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An experimental investigation of the competitive displacement of a native gecko by an invading gecko: no role for parasites

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Abstract On islands across the Pacific the invasion of the gecko *Hemidactylus frenatus* has caused a decline in the abundance of a resident gecko, *Lepidodactylus lugubris*. In a previous study we demonstrated that the prevalence of the cestode *Cylindrotaenia* sp. is higher in the resident gecko on islands where it is sympatric with the invader than on islands where it occurs alone. In the present study we experimentally test whether the presence of the invading gecko causes an increase in parasites, particularly *Cylindrotaenia* sp., in the resident. In addition, we test whether the effect of the invader on parasite prevalence in the resident is mediated through an increase in corticosterone in the resident. Corticosterone is the primary glucocorticoid, or "stress" hormone in lizards, and chronic elevation in corticosterone may suppress some types of immune responses. After experimental manipulations of interspecific interactions (single vs. mixed species treatments) and intraspecific densities (high vs. low), we detected no difference in parasite prevalence or circulating corticosterone among the experimental treatments in either *L. lugubris* or *H. frenatus*. Circulating levels of corticosterone were higher in geckos sampled at night than geckos sampled during the day, indicating a circadian cycle in corticosterone levels in these nocturnal animals. Circulating levels of corticosterone were higher in experimental geckos than in geckos that had not been used in the experiment, and, in some groups, higher in geckos infected with cestodes than in uninfected geckos. Circulating levels of corticosterone did not differ between non-experimental *H. frenatus* and *L. lugubris*, but when geckos used in the experiment were compared, circulating levels of corticosterone were significantly higher in *H. frenatus* than in *L. lugubris*.

Key words Apparent competition · Competitive displacement · *Hemidactylus frenatus* · *Lepidodactylus lugubris* · Corticosterone

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Introduction

Competitive displacement of one species by another can occur when one or more of the following processes take place: (1) individuals of one species interfere directly with individuals of another (interference competition), (2) one species sequesters a larger portion of common resources than another (exploitation competition) (Birch 1957; Case and Gilpin 1974; Schoener 1977), or (3) attacks by a predator or parasite on one species increase in the presence of the second species (apparent competition) (Holt 1977, 1984).

The ongoing competitive displacement of the native Pacific island gecko *Lepidodactylus lugubris* by the invading gecko *Hemidactylus frenatus* offers a unique opportunity to study the mechanisms of each of these avenues of competition as well as their interactions. On many islands *L. lugubris* and other nocturnal gecko species have been or are being competitively displaced by *H. frenatus*. On these islands, *H. frenatus* has typically replaced *L. lugubris* as the major component of the house gecko guild and the density of *L. lugubris* has declined dramatically (Petren et al. 1993; Case et al. 1994; D.T. Bolger and T.J. Case, unpublished manuscript). Experimental manipulations have demonstrated that it is the presence of *H. frenatus*, rather than a correlated factor, which drives this decrease in *L. lugubris* (Petren et al. 1993; Petren and Case 1996; D.T. Bolger and T.J. Case, unpublished manuscript).

Experimental studies of exploitation and interference competition between *L. lugubris* and *H. frenatus* (Petren

et al. 1993; Petren and Case 1996) have shown that *H. frenatus* disproportionately depletes insect resources shared by the two species, thereby causing a decrease in the body condition, fecundity, and survival of *L. lugubris*. Active interference (Maurer 1984), in contrast, is extremely rare, and other interference mechanisms are subtle and do not appear to account for the magnitude of the interaction (Petren et al. 1993; Petren and Case 1996).

