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AGGREGATION IN THE BANDED GECKO, *COLEONYX VARIEGATUS*

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ABSTRACT: Aggregation of *Coleonyx variegatus* in diurnal shelter sites is shown to be a statistically valid phenomenon, confirming earlier reports based on subjective impressions. Preliminary data on causative factors suggest that limited burrow availability promotes aggregation. Experiments in which two individuals were placed in cages having an excess of burrows revealed no indication of interindividual attraction. However, these results do not exclude the operation of social factors in aggregation. On the contrary, pilot data provide hints that the sexes may differ in aggregative behavior. We hypothesize that lizard density, sex, and physical variables such as temperature and moisture may be associated with joint burrow occupancy.

Key words: Sauria; Gekkonidae; *Coleonyx*; Aggregation; Burrowing; Deserts

AGGREGATION of banded geckos, *Coleonyx variegatus*, in shelter sites has been reported (Evans, 1967; Greenberg, 1943; Van Denburgh, 1922, cited by Smith, 1946) but not rigorously demonstrated. Aggregation appears to occur under daytime shelters such as bark, moss, and water dishes in a laboratory setting (Evans, 1967; Greenberg, 1943) and under stones in the field (Van Denburgh, 1922, cited by Smith, 1946). More recent extensive field observations (Vitt, unpublished) fail to substantiate a tendency to aggregate. This apparent discrepancy has many potential explanations, for instance, geographic variation, seasonal differences (Van Denburgh observed aggregation only in April), density-dependence, and environmental fluctuations in moisture, temperature, and food supply. Another possibility is that banded geckos do not actually aggregate. The observations of Evans (1967), Greenberg (1943), and Van Denburgh (see Smith, 1946) suggest that aggregation may occur, yet it would be premature to conclude that the geckos were nonrandomly distributed with respect to available shelter sites because neither author presented any relevant statistical evidence.

To determine whether *C. variegatus* aggregates under diurnal shelter sites, we conducted controlled observations which permitted comparison of the frequencies with which various numbers of geckos occurred per shelter with the Poisson distribution. Thus, lack of any statistically significant difference between observed frequencies and expected Poisson frequencies could be interpreted as consistent with a random distribution. Statistically significant differences between observed and Poisson frequencies would indicate either mutual avoidance or aggregation depending on the direction of the difference from expectation.

After it had been established that the geckos aggregated in shelter sites, two potential underlying factors promoting the contagious distribution were investigated. Because *C. variegatus* burrowed more and aggregated to a higher degree when no previously existing burrows were present, the possibility that availability of existing burrows might influence shelter site selection was investigated. Burrow construction in loose sand is not difficult for *C. variegatus*, but expenditure of time and energy in digging could be avoided by selection of shelters already suitable for occupancy. It was therefore predicted that geckos would prefer shelter sites with prepared burrows to those lacking burrows. Many factors other than burrow availability, including social variables, could conceivably affect choice of burrows; e.g., aggregation may depend on sex, age, and/or reproductive status. We hypothesized that if social factors promote aggregation, the presence of one gecko in a burrow might attract other individuals.

METHODS

Geckos used in this study were collected in May 1983 near Ocotillo, San Diego County, California. Observations and experiments were conducted between mid-July and mid-August 1983 at the Savannah River Ecology Laboratory in a laboratory building with translucent ceilings and walls, and continuously open doors at both ends. Light and temperature cycles in this building closely approximated the natural cycles in the vicinity except that there were slight lags in the thermal cycle and somewhat higher maximum temperatures. When not being used as observational or experimental subjects, lizards were housed individually in small glass or plastic terraria supplied with sand substrates and bark or plywood shelters. Food, primarily crickets and tenebrionid beetle larvae, and water were available ad libitum.

