OF BEHAVIOR IN COOTS

Twenty-three individuals (eleven watched from hatching)

m = minutes, h = hours, d = days

Coordination	*Number showing coordination*	*Age at first appearance*	
		Range	*Median*
Stage II			
Yawning	10	−1m-40m	3.5m
Snapping	5	20m-56m	35m
Pecking	5	26m-2h	1h1m
Preening	7	1h1m-3h3m	1h16m
Scratching head	5	20m-4h	1h12m
Eating	7	25m-2h30m	2h3m
Stage III			
Shaking selves	4	2h-18h	6h45m
Begging	4	4h-17h	6h30m
Stage IV			"Typical"
Strong on feet		20h-1d	1d
Stretching leg back	7	19h-4d	1d
Picking up food	6	3h25m-2d	2d
Catching insects	3	16h-3d	2d
Stretching wings back	3	2d, 12d, 30d	
Stretching wings up	2	2d, 25d	
Fanning wings	7	1d-4d	2d
Bathing	7	3d-5d	4d
Stage V			
Aggression	11	1d17h-7d	5d
Diving			6d*
Social preening	1		10d
Thrashing in bath	1		25d
Tipping up			28d*
Nest building	1		30d
Stretching wing and leg sidewise	1		45d
Standing on one foot	1		45d
Beginning to fly	1	88d	75d*

* Gullion, 1954.

The female usually seeks food for the first young while the male continues to incubate. "If the nest is disturbed during the hatching period, the female takes the older members of the brood away from the nest to safety while the male stays to defend the nest and the young and eggs remaining in it." In one case "the two- and three-day-old young got off the nest and swam several feet to await the approach of the food-laden hen. After being fed several times they returned to the nest and the protection of the incubating male."

5. Stage IV—Locomotory

At 24 hours our birds were strong on their feet. The first catching of prey was seen at the very early age of 16 hours with C18—amphipods in a bowl of water. At 46 hours C12 caught and ate ants, and at three days C19 picked up insects from the floor of the brooder.

a. *Begging.* Begging was seen with Coots from the age of four hours to 38 days. It was most frequent in 1952 from the age of four to nine days. The postures are even more extreme than with Soras: the little Coot, lying on the ground, extends and withdraws its head, weaving it from side to side, its bill aimed at the bill of the subject; it brings its wings forward and back, sometimes together and sometimes alternately.

For the first few days the Coots were apt to beg from our fingers, but on the whole they begged far more from other birds than from us. The first two years Franklin's Gulls were their favorite objects. In 1951 the gulls were slightly older, in 1952 slightly younger. Some Coots begged hardly at all, others a great deal.

C7 in 1952 was seen to beg to nine different objects: my fingers, gulls, three species of ducklings, a Red-necked Grebe, a brother, an electric light and the end of my pen. C14 in this same brood was never recorded as begging. In 1954 the oldest of the family, C19, was the most persistent beggar. It begged regularly from its shorebird companions—the Killdeer and Spotted Sandpipers. Once it begged to a Least Sandpiper with a broken wing that had been introduced into the pen. Once it begged to a younger brother.

C18, raised in 1953 with Sora 4 and Spotty 1, although devoted to the Sora, never begged from him, but regularly begged from the sandpiper.

C3 and C4, raised in Chicago with gulls about their age, never begged from us, but did beg to the gulls until their separation when the Coots were 37 and 38 days old. In nature young Coots may beg from their parents for a long time—"even as late as 70 days after hatching" (Gullion, 1954: 395).

The begging of our Coots to other birds was never rewarded, except that C3 and C4 occasionally picked food from the edges of the gulls' bills; yet it persisted for days and weeks.

Begging is a strong instinctive coordination in young Coots; under conditions of captivity it had no chance to function normally. The energy became dammed up and was released by new objects, and persisted through habituation.

Our Coots during their first day pecked at the white end of a pencil far more readily than at pencils of other colors. Perhaps this was an innate tendency to respond to the white frontal shield of the adult. There is some evidence that light-colored birds released begging more than dark ones—gulls and shorebirds, for instance, in preference to the Soras. Only once did we see a suggestion of begging to a Sora—C14 at 7½ hours to four-day-old Sora 2. The ducklings were light in color and so was the Killdeer.

6. Stage V—Socialization

Stage V starts earlier with Coots than with the other rails.

a. *Aggression.* Adult Coots are notoriously belligerent and this characteristic is reflected in the chicks which from the age of five days regularly attacked strange chicks of other species. Differences in the first appearance of aggression would seem to be both a matter of individual character and of opportunity.

Some individuals are more pugnacious than others. The two most aggressive individuals were C12 and C13, both males. When they were 45 and 41 hours old we introduced a fledgling House Sparrow; they begged to it, then attacked it fiercely, pecking at its open bill. At three days C12 attacked his companion, the Sora, as well as a newly hatched Redhead. At four days C13 attacked two newly introduced birds—a Pied-billed Grebe and a Ruddy duckling, the latter weighing twice as much as he. Other Coots attacking at four days were C14 and C15 (a female), their victim a newly hatched Pied-bill; C16 attacked the Sora when the latter was returned to the group after a short absence. In 1952 no aggression was noted before the age of five days, in 1951 not before six days. In 1954 no aggression was seen with the family for its first five to 10 days; the only stranger introduced, an adult Least Sandpiper, was met by begging. As for C18, raised with Spotty 1 and Sora 4, the first time "she" met a stranger was at the age of two weeks when a baby Blue-winged Teal of 24 grams was introduced; C18, weighing 95 grams, elongated her neck, then rushed away, followed by the duckling. Four days later she attacked the second stranger, a fledgling House Sparrow.

In 1952 the five- to seven-day Coots attacked the younger Gadwalls for the first two days, then accepted them. Only once did I record a Coot attacking a gull—seven-day C13 pecked a newly hatched Franklin's Gull. That year—1952—we did not rear these two species together. Young Yellow-headed Blackbirds were pecked by these Coots. When they were 12 to 15 days old they started to pester 17-day-old Sora 2 that had been raised with them; at this time he weighed 38 grams, while they weighed 108 to 122 grams. The only friction noted within a family was when C14 at 33 days pecked C15. No disharmony was seen between C3 and C4 before we took them to the Brookfield Zoo when 37 and 38 days old.

As to wild Coots, Gullion (1954:392) says they assume the "fighting position of adults" at six days. He explained in a letter to me that this occurred when he "had them cornered in the cat-tails and picked them up for examination. I don't recall any instances of them making aggressive moves towards other birds at that tender age."

b. *Social preening.* This was seen only once with young Coots: C19 at 10 days was noted preening eight-day-old C21 on its back. The babies appeared to enjoy being preened by ducklings; they stood still with hanging heads. Black Coot parents preen their small chicks (Kornowski, 1957). C3, C4 and C18 liked being stroked by us. Social preening is a part of courtship (Gullion, 1952b:89). We saw this mutual nibbling in the homosexual pair of males, C12 and C13.

c. *Bathing.* Simple bathing—head dipping and simultaneous use of the wings—was seen at three days with Coots 14, 15 and 20. Thrashing has been seen only once by us in our hand-raised Coots—C4 at 25 days.

Coots 3 and 4, which did not have a chance to bathe during their first week, were very slow in developing adequate coordinations in this line. Their companions, the Franklin's Gulls, took baths at seven and nine days, but it was not until 15 and 16 days that the Coots went through bathing motions and these were performed *outside* the water dish.

They continued to do this for the next week, putting their heads into the water dish and shaking them, but using no wing movement. At 24 days C3 took a bath in the grass beside the basin in which a gull was bathing. She bowed her head and breast and moved them from side to side, but no wing movement was apparent. At last, at 25 and 26 days, both Coots took thorough baths in the basin, one of them using both simultaneous and alternate wing movements.

July 20: C4 at 25 days "Taking a wonderful 'bath' outside water basin. Then *climbs in* and *bathes properly!!!* A great deal of dipping of head and breast, and waving of wings, *both together and alternately.* Wags tail in drying self. Returns in three minutes; bathes outside, then in."

Later C3, (26 days) "independently gets into basin and takes her *first real bath*—a great deal of head and breast motion, practically no wing motion. Gets out and finishes on the grass."

Mr. Gullion wrote me (August 14, 1954) that he did not recall having seen any wild Coots bathe. But later (October 7) he wrote that he had seen an adult bathe. "The bird was swimming among a group and proceeded to duck and work the water up over its body with its wings and preen with its bill in the same manner as ducks and other swimming birds."

On November 15, 1954 I saw two adult Coots bathe in the Lincoln Park Zoo in Chicago, one swimming, one standing. "Coot bathing while swimming; many dips, shakes water on back with head; almost no wing movement. Other Coot standing in four inches of water; dips, dips, dips, shakes water over back with head. Works furiously with head, much movement with posterior part of body; a little wing movement. Scratches head. Comes out, waves wings; wags tail; preens oil gland, rubs oil on wings and side, rubs face on oil gland, then on back. There was no thrashing with either bird."

It was not until November 2, 1958, that I saw a wild Coot bathe; it was standing in shallow water and it thrashed with its wings.

Bathing is seldom seen in the European Black Coot. It is not mentioned at all by the Heinroths (1924-33, III). Geyr (1939b) says he does not remember seeing it bathe and this was corroborated by half a dozen other German ornithologists. Ringleben (1939) reported seeing a Coot bathe once while swimming. Scharnke (1939) saw a Coot bathe in shallow water, apparently thrashing. Ruthke (1939b) says they bathe like ducks.

d. *Other coordinations.* At 34 days C3 gave a new note, deep and nasal, an early version of the characteristic *poonk* of the female (Gullion, 1952a). In the wild, Gullion (1954) recorded a "poorly developed adult *poonk*" at 36 days. Nest building was seen once by us; C3 at 30 days was observed putting grass over her shoulder, accumulating quite a little pile.

Neither Coot had been noted standing on one leg up to the age of 38 days when taken to the Zoo on July 31. At our first visit a week later C3 stood on one leg as she preened. Nothing new was seen on our next visit, August 20. The two Coots (C3 and C4) had a strong bond to each other, often lying down side by side. A month later C4 was seen to fly—when 88 days old. Gullion (1954) found wild Coots "beginning to fly" at 75 days.

D′. Comparison of the Three Rails

1. Nestling Plumage

All rails have black or dark brown down. As to the three species studied by us, the Virginia Rail, *Rallus limicola,* was completely covered with glossy black down, its crown only slightly bare, its bill buff

with a black ring near the center. The Sora, *Porzana carolina,* has a more noticeably bare crown, a bunch of orange whiskers and a red protuberance at the base of its bluish bill, which is tipped with yellow. (The value of the black plumage to these little rails was demonstrated to us when we lost a small Virginia Rail outdoors: as we searched through the grass we often snatched at shadows, convinced we were looking at our little bird.) The American Coot, *Fulica americana,* is a fantastic looking creature, its black down tipped all over with orange, its bald red crown very conspicuous, a huge ruff of orange around its neck and its bill crimson, white and black.

Boyd and Alley (1948) believe the head coloration of nestling Rallidae serves "to stimulate the adults to feed the young," as the brightly colored gape and palate of nestling passerines are supposed to do. "Bright head coloring becomes more frequent as we pass from the more primitive (for example *Rallus* and *Porzana*) to the more recently specialized genera" *(Fulica, Porphyrio* and *Gallinula).* They say that in presence of danger very young Black Coots attempt to conceal their heads.

2. Sanitation

All our rails were instinctively toilet trained, never soiling their sleeping quarters but doing their droppings in a particular place. The Coots in 1954 and Sora 4 were very apt to do this in water. The hand-raised King Rails seen in the Trailside Museum used a corner of their cage for this purpose. The Heinroths mention this trait in connection with the Water Rail and the Coot. This behavior would seem to be an instinctive adaptation to the practice of sleeping on a platform.

3. Earliest Coordinations

While drying after hatching, our three species yawned, preened, scratched their heads, snapped *in vacuo,* pecked at objects and progressed on their tarsi. They became strong on their feet at 11 hours (Virginias), 18 to 21 hours (Soras) and 24 hours (Coots).

4. Feeding

All took food from the forceps early—a Sora at nine minutes, a Coot at 25 minutes, a Virginia Rail at 102 minutes. A Coot picked up food at 3½ hours, a Sora at 27 hours.

5. Begging

This behavior was only slightly developed in the Virginias: it was noted from 10 to 20 days, usually directed toward us but occasionally toward a brother or a Sora. Begging was much more pronounced in the Soras, and Noll (1924) records the same thing of his hand-raised Baillon's Crake, *Porzana pusilla,* in comparison with the Water Rail, *Rallus aquaticus.* Our Soras begged from the age of 8½ hours to 22 days, to us, to a young bittern, to Spotted Sandpipers, and twice to ducklings. Begging behavior was most highly developed in the Coots; it was seen directed to a dozen different species and to two inanimate objects. It was first recorded at four hours and last recorded at 38 days, but may persist in nature as late as 70 days.

6. Aggression

Aggression towards strangers was pronounced in the Coots, appearing typically at four and five days but occasionally earlier, even at 41 hours. It was not seen until 14 days in the Soras and 16 in the Virginias. Sherman (1952:136) watched young Soras and Virginias from a blind; they were playful, chasing one another about; "although smaller the Sora beyond doubt was the master bird; it seemed to take delight in dashing at his handsomer cousin and putting him to rout." Hostility towards each other in a brood of nine hand-raised Water Rails was first seen at the age of 34 days (Sigmund, 1958).

7. Contact Notes

All our rails were very vocal, uttering little songs much of the time. With the Virginias and Soras these utterances sounded something like a watch ticking. For the Virginias I recorded: "9 days, 66 in a minute; 11 days, constant song; 14 days, continuous song when stroked in my hands; 22 days, busy little song; 30 days, sings while being weighed; 35 days, V2 and V3 sing in my hand, but V4 is silent." The Soras uttered the "watch" song for the first three weeks; when continuous, from 66 to 108 notes a minute were uttered. As to the Coots, I will give four observations on C18: "Second day, sings almost continuously; 12 days, soft little song, more rapid, more musical, about 60 a minute; 14 days, as I stroked her in my lap 22 *whee-ups* in one minute, 33 *spees* a minute; 15 days, singing *spee spee* in the box." The Coots' songs were the loudest and showed the most variety; the Virginias' and Soras' songs were much alike, the formers' somewhat

louder than the latters'. This continuous song was noted by the Heinroths in their hand-raised Water Rails, Spotted Crakes, Little Crake and Corncrake.

These "songs" evidently serve as contact notes under natural conditions where visibility is restricted. With the Soras the notes became louder when the little birds were hungry or cold.

8. Jump-and-Flap

All our birds occasionally jumped and waved their wings like a young gull. This was first seen at 19 and 20 days with the Soras, 24 and 29 with the Virginias, 26 and 38 with the Coots.

9. Standing on One Foot

The Virginias first stood on one foot at 15, 16 and 17 days, the Soras at 20 and 21 days, a Coot between 38 and 45 days.

10. Wing Movements

All our rails had very flexible wings that were used at first to help them in balancing. All rails have a claw-like appendage at the tip of the manus of the wing; this assists them in climbing about in thick vegetation. This use has been noted in Virginia Rails (Walkinshaw, 1937), Coot (Hendrickson, 1936), Purple Gallinule (Gross and Van Tyne, 1929), Common Gallinule (Miller, 1946).

The primaries started at about three weeks in the Soras and Virginias, and at 30 and 31 days in Coots 3 and 4. Wing-stretching movements were not established until late. Conventional stretching of wings up and a wing and leg sidewise were seldom seen, especially in the Coots. Stretching wings *back* and *down,* either by themselves or accompanied by stretching back of one leg was characteristic of the Virginias and Soras, appearing from 14 to 19 days. It was also seen in the 10-week-old King Rails. In Coots I recorded it only three times at 2, 12 and 30 days. Stretching of both wings down appears as a temporary coordination movement in many altricial birds (see Chapter XI), but the only species besides these rails in which I have found it recorded as a permanent coordination is Bourke's Parakeet (Hampe, 1939).

11. Sunning

Most rails sun in a peculiar way by stretching their wings back, fanning them out and arching them over their backs. This was first

seen in the Soras at 23 days and in the Virginias at 30 days and was noted in the 10-week-old King Rails. The Heinroths' Water Rail first sunned "like all rails" at 10 days. The Common Gallinule (Moorhen) and Corncrake also sun in this manner according to Heinroth, and so does the Black Coot (Kornowski, 1957). We never saw sunning with our Coots. At the Philadelphia Zoo I noted the Gray-necked or Cayenne Wood Rail, *Aramides cajanea,* sunning in typical rail fashion.

