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THE RELATIONSHIP BETWEEN CALCIUM GLAND SIZE, FECUNDITY AND SOCIAL BEHAVIOR IN THE UNISEXUAL GECKOS, *LEPIDODACTYLUS LUGUBRIS* AND *HEMIDACTYLUS GARNOTII*

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ABSTRACT: The three present experiments examined the relationship between calcium gland size, fecundity, and dominance/social behavior in the unisexual geckos, *Lepidodactylus lugubris* and *Hemidactylus garnotii*. Study 1 examined the above variables while the geckos were housed communally and solitarily. *L. lugubris* established stable dominance hierarchies through aggressive interactions, whereas *H. garnotii* neither established a dominance hierarchy nor displayed signs of aggression while housed communally. Eggs were developed by 4 of 4 dominant *L. lugubris* but by only 1 of 4 subordinate *L. lugubris* and 1 of 6 *H. garnotii*. Calcium glands decreased in size in the subordinate *L. lugubris* and *H. garnotii* during communal housing, then recovered when the geckos were housed solitarily. Study 2 examined the relationship between reproductive state and calcium gland size in *L. lugubris*. Calcium glands were found to be smallest prior to and immediately after oviposition and largest when eggs were yolking follicles. Study 3 examined the effect of sociality on fecundity in *H. garnotii*. Egg development was not related to whether geckos were housed solitarily or as dyads. Calcium gland size in geckos appears to be related to both stress and to the reproductive state of the gecko. We hypothesize that stress decreases the size of geckos' calcium glands resulting in decreased egg production in stressed animals.

Subordinates usually produce fewer offspring than dominants when species form strict dominance hierarchies (for example, primates, Abbot, 1987; birds, Ekman, 1987; reptiles, Brown & Sakai, 1988). Being a subordinate in a dominance hierarchy is stressful to an animal (Chapais

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& Schulman, 1983). Brown and Sakai (1988) found that the unisexual gecko, *Lepidodactylus lugubris*, formed stable dominance hierarchies in captivity and that fewer eggs were developed by subordinates when geckos were housed as quadrads. Further research on *L. lugubris* found that calcium gland size was also related to dominance rank (Brown et al., 1991). Subordinate geckos had smaller calcium glands than dominant geckos. The subordinates' calcium glands, however, increased in size after the geckos were housed solitarily. Research has shown that heat stress is related to decreased ionized calcium blood levels in chickens resulting in detrimental egg shell formation (Odom et al., 1986). Additionally symptoms of porcine stress syndrome are correlated with inefficient calcium storage in muscle mitochondria in pigs (Cheah & Cheah, 1979). Therefore the stress experienced by subordinate geckos may be affecting the availability of calcium and/or the storage ability of their calcium glands.

Calcium glands are found only in subfamilies of geckos that lay calcareous shelled eggs (Bustard, 1968). Ineich and Gardner (1989) found that calcium glands varied in size relative to the females' reproductive states. When Ineich and Gardner dissected geckos, they found that *L. lugubris* with small to moderately sized calcium glands were in an early stage of egg development, while geckos with larger glands had larger eggs. It was also observed that the glands varied in size just prior to egg laying. The variance in calcium gland size was believed to be associated with the timing of calcium deposition onto the eggs.

Little is known about the sociality of the unisexual gecko, *Hemidactylus garnotii*, and how the size of its calcium glands might be related to its social and reproductive states. Frankenberg (1982) reported little aggressive behavior between *H. garnotii* individuals. *H. garnotii* did not appear to form dominance hierarchies because, when one gecko moved into the vicinity of a second gecko, the first gecko always retreated.