Experiment 1

For observations of possible aggregative behavior, open-topped, transparent plexiglass arenas of dimensions 122 × 122 × 30 cm were constructed. Each chamber contained a sand substrate with a uniform depth of 3 cm and 16 shelter sites consisting of plywood sheets of uniform dimensions (14 × 14 × 3 cm). The floor of each chamber was divided into 16 squares of equal area; a single wooden sheet was placed at the center of each square (Fig. 1). During observation periods lasting several days, two water dishes were placed between central shelter boards and mealworms were released in each observation chamber.

Four groups of eight adult lizards matched by size and sex were drawn from the laboratory population; each group contained four males and four females. Each group of eight lizards was placed in a separate chamber and observed for three consecutive nights. Lizards were placed in the observation chamber shortly after dark and were returned to their home cages the following morning. During the first two observation days for each group, clean sand lacking burrows and clean plywood shelters were placed in the chambers. After lizards were removed following the first night, observation chambers were washed

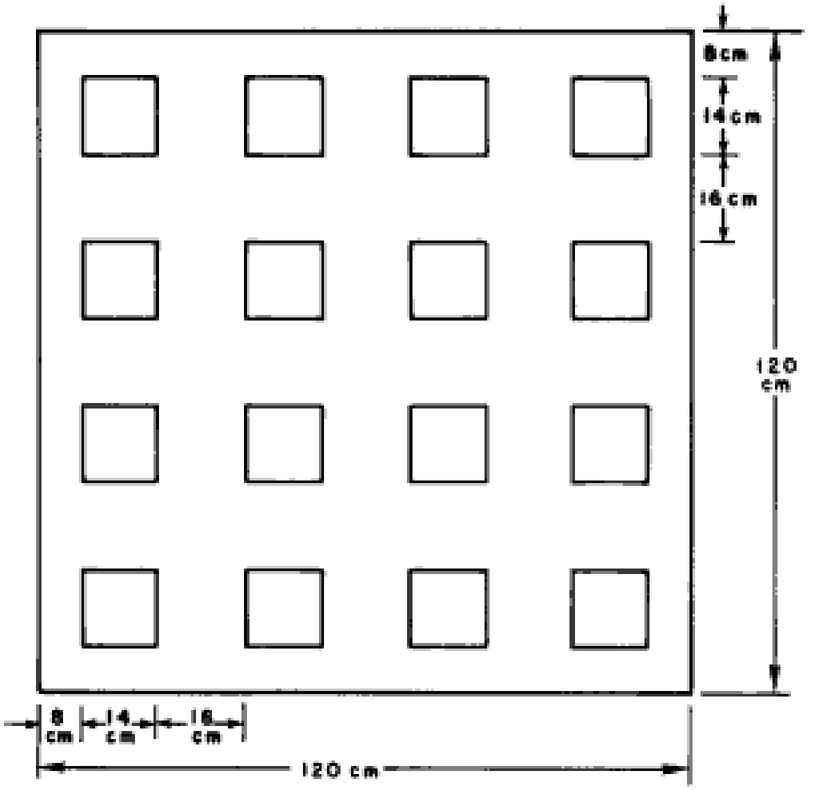

FIG. 1.—Plexiglass observation chambers contained a sand substrate and 16 evenly spaced plywood shelter sites (small squares).

with Alconox and fresh sand and shelters were added. On the third night, sand, shelters, and burrows were left undisturbed from the second night. One of the four groups, group 3, was left in its chamber continuously for eight more days following the third night. The position of each lizard, individually marked by toe-clipping, was recorded each day at approximately 0830 h ESDT after geckos had retreated to burrows under the shelter sites for the day (Cooper et al., 1985). Positions of burrows dug during each night and those remaining from previous nights were noted.

To detect aggregation, the frequencies of shelters harboring 0, 1, 2, . . . , 8 lizards on a given night were compared to Poisson frequencies by the *G* procedure incorporating Williams' correction factor (Sokal and Rohlf, 1981). Expected Poisson frequencies were calculated for 64 shelters (16 per group) with an expected value of 0.5 lizards per shelter as:

$$\frac{64(0.5)^x}{x!e^{0.5}}$$

Differences in degree of aggregation on the three nights were analyzed by McNemar's test of significance of changes. Possible position effects which might indicate that aggregation was induced by attraction of lizards to the same place were also examined. The possible attraction of lizards to particular quadrants or sides of the chamber or to edges was evaluated by two-tailed chi-square tests of independence of the distribution of occupied shelter sites and by binomial tests (Siegel, 1956). Influences of site fidelity were examined by binomial tests. All significance tests were two-tailed unless otherwise noted, $\alpha = 0.05$.