12. Social Preening

Social preening was most prominent in the Virginias, being noted from 15 days on. It was frequently indulged in by the Soras from the age of 17 days, but seen only once in young Coots. We saw it performed by the King Rails at Trailside Museum. Heinroth recorded it with the Water Rail and Common Gallinule, Meise (1934) for the Argentine Crake, and Baldwin (1947) for the Laysan Rail. All our birds liked being stroked by us. At Brookfield Zoo I noted a European Spoonbill vigorously preening a Crested Screamer on its back, neck, shoulders and breast, the screamer with closed eyes apparently enjoying the attention. Social preening is practiced by albatrosses, petrels, cormorants, penguins, herons, tree ducks, parrots, Bobwhites, Marbled Wood Quail, Ani, pigeons and some passerines such as Bearded Tit, Bullfinch, some weaver finches, and others. Goodwin (1956:31) suggests that with pigeons "mutual caressing" serves both physical and psychological functions—removal of ectoparasites or other foreign bodies from the mate's head, and sublimation of aggressive impulses between birds that have a definite social bond to each other.

13. Bathing

Simple bathing was seen very early in the Virginias and Coots. Thrashing was first noted at 18 days with the Virginias, 19 with the Soras and 25 with the Coots. With two of the Coots, bathing was long inhibited.

From 19 days on, the Soras dived ("scooted") in connection with bathing. This behavior was not seen in the Virginias before their release when 5½ weeks old. It was, however, noted in a young hand-raised King Rail, so probably is practiced by Virginias. Adult Coots do not often bathe. Diving in this connection does not seem to have been recorded. The Heinroths write that the Common Gallinule at one month dived, especially before bathing. Geyr (1939a) writes that

this species bathes often, occasionally diving, but usually standing more or less deep in water.

14. Escape Reactions

Young of all these species will scramble out of the nest in response to parental warning shortly after hatching. Gullion says that Coots leave "except those that are less than 15 to 20 minutes old" (1954:389). We found Soras at the age of six hours indifferent to the sound of chairs scraping over a cement floor and of wood being broken, but after nine hours they responded by crouching. Coot 22 made an escape movement at the age of four hours in response to scraping noises, while his three brood mates aged two to four days hid.

As to the Black Coot, Nylund (1945) writes: "The new-born young react positively (approaching, biting the finger-nails) to the human being, especially the hand, and exhibit no fear until they are 6 hours old, when the flight instinct ripens and the young are able to follow the parents." Alley and Boyd (1950:49) caught very young chicks that had left the nest in response to parental alarms, carrying them out of ear shot of the adults; the "young behaved towards us without fear, responded to our calls, followed us, and even accepted food from the hand. Apparently in very young birds alarm is a response to an auditory releaser, and does not appear in the absence of such evocation; but the association of this innate reaction with other 'relevant' sense impressions is not long delayed. We found that the period of initial tameness lasted at least eight hours."

Unlike the shorebirds (Charadrii), our rails paid no attention to the shrieking of gulls. Coot 4 when three weeks old rushed to me when a pigeon flew over. She and her sister also sought shelter when they heard the screeching of train brakes near our garden.

15. Bond to Parents

Our Soras and Virginias in 1954 had a close bond to us until we left, when they were about six weeks old. King Rail families may remain together for more than a month (Meanley, 1956:254), Clapper Rail families for five or six weeks (Adams and Quay, 1958).

Our Coots in 1951 were devoted to their "parent-companions," the Franklin's Gulls, until separated from them at the age of 5½ weeks. Gullion found young Coots independent at 30 days, "though still often feeding in company with their parents" (1954:395). Ruthke (1939b)

says Black Coots become independent at eight weeks, when they join other young, but continue to return to the parents.

16. Bond to Brood Mates

This bond lasts longer than that to the parents, as pointed out for Soras and Virginia Rails by Pospichal and Marshall. The Heinroths raised a Black Coot all alone and became very weary of its "continually lamenting" cry (1924-33, III). Gullion (1954) says young American Coots at 30 days "tend to become a closely knit group"; at 40 to 45 days they are "usually in company with one or more brood-mates."

17. Premature Breeding Behavior

Nest-building behavior was seen in all three species raised by us. Nest-molding was frequently practiced by one Sora (S8) from 17 days on, and occasionally by another.

Manipulation of materials was noted in S8 at 21 days, in one Virginia at 23 days and in one Coot at 30 days; also in an Argentine Crake at about eight weeks. A half-grown Common Gallinule helped its parent repair the nest (Hayman, 1955). Sora 4 attempted copulation at 33 days.

In some species of Rallidae, young of the first brood have been recorded as feeding young of the second. It has been noted with the Common Gallinule (Moorhen) in England by Grey (1927) and in America by McIlhenny (1934) and Miller (1946), the latter stating, "Young birds of the first brood feed the young of the second brood," but sometimes they "snatch food from the younger brood without any parental interference." Steinbacher (1939) reports first-brood young as never feeding second-brood young, but often snatching from parental bills food intended for the small chicks. In the Black Coot, Burkill (1933) and Ruthke (1939b) have occasionally seen older young feeding younger ones. With American Coots, Gullion wrote me: "I saw nothing but antagonism of parents against first brood young when the second brood hatched, in our coots. First brood birds never showed any interest in second brood young, even though occasionally second brood young would follow immatures around and beg of them, unsuccessfully."

A pair of Argentine Crakes (of the same genus as our Black Rail) bred in the Dresden Zoo. The eight-week-old chick of the first brood laid mealworms before the newly hatched young; it did this for three

weeks, even though it was itself being fed by the parents. It also shared in the brooding (Meise, 1934).

18. Parental Care

Typically rails are monogamous, both parents caring for the eggs and young. Feeding of the incubating partner has been recorded for Virginia (Walkinshaw), King (Meanley, 1957), and Water Rails (Zimmermann, 1937), and Argentine Crakes (Meise). In Gullion's (1954) table on breeding behavior of the Rallidae the making of brood nests is recorded for nine species of six genera. Building up of the nest during incubation in face of danger of flooding has been noted in several species, as King Rail—as much as a foot (Meanley, 1953), Common Gallinule (Bent, 1926; Miller, 1946), and Water Rail (Hosking *et al.,* 1946).

Three species of *Rallus* have been reported as carrying young in the bill: Virginia (Bent, 1926; Walkinshaw, 1937), Water (Zimmermann), and Clapper Rails; a parent of the latter species was also observed retrieving an egg between its mandibles (Pettingill, 1938). A pair of Water Rails, disturbed by an ornithologist's opening up of their nest for photographic purposes, moved their eggs into a "newly made little nesting hole just behind the nest"; they did this partly by "rolling" the eggs, and partly by carrying them in their bills (Woudstra, 1958). A Common Gallinule that had nested in a thick bush two meters above the water transported in its bill two young, one at a time, from the nest to the water where three chicks and the other parent were swimming (Wolff, 1953).

Incubating Virginia Rails may be fearless in defending their nests. When Walkinshaw extended his hand toward the nest "the parent fairly leaped at it . . . pecking it severely." One bird struck the lens of a camera (Bent, 1926). King Rails at hatching time have struck the observer on the chest or legs (Meanley, 1953).

The subject of parental recognition of young in the Black Coot is discussed in detail by Alley and Boyd (1950). Adults with young less than two weeks old may adopt strange chicks of about the same age, while attacking any conspicuously older or younger; afterward they attack any chick not their own, sometimes killing them (Alley and Boyd, 1947). Of the American Coot, Gullion (1954) describes behavior in broods where there may be a week's difference in the ages of the young; the parents may attack the oldest when they start getting

light in plumage, and after most become light, they may attack the youngest still in natal down. "The parent coots are obviously confused by this change in the appearance of their young, since they frequently will bill an odd-colored young, feed it, and then severely attack it, only to resume feeding it immediately afterwards."

C. Summary

Representatives of precocial chicks that follow their parents and are fed by them for longer or shorter periods are grebes, loons, a few pheasants, some shorebirds, and most cranes and rails.

Grebe chicks have short down; they are weak swimmers and must spend most of their time in their parents' feathers. We watched Eared, Pied-billed and Western Grebes hatch, but were not able to keep them alive for more than a few days. Examples are given of post-hatching behavior in two of these species. Ages at which seven coordinations appeared in eight individuals of the three species are given in Table 12. All the chicks were very active from the first and it proved difficult to distinguish stages of development.

Newly hatched loons have much thicker down than grebes. Two Common Loon chicks attacked each other at two days of age and at one week caught fish for themselves (Beebe, 1907).

Five Virginia Rails were watched, three from hatching; four were kept until they were 5½ weeks old. The ages at which 26 coordinations appeared are shown in Table 13.

We watched 11 Soras, seeing five hatch; four were observed to the age of six weeks. The activities during the first hour of one individual are described. Table 14 shows the ages at which 36 coordinations appeared. Begging behavior is pronounced in these birds.

Of our 23 American Coots, 11 were watched from hatching for one to 12 hours; two were brought to Chicago and kept until 5½ weeks old. One brood was over-wintered at the Station; a brother and sister nested together the next season, while two brothers formed a homosexual pair; one of them migrated the following winter, returned and nested two miles from the Station.

Examples of post-hatching activities of two birds are described. The ages at which 25 coordinations appeared are given in Table 15. Both begging and aggressiveness are pronounced in this species.

There are many similarities in the early behavior of these three species of rails. Conspicuousness of nestling plumage, begging behavior and aggressiveness become progressively more pronounced from the Virginia Rails through the Soras to the American Coots. Contact notes were softest in the Soras, louder in the Virginia Rails and loudest in the Coots. Social preening was most pronounced in the Virginias, less so in the Soras and observed only once in young Coots. The Soras dived in connection with bathing and so did King Rails. Adult Coots seldom bathe. The Virginias and Soras sunned by stretching their wings back, fanning them out and arching them over their backs. All three species have a strong bond to their brood mates.

CHAPTER IX

Semi-Precocial Chicks That Stay At or Near Nest, Though Able to Walk: Gulls, Terns

These chicks are as capable physically of following their parents on foot as are fully precocial young. The parents, however, obtain food at a distance from the nesting site, hence have to bring it to the chicks. Heinroth suggests that this precocity of Laridae young probably stems from their descent from the Limicolae (Charadrii). Many of the chicks leave the nest for short expeditions, returning to it for food and at night. In those species that nest on cliffs, as Kittiwakes, or on tree branches, as White or Fairy Terns *(Gygis),* the young stick exceedingly close to the exact place of birth.

A. Gulls

The Larinae, gulls, constitute a very successful subfamily distributed over most of the world. They are markedly social, yet at the same time aggressive.

Franklin's Gull, *Larus pipixcan,* which nests abundantly on the Delta Marsh, is a prairie species, subsisting largely on grasshoppers in the summer. It is a small black-headed gull with a red bill and red feet, and weighs from 246 to 264 grams, according to Roberts (1932, II:591). The male we raised to the flight stage weighed 248 grams at 38 days, the female 226 grams at 36 days. The European Black-headed Gull weighs from 211 to 292 grams (Niethammer, 1942:396).

Seventeen Franklin's Gulls came under our care.

Eight of these we watched from hatching for 1½ to seven hours, a total of 31 hours. In 1951 we raised G3 and G4 till they were flying strongly, then gave them to the Brookfield Zoo at the age of 38 and 36 days; G3 appeared from his behavior to be a male, G4 proved to be a female at her death in 1955 (Nice, C., 1956). The next two years birds were under observation for three and four weeks. In 1954 some notes were made on gulls raised at Delta by Martin Moynihan—seven Franklin's, a Herring, a California, and five Ring-billed.

The baby gulls were less active than the truly precocial species studied. They had a strong urge to be hovered. Some of them were markedly vocal, during the first hour or so giving a rhythmical, not unmusical utterance lasting eight to 40 minutes that I called the "red-eye song" from its resemblance to the song of the Red-eyed Vireo *(Vireo olivaceus).*

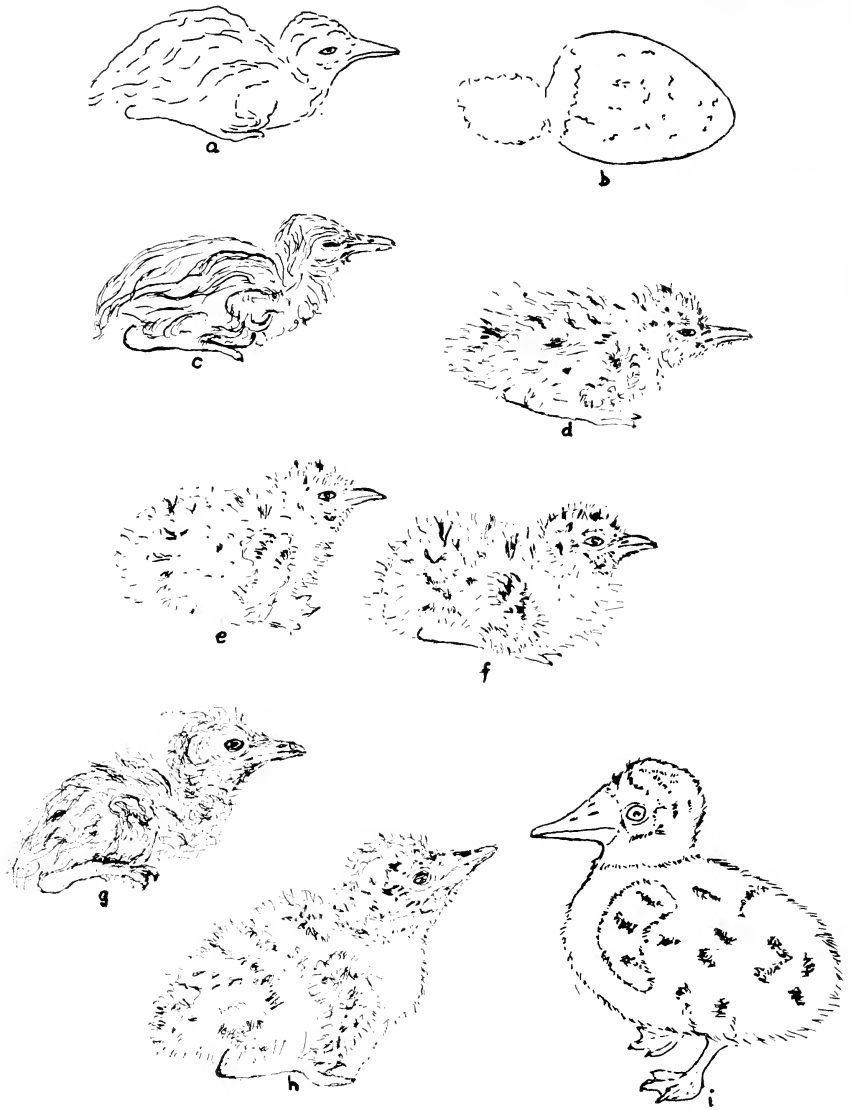

Figure 13. Baby FRANKLIN'S GULLS. *a-f*, G8: *a*, 40 minutes; *b*, hatched egg; *c*, 50 minutes; *d*, 2¾ hours; *e*, 11 hours; *f*, 24 hours. *g-i*, G1: *g*, 1½ hours; *h*, 24 hours; *i*, 2½ days.

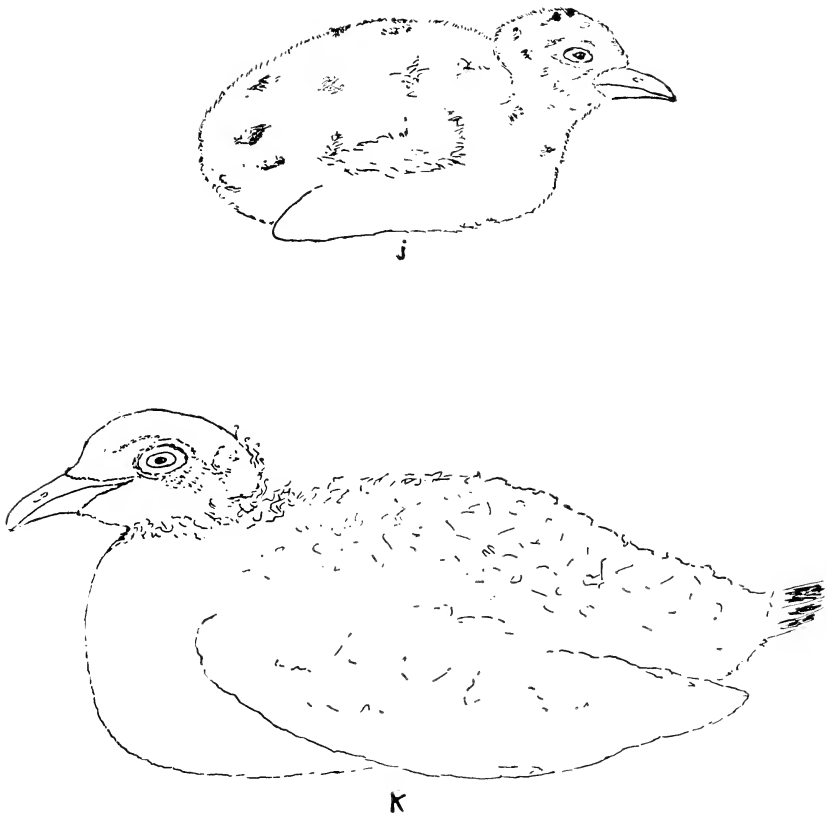

Figure 14. FRANKLIN'S GULLS. *j*, G1, 9 days. *k*, G3, 21 days.

