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FLAVOUR-MEAL SIZE CONDITIONING IN THE RAT (*RATTUS NORVEGICUS*): FAILURE TO CONFIRM SOME EARLIER FINDINGS

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ABSTRACT: A series of experiments was carried out in order to explore further the possibility that hungry rats, both mature and weanling, might learn to associate flavours with different sizes of meals made from the same diet. The general procedure used involved providing rats with either a large meal (e.g. 5 gm), usually consisting of wet mash with an added flavour such as anise, or a small meal (e.g. 1 gm) of the same diet with a second flavour such as vanilla added, on alternate days. Following a number of such discrimination training days, subjects were given a two-jar extinction choice test to assess their relative preferences for the two flavours. It was originally anticipated that rats would come to prefer the flavour associated with the larger meal (i.e., conditioned appetite), because the larger meal provided more calories. However, this result was never obtained. When a significant preference was acquired, this was for the flavour of the small meal instead, (i.e. conditioned satiety). The conditioned effects not only extinguished very rapidly but were also rather elusive at times. It is thought that the observed conditioned satiety effects were probably due to flavour-calorie rather than flavour-flavour associations.

A central theme in a number of current theories of food intake control is the idea that omnivores such as rats or human beings regulate their food intake on a short-term basis, that is, within a meal, by associating the caloric consequences of ingestion with the flavour of foods (e.g., Booth, 1985; Deutsch, 1987; Le Magnen, 1987). This phenomenon which is known as conditioned satiety is considered to be very important because it means that the omnivores do not necessarily have to wait until they have actually experienced the delayed results of digestion, namely, calories, before they terminate feeding. They can instead simply rely on their previous experience with familiar flavours

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as cues for satiety. Accordingly, inability to make such associations may be responsible for inducing some pressing human problems such as obesity (Booth & Mather, 1978), alcoholism (Deems, Oetting, Sherman & Garcia, 1986) and drug withdrawal problems (Le Magnen, Marfaing-Jallat & Miceli, 1980).

A complementary process known as conditioned appetite which also involves learning about flavour-food relationships has been implicated as a food selection mechanism on a more long term basis whereby omnivores choose their food after learning about the caloric values of different foods (Bolles, 1983; Bolles, Hayward & Crandall, 1981; Hayward, 1983; Mehiel & Bolles, 1984; Rozin, 1977). It is thought that rats are perhaps adept at learning about both of these types of conditioned preferences in much the same way as they acquire conditioned taste aversion (CTA) learning or bait shyness. In contrast to the very considerable and unequivocal evidence for CTA learning in rats which has been accumulated over the past three decades or so of research (see Riley & Tuck, 1985), evidence for positive conditioned flavour preferences, which include both conditioned satiety and conditioned appetite, is relatively less strong and unconvincing. This seems rather surprising in view of the fact that the idea of the involvement of such learning mechanisms in the regulation of feeding behaviour was originally proposed as early as 1955 by Le Magnen (see Le Magnen, 1969).

Although there is mounting evidence in support of the idea that rats are capable of learning about positive flavour preferences (e.g., Boakes & Lubart, 1988; Boakes, Rossi-Arnaud & Garcia-Hoz, 1987; Capaldi, Campbell, Sheffer & Bradford, 1987; Simbayi, 1987; Simbayi, Boakes & Burton, 1986) most of the evidence demonstrated conditioned appetite rather than conditioned satiety. It is interesting to note here that most of these studies had employed fluids such as glucose, saccharin and ethanol rather than solid food as reinforcers. In contrast, a relatively small number of studies have also demonstrated conditioned flavour preferences using solid food in other animals such as humans (e.g., Booth, Lee & McAleavey, 1976; Booth, Mather & Fuller, 1982) and chicks (e.g., see Capretta, 1961; Hogan, 1977, 1980). These studies could be considered more informative about conditioned preferences than those that used fluids as reinforcers, because most of the food of omnivores is in solid rather than liquid form.

The fact that the experimental demonstration of conditioned satiety has proved to be rather elusive has been hitherto acknowledged by Smith and Gibbs (1979). According to them, only two studies, one by Booth (1972) and the other by Booth and Davis (1973), had successfully

demonstrated conditioned satiety learning in rats. In his initial study, Booth (1972) found evidence for the ability of flavours to elicit conditioned satiety in rats. In this research, flavours were paired with high or low calorie diets during training and presented to the rats one at a time. During testing, when the two flavours were presented one at a time in isocaloric diets, the "low calorie" flavour was preferred more than the "high calorie" flavour. However, in a two stimulus preference test in which the flavours were presented simultaneously in isocaloric diets, the high-calorie flavour was preferred more than the low calorie flavour. This latter result demonstrated conditioned appetite. Similar findings have also been reported by Booth and Davis (1973). However, similar studies carried out by Bolles et al. (1981) and Hayward (1983) were only able to demonstrate conditioned appetite but not conditioned satiety. Perhaps even more interesting was Hayward's findings which also showed that young rats were capable of more diverse learning than adult rats.

The experiments reported in the present paper were undertaken in an attempt to explore further the positive conditioned flavour preference effects reported by Booth (1972), Bolles et al. (1981) and Hayward (1983) using wet solid food as a reinforcer. To test the validity of Hayward's (1983) developmental finding, conditioned flavour preferences were investigated in adult rats in Experiments 1, 2 and 4, and in rat pups in Experiment 3.

EXPERIMENT 1

This experiment was a partial replication of experiments carried out by Bolles et al. (1981), except for the following changes:

- a) The ratio of meal sizes was increased to 5:1 instead of 2:1. It was hoped that the ratio increment would serve to make the meal sizes more easily discriminable.
- b) To prevent rats from learning to anticipate or predict specific flavours during each subsequent training day, semi random presentations of flavour-meal size correlations replaced the alternating presentations every other day adopted by Bolles et al (1981).
- c) Control groups were added for which supplementary food (wet mash of standard laboratory chow) was made available 15 min after the

presentation of small meals. These control groups were somewhat similar to the Oral Group used in Bolles et al.'s (1981) Experiment 4 and were meant to equate the total caloric consequences of both meal sizes and thereby controlling for any possible confounding effects of differential hunger.

Basically, rats were given experience with two meal sizes of the same diet, each of which was marked by a distinctive flavour (anise oil or vanilla). Thus, the two distinctive flavours were correlated with the same pattern of oral cues and caloric density but different caloric consequences: that is, large meals yielded more calories than smaller ones. The conditioning of flavour preferences was assessed by the degree to which the animals tracked the flavours in an extinction choice test when they were no longer correlated with meal size.

METHOD

Animals

Twenty male hooded Lister rats were obtained from Sussex University's Laboratory of Experimental psychology breeding colony. They had been used previously in a food neophobia experiment but had no experience with either the reinforcer or flavours used in the present experiment. The rats were fed for only 2 h each day beginning at 1500 hrs and were food deprived for the rest of the day except for 30 - 60 mins beginning at 1000 hrs each morning when training or testing was conducted. More importantly, the animals also had some previous experience with feeding from jars and their mean consumption time for 5 gm of wet unflavoured mash was about 5 min. The average age and weight of the rats at the beginning of the experiment were 100 days and 250 gm respectively.

Materials

The experimental flavours, which were added to the chow diets, were made by adding 0.5 ml anise oil (Sigma London Chemical Company Limited, Poole, Dorset, England) and 2.0 ml vanilla (E.F. Langdale Ltd., New Addington, Surrey, England) extracts to 100 ml water. These flavour concentrations were chosen following a titration experiment which tested for sensitivity of rats to flavours relying on food neophobia as the dependent variable. Both the conditioning and testing diets consisted entirely of standard laboratory chow (Spratt's Expanded

Rodent Diet, Spiller's Limited, Newmarket, Suffolk, England) to which some water was added and yielded about 2 cal/gm.

All conditioning and testing was carried out in the animals' home cages where both the conditioning and testing diets were presented in feeding jars with holes in the lids large enough for the rats to insert their heads in order to reach the food. During testing the jars were attached in pairs to prevent rats from altering the position of each jar relative to the other. In addition, the pairing arrangement also made it possible to effectively counterbalance for any positional biases.

Experimental design

A 2 x 2 factorial design was used with large meal flavours (anise vs. vanilla) and supplementation (whether or not the animal had received supplementary food on small meal days during conditioning) as factors. The experiment had two major phases during which conditions were reversed. For each subject the treatments in each phase were identical except that the relation between flavour and meal size was reversed. Each phase consisted of two 8-day conditioning cycles, each of which were followed by a single test day. Finally, a 5-day interval separated the two phases during which no flavours were presented and the same food deprivation schedule as used in the actual experiment was also maintained.

Procedure

Conditioning involved presenting flavour-meal size correlations for blocks of 8 days in semi random order, that is, a total of 4 days with each flavour. The animals were randomly assigned to four equal groups ($n = 5$) namely, Groups V, VS, A and AS. Groups V and VS were presented with a large meal (5 gm) flavoured with 2.0 % vanilla on some days and a small meal (1 gm) flavoured with 0.5 % anise oil on other days. On the other hand, Groups A and AS were both presented with a large meal (5 gm) flavoured with 0.5 % anise oil on some days and a small meal (1 gm) flavoured with 2.0 % vanilla on the other days. However, in addition, Groups VS and AS also received a supplement of 4 gm of unflavoured plain chow (also in wet mash form) 15 min after consuming the small meals. On any given conditioning day, all the animals received the same flavour: for example, on a typical 'vanilla day', Group V and VS received large vanilla flavoured meals, while Groups A and AS received small vanilla flavoured meals, and only Group AS received the 4 gm of supplementary food after 15 min. The

flavoured meals used for conditioning were presented at 1000 hr while maintenance food was presented for 2 h beginning at 1500 hr.