Experiment 2

To test the effect of burrow availability on shelter site selection, lizards were placed in cages containing four plywood sheets, only one of which covered a burrow. The test arenas were plate glass cages of dimensions 50 × 50 × 31 cm containing clean sand spread to a nearly uniform depth of 3 cm. A clean plywood sheet of the same type used previously was placed at the center of each quadrant in all cages. The experimenter constructed a burrow approximating the size and depth of natural gecko burrows under only one shelter site prior to introduction of an experimental lizard. In the eight trials, burrows were assigned to each quadrant twice as in a doubly replicated Latin square design.

Four trials each were begun 2 and 3 August 1983. Each individual was randomly selected from the laboratory population and at dusk was placed in an arena containing no other geckos. At 0830 h ESDT the following morning, gecko locations relative to prepared burrows were recorded, as were burrowing activities. Association between lizards and prepared burrows was analyzed by the binomial test (Siegel, 1956). It was assumed that the probability of a lizard occupying any shelter site would be 0.25 if all sites were equally attractive. Because the burrows were predicted to increase the attractive-

TABLE 1.—The number of lizards per shelter site has a contagious distribution in which more individuals simultaneously occupy the same shelter site than would be expected in a random distribution.

Lizards per shelter	Expected Poisson frequency	Observed frequencies		
		Night 1	Night 2	Night 3
0	38.816	48	46	45
1	19.411	7	7	14
2	4.850	5	7	1
3	0.806	3	2	2
4	0.101	0	0	0
5	0.010	0	1	2
6	0.001	1	0	0
7	—	0	0	0
8	—	0	0	0

ness of shelter sites, a one-tailed test was used.

Experiment 3

A test of the hypothesis that the presence of conspecific lizards affects aggregation was conducted by placing an experimental lizard in a cage containing four shelter sites and a single conspecific. Cages were as described for the previous experiment with the following exceptions. First, a burrow was prepared under each plywood sheet prior to introduction of lizards. In one test, the conspecific was tethered under a plywood shelter by a short length of number 1 cotton suture thread tied around the body just anterior to the rear legs and anchored to a screw in the center of the plywood. Because tethering could have induced heightened aggression or increased activity sufficiently to disrupt aggregation, a second experiment was run in which an untethered resident conspecific was left continuously in the cage for three days prior to introduction of the lizard to be tested. Neither the resident nor the experimental lizard was restrained.

Experimental subjects were placed in the arenas at dusk. At 0830 h EDST the next morning, it was noted whether or not both lizards were found beneath the same board. In both experiments, equal numbers of experimental males and females were randomly selected from the laboratory population. Due to limited availability of lizards, one gecko was used in one of the experiments on the effect of conspecific presence and in the burrow availability experiment. The experimental lizards were tested equally often with male and female conspecifics. The experiment involving tethering was conducted from 4–7 August 1983; the other from 9–17 August 1983.

Association between lizards was analyzed by the binomial test (Siegel, 1956). Under the null hypothesis that the presence of a conspecific has no effect on diurnal shelter site selection, the probability that both lizards would occupy the same site is 0.25.

RESULTS

Experiment 1

Geckos aggregated under shelter sites on all three nights during which four groups were observed. More unoccupied shelters and more shelters harboring two or more lizards than expected were present each night (Table 1). Due to low expected frequencies of two or more individuals occupying the same shelter, all the frequency categories of two and above were pooled for analysis. On nights 1 and 2, the departure from randomness was highly significant (night 1: $G = 13.35$, $P < 0.005$; night 2: $G = 12.20$, $P < 0.005$). On the third night the observed distribution did not differ significantly from the Poisson values (night 3: $G = 2.56$, $0.1 < P < 0.5$) calculated as above. Note that this result is probably attributable to the lumping of frequency categories necessitated by small sample sizes. Even on night 3, two shelters covered five geckos each. The probability of even one occurrence of five or more lizards under a single shelter is only 0.00025.