Previous experiments did not rule out the potential for apparent competition to affect the observed effects of *H. frenatus* on *L. lugubris*. Indeed, an earlier survey of the helminths of both *H. frenatus* and *L. lugubris* on islands across the Pacific where the two are sympatric and islands where each occurs alone suggested a possible role for apparent competition (Hanley et al. 1995). Only one parasite of *L. lugubris*, the cestode *Cylindrotaenia* sp., infected more than 5% of the geckos surveyed. The prevalence of this cestode was significantly higher in *L. lugubris* in sympatry with *H. frenatus*. This biogeographic pattern cannot be attributed simply to the introduction of the cestode to *L. lugubris* by *H. frenatus*, because *Cylindrotaenia* sp. infects *L. lugubris* both in sympatry and allopatry with *H. frenatus,* and is also almost never detected in *H. frenatus*.

In this study we tested whether the presence of *H. frenatus* would cause an increase in cestode prevalence in *L. lugubris* in experimental enclosures. In addition, we investigated one potential mechanism by which *H. frenatus* might effect such an increase in cestode prevalence in its competitor. The documented effect of *H. frenatus* on the body condition of *L. lugubris* (Petren and Case 1996) suggested an avenue by which the invader could affect parasite prevalence in the resident. Many types of unfavorable conditions (i.e., starvation, cold, high density, intraspecific aggression and others) have been shown to cause increased secretion of their primary glucocorticoid hormone, corticosterone, in reptiles (e.g. Greenberg and Wingfield 1987; Elsey et al. 1990; Lance 1990). Increased corticosterone in reptiles has in turn been shown to lead to a decrease in circulating lymphocyte numbers (Saad et al. 1987; Morici et al. 1997) and to be associated with infection by malaria (Dunlap and Schall 1995). Therefore we hypothesized that exposure to *H. frenatus* and a consequent decline in body condition cause an increase in circulating corticosterone in *L. lugubris* which in turn increases their susceptibility to cestodes.

To test this hypothesis we measured circulating levels of corticosterone and gut, lung and ectoparasites of *L. lugubris* and *H. frenatus* that had been held in either single or mixed (*L. lugubris* + *H. frenatus*) species treatments at either high or low density for approximately 6 months. We predicted that if the stress of interacting with *H. frenatus* increases the susceptibility of *L. lugubris* to cestodes, then we should see a non-reciprocal increase in both the average level of circulating corticosterone and the average cestode prevalence of *L. lugubris* held in the mixed-species treatments compared to the single-species treatments.

Materials and methods

L. lugubris (abbreviated as *Ll* in this section and in Results) is a small (averaging 44 mm snout to vent in this experiment) parthenogenetic gecko; *H. frenatus* (*Hf*) is a larger (averaging 55 mm snout to vent) sexual species. Petren and Case (1996) stocked the two species in abandoned aircraft hangars (revetments) at Barber's Point Naval Air Station on Oahu, Hawaii. Hangars are concrete half-domes 17 m wide by 14 m deep by 6 m high; each was divided into two enclosures with a stripe of Fluon (a teflon-based paint on which geckos cannot walk) down the center of the hangar and along its walls and base. Fences were erected across the opening of each hangar to exclude terrestrial predators; flying insects had free access. Each enclosure was equipped with artificial refuges, water dishes, and a single fluorescent light. Aluminum baffles were placed between the two halves of each hangar so that geckos in one enclosure could not see geckos in the neighboring enclosure. A blind was erected in the center of each hangar for behavioral observations.

Geckos were stocked in enclosures as single- or mixed-species treatments at either high (14 geckos per species) or low (7 geckos per species) densities. The treatments were as follows, with abbreviations for each treatment in parentheses. Single-species treatments: 14 *Hf* (*Hf*-hi), 7 *Hf* (*Hf*-lo), 14 *Ll* (*Ll*-hi), 7 Ll (*Ll*-lo); mixed-species treatments: 14 *Ll* and 7 *Hf* (*Ll*-hi + *Hf*), 7 *Ll* and 7 *Hf* (*Ll*-lo + *Hf*). The densities of both species used in the experiment were chosen to bracket natural densities (Petren and Case 1996). Replicates were arranged in the following fashion: four hangars contained one *Hf*-hi and one *Hf*-lo replicate each, four hangars contained one *Ll*-lo and one *Ll*-lo + *Hf* replicate each, and 4 hangars contained one *Ll*-hi and one *Ll*-hi + *Hf* replicate each.