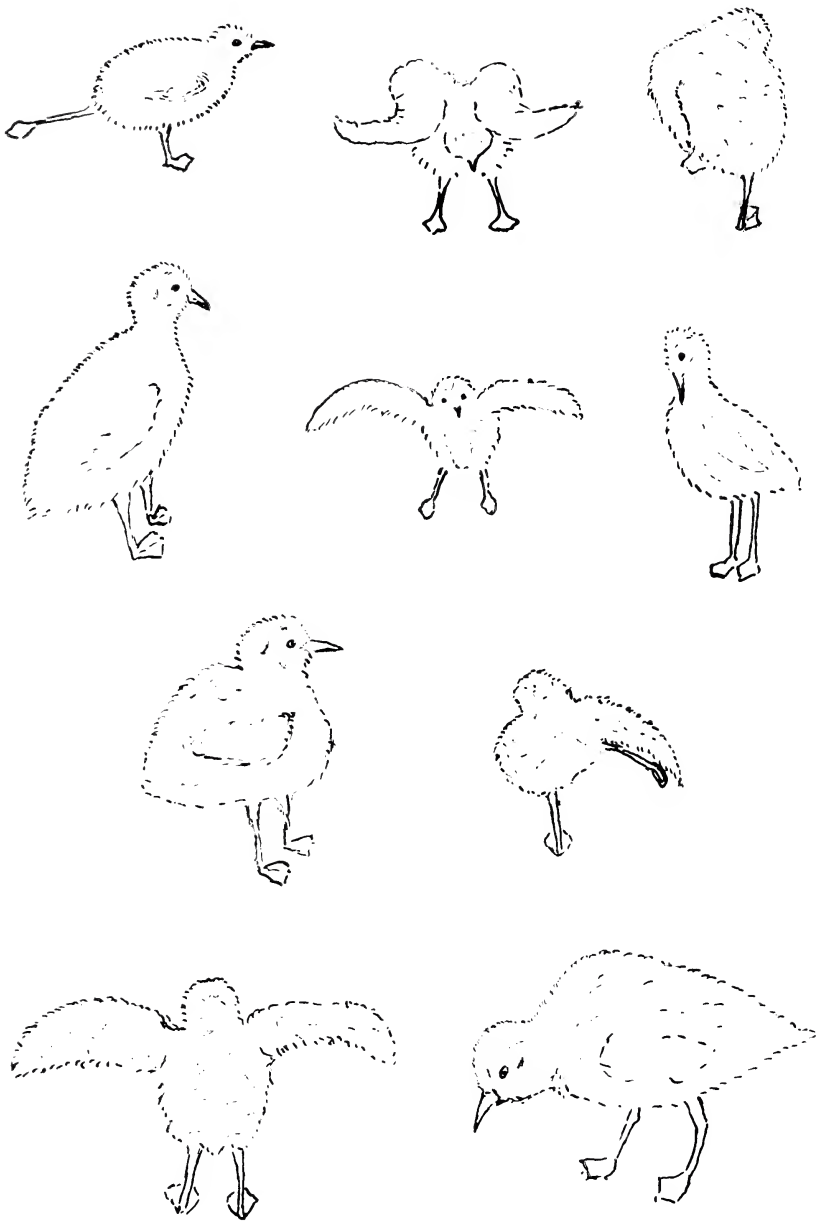

Figure 15. Two-week FRANKLIN'S GULLS. G3 and G4.

1. Example of Post-hatching Behavior

Our notes on the first four hours of G2 on the afternoon of June 21, 1951 follow:

0—Out very quickly at 4:14. In nest with Coot, Canvasback and Eared Grebe. Eyes closed. All curled up. Talking.
6m—Opens eyes a bit. Opens bill. *Pee-yap.*
9m—Yawns.
14m—Constant notes, 54 in a minute.
31m—Stands up on tarsi. Yawns; yawns.
34m—Still a constant song, 56 notes a minute. Something like a Red-eye.
41m—Yawns; backs.
58m—Yawns and backs.
1h31m—Quiet at last for a bit.
1h34m—Now a different song, less pretty.
1h46m—Quiet, sleeps all the time. Take him out; he gives a squawky note and a loose, green dropping.
1h53m—Yawns; holding his head up.
2h25m—Snatched at Coot's bill.
2h31m—Yawns; *tries to scratch head.*
3h16m—Quite transformed; pretty and fluffy.
3h18m—*Preens.*
3h25m—Yawns.
3h26m—*Eats some egg from forceps,* snatching at it. Pecks at red bill of Coot and red spot on grebe's head.
8h50m—*Eats well.*

2. Development of Behavior in Franklin's Gulls

The first appearance of motor coordinations in our Franklin's Gulls is shown in Table 16.

3. Stage II—Preliminary

During Stage II, the first four hours, all the chicks yawned, five of them pecked early at objects and six gave the red-eye song, but comfort movements were recorded only four times for all eight. There is no urgency towards independence.

4. Stage III—Transition

Stage III was counted as lasting about 20 to 24 hours, for it was not until two days of age that the gulls were strong on their feet. Picking up food and fanning wings regularly appeared during this stage. Lying with both legs outstretched was first seen at six to eight hours and persisted until the age of six, eight, and nine days. This

TABLE 16

DEVELOPMENT OF BEHAVIOR IN FRANKLIN'S GULLS

Seventeen individuals (eight watched from hatching)

m = minutes, h = hours, d = days

Coordination	*Number showing coordination*	*Age at first appearance*	
		Range	*Median*
Stage II			
Yawning	8	–1m-2h50m	9m
Pecking	5	34m-3h	2h27m
Eating	7	2h20m-3h26m	2h45m
Scratching head	2	2h31m-26h	
Stage III			
Picking up food	5	7h15m-1d8h	12h
Preening	9	3h15m-2d	14h
Stretching leg out	7	1h27m-2d	16h
Stretching both legs out	4	6h-1d	8h
Backing for dropping	5	8h30m-1d3h	23h
Fanning wings	6	16h-1d8h	1d
Stage IV			
Strong on feet	4	22h-1d12h	1d1h
Stretching wings up	4	1d15h-4d	3d
Jumping-and-flapping	6	2d-5d	3d
Swimming	1	3d	3d
Stage V			
Aggression	7	4d-6d	5d
Bowing in greeting	6	4d-10d	5d
Head in scapulars	3	5d-15d	7d
Catching insects	3	6d-8d	7d
Bathing	3	6d-7d	7d
Stretching sidewise	4	6d-9d	7d
Washing bill	2	12d, 14d	13d
Thrashing in bath	2	14d, 24d	19d
"Play-fishing"	4	18d-24d	21d
Flying a little	2	28d, 28d	28d
Flying well	2	31d, 33d	32d

was occasionally seen also in ducklings and Killdeer, and was observed in Sooty and Noddy Terns on the fourth day (Watson, 1908).

a. *Exploratory pecking.* The baby gulls pecked at objects very early. In ingenious experiments with incubator-hatched Franklin's Gulls at Delta, the Colliases (1957) offered pairs of differently colored models of bills to chicks from four hours to four days of age; 17

chicks, tested individually, pecked 3150 times at the red bill and 633 times at the green one, while 18 other chicks pecked 1076 times at the red bill and 143 times at the white bill. Many experiments have been carried out on this subject with Herring Gulls (Goethe, 1937: Tinbergen and Perdeck, 1950: Tinbergen, 1953a). Goethe reported the chicks pecking at moving stalks and at nest mates at about 12 hours, at which time they were usually first fed, although a precocious chick might be fed at the age of two hours. The young pecked at models showing a red spot far more than at uncolored models (p. 71). Tinbergen (1953a) concluded after exhaustive experiments:

"The object that releases the pecking (i.e. the bill of the parent bird) is characterized for the chick by (1) movement, (2) shape (elongate, not too short, thin), (3) lowness, (4) downward-pointing position, (5) nearness, and (6) the bill-patch, which must be (*a*) red and (*b*) differing, by contrast, from the ground-colour of the bill. Many of these properties are not quantities of something, but they are relationships" (p. 204). "The chick responds again and again, up to hundreds of times, to a crude dummy in spite of the fact that the dummy never provides it with food; it just cannot resist the few 'sign-stimuli'" (p. 232).

Kirkman (1937:103) describes begging by Black-headed Gulls: the chick "pecks at the breast of the adult, or, if within reach, at its neck and beak, and utters a querulous piping accompanied by upward jerks of the head." Young are fed by disgorging or from the tip of the mandible. "A chick in down, only one day old, is quite capable of picking up from the ground the worms and insects disgorged."

The Common or Mew Gull *(Larus canus)* chick does not at first pick food from its parent's bill; the parent puts regurgitated material into the chick's open bill (Pfeffer-Hülsemann, 1955). The Kittiwake "takes its food from the throat of the parent and food is rarely dropped" (Cullen, 1957:293).

b. *Backing to defecate.* One coordination appeared in this stage that did not occur in our precocial birds except grebes, namely backing to defecate. It was first noted from the ages of 8½ to 27 hours.

With healthy gulls it soon disappeared, but with G15 and G16 it persisted to a slight extent until they were 22 and 25 days old; G16, a female, died at four weeks, and G15, a male, at about six weeks. Portielje (1928) says this behavior in Herring Gulls raised by their parents in the Zoo was seen until 20 and 22 days of age; Goethe (1955) recorded it in one hand-raised Herring Gull as still occurring on the fifteenth day. Hazel Hen chicks at night backed to defecate (Krätzig, 1939).

5. Stage IV—Locomotory

At two days of age our gulls were well able to walk on their feet.

a. *Jump-and-flap.* The bird gives a little jump and flaps its wings, usually uttering a shout. This is practiced more and more until finally at about 4½ weeks the wings raise the bird off the ground and shortly afterwards the Franklin's Gull can fly. Jumping-and-flapping usually started at two to three days with our gulls.

It is reported as first seen on the third day with Kittiwakes, and the fifth day with the Black-headed Gull (Cullen) and seventh to ninth day with the Herring Gull (Goethe, 1955). Kittiwakes are far more cautious in the performance of this act than are ground-nesting gulls; for a long time they only flap their wings, not jumping until nearly ready to fly and then they "never lift their feet for more than an inch or so from the nest, whereas much smaller ground-nesting chicks can be seen jumping a foot or two in the air" (Cullen, 1957: 294).

The jump-and-flap is seen in all gulls and terns according to Ahlqvist (1937). It occurred in our American Coots and rails, Spotted Sandpipers and Killdeer, and in Seitz' Curlew (1949).

b. *Swimming.* Our chicks first swam at three to five days. We do not know how early they do it in nature. Ahlqvist's hand-raised Black-headed Gulls swam at eight days, his Herring and Great Black-backed Gulls at 19 days.

6. Stage V—Socialization

With these pugnacious birds hostility towards strangers appears early.

a. *Aggression.* At four to five days of age our Franklin's Gulls regularly attacked strange chicks of other species that were introduced into the group—duckling, grebes, American Coots, bitterns, Soras, Wilson's Phalarope, and House Sparrows, but never were antagonistic to younger gulls. Gradually they became used to these companions and forgot their animosity.

With our gulls we never saw any friction between individuals that had grown up together. But Martin Moynihan's young Franklin's Gulls, which were fed at longer intervals than ours, abused the youngest of the lot and also attacked a captured wild member of the species slightly older than they. We wonder whether food scarcity might have encouraged the development of hostility to an exaggerated degree in these gulls (Moynihan, 1959).

With wild Herring Gulls, Culemann (1928) saw chicks quarreling

over food at four and five days, and Goethe (1937) at eight days, while chicks of five and seven days pecked the observer when he handled them. Hand-raised young at six days snatched food from each other's bills; from the twenty-third day a peck-order became established that was still in force in the birds' third year (Goethe, 1955). Black-headed Gulls begin to show signs of aggressiveness at about two weeks of age; "a display very similar to choking, and actual attacks can be observed towards strange adults" (Tinbergen, 1956:403).

In contrast to the generally peaceful home life of ground-nesting gulls, fights are common between nest mates in the cliff-dwelling Kittiwakes. When the parent comes to feed, the older chick attacks the younger and the latter turns its head away to hide its beak. "The fighting between nest mates is probably concerned with establishing the peck-order . . . whose function it is to determine the order in which the young are fed. In the normal course of events the peck-order is settled at an early age, when both the young are small and weak and easily tired" (Cullen, 1957:298).

The big gulls at Delta in 1954 were consistently placid and non-aggressive. Ahlqvist's (1937) European Herring and Great Black-backed Gulls, on the contrary, attacked and killed one of the Black-headed Gulls. The others soon flew away, but always returned to bathe and preen with the big gulls, although keeping a weather eye out for danger.

b. *Bowing.* At four to six days the Franklin's Gulls started bowing as part of the greeting ceremony. They bowed and shrieked each time we appeared. G3 and G4 did likewise in response to the begging of their Coot companions. The Heinroths (1924-33, III:47) say of this behavior in hand-raised gulls that it easily leads the caretaker to overfeed his charges; it is a form of greeting and does not necessarily signify hunger.

c. *Sleeping position.* Heads were first placed "under the wing," i.e., in the scapulars, at five and seven days. At 17 days G4 squawked in this position, reminding me of my hand-raised Serin that sang under like circumstances (Nice, 1945).

d. *Catching prey.* G3 and G4 caught and ate ants when eight and six days old; G9 did so at nine days. At seven and five days the first two tried to catch flies.

e. *Bathing.* Simple bathing was first seen at six and seven days, thrashing at 14.

G7 at six days took a bath in the water dish and on the wet paper. It dipped in its head, waved its wings, and preened its oil gland and breast.

G3 and G4 were given their first opportunity to bathe on July 2 at nine and seven days. "G3 steps into the soup bowl and takes a sort of bath. G4 takes a pretty good 'bath' outside. Both scratch their heads, dip their heads in, shake heads, shake wings. Get pretty wet underneath." July 3, G3 was put in the bird bath; he took something of a bath, but made no attempt to dry himself. On July 6 we offered them water in a soup bowl and a jelly glass. Both gulls chose the glass, putting in their heads, shaking them, lying down, shaking their wings, later preening energetically. July 7, G4 took a good bath in the soup bowl. On the ninth we put them in the bird bath and both took thorough baths, G4 thrashing. Both gulls wagged their tails.

On July 30, 1954, at Delta, I watched a Franklin's Gull bathe; it was about a month old and not yet able to fly:

"Dips head, then thrashes energetically; leans to one side, thrashes with opposite wing three or four times, then vigorously with both wings. Scratches head. Dips head six times with wing shivering; then flaps wings. Comes out. Scratches head; preens tail. Shakes self so vigorously it nearly falls over. Wags tail. Preens, rubs head on body. Flaps wings and jumps. Nibbles oil gland. Rubs head on it. Rubs bill on breast."

On September 21 I watched an adult Ring-billed Gull bathing near Chicago. It dipped its head about 100 times, but hardly moved its wings at all.

Records of first bathing in other gulls are: Black-headed at eight days, Herring and Greater Black-backed 19 days (Ahlqvist, 1937); Herring 20 days (Goethe, 1955).

f. *Play-fishing.* When G3 and G4 were 22 and 24 days old they were first seen indulging in a game which Ahlqvist (1937) called "Play-fishing."

G4 picked up a small twig, carried it and dropped it; G3 came over and got it. Then G3 got a long stick and carried it 25 feet; G4 followed and took it herself. On August 7 at Brookfield Zoo when they were 7½ weeks old we watched them play-fishing for 20 minutes. "G3 has a little stick; G4 chases around squawking and gets it from him. He carries it, she wheedles and snatches it from him. She drops it and picks it up. Both pull at it. She gets it, he chases after, gets hold of it and tugs it away. She shrieks. She gets it. He gets it away, then she gets it. He chases her again for the stick." At our next visit August 20, no more playing with sticks was seen.

In 1952, G5 and G6, aged 19 and 18 days, played with a two inch piece of phragmites, one picking it up, the other snatching it from him. On August 5 Helen Hays wrote from Delta: "The gulls do a great deal of playing. One will pick up a stick or a pencil and dash away with it. The others will follow until he drops it, and then perhaps another will pick it up." They were then about seven weeks old; they could not fly as they had been wing-clipped.