Whether or not aggregation occurred on the third night, substantially fewer individuals shared shelter sites with other lizards at that time. On each of the first two nights, 25 geckos shared shelters, but this number dropped to 18 on the third

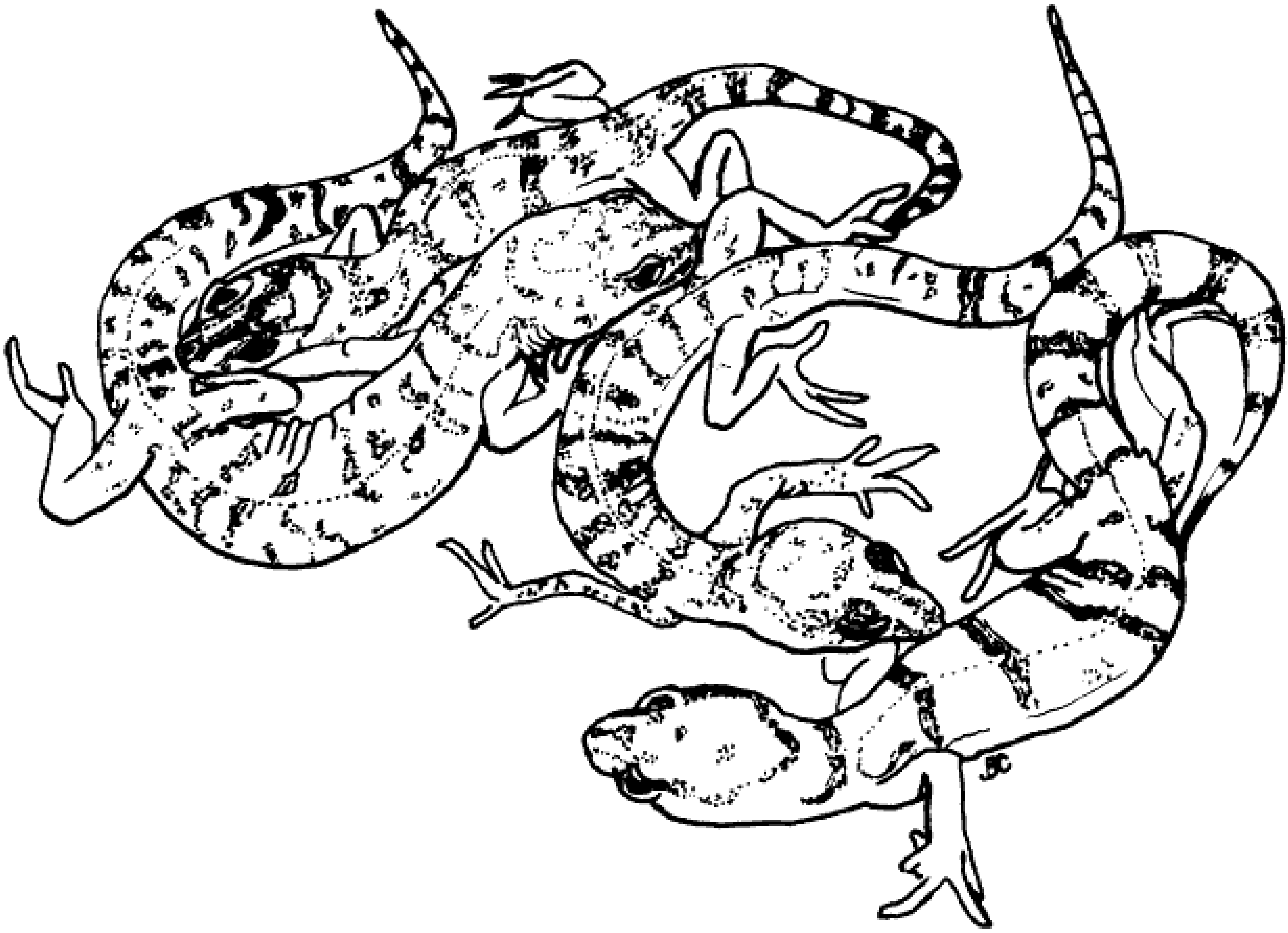

FIG. 2.—Individuals in burrows were frequently found to be in physical contact.