To further our knowledge of the reproductive behavior of these two unisexual gecko species, the present study examined (1) relationships between calcium gland size, egg development and the social behavior of *H. garnotii* and *L. lugubris* geckos; (2) the relationship between reproductive state and calcium gland size in *L. lugubris*; and (3) the effects of sociality on fecundity and calcium gland size in *H. garnotii.*

METHODS

Housing Conditions

All geckos were provided with fruit flies and meal worms ad libitum. The enclosures were misted with water daily to maintain a moist and humid environment. The floor of each enclosure was covered with approximately 2 cm of pebbles. A small wooden platform was constructed so that a 2 cm crack was formed between the top and bottom layers. The platform and a piece of bark provided daytime hiding places. Timed lights were used to maintain a 12-hour light/dark cycle.

Procedure

Study 1. The geckos were obtained from Wailoa Park, Hilo, Hawaii on 2/27/94. Three different species of geckos were collected, *L. lugubris* (n = 8), *H. garnotii* (n = 6), and *Hemiphyllodactylus typus* (n = 2). Measurements of their snout-vent lengths, calcium glands, and eggs were recorded within 24 hr of capture. Eggs and calcium glands were measured by placing the gecko in a narrow plexiglas box and examining the gecko's translucent ventral surface. Eggs greater than 1 mm in size and swollen calcium glands can be observed in this manner. The width and length of each calcium gland were measured, and the areas of both glands (right and left sides) were added together for a gecko's total calcium gland size. Each gecko was marked with non-toxic paint for identification and randomly placed with three other geckos in an aquarium (51 x 28 x 31 cm). *L. lugubris* were housed in Cages 1 and 2, and *H. garnotii* in Cage 3. Cage 4 was shared by two *H. garnotii* and two *H. typus*. *H. garnotii* are rare in Hawaii, and we failed to capture eight. Geckos were kept in the communal enclosures for 28 days. A ten minute serial record of the geckos' behavior was obtained five times per week (total observation time per cage = 3.2 hr). Observations were used to determine the dominance rank of each gecko. Dominance rank was calculated by dividing the number of times a gecko won an interaction (the interaction ended with other gecko moving away) by the total number of interactions in which the gecko participated.

After 28 days in the communal aquaria, the geckos were transferred to singleton plexiglas enclosures (32 x 18 x 23 cm) for an additional 28 days. Measurements of the geckos' calcium glands and egg size were recorded once a week during both communal and solitary housing conditions. A two-part experiment was performed.

Study 2. To examine the relationship between egg development and calcium gland size in more detail, 10 *L. lugubris* were studied. Measurements of the geckos' calcium glands were taken immediately after egg laying and weekly thereafter until a second egg clutch was laid. Calcium gland size was compared for the following reproductive periods: (1) immediately after egg laying, (2) when eggs were first observed in the geckos ($MN_{egg\ size}$ = 2.6, range: 1 - 5 mm; most likely ovarian follicles), (3) the week after eggs were first observed ($MN_{egg\ size}$ = 4.4 mm, range: 3 -6 mm; most likely ovarian follicles) (4) two weeks before the second clutch was laid ($MN_{egg\ size}$ = 6.7 mm, range: 6 - 8 mm; most likely oviductal eggs) and (5) the week before the second clutch was laid ($MN_{egg\ size}$ = 8.3 mm, range: 7 - 10 mm; most likely oviductal eggs: see Jones et al. 1979 for information on ovarian vs oviductal eggs).

Study 3. Because *H. garnotii* seemed more communally tolerant than *L. lugubris* in Study 1 and because other researchers (Crews & Fitzgerald, 1980) have proposed that some social behaviors, for example pseudocopulations, influence fecundity in unisexual lizards, we designed a study to examine sociality and its effect on fecundity in *H. garnotii.* Nine geckos with no signs of egg development were housed as dyads for 112 days and solitarily for 112 days (a tenth gecko whose data are not reported was used as a stimulus gecko for one gecko; we could not originally capture 10 *H. garnotii*). Geckos were housed in plexiglas enclosures (32 x 18 x 23 cm) with one platform. Housing conditions were counterbalanced across geckos, 4 received the communal treatment first (June - September, 1994), 5 the solitary treatment first. Geckos then received the counterbalanced treatment (September, 1994 - January, 1995;). Geckos were randomly assigned to initial housing conditions. None of the geckos had visible signs of egg development when they received the first half of the treatment. If geckos had observable eggs at the end of the first half of the study, their placement in the second half was delayed until oviposition.