Ahlqvist's Black-headed Gulls played with sticks and chased each other from the age of 12 to 35 days, the Arctic Skua from 20 to 32 days, the Greater Black-backed from 23 to 52 days. This was not seen with any of the birds after they were able to fly. Portielje's (1928) zoo-raised Herring Gull played with sticks in the water at the age of one month. Play-fishing with sticks and pieces of paper first occurred with Goethe's (1955:412, 424) Herring Gulls at 11 days; as a rule it was confined to the first month with both captive and free birds, but in several of the former it was noted at 80 days and with one individual at 1½ years.

g. *Flight.* The 1951 Franklin's Gulls started to fly at 28 days and were flying well at 31 (G4) and 33 (G3) days. Ages of flying of some other gulls are: Little, 24 (Heinroth, O. and M. 1924-33, IV); Skua, 32 (Ahlqvist); Black-headed, 35 (Ahlqvist); Kittiwake, 42 (Cullen); Herring, 52 (Portielje), 45 to 62, averaging 51 days (Goethe, 1955); Greater Black-backed, 58 (Ahlqvist).

h. *Standing on one foot.* This was not seen with Gulls 3 and 4 before we took them to the Zoo on July 31, nor was it noted during the two hours' observation on August 7, but both did so on August 20 at the ages of 46 and 48 days.

7. Escape Reactions

Kirkman (1937:173) could get no fear response with Black-headed Gulls for the first 12 hours and sometimes for 24 hours. Goethe (1937:68) noted a Herring Gull chick of 20 hours crouching at the parental alarm call. Tinbergen (1953a:180) reports the Herring Gull chicks' response to the alarm call as appearing very early: "Even when still in the egg a chick stops its squeaking when it hears the 'hahaha' call. . . . chicks of only a few hours of age crouch in the nest. Before they are a day old, however, they leave the nest when alarmed and crouch some distance away."

Our young gulls never showed fear of anything on the ground. G3 and G4 merely observed cats and dogs with interest. At six weeks G5 rushed with loud squawking at a Golden Labrador puppy that had wandered into the duck pen and drove off the intruder. Ahlqvist's young gulls, Arctic Skua and Common Terns evinced no fear of ground enemies, such as cats, but they noticed enemies in the air.

In Chicago G3 and G4 would hurry to cover at the harsh grating

sound of trains backing nearby, or at the starting of our car, and at the sound and sight of an airplane overhead. Goethe's Herring Gulls ignored a mounted Buzzard, but at 20 days fled from it as it was moved three meters above them.

8. Premature Breeding Behavior

G4 at about 3½ weeks showed intimations of begging behavior to our hands, running her bill coaxingly around our fingers. She also did this to G4, who once at the age of 30 days regurgitated food to her. Portielje's seven-week-old female Herring Gull carried twigs, straws and feathers into the sleeping hollow. This species does not breed until three years of age.

9. Social Bond

Franklin's Gulls were never devoted to us, as were the Killdeer, rails and some of the American Coots. Gulls 3 and 4 evinced a mild bond towards the two Coots with which they were raised, but it was much less pronounced than that of the Coots towards them. Neither species showed any interest in the other after their initial separation at the Zoo and subsequent reunion, eight weeks later.

Goethe (1955) raised several Herring Gulls in isolation ("Kaspar Hausers"); he found them quieter and less voracious than those raised with companions. When introduced at the age of three and four weeks to the other young, the "Kaspar Hausers" were frightened; they pecked any individual that tried to lie down beside them, and were themselves severely pecked, so that they finally wound up at the bottom of the peck-order.

B. Terns

Parent terns present food—fish or insects—to the chicks, not dropping it on the ground as gulls usually do. (But Noddy Terns sometimes disgorge food on the rim of the nests [Watson, 1908]). The Heinroths (1924-33, IV:61) say one can almost speak of gaping *(sperren)* by terns with their shrieking and holding open of their bills. But there are no bill-swellings nor bright colors nor shining configurations inside the gullet. Also, whereas it is necessary for passerine parents to put the food on the base of the tongue, a tern chick snaps at the food and snatches it from the parent.

1. Forster's Terns

In 1951 we hatched three Forster's Terns. Unfortunately, because of our inexperience, they died after a few days. T2 hatched at 8:20 p.m., June 16, yawned at five minutes, and gave a nibbling movement at 17 minutes. For its first four hours it napped in my hand most of the time, occasionally waking up to squawk. At 2 hours 20 minutes and at 3 hours, it almost preened itself. When put by itself into the Pintail nest, it squawked constantly, shaking its whole body with each note. It was on its feet at 18 hours; it scratched its head and fanned its wings. At three days it was noted picking up a piece of food from the dish. My daughter took most of the care of the chicks; when they were three and four days old they started their raucous shouts whenever they heard her voice.

2. Notes on Terns of Other Species

Studies on the behavior of several species of terns have been published: the Sooty Tern and Brown Noddy on the Dry Tortugas by Watson (1908) and Lashley (1915); the Common Tern in Massachusetts by Palmer (1941); the Caspian Tern in Finland by Bergman (1953, 1956, see Lawrence, 1957); and the Black Tern in Michigan by Cuthbert (1954), and in great detail in Holland by Baggerman and co-workers (1956).

a. *Feeding responses.* Caspian Tern chicks react "to the combined feeding and summoning call of the adults . . . even in the egg, uttering a weak begging call" (Bergman, 1956). An unhatched Sooty chick with only its beak protruding accepted and swallowed minnows offered by the experimenter (Watson, 1908:243). A newly hatched Black Tern was first fed by its parents at the age of 2 hours 2 minutes; at 2 hours 48 minutes "its down was dry and fluffy except for a few small patches" (Cuthbert, 1954:47).

Bergman (1953) made two series of experiments on baby Caspian Terns with paper models of bills; the strongest reaction of the five-hour to two-day chicks was to red or black with a different colored tip, corresponding to a fish. The chicks also pecked at yellow, white and reddish flowers waving in the wind and at the yellow bills of their nest mates, but not at green paper nor green vegetation. "Pecking at various small objects on the ground is stimulated by bright colours and by movements" (Bergman, 1956).

Figure 16. FORSTER'S TERN. *a-g*, T1: *a*, 3 minutes; *b*, 10 minutes; *c*, 25 minutes; *d*, 80 minutes; *e*, 90 minutes; *f*, 2½ hours; *g*, 12 hours. *h*, T1 and T2, 1 and 2 days.

Black Terns in Holland "do not yet show begging behaviour" for the first two days. "The food is held close to the bill of the young bird, which seems to aim at the tip of the parent's bill and thus gets the food. The young does not seem to aim at the food itself but at the tip of the beak, for we have sometimes seen small chicks pecking at other pointed objects, too, like the wing and tail tips of the parents." They show full begging behavior from about a week on, stretching their legs and necks, opening their bills widely and "squeaking" loudly (Baggerman *et al.,* 1956:33).

b. *Aggression.* Adult Sooty Terns are very quarrelsome with each other as they nest in close proximity on the sand, but Noddies nest farther apart in bushes. Only one egg is laid, so the chicks have no nest mates. The Sooty leaves within a few days and spends the day in weeds and bushes, coming out at night to be fed (Lashley, 1915). The Noddy stays in the nest until about 20 days of age. Watson raised several of each species by hand.

The most striking feature about both sets of chicks was their furious fighting, which started at three days with the Sooties and five days with the Noddies. In regard to the three-day-old Sooties, Watson writes: "The fighting instinct appeared today in almost completed form. Two of my young birds faced each other and began striking simultaneously. A hold is taken on the body and maintained with grim determination, the victor all the time shaking his opponent as does the adult" (p. 243). In nature the somewhat older young frequently engage in fights with each other, and they may attack adult Noddies, but never adult Sooties. With very young Caspian Terns the "strong begging call (with the bill wide open, close to the parents) is identical with the call of strong aggressiveness" (Bergman, 1956). Seven-day-old Caspian Terns participate in their parents' battles with neighbors, particularly when they are hungry (Bergman, 1953:37).

In contrast to the excessive aggressiveness of the Sooty Terns was the Heinroths' (1924-33, IV:59-62) experience with Caspian Terns. Three of these were raised with two Lesser Black-backed Gulls of like age; the terns begged shrieking from the gulls. The friendship had continued in the flying cage of the Berlin Zoo till the time of writing, i.e., for two years. Another Caspian Tern was brought up with a Razor-billed Auk of the same age; there was a strong bond between these two, both of them attacking older members of both species. At the University of Michigan Biological Station a Caspian Tern was

raised with two American Coots; "after the Station closed, the birds, when given their freedom, went for long walks together on the upper drive, calling softly to one another" (Nelson, 1956:19).

c. *Escape reactions.* The Sooty Tern chick makes a hole in the egg large enough for the bill to protrude two days before hatching; during this period it "makes no response to the warning cry of the adults" (Watson, 1908:242). The Caspian chick, on the contrary, does react to the alarm call before hatching (Bergman, 1956:244).

Two-day-old Black Terns responded to "shrill, short cries in slow cadence" of the parents by freezing in the nest, but dashed off it when "the cries had a rapid cadence" (Cuthbert, 1954). Up to three days, Sooties at alarms freeze in the nest or near it, while older chicks rush to the bushes (Watson, 1908). In Finland small chicks of the Caspian Tern are more cryptic in the nest than out of it; at the alarm call of the parents they freeze in the nest up to the age of 10 or 15 days, whereas Common and Arctic Tern chicks, which are less cryptic in the nest, at a very early age leave it to hide (Bergman, 1955).

d. *Other behavior patterns.* Like young gulls, a Black Tern at one day of age, "climbed to the edge of the nest, turned, placed its abdomen in the water and defecated. The nests remained completely clean" (Cuthbert). Noddy Terns were backing to defecate when 12 days old (Watson).

At seven days Sooty Terns began to hop an inch or two in the air, flapping their wings. On the same day they began to dig holes with backward strokes of the feet, the same movements as used by the adults in making a nesting scrape. "By digging such a hole, the bird secures a surface which is damp and cool" (Watson, 1908:245). The Noddies first sunned on the 19th day; "The wing turned to the sun is drooped so as to shield the body, while the opposite leg is stretched out, the body being supported by one leg" (Watson).

Some of the day-old Black Terns swam out a few feet when the observer entered the blind, but quickly returned (Cuthbert). Caspian (Bergman, 1953) and Common Terns (Culemann, 1928) up to the age of four days become wet in the water and drown, but after that can swim successfully for long periods.

As to flight, this is reported for Caspian Terns as starting at 25 to 28 days (Bergman, 1953:40), and with the Black Tern at about three weeks (Baggerman *et al.,* 1956:35), and "at approximately 25

to 30 days" (Cuthbert, 1954:62). The adults feed the flying juveniles "for a long time . . . in all species of terns" (Baggerman *et al.*).

As to the two hand-raised Caspians of Bergman (1956), "At the age of 60 to 62 days, fishing capacity developed rapidly. Earlier the primaries had been too weak to allow sudden movements such as diving. The chicks knew their human parent-substitute astonishingly well and independently of his varying clothes, recognizing him at distances between 50 and 150 meters. When hungry, they followed his boat, but as long as they were expecting to be fed, or when begging, they were incapable of fishing for themselves."

C. Summary

Semi-precocial chicks are physically capable of following their parents on foot, but owing primarily to the nature of their food, which must be collected by their parents at a distance, they remain on or near the nest.

We watched eight Franklin's Gulls from hatching, while nine others were observed from their first day on, two being kept until they flew. The activities of a gull for its first four hours are described. The ages at which 25 coordinations were first observed are shown in Table 16.

Experiments on the pecking response of Franklin's and Herring Gulls are summarized. At two to three days the little gull starts to "jump-and-flap," at the same time giving a shout. This is kept up until at 4½ to six weeks the wings raise the bird off the ground and shortly afterwards it can fly. This behavior is characteristic of Laridae in general, and also occurs in Charadrii and Rallidae.

Aggression toward strange chicks of other species appeared at four and five days. Simple bathing was first seen at six and seven days, the complete technique, including alternate movements of wings, at 14 days. Escape reactions, premature breeding behavior, and social bond are discussed, both as seen in our gulls and as reported for various other species.

While most baby gulls pick the food from the parents' bills or from the ground, little terns hold their bills wide open, then snatch the food from the parent. We hatched three Forster's Terns, but they did not long survive. Some aspects of behavior of four species of terns are summarized from other studies; these include feeding responses, aggression, escape reactions and a number of other behavior patterns.

CHAPTER X

Semi-Altricial Chicks Unable to Leave Nest But Covered With Down: Bittern, Condor, Owls

Precocial chicks can move about soon after hatching; they are covered with down; they can see. Altricial chicks are unable to move about; they have little or no down and they are blind. Semi-altricial chicks are unable to move about, but they are covered with down; some are blind at hatching and some are not.

Unfortunately our experience with semi-altricials is meager, being confined to the first few days of life of three American Bitterns.

A. Chicks Hatched With Eyes Open

Herons and hawks are the chief representatives of semi-altricial chicks hatched with open eyes.

1. Bitterns

We observed three American Bitterns, one of which, B1, we watched hatch.

B1 was free of the shell at 7:25 p.m., June 25, 1951, and was watched for 80 minutes. It was very inactive. At 35 minutes of age it gave a wheezy note; at 46 minutes it yawned and snapped with its bill. At 47 and 77 minutes I opened its bill and fed it some hamburger. At 80 minutes it started lunging at various objects. It weighed 25.2 grams. On June 27 it ate readily from forceps held crosswise; it also picked up some food itself. On July 1 it moved about on its tarsi using its wings as props. The next day it died, weighing 48.2 grams.

B2 was brought to us July 8, 1953, at about one day of age. It gave a series of distress notes from cold; it weighed 26.8 grams. On July 10 I put the two-week-old Eared Grebe into the brooder with the bittern; the latter hissed and lunged with extended wings at the visitor again and again. The next day the same thing happened, but after that they accepted each other. The bittern would give eager little notes and crawl over when it wanted to be fed. It liked to have a finger placed crosswise in its bill and to have the food massaged down its throat. At about six days it preened its breast and drank from the water dish. On July 16 it weighed 62.2 grams and ate four grams of fish for breakfast, but the next day it died. Possibly it had been injured by the grebe.

The last bittern hatched June 22, 1954, but did not come into our

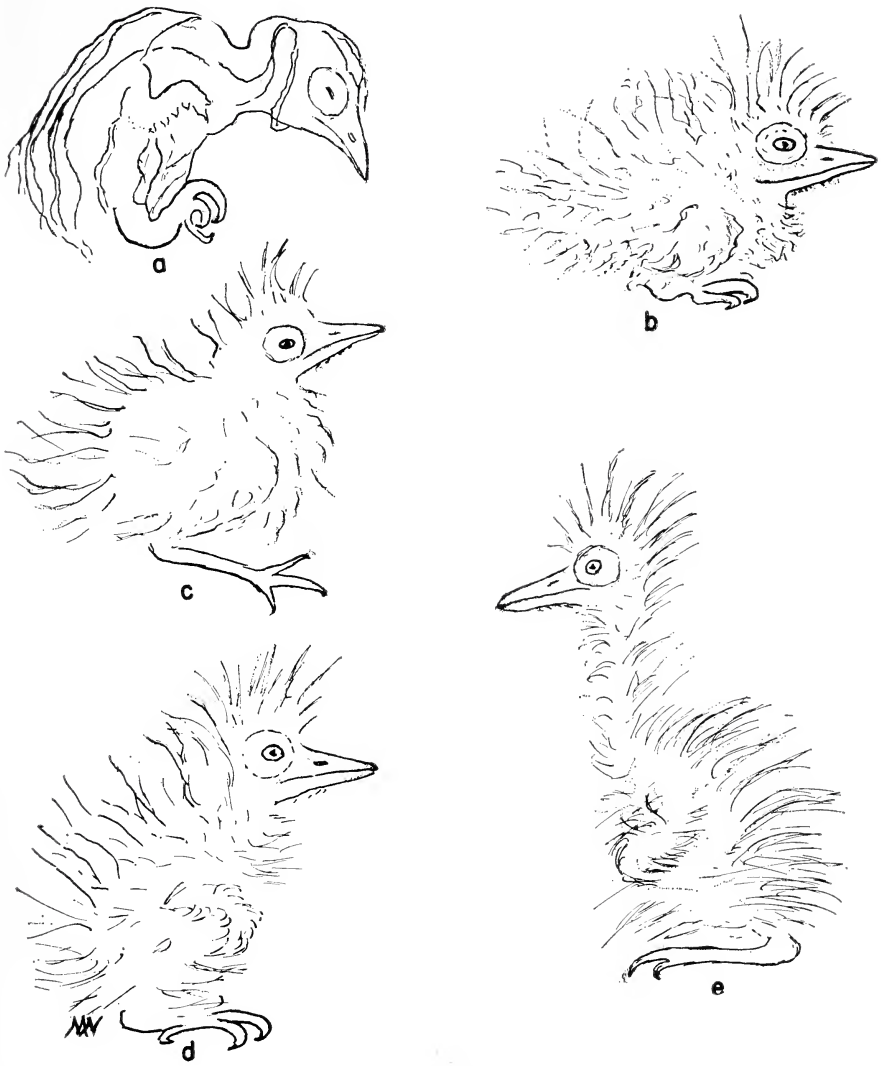

Figure 17. AMERICAN BITTERN. *a-e*, B1: *a*, 20 minutes; *b*, 12 hours; *c*, 24 hours; *d,e*, 48 hours.

care until the 27th, when it was emaciated, weighing only 21 grams. On this day it gave a pretty little song of contentment, 102 notes in a minute. When put in the brooder with the group of baby Soras, at first it tried to swallow S5, lunging at it. But after that it was peaceable with them, allowing them to cuddle under and against it. It weighed about 30 grams, the Soras about seven. At seven days we noted the first preening movements, awkward jabs at the breast. It actively sought the company of the Soras, shuffling over to join them. It stretched its wings forward and the next day drank by itself. As it was not thriving, it was killed July 3; its weight was 39.3 grams.