Testing was done using a two jar extinction choice paradigm which involved comparing the consumption of two diets presented simultaneously in equal amounts in two feeding jars. Each jar contained 20 gm of either anise or vanilla flavoured food in wet mash form. Testing lasted for only 10 min beginning at 1000 hr on each test day. The positions of test foods were counterbalanced for each pair of animals to minimise any positional biases. The first test was done on Day 9 (Phase 1) after which the conditioning cycle was repeated for another 8 days. Then, another choice test followed on Day 23 (Phase 2).

In order to further demonstrate the consistency and resilience of the phenomenon under investigation, the above procedure was repeated exactly except that the flavours were reversed during Phase 2 as mentioned earlier. A 5-day interval was allowed to reduce the chances of rats confusing flavour-meal size pairings used in Phase 1. However, no tests were carried out to ascertain whether or not preferences had remained unchanged during the intervening period. Thus, during Phase 2 Groups V and VS were presented with anise-flavoured large meals on some days and vanilla-flavoured small meals on other days while Groups A and AS were presented with vanilla-flavoured large meals on some days and anise-flavoured small meals on other days. Note that these flavour meal size correlations are exactly the opposite to treatments given in Phase 1. In addition, Groups VS and AS were retained as controls as in Phase 1, and they both received supplements of 4 gm of unflavoured plain mash 15 min after the presentation of food on 'small meal' days. However, as in Phase I, Groups V and A did not receive any supplementary food on their small meal days.

Relative preferences for anise-flavoured food in the extinction choice tests which followed each 8 day training cycle were calculated in terms of percentages of total food consumption by each subject during each test as follows:

$$\text{Preference for anise (\%)} = 100 \times \frac{\text{intake of anise}}{\text{intake of both anise and vanilla}}$$

Data analysis

Data obtained during each of the two phases of the experiment were initially assessed using separate three way analyse of variance (ANOVA) with repeated measures, comprising large meal flavour (anise versus vanilla), supplementation (supplement versus no supplement) and test

session (Test 1 versus Test 2) as factors. In order to determine how flavour preferences shifted after each 8 day training cycle, data obtained during each of the two test sessions in each phase were also separately assessed using two way ANOVAs with large meal flavour and supplementation as factors.

RESULTS

During conditioning, all animals ate all of the portions of food given to them every day. The data obtained from the extinction choice tests carried out at the end of each of the four 8 day training cycles in Experiment 1 are illustrated in Figure 1. This figure shows that although all groups highly preferred vanilla compared with anise in all choice tests (as revealed by low anise preferences ranging from 2 % to 35 %), quite clear group differences could still be seen.

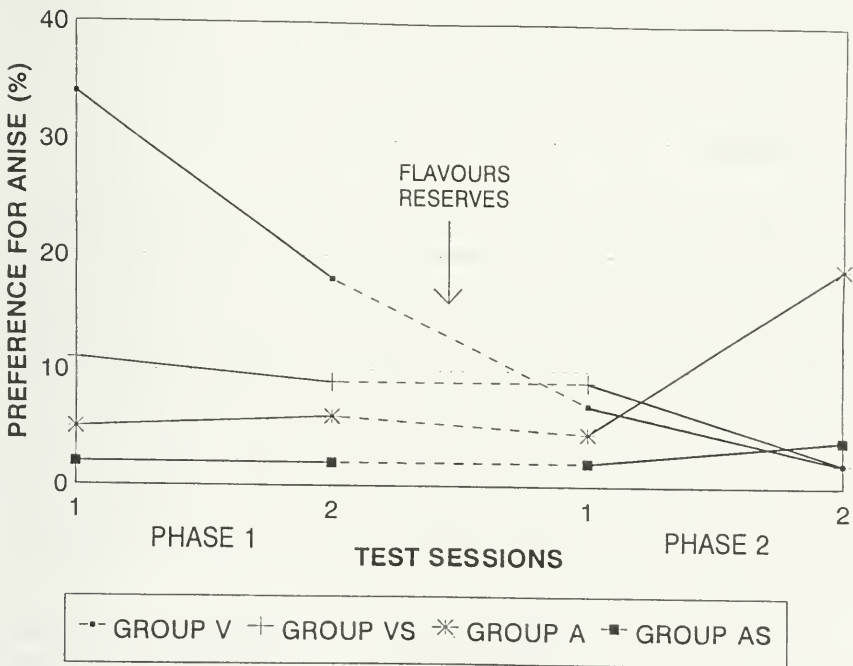


Figure 1. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 1 ($n = 5$). Note: Flavour-meal size pairings were reversed during Phase 2.

The ANOVAS performed on data obtained during each of the two phases of the experiment revealed a significant main effect of large meal flavour during Phase 1 only, $F(3,16) = 5.69$, $p < 0.01$. As can be clearly seen in Figure 1, this indicates that both Groups V and VS consumed significantly more anise-flavoured food than Groups A and AS during Phase 1. However, there were no such major flavour preference shifts observed during Phase 2 following reversal training, although the direction of the small preference shifts that had occurred was similar to that observed during Phase 1.

A two way ANOVA of data obtained during Test 1 of Phase 1 revealed reliable main effects of both large meal flavour and supplementation, $F(1, 16) = 8.17$ and 5.32 , $p < 0.01$ and 0.05 , respectively. However, there was no significant interaction between the two factors. As can also be clearly seen in Figure 1, supplementation of meals significantly reduced the magnitude of flavour preference shifts during Test 1. Another two way ANOVA of data obtained during Test 2 of Phase 1 revealed a significant main effect of large meal flavour only, $F(1,16) = 5.32$, $p < 0.05$. Similar statistical analyse of data obtained during each of the two tests in Phase 2 of the experiment failed to reveal any significant main effects or interactions.

DISCUSSION

Three main findings emerged from Experiment 1. Firstly, adult rats learned to prefer a particular flavour when it was previously correlated with small meals more than when the same flavour was correlated with larger ones. Secondly, supplementation of small meals initially slightly reduced the preferences for the flavour previously paired with the small meal, but had no effect on the preferences afterwards. Even though the rats had clearly a positive preference for vanilla and what appeared to be an unconditioned aversion to anise, it was also clear from the data that the flavour tracking effect was quite consistent throughout the experiment. Thirdly, although reverse flavour-meal size pairings reduced the preferences to non significance, they were still in the direction determined by meal sizes.

Although the first finding appears to be consistent with Booth's (1972) conditioned satiety findings, the extinction testing procedure which was used in the present experiment was different from that utilised by Booth. For instance, Booth's testing procedure involved presenting the two test flavours one at a time whereas in the present experiment the testing procedure involved simultaneous (or side by side)

presentation of the two test flavours. However, the same finding clearly contradicts reports by Bolles et al. (1981) and Hayward (1983) that adult rats can not learn taste preferences based on differing caloric outcome.

The second finding appears to be entirely consistent with those of Booth and Davis (1973) and Booth et al. (1982) who found that although the latter supplements failed to condition meal size per se, they did actually manage to condition flavour preferences. Finally, the third finding could be explained in terms of either overshadowing or proactive interference (or inhibition) of the subsequent learning during Phase 2 by learning which took place earlier during Phase 1.

EXPERIMENT 2

One criticism of the conditioned satiety hypothesis, namely that the animal will prefer the flavour not associated with satiety, is that it might instead avoid the flavour with a prolonged exposure due to an acquired aversion. In order to rule out this possibility, in Experiment 2 flavours were presented for an equal amount of time but were followed or preceded by different sized supplements. Therefore, for one half of the subjects, one flavour was followed by 4 gm while a second flavour was followed by 1 gm of plain mash. Hence, this procedure controlled both for flavour exposure time and for the disturbance factor involved when supplements are given after the presentation of flavour cues. Another important issue concerns the extent to which the relationship between the flavour cue and the caloric supplement could also be important, since cues presented at meal onset may have a different value compared with those at the end of the meal. In order to investigate this issue flavour cues were preceded by supplements for the remaining half of the experimental subjects. This allowed comparisons to be made to examine the extent to which conditioned satiety depended upon the relative temporal positions of flavour cues and supplements.

METHOD

Animals and materials

The subjects consisted of 24 male hooded Lister rats obtained from the same breeding colony as in the previous experiment. They were aged about 160 days and weighed 325 - 480 gm at the beginning of the experiment. The rats had previously been used in another flavour

conditioning experiment employing the Holman (1975) procedure using delayed reinforcement (Simbayi, 1987), but had no experience with the solid reinforcer, the two flavours (i.e., vanilla and anise) and the conditioning procedure used in this experiment. The subjects were allowed about 4 weeks of ad libitum feeding prior to being given another 2 weeks to adjust to new housing conditions and a new feeding schedule similar to that used in Experiment 1. In addition, they were allowed 6 days to accommodate to feeding on wet chow from feeding jars placed inside their individual cages before the actual experiment began.

All the materials used were similar to those used in Experiment 1.

