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DOMINANCE BEHAVIOR IN ASEXUAL GECKO, *LEPIDODACTYLUS LUGUBRIS*, AND ITS POSSIBLE RELATIONSHIP TO CALCIUM

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ABSTRACT: Investigations of dominance behavior and its relationship to calcium gland size were conducted in the asexual gecko, *Lepidodactylus lugubris*. In an initial study, geckos, immediately after laying eggs, were randomly assigned to one of six groups where time of social contact (2 vs. 7 days) and type of social contact (direct experience with a gravid or non-gravid gecko or indirect experience) were varied in a 2 × 3 factorial design. Behaviors displayed by geckos in social contact were systematically recorded. Dominance hierarchies were readily formed between gecko dyads that received 7 days of social contact with each other. Dominance was not related to gecko size or reproductive state. A second study examined the relationship between dominance, calcium gland size and egg development. Geckos were housed in groups of 4 for 28 days and were subsequently transferred into either dyads or housed individually for an additional 28 days. During the final 28 days, half of the geckos received extra calcium. Dominance, size of calcium glands and egg development were recorded. Dominant geckos developed a greater number of eggs and had larger initial calcium glands than subordinates, but extra calcium was not related to gland size. The function of dominance in *L. lugubris* populations may be two-fold: it may act as a spacing mechanism in low density environments and may facilitate the development and laying of eggs by more nutritionally fit individuals in high density environments.

Dominance hierarchies are well documented in a variety of sexual vertebrate species and are usually associated with aggression and lowered reproductive success of subordinates (i.e. primates, Abbot, 1987; birds, Ekman, 1987; wolves, Packard et al., 1985). The data on dominance and its relationship to aggression and reproductive success are more equivocal in asexual vertebrates. Leuck (1985) found that individuals of the parthenogenic species, *Cnemidophorus uniparens*, were less aggressive than sexual *Cnemidophorus* species and seldom engaged in biting or chasing. The asexual whiptails were also reported to form weaker dominance relationships than sexual whiptails. In contrast to Leuck's research, however, Grassman and Crews

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(1987) found that asexual *C. uniparens* readily formed dominance hierarchies.

Bustard (1970) found that female geckos of sexual species occasionally regulated their numbers through aggression, however, Frankenberg (1982) reported little aggressive behavior in the parthenogenic gecko, *Hemidactylus garnotti*. When one *H. garnotti* approached another, the stationary gecko usually attacked and the approaching gecko always retreated. *H. garnotti* did not form stable dominance hierarchies or establish territories even though they preferred certain locations in their enclosures. Again, in contrast, Brown and Sakai (1988) found that the mourning gecko, *Lepidodactylus lugubris*, formed dominance hierarchies and that egg development was related to dominance. Dominance behavior was also related to egg production in *C. uniparens* (Grassman & Crews, 1987; Gustafson & Crews, 1981).

Geckos are unusual among reptiles because they lay calcareous shelled rather than parchment shelled eggs (Bustard, 1968). Calcium glands are visible in most adult geckos' necks (Ruth, 1918) and change size relative to the female's reproductive state (Ineich & Gardner, 1989). The reduced fecundity of subordinates may be related to stress and its effects on calcium. Stress is related to decreased calcium levels in some species (i.e., chickens, Odom, Harrison, and Bot-tje, 1986; rats and mice, Watanabe, Ho, and Haskins, 1987) or altered and inefficient calcium storage as in porcine stress syndrome (Basrur, Frombach, and McDonell, 1983; Cheah & Cheah, 1979). Lowered calcium levels are also associated with increased mortality and abnormal eggs in chickens (Brugh & Beard, 1986). Therefore, a proximate cause of the decreased fecundity observed in subordinate mourning geckos may be decreased levels of available calcium.

The two present studies were designed to extend our knowledge of the variables important in egg development in *L. lugubris*. The first study examined the formation of dominance hierarchies in *L. lugubris*. The second study examined calcium gland size and its relationship to dominance and egg development in *L. lugubris*.