Peter Magosian watched an American Bittern nest at Delta from a blind in July, 1954. He reported that at six days of age the only activity he saw was sleeping, crawling into the shade, and eating. Food was taken from the mother's bill and also from the floor of the nest. Sometimes the mother caught fish from the nest. The next day he saw preening for the first time. This agrees with our observations on B2 and B3. At 11 days the little birds hissed and clapped their bills.

The Heinroths' (1924-33, IV:34-40) European Bitterns crept about in the nest at one week, made expeditions out and back at two weeks, and flew at eight weeks. The female young doubled its weight in five days, and tripled it in seven days, while at 24 days it was 25 times as heavy as at hatching.

It is difficult to classify the activities of these bitterns into stages. Perhaps Stage III was reached at six to seven days, for preening was first seen in two of our birds and in wild birds at this time, and B1, B3, and the European Bittern became more active at this age. Defense appeared with B2 at about three days.

2. Condor

Falconiformes have long incubation periods. That of the California Condor has not been determined, but that of the South American Condor with an egg of similar size lasts from 54 to 56 days.

About 350 B.C., Aristotle, on the basis of the known incubation periods of the domestic goose and domestic chicken, declared that the eagle incubates for about 30 days and the kite and hawk for about 20 days. (Actually the periods are about 45, 30 and 35 days respectively.) These ancient guesses were quoted for 2,200 years, and the original assumption that length of incubation was determined by size of egg was applied to birds in general from the end of the 18th century on (Nice, 1954a, 1954b). It was not until the careful researches of Evans (1891) and Heinroth (1908, 1922) that a body of tested facts on the subject of incubation periods became available (unfortunately these studies were largely

unknown in North America). These authors showed that the chief factor determining the length of incubation was *the rate of development* of the embryo. In general the fewer dangers to which the eggs and young are exposed, the slower their development.

Koford (1953:111) writes of the five stages in feather development of the young California Condor: "These stages correspond approximately with the five stages in the psychological development of passerines recognized by Nice (1943:14), and the first three stages correspond with the three main stages of growth in raptores recognized by Sumner (1933:284, 285)." Examination of pages 87, 111-123 and 148 enables us to construct the following schedule of the stages.

Stage I: Hatching to three weeks. Natal down; continuous brooding. Chick stays close to location of the egg. Threat attitude at eight days.

Stage II: Fourth and fifth weeks. Second down appeared. Brooding at night only. Chick can walk on tarsi at three weeks.

Stage III: Sixth through 20th week. Juvenal feathers appeared; not brooded, but still fed in nest. Walked on feet at eight weeks. Preening, exploratory pecking, fanning the wings, scratching the head, stretching wings up, wing and leg sidewise. What the author calls "frolicking" was noted at eight weeks: he saw the bird "jump up and down four times in rapid succession, turning completely around in this action, and then repeat the entire performance twice more" (p. 114).

Stage IV: Twenty-first through 31st weeks. Feathers completed growth; out of nest; flightless. Sunning, shaking, and later short flights were performed.

Stage V: Eight to 15 months. Volant, still somewhat dependent.

In a general way these stages correspond to those in the Song Sparrow, but in some respects there is greater advance in the semi-altricial than in the altricial. In Stage I the Condor's eyes are open, and a threat attitude was taken towards the observer. In Stage II the Condor can walk on its tarsi. Stage III corresponds in both birds in the exercise of comfort movements, but the Condor is ahead in walking on its feet, in exploratory pecking and in "frolicking." (See Chapter XII.) Stages IV and V are much alike in both species.

B. Chicks Hatched With Eyes Closed

Owls are good representatives of this class of semi-altricials.

Since the end of the eighteenth century owls have been assigned

Figure 18. SHORT-EARED OWLS. About 20 and 12 days.

too short incubation periods—two weeks for small owls and three weeks for large ones, and these are still occasionally quoted. In reality owls have been found to incubate from 26 (Screech Owl [Sherman, 1911]) to 36 days (Eagle Owl [Heinroth, 1922]).

In 1951 I sketched two nestling Short-eared Owls at Delta; each was hidden in its own little hut in the grass. Comparing these with the Heinroths' (1924-33, II:37ff.) photographs of hand-raised birds of this species, I estimate the younger to have been about 12 days old, the older perhaps 20 days. The Heinroths report a few data on their brood: eyes partly open at eight days, fully open at 12; at 17 days the birds began to leave the nest; at 27 days they ran around; at one month they could fly to the window sill, and a week later they flew well.

Sumner's (1934) Great Horned Owl opened its eyes and evinced fear at eight days; it was brought to the laboratory at 14 days; showed hostility toward its caretaker at 15 days and exploratory pecking at 19. It picked up pieces of meat and fed itself at 20 days and flew at 36 days.

C. Summary

The stages of development in semi-altricial birds may approximate in a general way those in altricial birds but in several respects the former show themselves more advanced. Herons and hawks hatch with open eyes, but are comparatively helpless for a considerable period.

One American Bittern was watched as it hatched, but it died at seven days. Two others were observed for about a week. Preening was first seen at six to seven days.

Hawks and owls have long incubation periods. In his intensive study of the California Condor, Koford divided development into the five stages found in altricial nestlings; these are summarized and discussed.

Owls are hatched at an earlier stage than are semi-altricials 1, since their eyes are closed. We were unable to make any observations on such birds, nor can I find in the literature any detailed study of their development.

CHAPTER XI

Altricial Chicks, Unable to Leave Nest, Naked or Nearly So: Passerines

Although most of my work since 1943 has been with precocial birds, I have had some experience with young altricials and this has corroborated earlier findings. I also had the opportunity of seeing five nestlings hatch. These altricials hatched very quickly in comparison to precocials.

A. Post-hatching Behavior of Altricial Birds

At Delta, nestlings of five passerine species were watched for periods from 20 minutes to an hour after hatching. The birds spent part of the time in a Kingbird nest under a lamp and the rest of the time in my left hand while I sketched and recorded behavior with my right. Gaping was spontaneous in every case but one—the first instance with the Barn Swallow. The records follow:

Catbird:
Gaped at one minute. Four gapes in first 20 minutes. Silent.

Barn Swallow:
0—Opens bill; rests.
1m—Tumbles over on back; rights self.
3m—Now on abdomen; humps up its back, struggles about.
4m—*Gapes* as I cough. Resting on forehead and pot belly. Scratches face with right foot in its random movements.
10m—Take it in my hand.
12m—Gaped three times.
13m—Gaped.
22m—Mostly resting. Gaped six times in the first 30 minutes, but gave no notes.

Yellow Warbler: Hatched feet first. Gaped 27 times in first hour, but made no sound.

Yellow-headed Blackbird: Gaped at two minutes; started *tchipping* at three minutes and kept it up almost continuously, seven notes in one minute. Gaped 14 times in 45 seconds. In nine cases the length of time the bill was held open was measured by stop watch: 7-, 5-, 19-, 7-, 13-, 7-, 4-, 11-, and 12 seconds. There were 55 gapes during the first hour.

Song Sparrow: Five gapes were given one minute after hatching; the first note was heard at seven minutes. There were 17 gapes during the first 12 minutes, no gaping during the next six minutes, and 51 in the last 42 minutes, 68 in all. The number of gapes per minute ranged from one to seven. They lasted about four seconds each. *Tchipping* was continuous. The rate ranged from four to 13 notes a minute, the median of 12 minutes being 10.5; hence this infant must have *tchipped* some 560 times during its first hour of life.

The energy shown by these tiny, newly hatched nestlings, immediately after the exertion of breaking out of the egg, is amazing. The altrical hatchling has to make itself seen and felt and sometimes heard; the first arrivals in order to change the parents' mood from incubating to feeding and brooding, the later arrivals to press their claims against their larger nest mates.

In his study of the physiology of the inborn releasing mechanism of gaping in young passerines Prechtl (1953) found that during the first few hours of life gaping is very often spontaneous. Movements involved in the begging of three species of buntings *(Emberiza)* are described by Andrew (1956b), while experiments on the stimuli inducing begging in Red-winged Starlings *(Onychognathus morio)* were made by Rowan (1955), and in European Blackbirds by the Messmers (1956:405). Observations on this subject in young hand-raised Whitethroats are reported by Sauer (1954); interestingly enough, a two-year-old hand-raised female responded to tape recordings of begging calls by bringing food to the loud-speaker.

B. Some Observations on Later Stages of Passerines

"The Behavior of the Song Sparrow and Other Passerines" (1943) was based on my personal observation of 24 hand-raised birds of eight species. Since then I have had some experience with eight individuals of three altricial species in the home or laboratory and with four individuals of two species in the field. A Red-winged Blackbird and five Yellow-headed Blackbirds were taken from the nest at about eight to nine days of age, while three Yellow Warblers that had just left the nest were kept in the laboratory for two days. A brood of two Least Flycatchers was watched several hours each day from hatching to fledging (Nice and Collias, 1961), and a brood of two Eastern Wood Pewees was watched from the estimated age of five to six days to their leaving 10 days later (Nice, 1961).

The first three species fall into Group V of Table V (Nice, 1943:70), i.e., the families (from Alaudidae through Fringillidae) in which young leave the nest at eight to 11 days, but the flycatchers fall into Group IV, where young usually leave at 12 to 15 days. The appearance of motor coordinations in the first three species corresponded closely to that found in the Song Sparrow (see Nice, 1950, for the account of the Redwing). The appearance of motor coordina-

tions in the flycatchers, however, matches that of the European Redstart, which left the nest at 14 days. "The Redstart is appreciably slower than any of the others, the period of rapid development of motor coordinations coming some 4 days later than with the other birds. This is evidently correlated with the date of nest-leaving, *stage 3 starting some 3 days before this event in all the birds*" (Nice, 1943:59). In those species that leave the nest early, the development of coordinations is accelerated.

Observations of special interest on four activities were made.

1. Stretching Both Wings Down

Formerly I had seen this coordination in six passerine species (1943:44); it also occurred in the five under consideration here: Yellow Warbler, about eight and nine days; Red-winged Blackbird, about 10, and rarely to 19 days; Yellow-headed Blackbird, about 9 to 11; Least Flycatcher, 12 and 13; Eastern Wood Pewee, about 15 to 16. Nicolai (1956) gives a photograph of a 14-day Bullfinch in a nest stretching backwards with both wings at once. Andrew (1956a) reports this movement as seen occasionally in adult buntings, "although it was most common in Reed Bunting fledglings."

2. Exploratory Pecking

This was noted from the age of 12 to 14 days both in the birds reported in 1943 and in those of the new observations. At 12 and 13 days the Least Flycatchers pecked at the rim of their nest and at the supporting branch, and the Wood Pewees did likewise the day they left. The start of this behavior was spectacular in a Yellow-headed Blackbird at the estimated age of 14 days:

"June 27, 2:40 p.m. Exploratory pecking at last. He has looked at food and at insects, but has done nothing. Now, all of a sudden, he first pecks at my pen, then at the twigs of the Catbird nest, tugging and tugging. Works at a screw in the table. Pecks at my watch. 4:40. Tugged at the blackbird nest. Determined to perch on my head. 7:00. Picked up a bit of food."

The White-throats started to peck at objects on the 14th day (Sauer, 1954: 22) and the European Blackbirds on the 13th, but it was not until the 18th day that one actually picked up and swallowed food (Messmer, E. and I., 1956:413).

3. Leaving the Nest

The Yellow-heads hopped first and started walking from one to three days later; the Redwing hopped first and walked two days later.

This is characteristic of many passerines that habitually walk when adult (Nice, 1943:49).

The 14-day-old Least Flycatcher left the nest before 9:37; its 13-day nest mate fanned its wings on the edge of the nest. During the next 45 minutes it was very active in stretching and shaking and preening, while its parents brought it five meals. Once it hopped from one rim of the nest to the other. At 10:25 the female fed and left; the little bird climbed out and fluttered 10 inches up the branch. It then flew a foot to a small branch where it perched a bit unsteadily. A parent came to the nest, picked up two fecal sacs and left. The fledgling preened. At 10:32 it turned about and flew out of sight.

One of the Wood Pewee nestlings stepped out of the nest at 10:25 a.m. just after a feeding, but remained cuddled close to it. At 6:52 p.m. the nest was empty; the chicks were close together on a branch two feet away. The next day they had moved to a perch 10 feet above the nest and the following day to a neighboring tree some 35 feet distant.

4. Standing on One Leg

A Yellow-headed Blackbird first stood on one leg at the estimated age of 17 days. The Redwing occasionally stood on one foot at 12 days; four days later this coordination was well established. Bullfinches sleep standing on one leg three days after leaving the nest, i.e., at about 19 days (Nicolai, 1956). European Blackbirds were able to do so at 14 to 17 days (Messmer, E. and I., 1956:403), King Birds-of-Paradise on the 15th day (Bergman, 1957).

C. Summary

Five altricial nestlings were watched for 20 minutes to an hour after hatching. The Catbird gaped four times in the first 20 minutes, the Barn Swallow six times in the first half hour. During the first hour the Yellow Warbler gaped 27 times, the Yellow-headed Blackbird 55 times and the Song Sparrow 68 times. The first three birds were silent, while the last two chipped almost continuously.

Some observations on later stages in 12 individuals of five species are reported. Stretching of both wings down was seen in all the species. The sudden appearance of exploratory pecking in a Yellow-headed Blackbird is described. The Red-winged and Yellow-headed Blackbirds hopped before they walked. Notes are given on nest leaving of the Least Flycatchers and Eastern Wood Pewees. The ages are reported at which standing on one leg appeared in birds of five species.

CHAPTER XII

Comparison of Behavior Development in Some Precocial and Altricial Birds

Some aspects of behavior development in seven species of five vertebrates, including a precocial and an altricial bird, were briefly touched upon in Chapter II and summarized in Table 1. In Chapter IV five stages in this development are described for an altricial bird, the Song Sparrow, and analogies shown in Table 5 between its behavior development and that of a small altricial mammal, the white mouse. In Table 6 analogies are further shown between the development of the Song Sparrow and the precocial Spotted Sandpiper.

Chapters V through XI describe behavior development in examples of the eight categories of birds from the most precocial to altricial as found by us and others. It is now appropriate to summarize the findings of these chapters and to see what light they throw on the concept of these stages as a helpful device in organizing our thinking on the behavior development of many birds.

A. The Basic Motor Coordinations and Their Stages of Appearance

In studying the observations on our precocial and semi-precocial birds and also on the Song Sparrow, I found that 17 motor coordinations appeared in all the species on which records were adequate—ducks, Killdeer, Spotted Sandpiper, White Rock chickens, Virginia Rails, Soras, American Coots, Franklin's Gulls, and Song Sparrows. An eighteenth—play-fleeing—appeared in all but the coots and gulls. These coordinations are shown in Table 17 arranged according to the stages in which they characteristically appeared.

Fifteen of the coordinations appeared *in the same stages* in all the birds. Two came one stage earlier in the precocials and semi-precocials than in the altricials; scratching the head and exploratory pecking reflect the urgency for comparative independence in precocial birds. Play-fleeing started in some of the precocials in Stage IV—Killdeer, Spotted Sandpiper, Virginia Rail and Sora, but in Stage V with Brush Turkeys, ducks and White Rocks, as well as with Song Sparrows.

In Stages II and III the little bird must perfect locomotor abilities

TABLE 17

Stage of Appearance of Basic Motor Coordinations in the Precocials, Semi-Precocials and Altricials Studied

Stage	*All Species*	*Precocials and Semi-Precocials*	*Altricials*
II. Preliminary	Yawning Preening Standing on tarsi	Scratching head	
III. Transition	Crouching Stretching legs and wings Fanning wings Shaking self Standing on feet	Exploratory pecking	Scratching head
IV. Locomotory	Leaving nest Fleeing Picking up food Simple bathing	Play-fleeing (shorebirds, rails)	Exploratory pecking
V. Socialization	Aggression Matured bathing Flight	Play-fleeing (megapodes, ducks, White Rocks)	Play-fleeing

and start the care of its plumage. In Stage III it typically crouches at loud, harsh sounds. In Stage IV it leaves the nest, it starts to feed itself and is ready either to freeze or flee at the approach of an enemy. In Stage V it is ready to attack strangers; it perfects its bathing technique and its ability to fly. These are the main outlines, filled in with many other activities common to all and by special activities peculiar to each species or group of species.