Procedure

The rats were housed, watered, fed and tested exactly as in Experiment 1. However, some major changes were made during training. Discrimination training commenced at the same time of day as in Experiment 1 and flavours were also presented in a semi-random order for 8 days. The subjects were randomly divided into four groups ($n = 6$), namely, Groups VS, AS, SV and SA. Groups VS and AS received flavoured mash initially before supplements of plain mash were presented whereas supplements of plain mash preceded the presentation of flavoured mash in Groups SV and SA. All four groups received 1 gm of either vanilla or anise flavoured mash, each flavour separately for a total of 4 days. On any particular conditioning day, all groups received only one of the two flavours which served as the conditioned stimuli. Group VS received 4 gm of plain mash 2 min after the presentation of 1 gm of vanilla flavoured mash on some days and only 1 gm of plain mash also 2 min after the presentation of 1 gm of anise flavoured mash on other days. Groups AS received a similar treatment to Group VS, except that flavour-meal size contingencies were reversed, that is, 4 gm of plain mash 2 min after the presentation of 1 gm of anise flavoured mash on some days and 1 gm of plain mash also 2 min after the presentation of 1 gm of vanilla flavoured mash on other days. However, Groups SV and SA were presented with the same flavour-meal size pairings, as Groups VS and AS respectively, except that the order of the presentation of the flavoured and plain mash were reversed. Therefore, Group SV received 4 gm of plain mash 5 min before the presentation of 1 gm of vanilla flavoured mash on some days and also 1 gm of plain mash 2 min before the presentation of 1 gm of anise flavoured mash on the other days. Similarly, Group SA received the same treatment as Group SV, except that the flavour-meal size pairing was reversed, that is, 4 gm of plain mash was presented 5 min before the presentation of 1

1 gm of anise flavoured mash on some days and 1 gm of plain mash 2 min before the presentation of 1 gm of vanilla flavoured mash on other days. The 2-min and 5-min intervals were introduced to enable the animals to eat all of the initial plain and flavoured mash respectively before additional food was presented. This procedure was adopted to prevent mixing of flavoured and unflavoured food and a possible reduction of the potency of the conditioned stimuli due to dilution.

Testing for changes in preferences of either anise- or vanilla-flavoured mash was performed using two jar extinction choice tests on 2 consecutive days and lasted for 10 min on each day as in Experiment 1. Rats were simultaneously presented with 30 gm of vanilla flavoured mash and 30 gm of anise flavoured mash in separate jars. Both Tests 1 and 2 were held under conditions of food deprivation similar to those employed during conditioning.

RESULTS

All animals consumed their food portions on all training days. The results obtained from the choice tests carried out at the end of the single 8-day training cycle are shown in Figure 2. During Test 1, both Groups VS and SV which had prior exposure to large vanilla-flavoured meals and small anise-flavoured meals had higher preferences for anise-flavoured mash than Groups AS and SA which had been exposed to large anise-flavoured meals and small vanilla-flavoured meals. There was a similar pattern of group preferences during Test 2. During both Tests 1 and 2, Groups VS and AS (which had received cues before supplements) had higher preferences for anise-flavoured mash than Groups SV and SA, which had received flavour cues after the meal supplements.

A two way ANOVA of data obtained during Test 1 revealed significant main effects for both large meal flavour and the timing of the supplement, $F_s(1, 20) = 10.43$ and 6.22 , $p_s < 0.01$ and 0.05 , respectively. However, there was no significant interaction between the two factors. The former main effect indicates that Groups VS and SV had significantly higher preferences for anise-flavoured mash than Groups AS and SA, whereas the latter one shows that flavour cues were more effective as conditioned stimuli during conditioning when they were presented at meal onset as in Groups VS and AV than at meal offset as in Groups SV and SA. When data obtained during Test 2 was also statistically assessed, neither the main effects nor the interaction between the two factors were found to be significant.

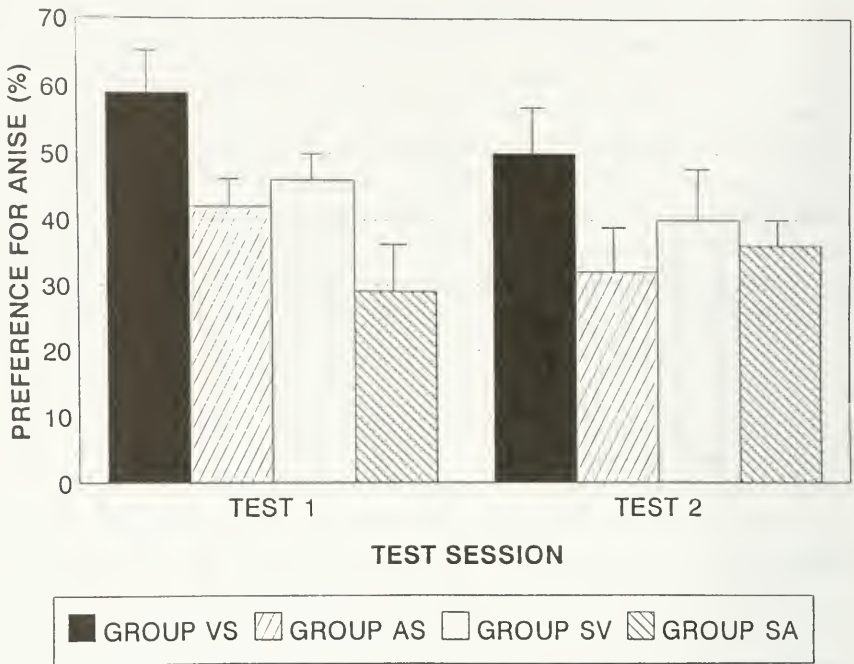


Figure 2. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 2 ($n = 6$). Bars represent standard errors.

DISCUSSION

Three main findings emerged from Experiment 2. Firstly, it confirmed the finding in Experiment 1 that adult rats are capable of learning about flavour-meal size associations. Even when flavour-exposure time was controlled, the rats learned to prefer a flavour previously associated with a small meal better than when the same flavour was paired with a large meal. Secondly, flavour-meal size effects were stronger when flavour cues were presented at meal onset than at meal offset. Thirdly, the conditioned effects extinguished very rapidly.

The finding that conditioned satiety effects could still emerge when flavour exposure time was controlled provides further evidence that satiety associated with the ingestion of large meals has no positive reinforcement properties. Similar conclusions have been arrived at by Van Vort and Smith (1983). The present finding also weakens the

argument that conditioned flavour preferences observed in Experiment 1 were due to an acquired aversion towards prolonged flavour exposure which was associated with large meals during conditioning.

The second finding that flavour cues were presented at meal onset rather than at meal offset suggested that the cues may be more salient and less interfered with at the former than at the latter stage. The presentation of flavour cues following supplements was still effective in conditioning satiety but it reduced the effects considerably. It is possible that when supplements preceded flavour cues, they interfered with the learning of the discrimination between the two flavours and the appropriate satiety signals derived from the two meal sizes. The result of such interference was probably some weakening of the effects of the conditioning.

An alternative explanation would be that the rats became satiated after consuming the supplements and perceived the appropriate satiety signals immediately afterwards before the flavour cues were even presented and perceived. Therefore, it would appear from the present data that the strength of any flavour-meal size conditioning is stronger when the flavour cues precede supplements than vice versa. This finding appears to contradict the findings reported by Booth and Davis (1973) in rats and Booth et al. (1982) in humans, where the later supplements failed to condition meal size per se and conditioned only flavour preferences at most. The third finding that the conditioned satiety effects were weak and extinguished rapidly was surprising when compared with the extreme persistency of the other types of flavour conditioning based phenomena (see Capaldi, Myers, Campbell & Sheffer, 1983; Logue, 1979; Revusky, 1974; although see Simbayi, 1987). The effects had disappeared as early as the second test day after an 8-day conditioning cycle during which each flavour-meal size pairing was presented four times only. Perhaps, the effects could have been more persistent and more resistant or less susceptible to extinction with additional conditioning.

EXPERIMENT 3

Both previous experiments demonstrated flavour-meal size conditioning in adult rats. The aim of Experiment 3 was to test Hayward's (1983) claim that rat pups are apparently capable of more diverse learning than adult rats. As indicated earlier, Hayward showed that rat pups, but not adult rats, could acquire a conditioned taste preference for a flavour paired with a diet that provides more calories

than another diet of equal caloric density. In particular in her Experiment 3, she obtained stronger conditioning of caloric effects with rat pups when a 4 cal/gm novel diet represented the major part of the animal's daily caloric intake for just 4 conditioning days. The pups were given unlimited access to 20 gm of the 4 cal/gm diet on one day, and three quarters of the previous day's consumption on alternate days. In order to control for differential hunger experienced on days when rats had inadequate food, the food supply of half of the animals was topped up with laboratory chow 8 h after presentation of the novel diet. Thus, the present experiment was meant to confirm such caloric effects by using a procedure almost identical to that employed by Hayward except for the following four minor changes which were made. Firstly, rats were first familiarised with the diets to reduce neophobia. Secondly, on small days the rats received only half of the amounts of food they received on large meal days to make the meal sizes more easily discriminable but, as indicated above, their training diets were also supplemented by laboratory chow pellets. Thirdly, the duration of testing was extended to cover a period of up to 24 h with intervals at 30 min and 4 h instead of only after 30-min and 3-h intervals as per Hayward (1983). This allowed monitoring of intake rates for a period longer than a meal which in turn made it possible for one to distinguish between aversions taking place early and throughout the meal as opposed to those taking place later. This in turn made it possible to distinguish between conditioned aversion and conditioned satiety respectively. Finally, in order to facilitate comparisons with other experiments reported in the present paper, conditioning lasted for 8 days instead of only 4 as in Hayward's study.

METHOD

Animals

Twenty four male naive Lister rat pups, 24 - 28 days old and weighing 46 - 91 gm at the beginning of the experiment, were used. The rat pups were weaned at the age of 21 days old and reared in colony cages (4 - 6 animals per cage). They had ad libitum access to dry laboratory chow pellets (Scientific Foods, Croydon, England) and tap water for 3 - 7 days before the experiment commenced. Following selection and assignment to groups, the weanling rats were housed individually in wire cages in a cage rack in an experimental room and had ad libitum access to water throughout the experiment.