METHODS

General Housing Conditions

The geckos were provided with water, food (meal worms, grasshoppers, and fruit flies) and a vitamin (Brand name Vionate)/corn syrup mixture ad libitum. To provide a humid and moist environment, the enclosures were misted with water each morning. Each enclosure floor was covered with approximately 2 cm of pebbles to per-

mit digging. Sphagnum moss was placed on the pebbles to provide the geckos with hiding places and to maintain the moisture within the enclosure. One platform, constructed of two pieces of wood so that a crack was formed, was placed in each enclosure. The platform was designed to mimic the geckos' daytime hiding places. A 12 hr light/dark cycle was maintained with lights turned on at 6.00 and off at 18.00 hr. Additional external fluorescent lights were placed near each enclosure providing the geckos with heat, and were turned on at 8.00 and off at 12.00 hr. The laboratory room was open to the natural tropical environment of Hawaii Island through windows along one wall; lab temperatures varied from 72 to 78°F.

STUDY 1

Procedure

Study 1 was designed to document how dominance hierarchies are formed in *L. lugubris* and whether dominance is related to the gecko's reproductive state. Sixty *L. lugubris* were collected on 21 and 22 January 1987 between 19.00 and 21.00 hr at the University of Hawaii, Hilo. The study began 21 January 1987 and continued until 10 August 1987 when the last gecko laid its eggs. Geckos were initially housed in aquaria (51 cm × 28 cm × 31 cm) and checked weekly for egg development. Eggs greater than 1 mm in diameter were observed by placing the animals in narrow plexiglass boxes and examining their translucent ventral surfaces. When egg development was first noticed, the geckos were removed from the communal enclosures and randomly assigned to single plexiglass enclosures (32 cm × 18 cm × 23 cm). Geckos that did not lay at least one egg were not used as subjects; therefore all experimental geckos were synchronized in terms of their reproductive cycles. The first 36 geckos (experimental geckos) to lay eggs were randomly assigned to one of six groups ($n = 6$) which comprised a 3×2 (condition X days) factorial design. Geckos were placed with 3 types of stimulus gecko (stimulus geckos were obtained from our lab collection): a gecko with no visible sign of egg development (non-gravid condition), a gecko with visible eggs (gravid condition), or in a divided enclosure in which the gecko was able to see and hear another non-gravid gecko but could not touch it (audio/visual condition). Geckos remained in the social situation for either two or seven days.

Eight 15 min event recordings were obtained each day for geckos that were housed with a stimulus gecko with which they could physically interact (2 and 7-days—gravid conditions; 2 and 7-days—non-gravid conditions) each hour between 6.00 and 10.00 hr and again

TABLE 1
Interactive Behaviors Observed Between Geckos with Descriptions

<i>Behaviors</i>	<i>Descriptions</i>
In proximity	Less than 3 inches apart, from 2 to 15 min.
Orient to	Gecko turns head toward another
Face to	Gecko turns body toward another
Approach	Gecko moves toward another, including mutual approaches and chases, but excluding lunges
Click	Rapid, sharp sound
Rurr	Extended, low guttural sound
Push-up	Gecko moves upper body up and down
Lunge	Gecko plunges toward another
Bite	Gecko mouths the other usually on the neck or tail
Touch	Physical contact excluding biting
Displacement	Gecko occupies the position of another after the second moves away
Orient away	Gecko turns head away from another
Face away	Gecko turns body away from another
Back-up	Gecko moves away from another using a backward motion
Move away	Gecko moves away from another in a forward motion

between 17.00 and 21.00 hr. Therefore, geckos in the 2-day condition were observed for 4 hr, while those in the 7-day condition were observed for 14 hr. The behaviors classified as interactive are summarized in Table 1. Dominant geckos were defined as geckos that did not flee as often as their cagemates in encounters where one gecko clearly fled from another. Stable dominance hierarchies were defined as those in which one gecko was consistently dominant to the other during the last half of the observations (i.e., the last 24 hrs in the 2-day condition and the last 3 1/2 days in the 7-day condition). The positions of the geckos relative to one another were also systematically recorded for geckos in the audio/visual condition.