night, suggesting a possible decrease in aggregation. Examination of individual data showed that the proportions of lizards changing from aggregated to isolated occupation of shelters and vice versa were similar between nights 1 and 2. Between the second and third nights, the number of lizards shifting from shared shelter to isolated ones was not significantly greater than that changing from isolation to cohabitation ($0.05 < P < 0.10$). However, the close approach to significance suggests a possible decline in aggregation.

As a group, the geckos showed no marked preferences for particular locations in the observation chambers. Lizards did not occur at higher than expected frequencies in any quadrant ($P > 0.50$), nor did they prefer the right or left side ($P > 0.10$) or the top or bottom half ($P > 0.50$) of the chamber as oriented in Fig. 1. Shelters adjacent to walls were no more likely to be occupied than were the four centrally located shelters ($P > 0.10$).

There were no indications of lasting associations between individuals in the data for all groups on the initial three days. However, there was evidence of site fidelity. Four of 32 lizards occupied the same burrow on both of the first two nights (binomial $P \geq 4 = 0.137$) and an additional individual remained on the surface at the same spot on both mornings (binomial $P \geq 5 = 0.047$). Site fidelity was much more pronounced between nights 2 and 3 when eight lizards occupied the same burrow for 2 successive days (binomial $P \geq 8 = 0.0006$). Several individuals in group three displayed short-term attachment to particular shelters. For example, one gecko occupied the same shelter on 10 consecutive days and another for seven of the 11 nights.

Despite the absence of prolonged asso-

TABLE 2.—Burrow construction by *Coleonyx variegatus* may be related to burrow availability and lizard density. For each night, the number of new burrows dug and the total number of burrows present on the following morning are given, the latter being a sum of newly constructed burrows and those remaining from earlier nights. The number of burrows per lizard is given by the total number of burrows divided by the number of lizards. The number of isolated lizards is simply the number found alone whereas the number of aggregated lizards is the number of individuals sharing shelter sites with one or more other geckos.

Night	Number of new burrows	Total burrows present	Burrows per lizard	Isolated lizards	Aggregated lizards
1	23	23	0.72	7	25
2	31	31	0.97	7	25
3	7	38	1.19	14	18

TABLE 3.—Observations of a group of eight geckos for 11 days suggest that aggregation continues well beyond the three day period of analysis and that aggregation may be influenced by sex and/or social factors.

Night	Number of male isolates	Number of female isolates	Number of females with other females	Number of males with other males	Number of females with males	Number of males with females
1	0	1	0	2	3	4
2	2	1	3	2	3	2
3	3	0	4	0	4	1
4	3	1	3	0	3	1
5	1	0	2	0	4	3
6	1	0	2	0	4	3
7	2	0	4	0	4	2
8	4	1	3	0	0	0
9	2	1	2	0	3	2
10	3	1	2	0	1	1
11	2	1	2	0	3	2

ciations between individuals in shelter sites, lizards at rest were frequently in physical contact with each other when their burrows were exposed in the morning. The geckos were touching each other even though the burrows afforded room for mutual avoidance (Fig. 2).