Materials

The recipe for the novel diet used was identical to that utilised by Hayward as the high calorie food. It consisted of 50% dextrin (Sigma), 15% calcium carbonate (chalk, East Anglia Chemicals), 2.5% mineral oil (liquid paraffin, British Drug Houses, now M. W. Scientific, Ltd., Poole, Dorset, England), 7.5% ordinary (domestic) vegetable cooking oil and 25% lactic casein (Sigma). The diet provided approximately 4 cal/gm. Either vanilla or anise extract was added to the diets separately in the following proportions: for vanilla, 10 ml of flavour was added to 100 gm of the diet mixture; for anise, 0.50 ml of flavour was dissolved in 20 ml of water and also added to 100 gm of the diet mixture.

Procedure

The rats were assigned randomly to four groups ($n = 6$), namely, Groups R-A, R-V, Ad-A, and Ad-V, with R and Ad standing for restricted and ad libitum conditions respectively, as explained below. Groups R-A and R-V represented Groups A and V in Experiment 1 in the present study whereas Groups Ad-A and Ad-V represented Group 2 (the chow group) in Experiment 3 reported by Hayward (1983). On familiarisation days, all the weanling rats were exposed to the unflavoured novel 4 cal/gm diet. First, all groups received 40 gm overnight. Then, Groups R-A and R-V received only 5 gm while Groups Ad-A and Ad-V continued to receive unrestricted access to 40 gm for every 24 h beginning at 1200 hrs for the next 3 consecutive days.

On conditioning days, Groups R-A received anise flavour in 5 gm of the novel 4 cal/gm diet on some days and vanilla flavour in 1 gm of the same diet on other days. The flavour-meal size pairing was reversed for Group R-V. Group Ad-A received anise flavour in 20 gm of the novel 4 cal/gm diet on some days and vanilla flavour in 10 gm of the same diet on other days. Similarly, the flavour-meal size pairing was reversed for Group Ad-V. Therefore, for all rats, the two flavours were correlated with the same pattern of oral cues but differing caloric consequences (i.e., 20 vs. 4 calories for Groups R-A and R-V and 80 vs. 40 calories for Groups Ad-A and Ad-V, both respectively). Altogether, rats in Groups Ad-A and Ad-V experienced 4 days with sufficient food (i.e., large meals) and another 4 days with an inadequate amount of food (i.e., small meals). In order to avoid the problem of differential hunger on days of inadequate food, the food supply was supplemented by 5 pellets of dry laboratory chow (weighing approximately 10 gm and containing 40 calories) 5 h after the presentation of the training diet.

For both Groups R-A and R-V, laboratory chow was removed 2.5 h prior to the presentation of the novel diet and returned 5 h afterwards. The remaining rats in both Groups Ad-A and Ad-V received no additional food except only as specified above, that is, on small meal days. Flavours were also presented in semi-random order as in previous experiments.

All groups were given an extinction choice test between the anise and vanilla flavoured diets on Day 9. Two jars of the 4 cal/gm food were presented simultaneously, and consumption was recorded at the end of 30 min, 4 h and 24 h for all four groups. As in previous experiments, preferences for anise-flavoured food were calculated as percentages of total food intake.

Data analysis

The data were first assessed using a three way repeated measures ANOVA with the following factors: duration of exposure to the training diet (restricted vs. ad libitum), the large meal flavour (anise vs. vanilla) and cumulative test intervals (30 min vs. 4 h vs. 24 h). Follow up limited pair-wise comparisons between groups trained under similar conditions of exposure to the training diets at each test interval were also carried out using independent *t* tests.

RESULTS AND DISCUSSION

All animals completely consumed their food portions on all training days. Figure 3 outlines the results obtained during the three cumulative intervals of the extinction choice test held on Day 9. It shows that the two groups which had received vanilla flavour paired with the larger meal during training (i.e., Groups R-V and Ad-V) generally had higher preferences for anise than the other two groups (i.e., Groups R-A and Ad-A) which had received anise paired with the larger meal during training. This effect was particularly marked after 24 h than after both the 30 min and 4 h cumulative intervals of the extinction choice test.

The repeated measures ANOVA failed to reveal any significant main effects (all $ps > 0.05$). However, the interaction between all three factors was significant, $F(2,40) = 5.82$, $p < 0.01$. Additional between-group comparisons also revealed a highly significant difference between Groups Ad-A and Ad-V after 24 h of testing only, $t(10, \text{one tailed}) = 5.07$, $p < 0.001$ (see Figure 3). This shows that the rat pups were clearly capable of learning to associate a taste with the size of the meal under

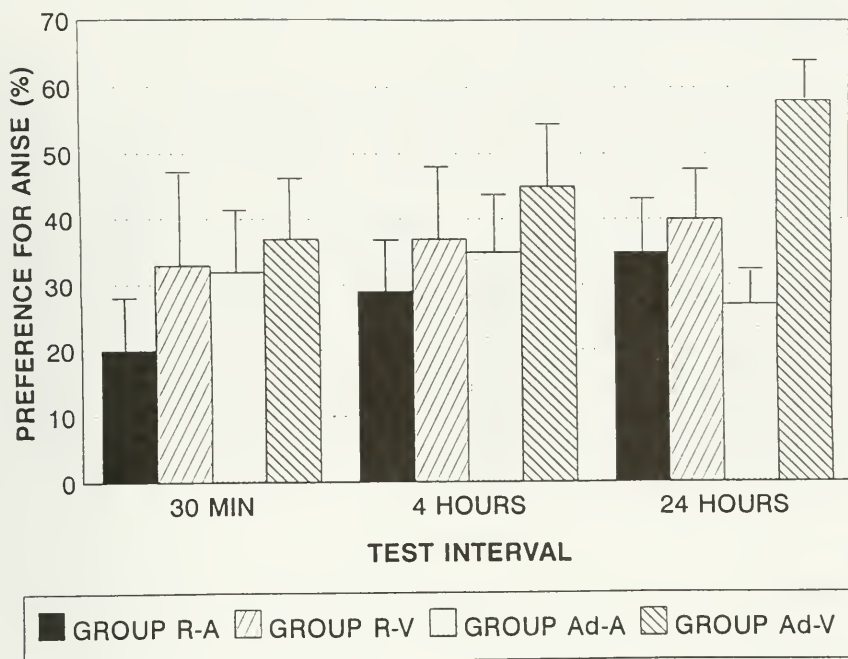


Figure 3. Mean preferences (%) for anise flavour during the two-jar extinction choice tests in Experiment 2 ($n = 6$). Bars represent standard errors.

the ad libitum feeding conditions, whereas they were not able to do so under restricted feeding conditions. Even more interesting was the fact that flavour preference shifts were most pronounced after 24 h of testing than earlier. This finding suggests that the flavour-meal size conditioning effects observed in these experiments might be attributed to satiety rather than aversions, because if the latter were involved, flavour preference shifts would have been observed throughout the test period. In particular, they would have commenced at the beginning of the test period rather than later, as occurred in the present experiment. The results are consistent with Booth's (1972) conditioned satiety ideas but they clearly contradict Hayward's (1983) findings. It is important to note here that the present experiment used a procedure similar to Hayward's except that the meal sizes and one flavour were different. However, her findings generally supported a conditioned appetite hypothesis whereby only young rats learned to prefer a taste which was previously associated with larger meal sizes or more calorific diets.

EXPERIMENT 4

As both the training and testing procedures employed in Experiment 3 did differ somewhat from those employed in both earlier experiments (i.e., Experiments 1 and 2), it is not only difficult but also rather unfair to make direct comparisons between their respective findings. Clearly, the best way to achieve such a goal would be to replicate Experiment 3 using naive adult rats. This was the aim of Experiment 4. According to Hayward (1983), an adult rat no longer attends to post-ingestional feedback since it is rarely hungry and therefore is not capable of learning conditioned taste preferences based on differing caloric outcome. Therefore, Experiment 4 investigated whether naive adult rats could be as responsive as naive young rats to flavours paired with differing caloric outcome when novel diets provided either only a small proportion or most of the rats' daily caloric needs.

METHOD

Animals

Twenty four naive male hooded Lister rats 81 - 126 days-old and weighing 245 - 420 gm at the start of the experiment were used.

Materials and Procedure

The materials and procedure were the same as for Experiment 3 except for the following three minor changes: both Groups R-A and R-V were allowed 25 gm of supplementary solid laboratory chow pellets at 17.00 hrs each day; during familiarisation, both Groups Ad-A and Ad-V received 30 gm of unflavoured and novel high calorie diet instead of 20 gm only as in Experiment 3; during training, both Groups Ad-A and Ad-V received 30 gm of the novel diet with no supplements on large meal days and 15 gm of the novel diet plus another 15 gm supplement of solid laboratory chow pellets on small meal days. All the changes were made to compensate for the larger size of animals used in the present experiment compared to those used in Experiment 3.