Results

Interactions between gecko dyads were highest during the first 24 hr after they were placed together, and most interactive behaviors significantly decreased during the second 24 hr (Table 2). Both experimental and stimulus geckos exhibited similar decreases in orienting

TABLE 2
Behavioral Differences Observed in Geckos Across the First vs. the Second 24 hr They Were Placed Together.

Behavior	0-24 hrs		25-48 hrs		$F_{(1,22)}$	p
	MN	SE	MN	SE		
<i>Experimental Gecko</i>						
Orient/face to	.4	(.3)	.2	(.2)	9.2	.006
Approach	.5	(.4)	.2	(.3)	9.3	.006
Click	3.0	(1.9)	.9	(1.3)	2.8	.11
Bite/lunge	.1	(.1)	.0	(.1)	3.8	.06
Orient/face away	.2	(.1)	.1	(.1)	6.1	.02
Move away	.3	(.4)	.1	(.3)	5.6	.03
<i>Stimulus Gecko</i>						
Orient/face to	.4	(.3)	.1	(.2)	10.6	.004
Approach	.5	(.4)	.1	(.2)	11.3	.003
Click	1.9	(2.4)	.8	(1.8)	3.2	.09
Bite/lunge	.1	(.1)	.0	(.1)	4.2	.05
Orient/face away	.2	(.2)	.1	(.1)	2.9	.10
Move away	.4	(.2)	.1	(.2)	13.8	.001

or facing to, approaching, clicking at, lunging and/or biting, orienting or facing away from, and moving away from the other gecko. In the 2-day groups, only 6 of the 12 dyads formed stable dominance hierarchies. In contrast, in the 7-day groups, stable dominance hierarchies were formed in 11 of the 12 dyads (the one exception was in the 7-day gravid condition). In the 7-day gravid condition, the gravid gecko was dominant 3 times and the experimental (non-gravid) gecko 2 times. Therefore, being gravid did not necessarily give the gecko an advantage in dominance contests. In both 7-day groups the dominant gecko was larger than the subordinate in 45% of the dyads, equal in size in 18%, and smaller than the subordinate in 36% of the dyads (Overall $\bar{X}(\text{DOM}) = 43$ mm, $s(\text{DOM}) = 1.5$ mm; Overall $\bar{X}(\text{SUB}) = 42$ mm, $s(\text{SUB}) = 2.7$ mm). In all stable dominance hierarchies (17/17) the dominant gecko controlled the platform by the end of the observations.

All geckos displayed behaviors associated with dominance behavior. Interactions between gecko pairs in the 7-day conditions were analyzed in detail. Dominant geckos were more likely to initiate and end encounters by clicking than subordinates; this difference was statistically significant using the Sign test ($T = 0$, $N = 11$; $p < .01$). Subordinate geckos usually initiated encounters by simply orienting

to or facing the dominant gecko without subsequently approaching; a behavior seldom observed in the dominant geckos. This difference was statistically significant using the Sign test ($T = 0$; $N = 6$; $p < .05$).

Whether the geckos were in the gravid condition influenced their reactions to another gecko. Geckos in the gravid condition many times displayed no visible reaction after their cagemates initiated an encounter (18/47 encounters). Geckos in the non-gravid condition, however, seldom reacted to an encounter by "not responding" (5/73 encounters). This difference was found to be statistically significant using the Mann-Whitney U ($U = 27$; $n = 5$ & 6 ; $p < .05$).

Geckos in the audio/visual conditions, although not able to physically interact, oriented themselves so that they could view each other in 36% of the observations. Five of the six geckos in the 7-day audio/visual condition were observed mutually clicking at each other at least 2 times during observations; this differed from clicking observed in the gravid and non-gravid conditions when only one gecko clicked at a time.