Enclosures were stocked with geckos from lighted urban areas where both species were present (see Petren and Case 1996 for details of the layout and protocols). Each gecko was marked with an unique pattern of toe-clips and a pattern of stripes of acrylic paint on its dorsum. Enclosures were censused every 14–21 days, at which time each gecko's length, weight, tail condition, and egg production were recorded.

The experiment lasted for 148 days between 10 February 1993 and 5–7 July 1993. Dead and missing geckos were replaced after each census to maintain experimental densities; consequently, the total number of days an individual gecko spent in an enclosure ranged from 12 to 148 days. At the end of the experiment, all geckos were collected and plasma and parasite samples were taken as described below.

Plasma collection

Basal levels of corticosterone can follow circadian (Lance and Lauren 1984) and circannual (Zerani and Gobetti 1993) cycles; to minimize variation due to such cycles, all geckos from the enclosures were collected between 1000 and 1445 hours on 5, 6, and 7 July 1993. To avoid a surge in corticosterone due to handling stress (Moore et al. 1991), each gecko was captured by one person and immediately handed over to another who decapitated and bled it into a 1.5-ml heparinized plastic tube. No more than 3 and usually only 1 min elapsed between initiation of pursuit and decapitation of any gecko. Each carcass and blood sample was placed into a labelled plastic bag and held in a cooler on ice until that evening. All geckos in both enclosures of a hangar were killed during one bout, which usually lasted about 30 min. On the same days, we collected 18 *Ll* and 25 *Hf* which were not being used in the experiment, between 1000 and 1445 hours; some of these were collected from the outsides of the bunkers and surrounding vegetation and some were geckos which had invaded the bunkers since the most recent census or had hatched from eggs laid in the enclosures. This group will be referred to as Day NE (for non-experimental). Because we needed to decapitate and bleed non-experimental animals quickly, we did not measure snout-to-vent length or weight of these geckos. To test for circadian cycling of corticosterone, we also collected 18 *Hf* foraging on vegetation and

the outside walls of hangars between 1900 and 2200 hours on 9 July 1993. We will call this group Night NE. Both experimental and non-experimental geckos were living in similar habitats and were sometimes intermixed in the enclosures, but non-experimental geckos had never been handled for marking or censusing prior to their capture for this study.

Red blood cells were separated in a desktop clinical centrifuge, and the plasma pipetted off into a new tube and stored on either liquid nitrogen or dry ice for shipment. Plasma samples were then held at −80°C until they were assayed for corticosterone. In total, 344 geckos were collected; some geckos died in the enclosures or escaped between censuses. Forty-five smaller geckos (30 *Ll* and 15 *Hf*) did not produce enough plasma for analysis. Fourteen of the plasma samples taken were excluded from analyses because of uncertainty about their identity.

Radrioimmunoassay

Because of the small volume of plasma available, usually between 1–20 μl from *Ll* and between 10–40 μl from *Hf*, only about half of the samples were analyzed in duplicate tubes; in the other half, the total volume of plasma was used in one tube. Plasma was aliquoted into individual tubes, extracted into 2 ml of 3:2 ethyl acetate:hexane mix, mixed for 20 s in a vortex mixer and then snap-frozen in a dry ice/methanol mix. The organic phase was decanted into clean 10 × 75 mm disposable culture tubes and evaporated to dryness under a stream of nitrogen in a 37°C water bath (technique modified from Lance and Lauren 1984). One hundred μl of ICN steroid diluent was then added and samples were mixed in a vortex mixer.