RESULTS AND DISCUSSION

All animals completely consumed their food portions on all training

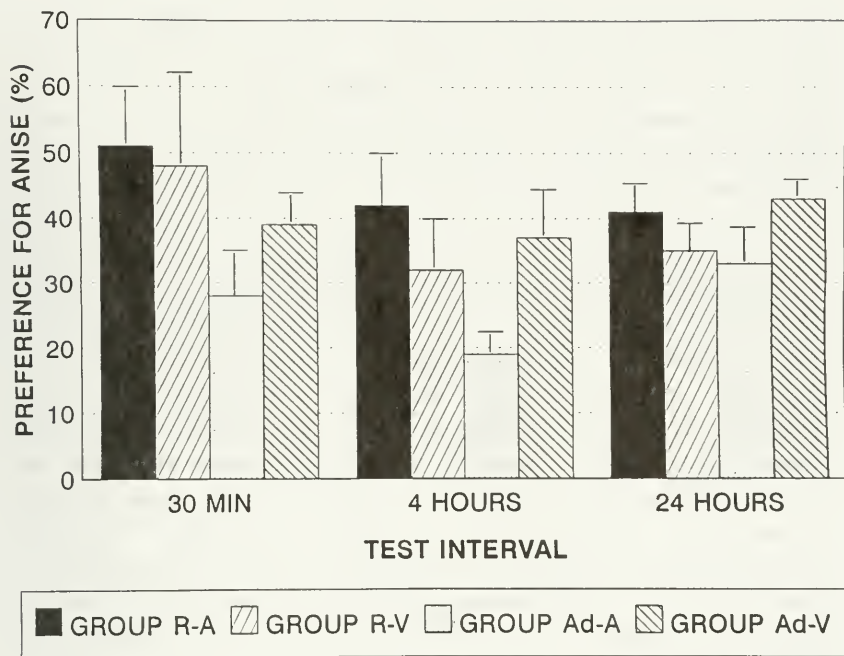


Figure 4. Mean preferences (%) for anise flavour during the two-jar extinction choice test in Experiment 3 ($n = 6$). Bars represent standard errors.

days. The results obtained during the three interval of the extinction choice test held on Day 9 are displayed in Figure 4. They show that Group Ad-V generally had higher preferences for anise flavour than Group Ad-A, whereas no such differences are evident between Groups R-A and R-V.

When the data were assessed using a three way repeated measures ANOVA as for Experiment 3, neither the main effects nor interactions were significant. However, additional between-group comparisons of anise preferences indicated that Group Ad-A had a significantly higher preference than Group Ad-V after the 4 h test interval only, $t(10, \text{one tailed}) = 2.20, p < 0.05$. Thus, these mature rats were also able to learn about flavour-meal size associations under ad libitum but not restricted feeding conditions, as did the weanling ones in Experiment 3. It is rather difficult to explain why adult rats appeared to learn conditioned satiety only when flavour-meal size pairings were presented on an ad libitum basis (30 gm vs. 15 gm) but not when access was restricted to

much smaller amounts (5 gm vs. 1 gm). Perhaps, in the latter condition adult rats simply ignored post-ingestional feedback of the small snacks with a novel flavour and concentrated mostly on the bigger supplementary meals from which most of their daily caloric requirements were derived. Such a view is consistent with that of Bolles et al. (1981) and Hayward (1983) who used this fact to argue why adult rats should fail to learn to associate a flavour with a diet that provides more calories under such conditions. Nevertheless, the fact that, like weanling rats, adults can acquire flavour-meal size effects, appears to contradict these authors' findings. Another interesting aspect of the present results is that preference shifts in those groups which displayed them were most evident only after 4 h of testing. This differs from Experiment 3 where preference shifts were most notable in the groups concerned after 24 h of testing. Although the reasons for this disparity are unclear at present, one possibility is that older rats may experience the onset of satiety much sooner than younger ones. Nevertheless, this issue needs to be investigated further. Experiment 4, therefore, has shown that adult rats appear to learn to make flavour-meal size associations just as well as weanling rats especially when the diet provides for most of the animals daily caloric needs.

GENERAL DISCUSSION

The present research showed that both weanling and mature rats are capable of learning to associate a flavour with the size of a meal. In particular, these findings demonstrated flavour-meal size conditioning effects whereby an animal learns to prefer a flavour not associated with a larger meal. It is however important to note here that, as Capaldi and Myers (1982) and Davidson-Codjoe and Holman (1982) have pointed out, the preferences demonstrated in experiments of this sort are relative, rather than absolute. The data really do not distinguish a preference for the flavour consumed when rats received the small meal from an aversion for the flavour consumed when they received the large meal. Furthermore, as Capaldi et al. (1983) also pointed out, the word "preference" is usually intended as a neutral term accommodating either a learned aversion for the flavour associated with the large meal, learned liking for the flavour associated with the small meal, or both.

As the present results are consistent with Booth's (1972) and Booth and Davis' (1973) findings, a phenomenon very similar to Booth's conditioned satiety may be implicated. Conditioned satiety involves an increment in the size of the feeding bout on the dilute nutrient (or, small

meal, few calories, etc.) more than on the more concentrated nutrient (or large meal, many calories, etc.) after several pairs of presentations. This takes place in order to compensate for calories depending on the nature of the concentrated diet. Booth suggested that such conditioning of satiety may be important in the control of food intake only under conditions which are put on the timing of meals, that is, under high food deprivation schedules. Perhaps, different mechanisms are involved under normal ad libitum feeding conditions. This might explain why stronger evidence of conditioned satiety learning was obtained under restricted feeding conditions in both Experiments 1 and 2 in the present study than was the case under ad libitum feeding conditions in both Experiments 3 and 4. Nevertheless, the present findings clearly demonstrated the existence of an acquired oral and/or olfactory sensory control of the satiation process just as Booth's conditioned satiety study did. The present findings are also in agreement with those of Le Magnen (1985) and Deutsch (1982).

The present findings suggest that oral qualities of a familiar food may enable a mammal to react in anticipation of that food's caloric value or the duration of its satiating effect. According to such a view, animals stop eating at an appropriate stage even though absorption has barely started or possibly has not even started at all as in the case of a rapid feeder such as a dog. However, our findings clearly contradict Hayward's (1983) findings which generally demonstrated conditioned appetite in weanling rats but not in adults. Apart from strain differences, it is unclear at present why our results contradict Hayward's.

One hypothesis which explains the present findings is that the flavour tracking may be due to an acquired difference in the development of feeding inhibition during meals. This is because there were no differences in basal acceptability since both meals consisted of the same diet, except for flavours which were added to them. This view is consistent with that of Booth (1972). The higher preference for the flavour which had been paired with a small meal demonstrated in the present study could be attributed to a difference in the speed of onset of the suppression of intake in the later stages of the meal. This might suggest that an acquired oral and/or olfactory factor contributed to the development of the satiety which ended the meal to which the flavour previously associated with the large meal was added. When faced with a choice between flavour cues previously associated with large and small meals during conditioning, a satiety signal switched off eating immediately after the animal had perceived that the flavour was previously correlated with a large meal which was too satiating. However, there was no such satiety signal forthcoming from flavour

correlated with less satiating small meals and consequently, rats consumed significantly more food with a flavour which was previously associated with a small, less satiating meal. Hence, satiety had no positive reinforcing effects and might have been aversive. As was mentioned earlier, such a conclusion is consistent with that of Van Vort and Smith's (1983) who found that satiety had no positive reinforcing effects on flavour preferences at all whilst using sham feeding techniques and a similar flavour tracking procedure.

An alternative explanation is that when rats were exposed to flavours correlated with large meals, they developed slightly stronger aversions to them than when exposed to flavours correlated with small meals. However, since Experiments 2 - 4 controlled for the amount of flavour exposure, this hypothesis is highly improbable. Furthermore, the mere fact that all groups in Experiment 1 ate in excess of 60% vanilla-flavoured food during choice tests further weakens this argument.

The conditioning of flavour preferences based on meal size demonstrated in the present research does not in any way contradict Le Magnen's (1969) findings of conditioned appetite at all. Conditioned discriminative (also referred to as selective or differential) appetite induced during conditioning causes a rat to eat more of the reinforced, and hence beneficial food, and less of the non reinforced food in the final choice test. As Bolles et al. (1981) pointed out, conditioned satiety and conditioned appetite merely represent complementary aspects of intake regulation. Whereas the phenomenon proposed by Le Magnen (which Bolles et al. later failed to demonstrate) was basically concerned with food selection through learning about the caloric potential of different foods, the phenomenon demonstrated in the present study more likely operates after the selection of the diet offering optimum caloric consequences has been completed. Hence, the animal learns to eat less of that diet on a day-after-day basis under conditions in which constraints are put on the timing of meals.

According to Capaldi et al. (1987), shifts in preferences such as those demonstrated in the present study can be viewed within either a classical conditioning or an instrumental learning paradigm. In a classical conditioning framework, the flavours are the conditioned stimuli (CSs) and they are being associated with some unconditioned stimulus (US) that is produced by consumption of meals of different sizes made from the same diet. In an instrumental learning paradigm, the flavours are the discriminatory stimuli (SDs) signalling the reinforcement produced by the instrumental response of consuming meals of different sizes. The important question therefore concerns what is the US or reinforcer in either paradigm.

One of the best candidates for the US or reinforcer in the type of learning demonstrated in the present study is the post-ingestive consequences of ingesting meals such as calories. Supporting evidence for flavour-calorie learning in rats has been reported elsewhere (e.g., Capaldi et al., 1987; Deems et al., 1986; Hayward, 1983; Holman, 1975; Mehiel and Bolles, 1984; Sherman, Hickis, Rice, Rusiniak & Garcia, 1983). Another possible candidate for the US or reinforcer is some oral stimulus such as flavour (or taste). However, this is very unlikely because the different sized meals in each experiment in the present study consisted of exactly the same diet, which meant that the flavour of the food contained in the two meals was identical. Thus, the flavour-meal size conditioning effects demonstrated in the present research were most probably the result of flavour-calorie rather than flavour-flavour associations.