The course of development runs parallel in all the birds, but with modifications adapted to the varying conditions of life of each species. Precocials and altricials pass through the same stages, but the latter are hatched in what corresponds to an embryonic condition in the former. Most of the coordinations of the precocials maturate before hatching, so that within a few hours of liberation from the egg the chick is

capable of leaving the nest, caring for its plumage, finding its own food (Precocials 1, 2 and 3), and responding with appropriate behavior to the threat of enemies.

B. Discussion of Some Behavior Patterns in Precocials and Altricials

Three behavior patterns will be discussed: imprinting, aggression and play-fleeing.

1. Imprinting in Precocials and Altricials

The rapid learning of the characters of the parent which occurs very early in the life of some precocial birds has been called imprinting *(Prägung)* by Lorenz (1935:163ff.). He states that this learning is confined to a very definite period of extremely short duration; that "once accomplished [it] is totally irreversible"; that it determines reactions that mature many months later, and that it "establishes a sort of consciousness of species in the young bird" (1937:264-265). Thus the object of social responses during immaturity may determine the object of sexual responses in maturity.

In his detailed discussion of this subject, Thorpe (1956) states that it has been shown to occur in some insects, fishes and mammals. Hess (1958) mentions imprinting of a number of precocial mammals—guinea pigs, sheep, goats, deer and buffalo; the following year (1959a) he gives a Table, rating the imprintability from poor to excellent of 20 kinds of fowl with which he has experimented.

a. *Imprinting in precocial birds.* Considerable research has been done on imprinting precocial birds. Geese have afforded some of the most striking cases, as reported by Heinroth (1911) and Lorenz (1949); typically the first moving object a gosling sees after hatching is adopted by it as parent-companion and this choice is adhered to steadfastly. Nevertheless, a Lesser White-fronted gosling, captured when between one and two weeks old, six days later followed human beings and continued its attachment to them (Steven, 1955). In Iceland the tendency of Pink-footed goslings to "regard human beings as their parents was frequently observed. On several occasions it was difficult to get away after marking a young brood without being followed by them." No age is specified. Whooper Swan cygnets "would sometimes follow humans even when at least a week old. Newly hatched cygnets usually

followed, and a hasty retreat was necessary if they were not to be led away from the nest" (Scott *et al.*, 1953).

With most Anseriformes it is a matter of life or death for the chicks to follow their mother closely. Velvet Scoters, normally nesting on small inland ponds where a strong child-mother attachment is not obligatory, lose the majority of their young when they colonize the seacoast (Koskimies, 1955, 1957). Pioneer experiments on imprinting ducklings were made by Fabricius (1951); he found the first 12 hours most favorable. At Delta I imprinted 12 ducklings of five species from hatching to about 12 hours by saying *kom kom kom* and moving my hand or myself away from them (1953). In a series of carefully planned tests on 92 Mallards Ramsay and Hess (1954) found that from 13 to 16 hours proved to be the best age for imprinting and that "only one duckling showed any imprinting beyond 24 hours." With baby chicks, 13 to 16 hours also proved to be the critical age (Hess, 1959b).

In a report on further ingenious experiments on ducklings, Hess (1958) showed that "the strength of imprinting appeared to be dependent not on the duration of the imprinting period but on the effort exerted by the duckling in following the imprinting object." He therefore proposes this formula: "the strength of imprinting equals the logarithm of the effort expended by the animal to get to the imprinting object during the imprinting period, or $I_s = \log E$" (1959a).

He suggests that this necessity of effort may be the explanation of the failure to imprint 30 Mallards exposed 48 hours before hatching to a constantly played tape recording of a female calling her young. It was "not possible for the animals still in the eggs to exert effort toward the source of sound" (1959c:59).

Except for Fabricius' and my studies, most experiments have dealt primarily with the first few days. Fabricius concerned himself constantly with his ducklings and they remained attached to him. Mine followed me until seven and 12 days old; but after an interim of five days they failed to respond. Fabricius wrote me that in later experiments "if our ducklings were not allowed to follow the model for at least about 15 minutes every day, they soon 'forgot' the following."

As to the lasting effects of imprinting young Anatidae on a different species there do not seem to be many examples, considering how often domestic ducklings are raised by domestic fowl. Lorenz (1937: 263) reports that a young Muscovy drake, raised along with his

sisters by Greylag Geese, attempted to copulate with Greylags. Another, raised by Lorenz with a brood of Mallards was sexually imprinted on Mallards (1935:173). A drake Goldeneye, raised in a zoo with Mallards and Pochards, ignored a hen of his own species and courted a Mallard, seizing her rightful mate by diving underneath him (Bernhardt, 1940). Thus in one case the bird's sexual behavior was switched to the species of the foster parent, in two to a species of the foster brood mate.

A European Oystercatcher, hatched and reared by a Silkie Fowl, had no opportunity to meet with its own species. "When mature it 'trilled' frequently at Silkie Fowls but not at any other species of bird" (Rollin, 1957).

The Heinroths, when raising European Curlews, found the young shy, and Lorenz (1937:267) concluded that this species possessed innate releasing mechanisms responding specifically to stimuli from its own parent. Seitz (1950), however, thought that the Heinroths' Curlews were frightened by the large size of their caretakers; he therefore kept two hatchlings separately in cages from which one could see only his head, the other the upper part of his body; both accepted him as their parent. Finally, four of Otto von Frisch's (1956) Curlew chicks became attached to him and remained tame to adulthood, even although three of them had been with their parents from 18 hours to four or five days. Two others, one hatched in the incubator, the other taken from the nest before it was dry, were always shy. The author explains the difference as due to his own behavior: he spent much time with those that became tame and very little with the others. From a curlew egg placed in a Lapwing nest, there hatched a chick that accepted its foster mother. Moreover, none of his chicks paid any attention to mounted specimens of adult Curlews, nor to the captive year-old birds of this species.

In 1873 Spalding wrote: "Chickens as soon as they are able to walk will follow any moving object. And, when guided by sight alone, they seem to have no more disposition to follow a hen than to follow a duck, or a human being." His chickens followed him for miles. A White Leghorn chick became imprinted on "an African gosling (a domestic breed of the Swan Goose)"; not only did it follow its parent-companion, but it learned to eat freshly cut grass and surprisingly, the phraseology and modulation "of its vocalizations became modified and resembled those of the gosling" (Klopfer, 1956).

My hand-raised Bobwhite (Nice, 1939) had the companionship of brothers and sisters for the first nine days of his life; this circumstance probably accounted for the fact that he accepted people as parent- and social-companions, but not as sex-companions.

The experiment by Hinde, Thorpe and Vince (1956) on "The following response of young Coots and Moorhens" hatched in incubators and reared in brooders showed that their subjects might follow "almost any moving object independently of any prior learning process." But Coots and Moorhens (gallinules) stay on territories and their young do not have to follow their parents closely; they wander about in the territory and swim to the parents for food. I do not feel that the authors were really investigating imprinting (Koehler, 1956; Nice, 1957). To study *following,* a species should be chosen that in nature is obliged to follow its parent. Many of the Coots we raised at Delta appeared to be imprinted on us; during their first day or two they sought our hands to nestle in and when resting in the nest-basin they customarily lay with their heads oriented towards us. When aged eight hours to two days they came dashing at my call of *kom-kom-kom.* They followed me along with the ducklings when aged from one to 12 days, but after a five-day interval, attempts to induce following met with no success.

Two Corncrakes were raised by the Heinroths (1924-33, III:218); the male courted Frau Heinroth, but when she stopped playing with him he mated with his sister.

In 1953 we raised Sora 4 with Spotty 1 and a Coot; the two former when five weeks old were given to the Philadelphia Zoo. Sora 4 was put in a large cage with a pool and marsh; here there were a variety of other birds including three adult Soras. Spotty 1 was placed in a different cage with a number of passerines, but in the late summer of 1955 she was transferred to the large cage where Sora 4 was busy attacking the Ruffs as they attempted to display.

On September 4 my daughter, Constance, wrote me: "When Midget [Sora 4] chased a Ruff, Spotty very definitely chased *him* and he retreated! She spread her tail wide, something I had not noticed before. She also chases the other Soras, but not fiercely, and they don't retreat so precipitately. I think it very possible that Spotty considers herself a Sora, although she does seem much interested in her image in the glass at the edge of the cage. I also think it possible that Midget considers

himself a Sandpiper. Otherwise why should he chase the Ruffs so persistently?"

Here the "brood mates" of two different avian orders may have become imprinted on each other.

b. *Imprinting in semi-altricial birds.* Two instances of this behavior are of interest. A Purple Heron, taken from the nest at about 10 days of age and raised by hand, courted his fosterer, building a nest with him and making copulatory attempts; he was consistently devoted to his human "mate" and hostile towards all other people (von Frisch, 1957). When less than a year old, the male Eagle Owl raised by the Heinroths (1924-33, II:34) courted Dr. Heinroth, while his sister courted Frau Heinroth; shortly afterwards both birds were given to the Berlin Zoo.

c. *Imprinting in altricial birds.* Lorenz (1935:171) points out the difficulty in deciding when imprinting takes place in altricial birds. He once took six Jackdaws nearly ready to leave the nest and three that were still unfeathered; all begged from him and were equally tame while still dependent on him, but afterwards the older ones became shy whereas the younger ones courted him.

Whitman (1919) was able to hybridize many species of pigeons by letting birds be reared by foster-parents. Goodwin (1948b) on the contrary, found that "the young bird may be influenced in this direction by species which it habitually sees in its neighborhood, even if they have never stood in the 'parent-companion' (to use Lorenz's term) relationship to it." Thus, a Turtle-dove, Wood-pigeon and Magpie, raised by their own parents for 10, about 12 and about 14 days respectively and after that by hand, all sought mates among Domestic Pigeons which they saw and heard about them. A male Domestic Pigeon, however, raised by its parents for seven days, then by hand along with two Stock Doves mated the following spring with one of the latter.

Lovie Whitaker writes me that she found imprinting occurred when the baby bird was raised without a fellow member of its species. A Mourning Dove raised alone adopted her as its mate, while two others, taken even earlier and raised together, were just as tame as the first dove but never reacted sexually to her. "A Pyrrhuloxia," she wrote me, "raised with a baby Desert Sparrow adopted me, while two others raised together did not, though these were tame throughout their lives."

Bullfinches reared in isolation become very attached to their care-

takers, but if given mates of their own species during their first winter they make a normal adjustment. However, if kept exclusively with people, it "later accepts one of them as a permanent mate. It is only then that the sexual imprinting to humans has become irreversible. Males reared in isolation behave very tenderly to their human partner, attempt to feed him and are strongly personally attached to him. . . . Females are very aggressive and furiously attack humans" (Nicolai, 1956).

Song Sparrows, when taken from the nest at five or six days of age, accepted us as parent-companions for about a month, but after that lost their attachment to us. A male Eastern Meadowlark, rescued from a dog before it was ready to leave the nest, was raised as a pet by a family who gave him to me at the age of approximately 10 weeks. He never saw his own species after his rescue and very few other birds while with us. In the spring he adopted me as his mate.

It would seem as if altricials in general become imprinted on their parents while in the nest, although with nest parasites, such as European Cuckoos, Cowbirds, and Honey-guides, the knowledge of species must come after independence from foster-parental care. Most altricials must be primarily imprinted—to the parents—while in the nest, probably in Stage III, but learning characters of the sex partner may come later, as shown by Goodwin's observations on pigeons and a Magpie, and Nicolai's on Bullfinches.

d. *Some conclusions.* Imprinting is primarily concerned with learning the characters of the parent-companion, and secondarily with learning the characters of the future sex-companion. It has been found that much imprinting needs reinforcement and that cases of birds preferring the wrong species as their mates usually involve long continued association of the two species. Imprinting is clearly less irreversible than Lorenz at first believed. Birds raised alone are more prone to imprinting that determines a wrong species of sex partner than are those raised with brood mates.

At what stage does imprinting occur with precocials? Typically it would seem at the end of III and start of IV. Hess (1959c) states that the critical age for imprinting comes just before the onset of fear. His criterion was the response of the chick to the first *sight* of an imprinting object. Alley and Boyd (1950) concluded from their experiments with Black Coot chicks during the first eight hours that "apparently in very young birds alarm is a response to an auditory releaser."

This was also our experience with our hand-raised chicks; in Stage III they crouched at loud, harsh sounds, but showed no fear of objects.

The only ones of our hand-raised birds at Delta that became wild were the Spotted Sandpipers in 1954; this occurred when they were four and six days old. The other chicks accepted us as parent-companions or food-dispensers, but with the exception of the 12 ducklings I deliberately imprinted in 1952, it is a question how many of the birds became "imprinted" on us. Certainly Killdeer 1, kept in constant contact with us for his first eight hours, showed not the slightest hesitation in accepting his own parents at the end of this period.

2. Aggression in Precocials and Altricials

The first appearance of aggression is one of the chief criteria of Stage V—Socialization. This was true of Song Sparrows and a Cowbird at 17 and 18 days, Chaffinches at 21 days (Marler, 1956) and of King Birds-of-Paradise at 15 and 16 days (Bergman, 1957). With the precocial and semi-precocial birds it appeared early in some of the most precocious of the former: at two days in one megapode, five days in another; at 29 hours in a Ruddy duckling, and three to seven days in other ducklings, as well as in species where the adults are particularly aggressive: at 41 hours in a Coot (typically at five days), at four to six days in Franklin's Gulls and three days in Sooty Terns. With the White Rocks it first appeared at six to seven days, with the shorebirds at seven and nine days, with the rails at 14 and 16 days.

The precocious Common Loon chicks in Beebe's (1907) care fought each other ferociously when two and four days old, and a two-day-old European Crane attacked its newly hatched nest mate furiously and continued its hostility so the two often had to be separated (Heinroth, O. and M., 1924-33, III:94).

With some semi-altricials and altricials a temporary spell of aggressiveness towards nest mates appears very soon after hatching. This has often been noted in certain eagles, in three species of which the older nestling seems rather regularly to dispose of the younger one. Wendland (1958) tells that the Lesser Spotted Eagle lays two eggs but only once have two young been known to have fledged; he found that the older nestling squatted on top of the younger and thus prevented its being fed. When removed by the observer "Cain" crawled

about and once again sat upon the three-to-four-day-younger "Abel." The maltreatment of the younger Verreaux's Eagle by the three-day-older nest mate is told in text and Table by Rowe (1947:582). During 40 hours' watching during the week of C2's life there were 36 attacks and 10 "squats" by C1. On its first day C2 fought back, but the next day it soon tired. "Pecking C2 on neck, back and wings, C1 several times gripped it with its bill and shook it as a terrier shakes a rat." Both "fights and squats were specially related to meals. Either C1 would interrupt its own meal to savage C2 and often squat on it and continue its own meal in that position, or C1 would wake up to find C2 being fed and immediately attack it." No wonder the younger chick succumbed to "maltreatment, starvation and exposure."

Sumner (1934:345) describes the behavior of the elder Golden Eagle chick shortly after the younger had hatched. The former, which weighed almost exactly twice as much as the smaller, "would dig its beak into its nest mate with a force and energy out of all proportion to its size. Repeatedly it dug and pulled, until pieces of down were scattered through the air and the helpless victim was yelling its loudest. . . . I was impressed by the singularly mechanical, almost reflexive aspect of the performance, and by its remarkably slight resemblance to the behavior of other young birds which are merely hungry." Sumner, Wendland, and Ingram (1959) cite many references to this subject in young raptors. The last author considers it a beneficial device in hawks and owls, ensuring the survival of a few healthy birds in times of scarcity, but he fails to see its utility among eagles "which lay only two, or at most three, eggs."

The Greater and Lesser Honey-guides are parasitic on hole-nesting birds; the bills of the newly hatched nestlings possess sharp hooks at the tip. A two-day-old Lesser Honey-guide bit its Black-collared Barbet nest mate "savagely in great gasping bites, the jaws widely opened in its attacks"; three days later the victim was dead (Friedmann, 1955:206).

Wendland speaks of the behavior of the Lesser Spotted Eagle as an inborn drive, comparable to similar actions in the European Cuckoo. Sumner's description bears out this instinctive aspect. In the eagles, the Cuckoo, and the Honey-guides, this drive to eliminate competition appears at or very soon after hatching and later disappears. Hence it seems to be a special kind of "aggression," different from that appearing in the birds watched by us in Stage V.