STUDY 2

Procedure

Study 2 was designed to see if calcium gland size was related to dominance in *L. lugubris*. Thirty-two *L. lugubris* were collected on 31 January ($n = 16$) and 14 February 1989 ($n = 16$) at the University of Hawaii, Hilo. Only geckos that showed no visible eggs were collected. Two replicates of the study were conducted. In both replicates 16 geckos were randomly assigned to one of four communal enclosures ($n = 4$) after their snout-vent lengths and calcium glands were measured, and after they were paint marked with non-toxic tempera paint. Two observers, blind to the geckos' dominance status, independently measured the calcium glands (inter-observer reliabilities ranged from + .5 to + .84 with a mean of + .72).

Geckos were kept in the communal enclosures for 28 days. Fifteen minute event recordings were obtained on each enclosure in a random sequence between 8.00 and 9.00 hr five days a week (total observation time per enclosure = 5 hr). Observations were done in order to determine the dominance rank of each gecko. Dominance was defined by the number of times a gecko ended an interaction with the other gecko moving away and by the ability of a gecko to maintain control of the platform over other geckos in the enclosure (See results obtained in Experiment 1 above).

After 28 days in the communal enclosures, calcium glands were

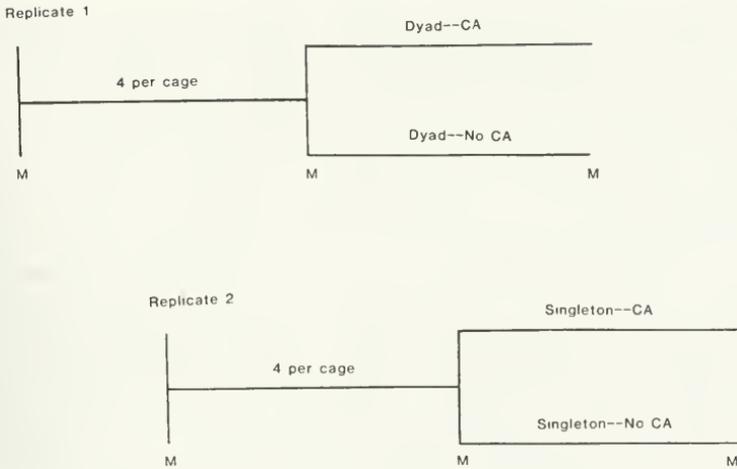


FIGURE 1. Experimental design for experiment 2. M indicates when a measurement of the geckos' calcium glands was obtained, CA indicates groups that received extra calcium in the form of gecko egg shells, and horizontal lines represent 28 day periods.

remeasured (See Figure 1). The geckos in Replicate 1 were divided into dyads and transferred to smaller plexiglass enclosures. The most dominant and most subordinate geckos were housed together and the intermediately ranked geckos were housed together. One gecko in Replicate 1 escaped during the first 28 days. Only the most dominant and subordinate animals were kept from this cage; the remaining gecko was released ($n = 14$). Calcium supplements which consisted of gecko egg shells were supplied to 3 of the 7 dyads (2 cages containing dominant/subordinate geckos and 1 with intermediate geckos). For the next 28 days, the geckos' positions in the enclosure were noted each morning with special attention to which gecko controlled the platform.

In Replicate 2 after the communal experience, the geckos were housed alone for 28 days. This was done to observe how a less stressful environment in terms of dominance would affect the size of their calcium glands. Geckos were checked weekly for egg development and enclosures daily for oviposition. Calcium glands for both replicates were measured 28 days after the geckos were transferred from communal cages (See Figure 1). All geckos at the end of the study were released near their capture sites.