Finally, it must be noted here that although only four experiments are reported in the present paper, six additional experiments were also carried out which consistently failed to yield any significant effects. However, preferences were mainly in the direction which is predicted by the conditioned satiety hypothesis, that is, the small meal flavour was relatively more preferred. These findings also suggest that the flavour-meal size conditioning effect definitely occurs but we have not yet been able to identify all the conditions which enable consistently reliable effects.

In conclusion, both mature and weanling rats appear to be capable of learning about flavour-meal size associations. In particular, they acquired conditioned satiety, albeit very weakly, rather than conditioned appetite as previously demonstrated by both Bolles et al. (1981) and Hayward (1983) in their similar studies. These conditioned satiety effects, which are most probably due to flavour-calorie rather than flavour-flavour (or tastes) associations, are also distinctly elusive.

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LIGHT MEDIATION OF CIRCADIAN PREDATORY BEHAVIOR IN THE YOUNG ALLIGATOR

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ABSTRACT: Minnow predation by 10 young American alligators (*Alligator mississippiensis*) was systematically measured during four daily time periods under four different conditions of lighting in order to investigate a circadian rhythm of predatory behavior. The four daily time periods were night (1:00 a.m.-7:00 a.m.), morning (7:00 a.m.-1:00 p.m.), afternoon (1:00 p.m.-7:00 p.m.), and evening (7:00 p.m.-1:00 a.m.). Each of the following lighting conditions had a duration of 4 weeks: continuous complete darkness (DD); continuous artificial illumination (LL); naturally varying light-dark conditions (natural LD); and reversed light-dark conditions with artificial lights on at sunset and off at sunrise (reversed LD). Predatory behavior (i.e., the number of prey fish consumed wholly or partially during each test session) varied significantly as a function of the interaction between time period and lighting condition. Under natural LD, the mean number of prey killed during night sessions was significantly higher than either morning or afternoon sessions. Under reversed LD, the pattern of predation reversed from that exhibited under normal lighting, with both morning and afternoon predation significantly higher than either evening or night. Under conditions of continuous illumination (LL and DD) the natural LD circadian pattern persisted for over 1 week with significantly higher predation rates during the night periods as compared to the morning and afternoon periods. The gradual transition of predation pattern in response to manipulations of the light-dark cycle suggests that the circadian rhythm of alligator predation is dependent upon light-dark variation for entrainment.

INTRODUCTION

The adult American alligator (*Alligator mississippiensis*) has been described as an opportunistic scavenger as well as an active predator

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(McIlhenny, 1976; Pooley, 1989; Weldon, Swenson, Olson, & Brinkmeier, 1990). Hatchling alligators eat insects, small crustaceans, and small fish (Coulson & Hernandez, 1983), whereas adult alligators prey upon frogs, snakes, birds, muskrats, nutria, and larger mammals (McIlhenny, 1976; Pooley, 1989; Ross & Magnusson, 1989; Scott & Weldon, 1990). The alligator is generally considered a nocturnal species with most of its feeding behavior and general activity taking place during the night (Lang, 1976; McIlhenny, 1976; Murphy, 1981; Pooley, 1989). Alligator predatory behavior appears to follow a circadian rhythm, but this has not been systematically investigated and reported.

In almost all vertebrates, endogenous circadian rhythms regulate temporally certain types of behavior (e.g., sleep) and bodily functions (e.g., hormone secretions, Aschoff, 1989). The rhythm itself is often entrained or synchronized by environmental cues such as daily cycles of light-dark and temperature change (Aschoff, 1989; Griffiths, 1986). These environmental cues that set the timing of circadian behavior are referred to as *zeitgebers* (Aschoff, 1989). Aschoff reports that the most powerful of all *zeitgebers* is a light-dark cycle. In the absence of *zeitgebers* (e.g., an environment of continuous darkness), circadian rhythms are free-running and self-sustaining. The free-running rhythm may cycle every 24 hours, be slightly longer, or slightly shorter.

In lower vertebrates, light mediates circadian rhythm via the photosensitive pineal gland. Although alligators lack pineal glands, studies have indicated that some circadian rhythms in alligators are controlled or mediated by light cycles. Circadian rhythm of young alligator motor activity was documented by Kavaliers and Ralph (1980). Lang (1976) found that movement between land and water in juvenile alligators varied as a function of circadian rhythm cued by light-dark cycles. A study by Murphy (1981) indicated the existence of an endogenous clock synchronized by the circadian light-dark cycle which enabled young alligators to use solar compass orientation. Kavaliers (1980) demonstrated that extraretinal responses to light pulses varied according to circadian phase. Moreover, photoperiod manipulation indicated exogenous entrainment of the extraretinal responses by light-dark cycles. In light of the alligators' lack of a pineal gland, Kavaliers and Ralph (1981) argued that overall organization of circadian rhythm and period length depends on a complex interaction of retinal inputs, extraretinal inputs, and other neural areas.

This study sought to determine if alligator predation was subject

to circadian rhythmicity. Minnow predation (i.e., number of minnows wholly or partially consumed) by young alligators was systematically measured during four daily time periods under different conditions of lighting. It was hypothesized that predation rates would peak during the dark periods of 24-hour natural and reversed light-dark cycles, and that an endogenous circadian rhythm would persist under continuous illumination. It was predicated that the circadian fluctuation could be altered by manipulating the light-dark cycle, thus supporting dependence upon light-dark alternation as a zeitgeber. A gradual transition of predation pattern in response to light-dark cycle manipulations would indicate entrainment by a light-dark zeitgeber.

TABLE 1
Subject Size After the Study Compared with Number of Prey Captured During 6-Hr Sessions

Subject	Subject Size		Number of Prey Captured		
	Length	Weight	Range	Mean	SD
1	46.0	304.0	0-9	1.89	2.28
2	46.5	285.5	0-10	2.77	2.94
3	42.5	215.0	0-10	2.57	2.97
4	42.5	203.5	0-10	2.36	2.78
5	41.9	208.5	0-10	2.28	2.84
6	38.5	176.5	0-9	2.16	2.37
7	39.0	164.0	0-6	1.59	1.84
8	44.0	228.5	0-10	2.71	2.94
9	37.0	148.5	0-5	1.65	1.73
10	38.0	151.5	0-10	2.08	2.48

METHOD

Subjects

Ten 1990 hatchling alligators (*Alligator mississippiensis*), 27 to 29 cm in length and weighing 56 to 80 gm, were obtained from the Rockefeller Wildlife Refuge, Grand Chenier, Louisiana when they

were approximately 1 month of age. (Age is approximate because exact date of hatching is not known). Testing began when subjects were approximately 6 months old and continued until subjects were approximately 14 months old. At the completion of testing, subjects ranged from 37 to 46 cm in length and 148.5 to 304 gm in weight (Table 1). Individual subjects were identified by removing a specific tail scute.

Maintenance

When not being tested, all 10 alligators were maintained in a home pool measuring 45.72 cm deep and 2.44 m in diameter. Ten cm of water covered the bottom, and a 60.96 cm diameter gravel-surfaced concrete "island" was situated near the center of the pool. The pool was retained in a heated enclosed garage with windows facing north and east. Air temperature ranged from 21 to 28°C with an average of 25°C. Water temperature ranged from 20 to 27°C with an average of 24°C. The pool was drained and filled with fresh water as necessary (usually once each week).

Food included two species of live minnows (*Notropis cornutus* and *Cyprinus idus idus*) and Burris Alligator Feed. Alligators were permitted to obtain live prey (minnows) beginning when they were 2 months old. Once testing began, live prey was available only in the testing arenas during test sessions. Burris Alligator Feed was provided ad libitum in the home pool.

Live minnows were obtained as needed (about every 2 weeks) from local bait shops and fish supply outlets. They were maintained in a plastic barrel, 55.88 cm in diameter and 71.12 cm high, filled with water. Aeration was furnished by an electric Second Nature Whisper 400 aquarium pump. Water and air temperature were the same as that for the alligators. The minnows were fed an adequate amount of Wardley Tropical Flakes fish food every evening.

Apparatus

Each test arena consisted of a plexiglass tray 45.72 cm x 25.4 cm x 12.7 cm high with a grill-type metal lid that allowed air circulation but prevented escape. Each arena was filled with 7.62 cm of water. The test arenas were located in the same room as the alligator home pool. Water temperature was the same as that in the home pool.

Procedure

All subjects were tested under all conditions. A two-factor (4 x 4) within-subjects experimental design was used, with one factor (daily time period) nested within the other factor (lighting condition).

The four lighting conditions were continuous complete darkness (DD), continuous artificial illumination (LL), naturally varying light-dark (natural LD), and reversed light-dark with artificial light on at sunset and off at sunrise (reversed LD). Each lighting condition was maintained for 4 weeks, and each followed a 2-week period of natural lighting to control for carryover effects. (Kavaliers and Ralph [1980] demonstrated that, following light manipulation, 10 days of natural light were sufficient to restore normal circadian rhythmicity of alligator motor activity).

Artificial illumination was provided by a Power-Glo 40-watt full spectrum fluorescent lamp. When necessary to shut out natural light, the windows were covered with black shades taped tightly against the walls so that no light could enter.

A total of 640 predation test sessions of 6-hour duration were conducted (160 test sessions per lighting condition). Predation test sessions were alternated randomly among four time periods: night (1:00 a.m.-7:00 a.m.), morning (7:00 a.m.-1:00 p.m.), afternoon (1:00 p.m.-7:00 p.m.), and evening (7:00 p.m.-1:00 a.m.). No time period was repeated until the other three had been used. All four time periods were tested each week.