Samples were analyzed at random in one of four separate corticosterone assays (150–200 samples per assay) using the ICN rat ^{125}I corticosterone kit with the following modifications: (1) the standard curve was extended from 10 ng/ml (rather than 25 ng/ml) to 1000 ng/ml by diluting the calibrators; (2) gecko samples were only diluted ×20–×100 (depending on total volume available) rather than the ×200 recommended by the kit protocol; (3) two different samples (alligator) were run in every assay to determine interassay variability (inter- and intra-assay variability were 18% and 24%, respectively).

Parasites

A number of parasites have been identified from *Hf* and *Ll* on Oahu, including seven species of coccidia (Upton et al. 1991, 1994), seven species of nematodes, two species of cestodes, one pentastomid species (Bursey and Goldberg 1996, and unpublished data) and two species of ectoparasitic mites (Tenorio 1985).

We examined each carcass with a ×10 magnifying lens for ectoparasites and assigned it a rank of 1 (0–10 mites), 2 (10–100 mites), or 3 (> 100 mites) (the heads of the geckos were often lost during decapitation so this survey only covered the trunk and limbs). We then opened the carcass, and if a fecal sample was available, pressed it from the lower gut and placed it in 2.5% $K_2Cr_2O_7$ and removed the gut and lungs into 95% ethanol. We collected a total of 344 gut and lung samples, but 11 samples leaked ethanol and rotted prior to examination. Fecal samples were surveyed for coccidia oocysts (methods in Upton et al. 1991) and guts and lungs were opened and surveyed for helminths under a dissecting microscope. All helminths were identified by Charles Bursey (Pennsylvania State University-Shenango Campus) and Stephen Goldberg (Whittier College). Mites were identified by Wayne Brown (University of Hawaii at Manoa). Coccidia were identified by one of the authors (KAH) and confirmed by Steve Upton (Kansas State University). We did not attempt to survey for blood parasites in this study because we had not found any in an exhaustive survey of Pacific islands (Hanley et al. 1995).

Statistical Analysis

We manipulated two factors in this experiment: intraspecific density and presence of a competing species. These factors were completely crossed for *Ll* and their effects were analyzed using a two-factor ANOVA. These factors were not completely crossed for *Hf*, so for this species the effect of treatment was tested using a one-factor ANOVA or, to test the effect of treatment on the prevalence of multiple species of parasites, MANOVA. Because geckos in a replicate do not represent independent data points, the mean values per replicate (for continuous data) or the arcsin-transformed proportions per replicate (for nominal data) were used in the ANOVAs outlined above (following Petren and Case 1996).

To compare experimental and non-experimental geckos, we randomly assigned each of the non-experimental geckos within a species to one of four groups and calculated the mean value or the proportion per group. Analyses of parasites were limited to parasites with an overall prevalence (percentage of host population that is infected, Margolis et al. 1982) greater than 15%. In comparisons for which we used multiple parasite species from the same animals, we corrected for multiple comparisons using a sequential Bonferroni technique (Rice 1989) and report the corrected *P*-values.

Results

Corticosterone

Corticosterone concentrations ranged from 1 to 38.7 ng/ml in *Ll* and 1 to 145 ng/ml in *Hf* (Fig. 1). After log-transformation, the distribution of corticosterone concentrations did not differ significantly from normal for the 18 Night NE *Hf* (chi-square test, $P = 0.9$), 15 Day NE *Hf* ($P = 0.1$), 17 Day NE *Ll* (P = 0.1), and 108