Burrowing was not clearly related to aggregation. When fresh sand and clean shelter boards were presented (nights 1 and 2), geckos constructed 23 and 31 burrows by digging sand out from beneath the shelter sites. Only seven additional burrows were dug on the third night, giving a total of 38 burrows at the end of that night, or 1.19 per lizard. The lizards readily dug burrows when none were present but decreased burrow construction when ample shelters sites with burrows were available (Table 2). In the group of eight lizards observed for 12 days, seven burrows were built on the second night and one more was dug on night 5. No further burrow construction took place. Thus, burrow construction ceased in this group when one burrow was available for each lizard. Despite the presence of sufficient burrows to shelter each individual in isolation, half or more of the lizards occupied shelters with other individuals on all but the eighth morning (Table 3).

No sex difference in tendency to aggregate was found on any of the first three nights. Nevertheless, observations of group 3 for 11 consecutive nights revealed clues regarding a possible sexual influence on aggregative behavior. Because the same individuals were observed repeatedly, statistical tests requiring the assumption of independence could not be used. Therefore, we merely point out several suggestive features of the data summarized in Table 3. First, more males than females were isolated on 10 of 11 mornings. Also, the number of males sharing shelters with females was greater than the number sharing shelters with other males on nine of 11 days. Finally, females shared shelters with other females more than males shared shelters with other males on 10 of 11 days.

Experiment 2

In six of the eight trials, geckos were found the following morning in the shelter site with the prepared burrow. The lizards thus occupied the prepared burrows at much greater than chance frequency (binomial $P = 0.004$). All but two of the lizards constructed burrows under shelter blocks other than the one covering the prepared burrow. Both of the lizards which did not dig new burrows occupied the prepared burrow, yet engaged in burrowing activity by extending the burrow area in the same shelter site.

Experiment 3

Three of 12 experimental lizards occupied shelters with tethered lizards. The probability of three or more of 12 pairs occupying the same burrow is 0.609, which is hardly indicative of interindividual attraction. In the experiment involving only unrestrained lizards, seven of the eight pairs were found under separate shelters. These results obviously do not suggest aggregation, but neither do they demonstrate that the lizards avoided joint occupation of shelters (the binomial probability that only one pair or no pairs would occupy the same burrow is 0.367).

DISCUSSION

Banded geckos definitely aggregated in the observation cages, confirming the subjective reports of earlier herpetologists (Evans, 1967; Greenberg, 1943; Van Denburgh, 1922, cited by Smith, 1946). The degree of aggregation observed was surprisingly high (Table 1) considering that banded geckos encountered under objects in the field are usually solitary (Vitt, personal observations). This suggests that aggregation could be a response to some novel aspects of the observational milieu, such as unfamiliarity with the cage, shelter sites and cagemates. The possible importance of novelty is supported by the tendency toward increasing isolation on the third night. However, the geckos of group 3 continued to aggregate throughout the 11 day observation period.

Another factor on the first two nights could have been the initial lack of burrows under the plywood sheets. On these nights, the geckos burrowed extensively, producing enough burrows to have allowed most lizards to occupy shelter sites alone, yet showed pronounced aggregation. On the third night, only a few additional burrows were constructed. The coincident increase in isolated geckos enhances the possibility that some aspect of burrowing behavior or burrow availability may affect the tendency to aggregate.

The results of experiment 2 show that burrow availability is an important factor in selection of shelter sites, at least initially. Geckos may choose shelter sites in part for burrow presence and qualities. Burrow features and other factors (such as social factors) could interactively affect shelter selection. At high lizard density relative to available shelter sites, geckos might be forced to share shelters. Where a superabundance of shelter sites exists, social (and other) factors affecting aggregation may operate independently. Burrow availability cannot completely account for the high degree of gecko aggregation observed because numerous completed burrows were empty every morning. The dependence of aggregation jointly on lizard and shelter site densities remains to be determined.

The absence of group preferences for any particular portions of the observation chambers indicates that aggregation was not induced by variation of external physical variables such as light and temperature within the observation cages. This does not show that these factors are unimportant, only that they had little influence in this study.