Because movement between land and water has been demonstrated to follow a circadian pattern itself (Lang, 1976), alligators and prey animals were placed in test arenas to control for this possible confound. Each test session was conducted as follows: ten minnows, five specimens each of *Notropis cornutus* and *Cyprinus idus idus*, were moved with a net by the investigator from their home barrel to a test arena at the beginning of the designated 6-hr time period. An alligator was then carried by the investigator by hand from its home pool to the test arena. A grill-type metal lid was then placed on the test arena. During the 6-hr test session, the animals were not disturbed. At the end of the session, the number of prey killed (i.e., number of minnows missing or partially consumed) was recorded. The alligator and remaining minnows (if any) were then returned to their respective homes. The water in the test arena was emptied and replaced with fresh water after each test session.

RESULTS

The dependent variable, number of minnows consumed wholly or partially, was analyzed with a repeated measures analysis of variance (ANOVA), in which time period and lighting condition were independent variables (both repeating) with time periods nested within lighting conditions. Predatory behavior varied significantly as a function of the interaction between time period and lighting condition, $F(9,270) = 15.79$, $p < .001$. Mean prey killed for each time period within each lighting condition are reported in Table 2.

TABLE 2
Means and Standard Deviations of Prey Killed During Time Periods Under Different Lighting Conditions

Lighting Conditions	Time Periods			
	Night	Morning	Afternoon	Evening
Continuous Dark				
Mean	0.393	0.260	0.065	0.203
SD	(0.507)	(0.404)	(0.227)	(0.377)
Continuous Light				
Mean	2.775	2.975	2.800	2.350
SD	(2.769)	(3.109)	(2.757)	(2.107)
Natural Light				
Mean	2.700	1.300	1.250	2.075
SD	(2.221)	(1.488)	(1.256)	(1.542)
Light Reversal				
Mean	2.600	4.500	4.600	1.750
SD	(1.646)	(2.491)	(3.177)	(1.932)

Figure 1 compares the predation patterns that occurred under natural LD and reversed LD cycles. Tukey HSD multiple comparisons showed that under natural LD the mean number of prey killed at night was significantly higher than either morning ($p < .01$) or afternoon ($p < .01$). Although mean number of prey killed was higher during evening than either morning or afternoon, the differences were

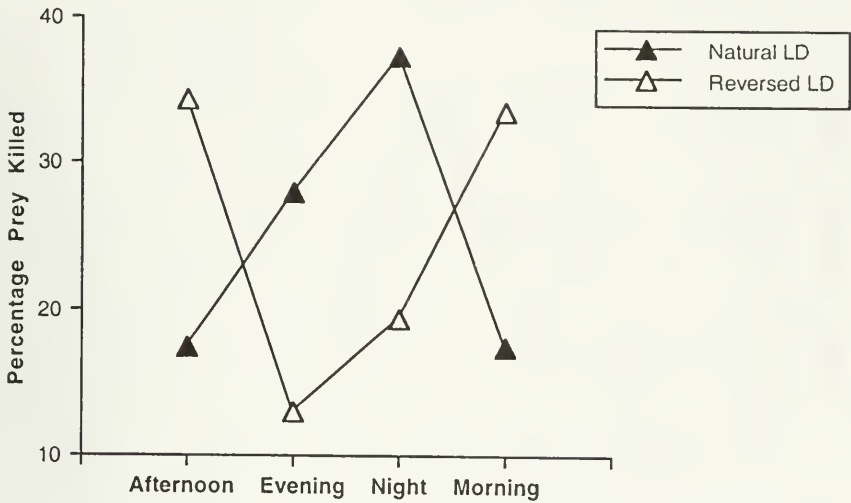


Figure 1. Circadian predatory behavior patterns under lighting conditions natural and reversed LD.

not significant. Kill rates for evening and night sessions did not differ significantly from each other. Morning and afternoon kill rates also did not differ significantly from each other.

Under reversed LD conditions, the pattern of predation reversed from that exhibited under natural LD. Tukey HSD multiple comparisons revealed that morning predation was significantly higher than either night ($p < .001$) or evening predation ($p < .001$). Afternoon predation was also significantly higher than either night ($p < .001$) or evening predation ($p < .001$). The reversed LD condition produced no significant differences between morning and afternoon predation. However, night predation was significantly higher than evening predation ($p < .05$).

Under DD, night predation was significantly higher than afternoon predation ($p < .01$). Under LL, no significant differences were found among the time periods.

The data for the initial week under each of the two constant conditions, LL and DD, were examined to see to what degree the natural LD pattern persisted. Figure 2 illustrates that the natural LD pattern did persist during the first week of LL and DD with predation rates peaking during night periods. Tukey HSD multiple comparisons determined the following significant differences. Under DD, night predation was significantly higher than after noon ($p < .05$)

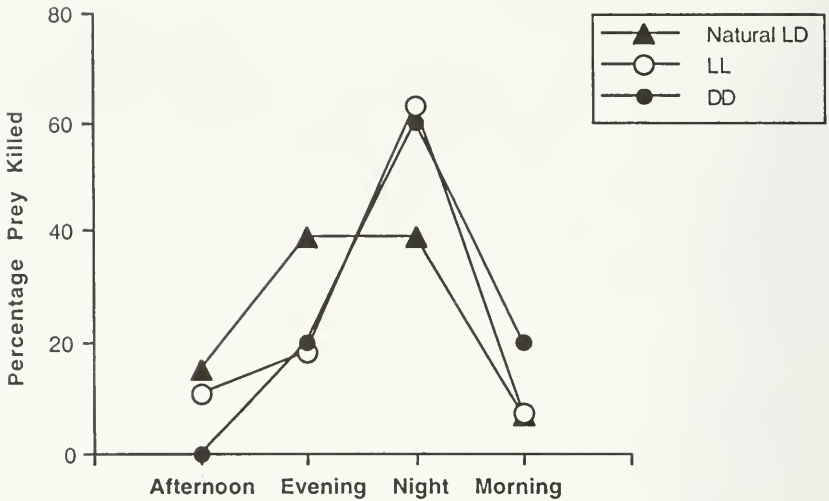


Figure 2. Circadian rhythm of predation during the first week of LL, DD, and natural LD conditions.

predation. Under LL, night predation was significantly higher than morning ($p < .01$), afternoon ($p < .01$), and evening ($p < .05$) predation.

Table 1 displays the mean number of prey killed by each subject. Predation rates of the 10 subjects were analyzed with a one-way ANOVA to determine if predation differed among subjects. No significant differences were found.

DISCUSSION

Alligators as young as 2 months of age are capable of capturing very active prey. The evidence accrued in this study suggests that predatory behavior in the young alligator varies as a function of light-mediated circadian rhythm. Light plays a critical role, as predation during dark periods was significantly higher than during light periods, whether lighting conditions were natural or reversed. Predation rates during natural and reversed LD climaxed during the second contiguous time period of darkness (i.e., night period of natural LD and afternoon period of reversed LD). This suggests that, in the wild, predatory behavior of the young alligator reaches a peak during the hours before dawn, declines sharply after daybreak, remains low throughout the day, and then rises steadily after nightfall. Such an

activity cycle is similar to the circadian rhythms of alligator motor activity found in other research (Kavaliers, 1980; Kavaliers & Ralph, 1980, 1981; Lang, 1976).

Aschoff (1989) describes circadian rhythms as "self-sustaining oscillations", and the test for such persistence is a recording of the activity under continuous non-varying illumination. Under DD, a predation pattern similar to natural LD persisted (i.e., night predation was significantly higher than afternoon), although predation was relatively suppressed during all time periods (see Table 2). Examination of predation rates of the first week under conditions of LL and DD showed that a general pattern of circadian rhythm, similar to the natural LD pattern, persisted. During the second week of LL, the pattern became arrhythmic. This is in accord with Kavaliers and Ralph's (1980) study where the free-running circadian rhythm of alligator motor activity became arrhythmic after 10-15 days of LL.

The suppression of predation during DD may have been due to melatonin, a hormone that increases during periods of darkness (Galluscio, 1990) and appears to regulate cycles of sleep and activity in many animals (Wurtman & Lieberman, 1987). Melatonin is present in the blood of alligators (Gern, Owens, Ralph, & Roth, 1978), but its exact role is not known. In birds, the increase in melatonin appears to cause a decrease in activity and in body temperature (Binkley, 1979). Although alligators are poikilotherms, an increase in melatonin due to continuous darkness may suppress predatory behavior.

Figure 3 provides further evidence of an endogenous circadian rhythm of predatory behavior. If the temporal occurrence of the young alligator's predatory behavior was solely under light stimulus control with no endogenous circadian rhythm, then an abrupt change in predatory behavior should occur immediately following light reversal. However, Figure 3 demonstrates a gradual transition of predation pattern in response to reversed LD, more indicative of a circadian rhythm being reprogrammed by the zeitgeber than behavior cued directly by light. Alligator predation follows a circadian rhythm and appears to be dependent upon light-dark variation for entrainment.