Results

At the end of 4 weeks, 13 out of the 15 dominant geckos had developed eggs whereas only 4 out of the 15 subordinates had devel-

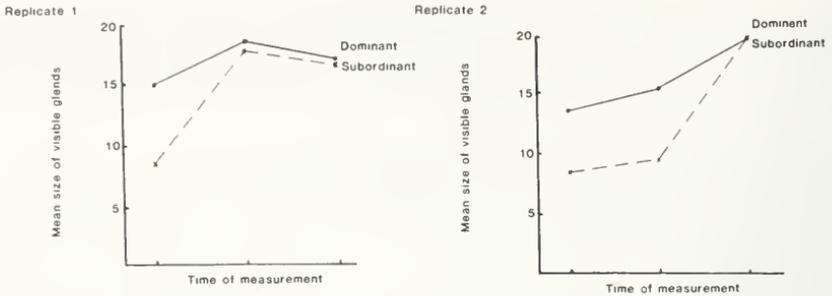


FIGURE 2. Summary of the calcium gland measurements for both Replicate 1 and Replicate 2. The first measurement was made the morning after the geckos were captured, the second measurement 28 days later after the geckos had been housed as quadruplets, and the third measurement 28 days later after geckos had been housed as either dyads (Replicate 1) or alone (Replicate 2).

oped eggs. The difference in egg development between dominant and subordinate geckos was significant ($\chi^2_{(1)} = 11.0$; $p = .01$; data from both replicates are included). Subordinates in both replicates had significantly smaller initial calcium glands than the dominants ($F(1,28) = 6.2$; $p < .05$; Figure 2). In Replicate 1, the subordinates' calcium glands increased up to week 4 whereas the size of the dominants' calcium glands remained relatively stable for the entire 8 weeks (Trials effect was significant; $F(2,24) = 7.2$; $p < .006$ using Greenhouse Geisser probability). On the other hand, in Replicate 2 the subordinates' calcium glands remained smaller than the dominants' through week 4 of the study and then increased in size after the geckos were housed alone (Trials effect was significant; $F(2,28) = 12.1$; $p < .0005$ using Greenhouse Geisser probability). The extra calcium some groups received in the form of gecko egg shells did not affect the size of geckos' calcium glands.

There were 13 geckos from both replicates with no eggs at the end of week 4, seven of these subsequently received extra calcium and six did not. Five of the seven that received calcium supplements developed eggs whereas only one of the six that did not receive calcium supplements developed eggs. Therefore there was a tendency for geckos that received calcium supplements to develop eggs over those which did not receive extra calcium.

DISCUSSION

All gecko dyads and quadruplets in the present studies attempted to establish dominance hierarchies; hierarchies stabilized by day 7

and half (6/12) by the end of 2 days. Dominance was unrelated to the reproductive state of the gecko. The behaviors displayed by both dominant and subordinate geckos were stereotypic with dominants much more likely to vocalize than subordinates. Unlike the parthenogenic gecko, *H. garnotti*, which defended a relatively small moveable area surrounding its body (i.e. its personal space, Frankenberg, 1982), *L. lugubris* dyads established stable dominance relationships, and the dominant gecko gained a resource, the small platform. Geckos are crack dwelling animals (Jones et al., 1978), and because the platform provided the only "crack" in the enclosure, dominant geckos obtained the best hiding place.

Dominant animals in Study 2 developed more eggs than subordinates. Brown and Sakai (1988) also found that dominant *L. lugubris* developed more clutches of eggs than subordinates, and dominant *C. uniparens* were found to be more fecund than subordinates (Grassman & Crews, 1987; Gustafson & Crews, 1981). Dominance may work as a spacing mechanism in geckos. For example, if a particular gecko is subordinate, it may be advantageous for it to move to a different place where there are either no geckos or where it can dominate. On the other hand, when geckos become numerous, as they are in many areas on the island of Hawaii, the most fit animals (i.e. dominants) may be the ones laying the majority of the eggs.

Because geckos lay calcareous shelled eggs (Bustard, 1968), animals with higher levels of calcium could be considered more fit than those with lower levels. We found that subordinate geckos in our quadruplets (Study 2) had initially smaller calcium glands than dominants, and that the calcium glands of subordinates increased in size when they were removed from social situations. Additionally, geckos that had not previously shown signs of egg development began to develop eggs when they received supplemental calcium. A proximate cause of decreased egg development in subordinate *L. lugubris* may therefore be decreased levels of calcium for egg shell formation.

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