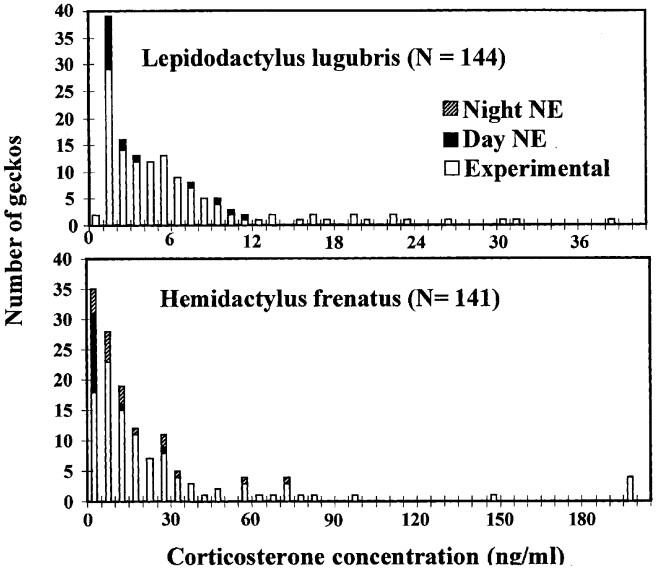

Fig. 1 Histograms of the distribution of corticosterone concentrations (in ng/ml) in all *Lepidodactylus lugubris* and *Hemidactylus frenatus* surveyed in this study. *Open bars* represent geckos used in the experiment, *black bars* represent non-experimental geckos collected during the day (Day NE), and *hatched bars* represent non-experimental geckos collected at night (Night NE). Note that the scale for corticosterone concentration (*x*-axis) is not the same for the two species

experimental *Hf* ($P = 0.5$). However, the distribution of corticosterone concentrations in the 127 experimental *Ll* were significantly different from normal ($P < 0.01$) after log-transformation. Unless otherwise noted, all statistical tests report results for transformed data.

Corticosterone concentrations in some individuals fell either above or below the range of the assay; we arbitrarily assigned values of 1 ng/ml to low-concentration individuals (3 *Hf* and 25 *Ll*) and 200 ng/ml to high-concentration individuals (3 Hf). We repeated all comparisons of experimental treatments without these arbitrary values and in no cases did the results change. One-third of the non-experimental *Ll* had low corticosterone concentrations; excluding these values did render significant differences within this group (comparisons of cestode-infected and uninfected geckos) and between this group and other groups (comparisons of enclosure occupancy time) non-significant because sample sizes became extremely small, but did not qualitatively alter relationships.

Corticosterone levels were significantly higher in Night NE *Hf* than in Day NE *Hf* (*t*-test, $n = 33$, $P = 0.002$: mean Day NE *Hf* concentration = 4.9 ng/ml, mean Night NE *Hf* concentration = 17.4 ng/ml), suggesting a circadian cycle of corticosterone in this species. Consequently Night NE *Hf* are analyzed separately from experimental *Hf* and Day NE *Hf* in all of the following analyses.

Mean corticosterone levels of Day NE *Ll* and Day NE *Hf* were not significantly different (*t*-test, $n = 32$, $P = 0.31$: mean *Hf* concentration = 4.9 ng/ml, mean *Ll* concentration = 3.4 ng/ml). In contrast, corticosterone levels were significantly higher in experimental *Hf* than experimental *Ll* (Mann-Whitney *U*-test, $n = 235$, $P < 0.0001$; mean *Hf* concentration = 28.3 ng/ml, mean *Ll* concentration = 6.4 ng/ml).

Handling and captivity can cause an increase in corticosterone in lizards (Moore et al. 1991). Although they were held under conditions that closely mimicked their natural environment, experimental geckos were handled every 2 weeks and they were prevented from emigrating from the enclosures. Mortality over the entire course of the experiment averaged 32% (± 0.13 SD) for *Ll* and 30% (± 0.1 SD) for *Hf*. Because some geckos died or escaped and were subsequently replaced over the course of the experiment, the length of time geckos spent in the enclosures ranged from 0 days (for non-experimental geckos) to 148 days (the maximum time). Mean occupancy time in the enclosures among experimental geckos did not differ among treatments for either *Hf* or *Ll* (two-factor ANOVA, $P > 0.15$ for both factors and for the interaction between factors). Mean occupancy time did not differ between the *Hf* and *Ll* used for hormone analyses (Mann-Whitney *U*-test, $n = 235$, $P = 0.13$), although when all experimental geckos are included in the analysis, *Ll* spent significantly longer in the enclosures than *Hf* (mean occupancy for Ll = 107.1 days, for *Hf* = 91.9 days; Mann-Whitney *U*-test, $n = 279$, $P = 0.03$).