As an ancient species that has evolved in latitudes subject to seasonal shifts in photoperiod, the alligator is an excellent subject for the study of endogenous circadian clocks that are fine tuned by environmental cues (eg., light-dark, temperature variations). Whether there is one circadian clock or a number of subordinate circadian clocks each kept in synchronization with the others by natural

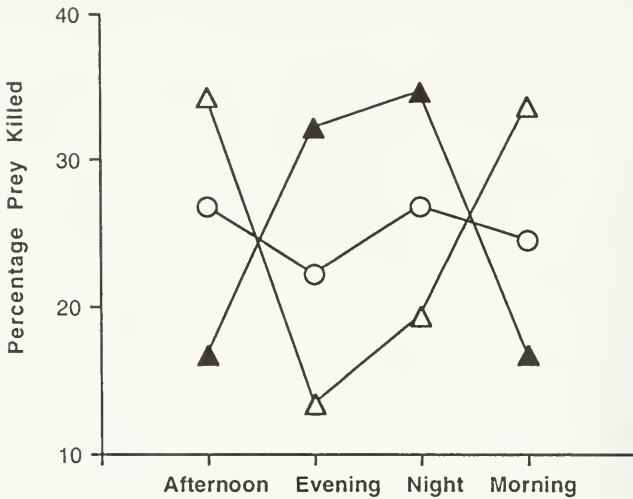


Figure 3. Transition of circadian predatory pattern from natural LD (solid triangles) to the first week (open circles) and fourth week (open triangles) of reversed LD.

zeitgebers can only be determined by extensive research. Amphibious behavior, solar compass time compensation, photoreceptor sensitivity, motor activity, and predatory behavior all may be controlled by one "master" circadian clock, or each behavior may have its own independent circadian clock. Conversely, all of the above behaviors may reflect variations symptomatic of the animals' activity cycles. To resolve these issues, it would be necessary to measure continuously and concurrently all of these behaviors under controlled laboratory conditions. By manipulating light and temperature cues, it may be possible to produce desynchronization of the behaviors from each other thereby demonstrating subordinate circadian clocks for some or all of these behaviors.

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PORTIA LABIATA, A CANNIBALISTIC JUMPING SPIDER, DISCRIMINATES BETWEEN OWN AND FOREIGN EGGSACS

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ABSTRACT: Eggsac recognition was investigated in *Portia labiata*, a jumping spider (Salticidae) that routinely feeds on the eggs of conspecifics, but does not normally feed on its own eggs. In laboratory experiments, we demonstrate that *P. labiata* females can discriminate between their own and foreign eggsacs. The cues by which these discriminations are made are discussed.

INTRODUCTION

Various types of parental care are known in spiders, including guarding eggs against predators (Eberhard, 1974; Kessler & Fokkinga, 1973; Pollard, 1984; Fink, 1986, 1987; Willey & Adler, 1989), providing food for young (Nørgaard, 1956; Bristowe, 1958; Kullmann, 1972; Shear, 1970) and opening the eggsac to allow emergence of spiderlings (Whitcomb & Eason, 1967). Generally, if a female that does not have eggs is offered eggs of a conspecific, she will reject, and sometimes eat, them (Bonnet, 1940; Palmgren, 1944; but see Nørgaard, 1956; Pollard, 1984). Yet females do not normally eat their own eggs.

In vertebrates, the stimuli by which females recognize their own offspring have been well studied (Fletcher & Michener, 1987), but the stimuli by which female spiders discriminate between their own eggs and those of conspecifics have received little attention. Previous studies suggest that eggsac discrimination by spiders is mediated by one or more of four cues (Kraft, 1982): (1) tactile cues based on the physical

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characteristics of the eggsac; (2) chemical cues associated with the eggsac's silk; (3) chemical cues associated with the spider's web; (4) cues based on the geographic location of the eggsac, the web or both.

Portia is a web-building jumping spider that specializes in preying on other spiders, including conspecifics (Jackson, 1992). *Portia* females enter the webs of conspecifics, where they attack or sometimes kill the resident female, then eat any eggsacs that are left behind (Jackson & Blest, 1982; Jackson & Hallas, 1986). Upon encountering eggsacs, *Portia* females open them by chewing and tugging with their chelicerae, then using their front pair of legs to rake the eggs forward into their mouths (Jackson & Blest, 1982).

Portia females have never been observed eating their own eggs. Yet females leave, then return to their webs during the incubation period (Jackson & Blest, 1982). Also, incubating *Portia* females in nature have been observed to eat eggs of conspecifics (Jackson & Blest, 1982; Jackson, unpubl. data). This suggests that *P. labiata* females have evolved an ability to recognize their own eggs or web. We investigated this hypothesis using a representative species, *P. labiata*, from Sri Lanka.

MATERIALS AND METHODS

Standard maintenance procedures were used, as described elsewhere (Jackson & Hallas, 1986). Tests were carried out in cages with removable glass sides (Fig 1A). An internal metal frame was positioned inside each cage (Fig 1B). Spiders attached their webs to the metal frame instead of to the glass, enabling the cages to be opened without damaging webs.

All females used in tests were randomly selected from the laboratory stock. Though a given female was used in more than one (maximum of two tests) test, no eggsac-female pair was used more than once. Also, no eggsac was used more than once, except for instances in which it had previously been paired with its parent. All eggsacs used in tests were of approximately (maximum difference of 3 days) matching age.

Before each test, the parent spider (test spiders and spiders that provided foreign eggsacs and webs) was deprived of contact with its eggsac and web for a 2-h period. After the 2-h period, the test female was placed in a cage containing one of the following treatments: (1) the test female's own eggsac in the test female's own web; (2) the eggsac and web of another conspecific female ('foreign eggsac in foreign web'); (3) the test female's eggsac in another conspecific female's web ('own eggsac in foreign web'); (4) the eggsac of another conspecific in the test

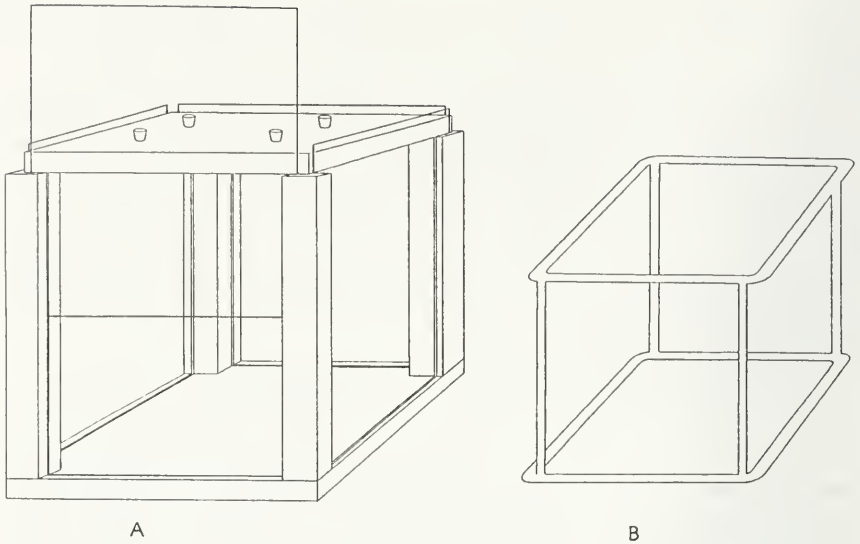


Figure 1. Cage (30 cm x 30 cm x 30 cm) used in testing *Portia labiata* for eggsac recognition. A: Wooden outer frame with sliding glass sides, one of which is shown partially raised. Prey were introduced through the four holes (plugged with corks) on top of the cage. B: Inner metal frame that is slightly smaller than the inside dimensions of outer cage. Inner frame is shown separately for clarity, but is normally positioned inside the outer wooden frame.

female's web ('foreign eggsac in own web'). The test consisted of leaving the test female in the cage for one week, during which time the eggsac was checked daily for evidence of having been fed upon.

Treatments 3 and 4 were obtained each time by taking a pair of incubating females' webs and trading the eggsacs: eggsac of female 1 placed in web of female 2 as close as possible to previous location of eggsac of female 2, and likewise for eggsac of female 2 placed in web of female 1.

RESULTS

Eggsacs encountered by test females in their own webs were treated differently depending on whether they belonged to the test female or another conspecific female ($\chi^2=47.62$, $N=59$): test females in their own webs resumed guarding their own eggsac in 19 out of 20 tests, and ate the foreign eggsac in only 6 out of 12 tests.

Test females in foreign webs resumed guarding their own eggsacs

in 13 out of 14 tests and ate the eggsacs in 12 out of 13 tests. Eggsacs which the test female did not resume guarding were invariably eaten.

DISCUSSION

Evidently, *P. labiata* females can discriminate between their own eggsac and a foreign eggsac. In the present study, females usually guarded their own eggs and ate foreign eggs. How widespread eggsac recognition abilities may be in salticids is unknown because species other than *P. labiata* have not yet been studied. However, an ability to recognize their own eggs may be especially advantageous in *Portia* because this is a genus of salticids known to feed frequently on eggs of other spiders, including conspecifics.

This study raises questions about the cues by which *P. labiata* distinguishes between its own and foreign eggsacs. In some vertebrates, cues from the geographic locations of the eggs are known to be important (Colgan, 1983). However, for *P. labiata*, cues other than location must be of primary importance. In our tests, when females' own eggsacs were placed in foreign webs, they were not placed in a location comparable to their original positions in the parent webs but, instead, as close as possible to the previous location of the foreign eggsac. Therefore, if the location of the eggsac in the web was the most important cue for eggsac recognition, then test females would have been expected often to eat their own eggsacs. However, test females usually guarded their own eggsacs, instead of eating them, regardless of whether they were in foreign webs or the females' own webs. Probably, in *P. labiata*, eggsac discrimination is based primarily on chemical cues.

However, it is interesting that, when we placed foreign eggsacs in the webs of test females, the test females accepted (i.e., did not eat) the foreign eggsac half the time. Yet, when test females encountered foreign eggsacs in foreign webs, they usually ate them. This suggests that cues from the female's own web are important in addition to cues from her eggsac. It is probably unlikely in nature for a female to encounter foreign eggs in her own web and, therefore, it might be advantageous for females to be reluctant to eat eggsacs encountered in their own webs, despite dissenting chemical cues.

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