Geckos were examined each month for signs of egg development and their eggs and calcium glands were measured unless they were shedding. Data on platform use were systematically obtained across the study. Eighty-six observations were obtained in the first 112 days and 90 observations in the last 112 days of the study.

RESULTS

Study 1

Twenty-four aggressive interactions were observed between *L. lugubris* geckos housed in Cage 1 and 23 aggressive interactions between geckos in Cage 2. In contrast, no aggression was observed in the cages housing *H. garnotii* and *H. typus* geckos. Dominance hierarchies were therefore calculated only for *L. lugubris* geckos. Dominance was not significantly related to the snout-vent lengths of the geckos. For example, in Cage 1 the largest gecko was the beta animal

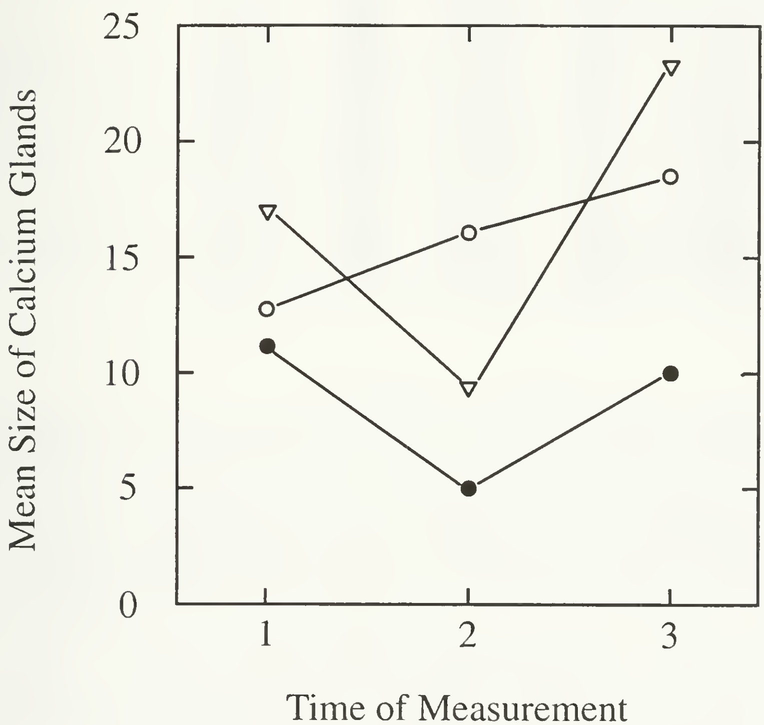

Figure 1. Size of the geckos' calcium glands in mm. The glands were measured (1) within 24 hr of the gecko's capture (2) after the geckos were housed communally for 28 days, and (3) after the geckos were housed solitarily for 28 days. The open circles represent dominant *L. lugubris* (S.D.s for dominant geckos at the 3 measure-ment times are 1.5 mm, 8.1 mm and 14.4 mm), the filled circles subordinate *L. lugubris* (S.D.s are 3.7 mm, 4.6 mm and 2.2 mm), and the open triangles *H. Garnotii* (S.D.s are 9.5 mm, 6.4 mm and 15.6 mm).

(44 mm); the alpha was 40 mm. In Cage 2 the largest gecko was the alpha (44 mm), but the second largest gecko (43 mm) was the most subordinate having 2 geckos measuring 40 mm dominant to it. Brown et al. (1991) also failed to find a relationship between size and dominance in *L. lugubris*.