3. Play-fleeing in Precocials and Altricials

In 1943 (pp. 51, 67) I called the chief form of play in the young Song Sparrows "frolicking." This behavior appeared first in the hand-raised birds at 17 and 18 days, was indulged in during all that first fall and occasionally practiced to the age of three years. It was also noted in young Song Sparrows in the wild. It "is characterized by sudden, rapid runs or flights with sharp turns." Konrad Lorenz wrote me:

"Most of what you describe as frolicking are emotion-dissociated fleeing movements! The most impressive instance of such frolicking is the pre-bathing play of Anatidae. They do every single stunt that is applied when the eagle is behind them—diving and taking wing at the very moment of emerging and taking a header from the air right under the surface, with a long under-water swim following, and last, but not least, repeated performance of *Hakenschlagen*—'hooks' or sudden turns. Yet apparently the ducks and geese are not afraid, e.g., the whole performance is really dissociated from the emotion which is correlated with all these instinctive actions when they are used in earnest.

"One of the best examples of the playful fleeing-and-defense reactions can be found in smaller stork species. When Black Storks and most of all the small African Abdim *(Abdimia abdimi)* are let out into a larger enclosure (so that the situation is absolutely that of frolicking), they begin a curious dance, evading by 'hooks' and sudden ducking the non-existent attacks of an imaginary eagle, even thrusting at him vertically upward with their bills. The fact that their coordinations of movement are calculated at an enemy attacking from above is very apparent."

"Frolicking" was not a good term. This is shown by Guhl's (1958) use of the word in regard to White Leghorn chicks—"a spontaneous activity in which individuals ran briefly with wings raised. . . . By the second week frolicking led to sparring."

The distinctive character of what I called "frolicking" lies in the *sharp turns* made by the animal. In discussing different types of play of young animals—fighting, hunting and fleeing—Eibl-Eibesfeldt (1950a:345) states that in his opinion every sudden change of direction is in itself an inborn movement of fleeing. "Play-fleeing" would seem a good word to denote this activity.

Play-fleeing has been reported in a number of young mammals belonging to prey species, such as Norway rats (Eibl-Eibesfeldt, 1950b:581), rabbits, badger, roe-deer, horses (Eibl-Eibesfeldt, 1950a: 345-352), and a six-day snowshoe hare (Nice *et al.,* 1956). Darling (1937:87) describes play of red deer consisting in sudden turns of direction; "in ungulates play may take . . . the . . . form of evading capture."

In our experience with precocial birds we saw play-fleeing in ducks, a Killdeer, Spotted Sandpipers, domestic chickens, a Bobwhite, and Virginia and Sora Rails. We did not note it in our grebes, Coots or gulls, nor does it seem to have been reported by others who have watched these species in the wild. It has been described in the Brush Turkey and in two genera of storks.

Surprisingly enough it also occurred in two young Ostriches in the Zoo at Basle: from their fifth week on, when let out in their yard they would turn themselves from one to four times in one direction and then in the other, then start rushing zig-zagging around, turning themselves about (Brinkmann and Haefelfinger, 1954).

In the semi-altricial California Condor at eight weeks Koford (1953:114) described jumping up and down and turning completely around, actions he considered "analogous to what Nice (1943:51) calls 'frolicking' and an evidence of 'surplus of energy.'" "Frolicking often ensued when the juvenile seemed to be frustrated by its inability to reach some higher perch." Whether or not this behavior should be considered analogous to play-fleeing is a question.

With passerines I have seen play-fleeing only in Song Sparrows (both wild and hand-raised) and in a hand-raised Eastern Meadowlark.

It has been noted most often in the Anatidae and Phasianidae (six genera). It has been recorded in many species of seven orders. It often seems to be a juvenile manifestation, but is carried on to maturity in some birds, for instance the two passerine species. With Anatidae it has been incorporated into a regular part of the bathing technique.

C. Summary

Seventeen basic coordinations were found in the precocial and semi-precocial birds watched as well as in the Song Sparrow.

An eighteenth—play-fleeing—was observed in all but the grebes, Coots and Franklin's Gulls.

Fifteen appeared in the same stages in all the birds as shown in Table 17.

Imprinting is concerned primarily with learning the characters of the parent, secondarily with learning the characters of the sex-companion. Many experiments have been made on primary imprinting with precocial birds, but very few on this subject with altricials.

The first appearance of aggression is one of the key coordinations for the start of Stage V—Socialization. Aggression toward strangers appeared early in pugnacious species. It appears a few days after hatching in some cranes, loons, and eagles and is directed toward newly hatched nest mates.

Play-fleeing, which in 1943 I called "frolicking," is characterized by sudden, sharp turns. It has been recorded in mammals of prey species and in seven avian orders.

CHAPTER XIII

Embryological Development in Precox and Altrix

We have compared behavioral development of precocial and altricial birds; let us make a brief survey of some of the work published on some features of anatomical development.

In his detailed study "An Embryological Comparison of the Domestic Fowl and the Red-winged Blackbird," Daniel (1957) found a close correspondence between the development of the two species up to the time of the hatching of the blackbird. "Essentially both birds are equally well developed, both morphologically and physiologically, except possibly in the nervous and digestive systems, by twelve to thirteen days of incubation."

A. Precocial Embryos at Twelve to Thirteen Days

A 12- to 13-day precocial embryo may look very much like a newly hatched altricial nestling. This can be seen in Fabricius ab Aquapendente's (1621) illustration of the 12-day domestic chick embryo; the caption reads *"digiti difereti"* (toes separated). It is shown in the 12- and 14-day examples of Weller's (1957) series of photographs of Redhead embryos at two-day intervals.

McCabe and Hawkins (1946:37-42) give illustrations and descriptions for each of the 23 days of the embryonic life of the Gray Partridge. 10 days: "Front toes visible but not separated." 11 days: "Toes separated . . . feather papillae along entire back." 12 days: "Live embryo is able to open and close the mandibles and to move its limbs." Feather papillae on dorsal surface elongate. "Nostrils formed. . . . Toes and legs finely scaled." 13 days: "auditory opening visible." (For the Domestic Fowl see Romanoff, 1960).

B. Comparison of Internal Organs

"The spinalis and biventer muscles, used to extend the head and neck, may be heavier in the Red-wing" at the time of hatching than in the 12-day chick embryo, "possibly correlated with their use in breaking the shell," and "their immediate need in food-getting" (Daniel, 1957:353). This author also found the digestive tract better developed

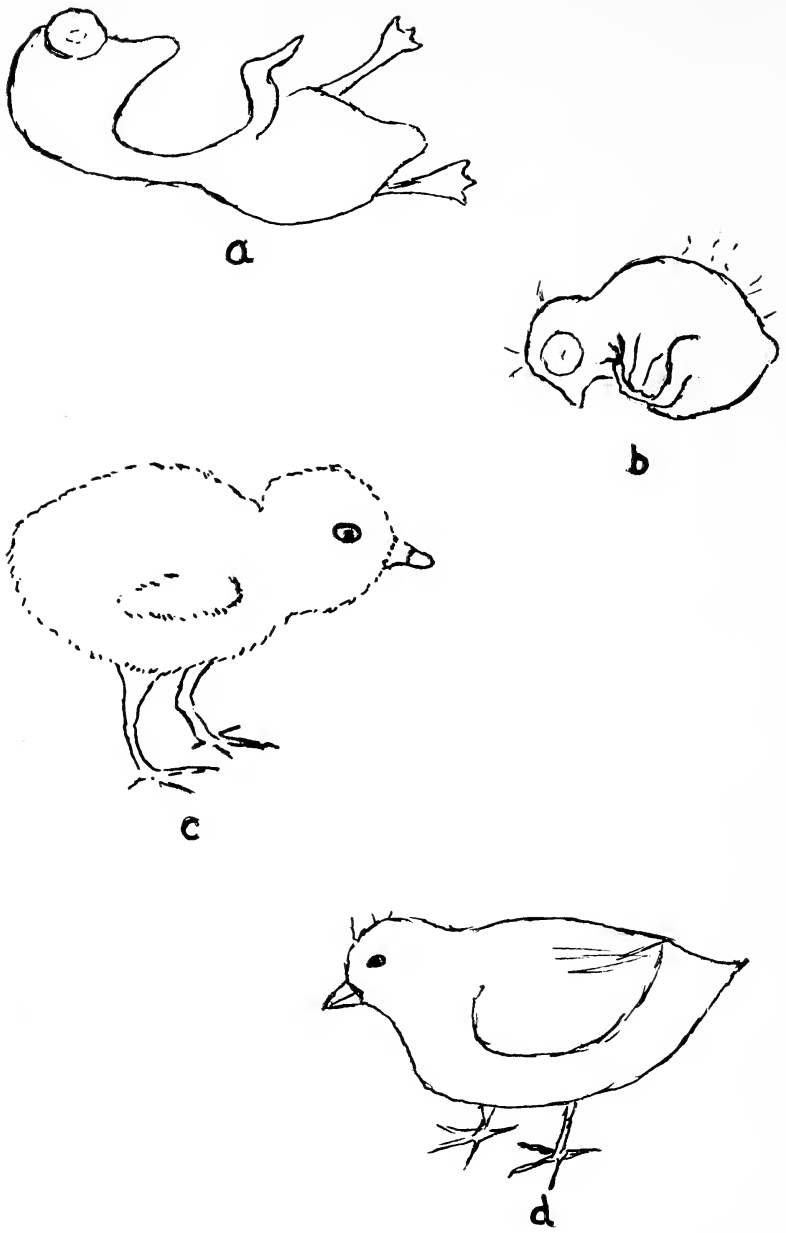

Figure 19. PRECOCIAL EMBRYO and NEWLY HATCHED ALTRICIAL; 3-DAY PRECOCIAL and 14-DAY ALTRICIAL. *a*, Redhead embryo of 12 days; *b*, Brown-headed Cowbird, newly hatched; *c*, Virginia Rail, 3 days; *d*, Song Sparrow, 14 days.

in the hatching Red-wing than in the domestic chick of like age. He points out that "without a doubt the nervous system is the seat of the greatest developmental discrepancies" (p. 345).

Portmann (1947) in his Table II compares percentages of total body weight of various organs in 10 newly hatched species, each precocial species (without its yolk) matching in weight an altricial species. The figures for digestive tubes ranged from 6.1 to 10.5 per cent for the precocials and 10.3 to 14.6 per cent for the altricials, whereas those for the brain ranged from 5.3 to 7.2 per cent for the precocials and 2.9 to 3.6 per cent for the altricials. Since the main business for altricial nestlings is to sit, ingest vast amounts of food, and grow—many of them reaching in the process weights greater than their parents—the need for heavy development of the digestive tracts is clear. On the other hand, this kind of life calls for little exercise of brain power.

In his paper on "Growth and differentiation of the brain in nidifugous and nidicolous birds," Sutter (1951) shows Portmann's Table in a graph and supplies photographs and sketches of the brains of precocial and altricial birds at hatching and maturity. "The cerebellum of the hatching Starling (incubation period 13 days) corresponds to that of a 12 day old chick embryo. Myelinated fibres are not yet formed. In the newly hatched chick (incubation period 21 days) we find a cerebellum, which does not differ essentially from the adult one. . . . The nestling of *Sturnus* does not reach an adequate point of myelinisation till at the age of 12 days." Both Portmann and Sutter emphasize the fact that adult precocial birds have relatively smaller brains than do adult altricials.

C. Newly Hatched Precocials and Altricials of Like Age

To turn to the newly hatched precocial, in many ways a Bobwhite that has just left the nest corresponds well with a Song Sparrow one day out of the nest (Nice, 1943:73). Witschi (1956) compares the embryonic and post-embryonic stages of House Sparrow and domestic chick, finding fair correspondence; the newly hatched sparrow at 13 days from start of incubation closely resembles the embryonic chick of 14 or 15 days, except that the former is entirely naked. At "total age of 21 days the nestling sparrow and the hatching chick have attained corresponding stages of differentiation." One week later,

both are able to fly to some extent (probably his chick belonged to a Mediterranean breed).

Daniel suggests that "The nidicolous birds, arriving later in the avian evolutionary sequence, could have evolved a twelve- to thirteen-day incubation period, because the ancestral nidifugous forms were in essentially hatchable condition at that age. There, the opportunity existed to select the shorter incubation time from the longer" (1957: 354).

D. Summary

When comparing species with rapid development, a marked correspondence is found between a precocial embryo aged 12 to 13 days and a newly hatched altricial.

The digestive system is more highly developed in the altricial than in the precocial bird. Attention is called to the work of Portmann and Sutter on comparison of the brains of precocials and altricials.

Precocials a day old may resemble in many respects altricials a day or two out of the nest.

CHAPTER XIV

Development of Temperature Regulation in Birds

Birds have the highest body temperatures of any animals. Minimum temperatures of 29 passerine species was found to be 40.4°C. (Baldwin and Kendeigh, 1932), and of 311 passerines of 42 species 40.6°C. (105°F.) and of 90 Charadriiformes of 13 species 40.09°C. (104°F.) (Udvardy, 1953).

Homeothermy is acquired during development. With altricial species it is not present at hatching, and young nestlings can withstand considerable exposure to low temperatures without damage. In the first two days after hatching Field and Chipping Sparrows tolerated body temperatures as low as 15°C. (60°F.) for an hour without harm (Dawson and Evans, 1957). The temperatures of semi-altricial Snowy Owls during the first two days of life dropped to 25° and 29°C. after half-hour absences of their mother; at 11 and 12 days they remained at 36.6° after 20 minutes without brooding (Barth, 1949).

Precocial species, however, are hatched possessing a greater or lesser degree of homeothermy. The start of temperature regulation in the egg after about nine days of incubation has been reported for ducks (Meyer and Stresemann, 1928); domestic chickens (Romanoff, 1941); Ring-necked Pheasants (Odum, 1942, Westerskov, 1956); Turnstones and terns (Bergmann, 1946:44-45). On hatching, a few precocial birds need no outside heat, e.g., megapodes, while others need little, e.g., Ruddy Ducks and Ancient Murrelets. Most, however, are absolutely dependent for a while on parental brooding. Capercaillie chicks in bad weather may have to spend so much time keeping warm under their mother that they do not have enough time left to procure sufficient food for themselves (Höglund and Borg, 1955). It would be impossible for California Quail "to breed in a region where the fog did not disappear for a long enough period each day to allow adequate foraging on the part of the young" (Sumner, 1935:219).

A. Attainment of Temperature Regulation in Species That Develop Rapidly

Many small passerines nesting in the open develop extremely rapidly. Field and Chipping Sparrows at three days of age "showed

improved capacities for remaining warmer than their environment above 25°, but they behaved like younger nestlings when exposed to cooler temperatures. The improvement of temperature control noted on the third day after hatching marked the beginning of a trend toward homeothermy that was almost completed at fledging, at least in the temperature range studied [10° to 40°C.]. Birds 7 to 10 days old were essentially homeothermic" (Dawson and Evans, 1957:322).

Even in the Arctic, temperature control is attained at about seven to 10 days (Irving and Krog, 1956) with many small passerines, and these leave their nests at ages corresponding to those in temperate zones. A spell of bad weather occurring just about fledging time may result in mortality; for example, in Horned Larks in Colorado about nine days old (Kelso, 1931), and on Baffin Island "in or near their nests" (Sutton and Parmelee, 1954b); and many well-developed Water Pipits in their nests dead "from starvation or exposure or both" (Sutton and Parmelee, 1954a). The insect supply for the Baffin Island birds was sharply curtailed during severe weather so the pipits and larks were undernourished and probably unbrooded. In Columbus, Ohio, two Song Sparrows nine days old in one nest and a lone Cowbird 10 days old in another, died in cold, rainy weather when unbrooded; all were definitely retarded because of parental neglect in feeding.

Many of the investigators of this subject agree that homeothermy comparable to that of the adult is not attained for some time: in the House Wren "after the fall molt" (Kendeigh, 1939); in gulls "some time after fledging" (Barth, 1951); in domestic chickens, after the down has been well replaced by adult feathers (Randall, 1943), and not completely homeothermic till mature (Moreng and Schaffner, 1951). See also Ryser and Morrison (1954) on Ring-necked Pheasants.

Yet birds early attain a practical degree of temperature control, which enables them to leave the shelter of the nest or parental body without harm if the weather is not too unfavorable. Let us use as the criterion for attainment of this degree of temperature regulation the age at which the young birds are potentially independent of protection from cold or heat provided by parents and/or nest and siblings.

In Table 18 data are summarized on the ages of attainment of temperature regulation in six altricial and 15 precocial species. All of these birds develop more or less rapidly in the egg, and the altricials also in the nest. (For discussion of fundamental differences in rate of development of birds, as well as of mammals, see Nice [1954a] and

Nice *et al.* [1956].) The start and attainment of temperature regulation in the altricials are based on intensive studies involving taking of temperatures. With the precocials, the same is true with the eggs of the Turnstone, domestic fowl and Ring-necked Pheasant, and with chicks of the Capercaillie and California Gull. The ages of attainment of temperature control in all but these last two species are based on observation of the length of time the chicks were brooded.