Site fidelity, as revealed by the marginally significant return after night 2 to the same burrow occupied on night 1 and the highly significant return after night 3 to shelters occupied on night 2, may be selectively beneficial because use of known shelter sites allows more reliable withdrawal from adverse environmental conditions and escape from predators. That twice as many geckos returned to the same burrows used the previous night on night 3 as on night 2 suggests at least two possibilities. Increased familiarity with the cage may have produced stronger attachment to burrow sites. However, since burrows constructed on night 2 were left intact whereas fresh sand was used at the outset of night 2, familiarity with the burrows themselves, perhaps including recognition of chemical stimuli, may also be important. We emphasize that only a minority of geckos in the laboratory displayed site fidelity, which may indicate the existence of alternative strategies of space utilization in *C. variegatus.*

Aggregation may often represent a response to physical variables among invertebrates (Fraenkel and Gunn, 1960), but in many vertebrates and social invertebrates, it is sometimes a social response. One indication of the possible influence of social factors was the apparent relationship between sex and aggregative tendency in group 3. Although the data suggest that sex and, by implication, social behavior may be important determinants of gecko distribution in shelters, they must be interpreted cautiously. Group 3 consisted of only four males and four females, and these same individuals were observed repeatedly for 11 nights. Therefore, the observed differences cannot by unequivocally attributed to sex. Further evidence favoring a social influence on aggregation is the frequent touching observed between individuals in burrows.

Experiment 3 failed to demonstrate any social stimulation of aggregation, but this failure cannot be interpreted as indicating that no social factors are involved. In the presence of a surplus of burrows and a single conspecific, geckos did not jointly occupy shelter sites at greater than random frequency. What would have happened at higher lizard densities and reduced burrow densities is conjectural, but a factorial experimental approach is strongly indicated. The observation of pronounced aggregation in the presence of more conspecifics and lower burrow density suggests that lizard and burrow densities could affect aggregation interactively.

In the laboratory, banded geckos aggregate in diurnal shelter sites and prefer sites which have already been excavated. The observations that these geckos show well developed aggressive behavior and are often found alone in shelter sites demand caution in the interpretation of proposed relationships between isolation in shelter and aggressive behavior. Spacing patterns and related social behaviors in geckos have not been studied extensively, but several diurnal species are territorial, including *Gonatodes vittatus* (Stamps, 1977), *Lygodactylus picturatus* (Greer, 1967), *L. somalicus* (Greer, 1967), *L. klugei* (Vitt, personal observation), and several species of *Phelsuma* (Kastle, 1964). Among nocturnal geckos, aggressive behavior and territoriality have been described in a number of species. Furthermore, solitary occupation of diurnal shelter sites has been interpreted as possibly indicative of active defense of shelter sites against conspecifics (Bustard, 1965, 1967, 1968, 1969, 1970, 1971). Although aggressive behavior may account for exclusive occupation of diurnal shelter sites in some nocturnal geckos, it does not follow that nocturnal geckos showing intraspecific aggression must exclude conspecifics from burrows or other shelter. On the contrary, *C. variegatus* is characterized by frequent fighting among males but also aggregates. It is quite possible that some nocturnal geckos do aggressively exclude conspecifics from shelter sites (Bustard, 1965, 1967, 1968, 1969, 1970, 1971). Aggressive displacement may occur at times even in *C. variegatus.* However, further study is needed before conclusions may be drawn regarding the roles of agonistic behavior in solitary occupation of shelters.

The ultimate causation of aggregation by banded geckos is not known. Greenberg (1943) believed that survival of nocturnal species would be promoted because aggregation brings individuals together especially for reproduction. Even ignoring the implication of group selection, there is insufficient evidence to accept Greenberg's hypothesis. That several nocturnal geckos locate mates without aggregating in shelter sites suggests that the hypothesis could be incorrect. Selection of shelter sites could be based largely on physical features of shelter and on environmental conditions. Aggressive interactions unrelated to shelter preferences might account for apparent sexual differences in aggregation. It may be expected that shelter-seeking behavior is selectively reinforced by avoidance of predation and harmful environmental conditions. Whether aggregation has any additional independent impact on avoidance of predation, extreme temperature, or low moisture levels remains to be determined.

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