Calcium gland size of dominant *L. lugubris* remained relatively stable throughout the course of the study. In contrast, calcium gland size of the subordinate *L. lugubris* and of the *H. garnotii* decreased during the time the geckos were housed communally but later increased after the geckos were housed alone (see Figure 1). All of the dominant (2 most dominant geckos in each cage) *L. lugubris* (4/4) developed eggs during the study while only one subordinate L. lugubris (1/4) and one *H. garnotii* (1/6) developed eggs.

The time the geckos were observed in proximity (less than 3 cm apart, for 2 to 10 min) in the platform or under the bark without displaying aggressive behavior was compared across the species. *H. garnotii* geckos spent significantly more time in proximity (7.4 min/10 min) than the *L. lugubris* (1.4 min/10 min), $\underline{F}(1,13) = 69.7$; $N = 14$; $p < .01$. *H. garnotii* housed in Cage 3 were observed in proximity in 9 dyads, in 11 triads, and 2 quadrads. Cage 4 *H. garnotii* were observed in proximity in 18 dyads, in 3 triads, and once in a quadrad.

Study 2

Geckos' calcium glands were smallest prior to and immediately after oviposition. The glands were largest the week that eggs were first observed in the geckos and remained large through the week before oviposition (Figure 2). The overall difference between calcium gland size across the geckos' reproductive states was significant, $F(4, 36) = 4.29$; $p < .01$. As can be observed in Figure 2, the mean calcium gland size immediately after laying and the week before the second clutch was laid are equal. Subsequent tests (Neuman-Keuls) found that calcium gland size at the above two reproductive periods differed significantly from the gland measurement when the eggs were first observed ($p < .05$) and the week after eggs were first observed ($p < .05$). Other pair-wise comparisons were nonsignificant. Although increases in calcium gland size were observed in 9/10 geckos, one gecko developed and laid eggs without visible signs of calcium glands.

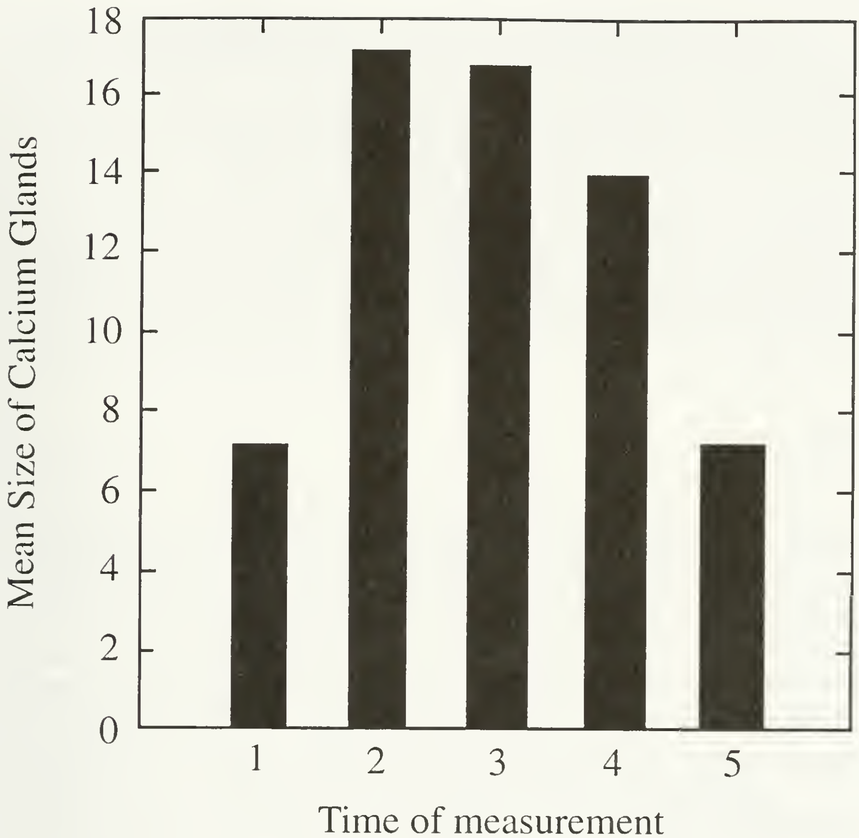

Figure 2. Size of the geckos' calcium glands by reproductive periods: (1) immediately after egg laying (SD = 10.3), (2) when eggs were first observed in the geckos (SD = 14.0), (3) the week subsequent to first egg observation (SD = 11.9), (4) two weeks before the second egg clutch was laid (SD = 13.8), and (5) the week before the second clutch was laid (SD = 9.4).