In some cases chicks seek brooding for longer periods. Turnstone young are repulsed by their parents after they are two weeks old. Two Red-legged Partridges reared by a domestic hen were not brooded by her after 18 days, yet showed no check in growth, but partridge chicks raised by their parents in captivity sought brooding until five to six weeks of age (Goodwin, 1953:604).

With the altricial species, *counting from the beginning of incubation,* development of temperature control starts at about 15 days in the sparrows and at about 17 days in the other species, three of which are hole-nesters. It is attained at about 20 days in the sparrows and from 25 to 29 days in the others, the whole process having lasted some 5, 8, 10, 11 and 12 days. A female Anna's Hummingbird no longer brooded the young night or day by the time they were 12 days old, i.e., 28 days from the start of incubation; by means of a thermocouple in the nest it was found that at this age they had attained good temperature control at air temperatures of 15° to 25°C. (Howell and Dawson, 1954).

For only three of the precocial species in the Table have temperature records been made throughout incubation; from these experiments and also from those mentioned earlier it would seem probable that temperature control begins to develop fairly early in embryonic life with other precocials. With the Turnstone, development lasted some 28 days, with the domestic fowl and pheasant about 34. Shorebirds appear to have attained fair temperature control at 37 to 48 days from the start of incubation, the galliforms at about 44 to 45 days, and the Coot and California Gull at about 44.

The precocial genus with the shortest known incubation period is the Button-quail (belonging to the Gruiformes), namely 13 days (Heinroth, 1922:245; Hoesch, 1959). A number of species have been bred in captivity. The chicks of *Turnix atricollis* [*?-nigricollis*] weigh four grams at hatching and are fed by their father for many days; they need a great deal of parental brooding (Heinroth, 1922:197, 245). A

TABLE 18

AGE IN DAYS OF ATTAINMENT OF TEMPERATURE REGULATION

	From Hatching		*From Start of Incubation*				
	Temperature Control			*Temperature Control*			
	Begun	*Reached*	*Age when Hatched*	*Begun*	*Reached*	*Duration of development*	
Altricials							
Field Sparrow[1]	3.5	8.5	11.5	15	20	5	Dawson *et al.*, '57
Chipping Sparrow[1]	3.5	8.5	11.5	15	20	5	Dawson *et al.*, '57
Black-capped Chickadee[1]	4	12	13	17	25	8	Odum, '41
House Wren[1, 2, 3]	3	15	14	17	29	12	Kendeigh, '39
Red-backed Shrike[1, 4]	2	13	15	17	28	11	Böni, '42
Wryneck[1, 4]	4	14	13	17	27	10	Böni, '42
Range	2-4	8.5-15	11.5-15	15-17	20-29	5-12	
Precocials							
Turnstone[2]	–14	14	23	*ca.*9	37	28	Bergman, '46
Redshank		17	23.5		40.5		Bergman, '46
Lapwing		17	25		42		Laven, B., '41
Curlew		14	29		43		v. Frisch, '56
Ringed Plover		22	24		46		Laven, H., '40
Piping Plover		20	28		48		Wilcox, '59
Domestic Fowl[2]	–12	24	21	*ca.*9	45	34	Romanoff, '41
Pheasant	–15	21	24	*ca.*9	45	34	Westerskov, '56
Red-leg Partridge		18	23.5		41.5		Goodwin, '53
California Quail		20	23.5		43.5		Sumner, '35
Sage Grouse		21	23.5		44.5		Girard, '37
Capercaillie[1, 5]		18	27		45		Höglund *et al.*, '55
Black Grouse		18	26		44		Koskimies, '57
American Coot		20	23.5		43.5		Hollister, '19
California Gull[1, 6]		*ca.*20	24		*ca.*44		Behle *et al.*, '57
Range	–12–15	14-24	21-29	*ca.*9	37-48	28-34	

For footnotes see opposite page.

South African Button-quail father brooded his chicks for the greater part of the day even with temperatures of 22°C. (72°F.) (Hoesch). After the age of 10 days chicks of this species were brooded only at night (Butler, 1905b). Painted Button-quails of southwestern Australia at 16 days "were perfectly feathered and capable of existence without their parent" (Seth-Smith, 1905). Yet Butler (1905a) reports that the Madagascar Button-quail chick ate almost unaided in the third week, "was moreover little brooded, but was still led about." At the end of the third week the chicks were fully feathered, in the fourth week they appear to separate from the adult. "Even in the fifth week the old male frequently took them under his wings." Thus for the attainment of a practical degree of temperature regulation from the start of incubation we have in this genus a minimum of 29 days from Seth-Smith and a longer indefinite period from Butler (1905a).

Megapodes are homeothermic at hatching. Although natives of hot regions, chicks of at least one species, the Scrub Turkey *(Alectura)* need no protection from cold when hatched in France (Delacour, 1935), or Berlin according to Heinroth (Böni, 1942:54). Information on the Mallee Fowl *(Leipoa)* was given me by letter by Harold J. Frith, Wildlife Survey Section, C.S.I.R.O., Canberra, Australia. The parents try to keep the temperature of their mounds close to 92°F.; the eggs hatch in about 57 days, but an egg laid in summer may hatch in 50 days, while with declining temperatures in autumn, incubation is prolonged, even to 78 or 90 days. "I incubated two eggs artificially at 100°F. and they hatched successfully at 44 days. However, both chicks were premature, having yolk sacs still attached but

Footnotes for Table 18

[1] Data on chicks based on taking of temperatures.

[2] Data on eggs based on taking of temperatures.

[3] "With a drop in air temperature, the body temperature of nestling house wrens also drops until an age of 15 days is reached" (Kendeigh, 1939).

[4] Based on Böni's Table III.

[5] Thirty Capercaillie chicks, hatched in an incubator and raised in a brooder, were tested every day for 50 days; their temperature rose continually until the age of 18 days when the normal body temperature of the adult—41.6°C. (107°F.)—was reached (Höglund and Borg, 1955).

[6] When the California Gulls studied at a colony on Great Salt Lake, Utah, by Behle and Goates (1957) reached a length of 12 inches at an estimated age of some 20 days, the cloacal temperatures were fairly stable.

otherwise normal. One survived; one did not. I feel sure eggs would hatch all right at about 46 days."

Romanoff (1960), working chiefly with domestic fowl, considers 37.5°C. (99.5°F.) "optimal" incubation temperature in general. If an egg of the Mallee Fowl weighing approximately 180 grams takes 45 days to hatch at temperatures comparable to those of the other species in the Table, how should it be classed as to rapidity or slowness of development? The only other egg of similar weight listed by Heinroth (1922) of one of the galliforms is that of the Curassow *(Crax globulosa);* this took 29 days to hatch. The Mallee Fowl embryo develops more slowly than those of a goose or crane, but faster than those of eagles or large vultures that take 45 and 55 days to hatch semi-altricial chicks. *Apparently the megapode needs about the same length of time to develop temperature control as do the seven other galliforms listed in the Table.*

B. Attainment of Temperature Regulation in Some Species That Develop Slowly

Experiments on temperature regulation have been carried out on Adélie Penguins by Sapin-Jaloustre (1951, 1955). The 130-gram egg hatches after 34 days into a semi-altricial chick; temperature control is attained at the age of 15 days.

Procellariiformes have protracted incubation periods: 40 days for the seven-gram egg of the Storm Petrel to 80 days for the Royal Albatross; about 56 days seems to be typical for many species. Eggs of two species have been found to hatch after days of cooling—five days in the Storm Petrel (Davis, 1957:99), seven in the Manx Shearwater (Matthews, 1954). Chicks of Wilson's Petrel fledged despite starvation periods due to snow blocking the burrows for as long as 11 and 20 days (Roberts, 1940). The body temperature of the adults is rather low: that of 10 Wilson's Petrels in the breeding season ranged from 36.5° to 40.5°C., averaging 38.8°C. (Roberts), that of 14 incubating Leach's Petrels ranged from 35.5° to 38.8°C., averaging 37.2°C., while that of six paired birds in burrows without eggs ranged from 37.7°C. to 39.9°C., averaging 39.0°C. (Folk, 1951). Each bird incubates three to four days at a time; Folk (1949) suggests that they may go into a stage of semi-torpidity (see Bartholomew *et al.,* 1957).

Leach's (Gross, 1935) and Storm Petrels (Davis, 1957:373),

both in the North Atlantic, are brooded by their parents for a week. Chicks of some species in the South Pacific are left alone very early. The Great-winged Petrel broods for only two to three days in the daytime; many nests are in the open and young may die in cold rains (Warham, 1956). Slender-billed Shearwaters (Farner and Serventy, 1959) and Wilson's Petrels (Roberts) almost never cover the chicks during the day after they are 48 hours old; air temperatures in the burrows of the first species averaged 22°C., and of the second ranged from 0° to 5°C.

Fifteen Slender-billed Shearwater chicks averaged temperatures of 37.9°C. on the first day, rose to 38.2°C. on the second, and soon stabilized at the temperature of the adults when in the burrows—about 38°C. Temperatures of the Wilson's Petrel chicks were 25°C., 27°C. on the first day, 28°C., 30°C. on the second, 32.8°C. on the fourth, and 36.5° to 37.5°C. from the seventh to fortieth day (Roberts, 1940:172). These chicks when forced to fast for extended periods must go into torpidity as do young European Swifts (Koskimies, 1948).

It would seem that these Procelariiformes chicks that need so little brooding must develop considerable temperature regulation during their long development in the egg.

C. Discussion

During five days on an island in the Gulf of California, Bartholomew and Dawson (1954) found that under severe conditions of radiant heat the varying degrees of temperature regulation of the chicks of an altricial, a semi-altricial and a semi-precocial species were compensated by different degrees of parental care—great in the Brown Pelican, somewhat less in the Great Blue Heron and only moderate in the Western Gull. "The degree of attentiveness of adults decreases as the homeothermy of their nestlings increases."

Development of temperature regulation is adapted to the conditions of life of the different birds. The altricial must have attained it by the time it leaves the nest, whereas with the precocial there is an advantage in slow development, because it prolongs the bond to the parent, to the advantage of the chick both in actual protection from enemies and in a certain amount of education as to the identity of enemies and in some cases choice of food (Nice, 1943:268). The rapidity of development of temperature control in altricials and its

leisurely pace in precocials go hand in hand with the rate of growth in the two categories of birds.

D. Summary

Homeothermy is acquired during development. In Table 18 information on this subject is summarized on 21 species that develop rapidly. In six small altricial species that have been carefully studied, temperature regulation starts several days after hatching and develops quickly, taking no more than five to 12 days. In 15 precocial species temperature regulation starts during incubation and develops comparatively slowly, taking from 28 to 34 days.

Reckoning *from the start of incubation* these altricials become independent of parental brooding and shading at about 20 to 29 days, the precocials at about 37 to 48 days.

The Button-quail with the shortest known incubation period for a precocial bird—13 days—is reported as becoming independent at only 16 days after hatching, although in one case a longer, rather indefinite period is noted.

Megapodes are homeothermic at hatching, even when transplanted to cool climates. Under natural conditions incubation lasts about 57 days at 92°F. (33.3°C.), but eggs artificially incubated at 100°F. (37.8°C.), hatched in 44 days, a period similar to that needed by several other galliforms for the attainment of temperature regulation.

Petrels have very long incubation periods; temperature regulation in a number of species is established a few days after hatching.

With many precocials the comparatively slow development of temperature regulation constitutes a strong bond to the parent.

GENERAL SUMMARY

The most significant points in the 14 chapters follow.

I. Among living creatures two chief methods have evolved for the perpetuation of species: many offspring and no care; few offspring and care. The more efficient the parents, the more helpless are the young. In all the main animal phyla some forms show parental care. The primary functions of this care are defense and provision of nourishment; secondary functions are provision of heat, guidance and sanitation. Strange devices have been evolved in invertebrates and vertebrates to care for the young. Parental care is best developed in some insects, some fishes, and in all birds and mammals.

II. Table 1 summarizes various aspects of development in five precocial animals—a fish, amphibian, reptile, bird, and mammal—and in an altricial bird and mammal. Reports on the early behavior of some very precocial mammals are noted.

III. In an attempt to clarify concepts of precocial and altricial and the intermediate stages, Table 2 divides birds into eight classes from the most precocial to the fully altricial. In Table 3 relative precocity of hatchlings is listed for all the orders of living birds (as listed by Wetmore, 1951) and for most of the families in eight of the orders. Percentage of yolk in fresh eggs decreases from about 60 in megapodes to about 20 in altricials.

IV. Five stages in behavior development are described and compared in an altricial bird and altricial mammal, and in an altricial and a precocial bird.

V. Megapode eggs receive much parental attention, the chicks get none. The chief condition underlying their greater independence than that of other precocials is their hatching with well-developed temperature regulation.

VI. As examples of precocial chicks that find their own food, yet follow their parents, we watched 39 ducklings of 12 species, four Killdeer, and five Spotted Sandpipers. The ages are given for the appearance of 17 coordinations for the ducks, of 35 for the plover, and 27 for the sandpiper. Bobbing was first seen at 51 minutes with a Killdeer; teetering at 29 and 31 minutes with two sandpipers. Head-scratching and foot-patting in plover and other birds are discussed.

VII. Large numbers of domestic chicks were watched as examples of precocial chicks that are shown food by their parents. The ages are

given at which 22 coordinations appeared. Scratching on the ground, rushing away with large morsels, play-fighting, dust-bathing, play-fleeing, and escape responses are discussed for these and other species.

VIII. The precocial chicks we watched that follow parents and are fed by them were three species of grebes and three of rails. All the grebes were very active from hatching. Ages are given at which seven coordinations appeared. Time of appearance of 26 coordinations is shown for five Virginia Rails, of 36 for 11 Soras, and of 25 for 23 Coots. The early behavior of these three rails is compared. Social preening in these and other species is discussed, as well as diving in connection with bathing by the Soras and a King Rail, and the peculiar wing postures assumed by rails in sunning themselves.

IX. Semi-precocial chicks are physically able to move at an early age, but owing principally to the nature of their food remain on or near the nest. The ages at which 25 coordinations were first seen in 17 Franklin's Gulls are given. Three Forster's Terns were hatched by us; behavioral development of other species of terns is summarized.

X. Semi-altricial chicks are unable to leave the nest, but are well covered with down. Herons and hawks are hatched with open eyes, owls with closed eyes. We watched one American Bittern hatch. The development of behavior of the California Condor is summarized from Koford's (1953) monograph.

XI. Altricial chicks are unable to leave the nest and are covered with little or no down. Five passerine species were watched for 20 minutes to an hour after hatching. The Yellow Warbler gaped 27 times in the first hour, the Yellow-headed Blackbird 55 times and the Song Sparrow 68 times. The first was silent but the other two chipped almost constantly.

XII. Seventeen basic coordinations were shown by our precocial, semi-precocial, and altricial birds; fifteen of these appeared in the same stages in all the birds. The subjects of imprinting, aggression, and play-fleeing are discussed in precocial and altricial birds and in other animals.

XIII. Among species with rapid development, a precocial embryo of 12 to 13 days corresponds in many respects to a newly hatched altricial chick after an incubation period of this length. Day-old precocial chicks resemble in many ways an altricial bird a day or two out of the nest, both being approximately the same age from the start of incubation.

XIV. All chicks but megapodes need parental heat. In altricials that develop rapidly, temperature regulation starts several days after hatching and attains a fair degree of control at the time of nest-leaving, the process lasting from five to 12 days in six species that have been studied. With precocials that develop rapidly, temperature regulation begins during incubation and is sufficiently developed for independence at two to three weeks after hatching, the process lasting about 28 to 34 days in three species where this subject was investigated. The comparatively slow development in precocial birds prolongs the bond to the parent. From the start of incubation the altricials attained temperature control at 20 to 29 days, the precocials at 37 to 48 days. Megapode eggs artificially incubated at 100°F. hatched in 44 days, so apparently, under similar incubation temperatures, temperature regulation would be attained at about the same age (from the start of incubation) as in other galliforms. Petrels have very long incubation periods; in two North Atlantic species temperature regulation was fairly well established at seven days, in three South Pacific species at two to three days.

To sum up: The behavior patterns of these precocial, semi-precocial, semi-altricial and altricial birds have been found to develop in a regular order of sequence with basic likenesses between the different categories of birds, as well as with some other vertebrates. Our studies have given us a glimpse into the fundamental kinship of all life, into the unity in its infinite diversity.

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Editorial Committee

The members of the Editorial Committee for the years 1960 to 1962, who participated in the preparation for publication of this volume of the *Transactions,* were Robert S. Arbib, Jr., Paul A. Buckley, Geoffrey Carleton, Eugene Eisenmann, Lisa McGaw, Theodora Nelson, and Joshua Wallman. Helpful comments and suggestions were received from Marjorie P. Chamberlain, Helen Hays, Wesley Lanyon, and Helen J. Williams. I am grateful for all their help.

—Anne W. Wachenfeld, *Editor*

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