Study 3

The geckos were more likely to be in the platform when observations were made with the lights on (M(proportion of time in platform) = .89) than when the lights were off (M(proportion of time in platform) = .31). A highly significant difference was found, $F(1,8) = 109.84$; $p < .0001$. Similar data were obtained during the second half of the study (M(lights on) = .82; M(lights off) = .03). Therefore subsequent analyses on time observed in the platform were conducted only when the data were obtained with the lights on.

H. garnotii geckos spent a significantly greater percentage of time in the platform when they were housed solitarily (M = .93) than when they were housed as dyads (M = .79), $F(1,8) = 10.34$; $p < .02$. When geckos were housed as dyads, the geckos were observed together in the platform in 63% of the observations (range: 36% - 96%). There was no difference in egg development and laying between the solitary (3/9) and the dyadic (3/9) conditions. Additionally the average size of the geckos' calcium glands did not significantly differ between the solitary (M = 9.56; s = 8.06) and the dyadic (M = 7.13; s = 8.4) conditions, $F(1,8) = 1.66$; $p > .05$.

DISCUSSION

The *L. lugubris* geckos in the present study formed strict dominance hierarchies in which the subordinate geckos developed fewer eggs than the dominants. These findings replicated our previous results (Brown & O'Brien, 1993) and the findings of other studies on unisexual lizards (Grassman & Crews, 1987). We found that calcium gland size was not only related to the gecko's position in the dominance hierarchy but also to the phase of the gecko's reproductive cycle. Dominant geckos and those geckos with yolking follicles possessed the largest calcium glands. We hypothesize that the decreased egg development observed in subordinate *L. lugubris* was related to the small size of their calcium glands. The pathway we propose is that subordination is stressful, stress causes the gecko to experience decreased levels of available calcium, and decreased calcium levels result in decreased egg production. This process is modulated by the reproductive cycle of the gecko.

The *H. garnotii* geckos in Study 1 resembled the subordinate more than the dominant *L. lugubris* in terms of egg production and calcium gland size. Additionally, Study 3 found that the *H. garnotii* produced few egg clutches regardless of their housing conditions. Meshaka (1994) proposed that *H. garnotii* should produce an egg clutch every three months; therefore in Study 3 the *H. garnotii* should have produced 18 clutches rather than the 6 observed. The calcium glands of the *H. garnotii* in Study 3 were also the same size as the communally housed geckos in Study 1. Some reptiles are extremely stressed by captivity (Cowan, 1980). It may be that the long-term captivity experienced by the *H. garnotii* in Study 3 produced stressed animals and subsequently stressed behaviors. The stress of captivity was most likely responsible for the *H. garnotii's* decreased calcium gland size and egg production paralleling the stress of subordination in *L. lugubris*. If captivity is indeed stressful for *H. garnotii*, the fact that the same number of geckos produced egg clutches in dyadic and solitary conditions in Study 3 cannot answer the question of whether or not *H. garnotii's* fecundity is increased by pseudosexual behavior as has been proposed for whiptail lizards (Crews & Fitzgerald, 1980).

In the present studies *H. garnotii* geckos were not observed defending personal space as reported by Frankenberg (1982) for a Florida population. The fact that several clones of *H. garnotii* (Moritz et al., 1993) exist suggests that the Hawaii and Florida populations might have been founded by different females from different clones and therefore display behavioral differences.

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