To analyze the effect of duration of captivity on corticosterone, we assigned each individual to one of the following enclosure occupancy categories: Day NE (0 days in the enclosure, 32 geckos), very short (1–15 days, 37 geckos), short (15–60 days, 30 geckos), medium (61–120 days, 57 geckos), and long (121–148 days, 111 geckos); divisions were based on natural breaks in a histogram of enclosure occupancy times. We compared corticosterone levels among enclosure occupancy categories using a Kruskall-Wallis test. Note that this test treats individuals as independent. This is justified because the comparison being made is outside the design of the experiment; individuals from a single replicate are assigned to multiple different enclosure occupancy categories. Corticosterone levels differed significantly among the enclosure occupancy categories in both *Hf* (Kruskall-Wallis test, $n = 123$, $P = 0.0004$) and *Ll* (Kruskall-Wallis test, $n = 144$, $P = 0.02$). Pairwise comparisons among groups revealed that among *Hf* all time categories in the enclosure were significantly higher than Day NE (Mann-Whitney *U*-test, *P* for all comparisons < 0.005), but that none of the time categories in the enclosure differed from each other ($P > 0.1$ for all comparisons Fig. 2). Among *Ll*, corticosterone levels were significantly higher in medium and long time categories than in Day NE or the very short time category ($P < 0.05$ for all comparisons); no other categories differed significantly ($P > 0.09$ for all comparisons, Fig. 2).

Various physical characteristics, such as sex, size, body condition and reproductive state, have been shown to affect or be correlated with corticosterone concentrations in some reptile species (e.g. Elsey et al. 1990; Wilson and Wingfield 1992). Among non-experimental geckos, corticosterone levels did not differ between gravid and non-gravid *Hf* females (*t*-test, Day NE:

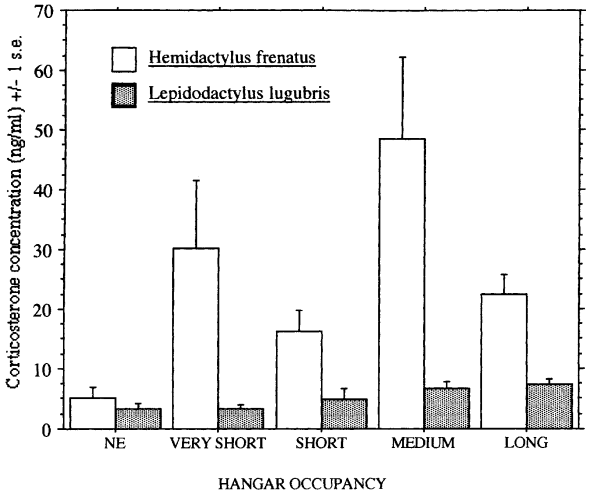

Fig. 2 The average corticosterone concentration (ng/ml) ± 1 SE of geckos held in the experimental enclosures for one of the five enclosure occupancy categories described in the text. *Open bars* represent values for *H. frenatus*, *shaded bars* represent values for *L. lugubris*

$n = 12$, $P = 0.21$; nighttime controls: $n = 10$, $P = 0.21$) or gravid and non-gravid *Ll* (*t*-test, $n = 9$ because not all geckos were checked for eggs, $P = 0.32$) or between male and female *Hf* (*t*-test, Day NE: $P = 0.5$; Night NE: $P = 0.75$). Length and weight measurements were not taken for non-experimental geckos. Among experimental geckos, corticosterone levels did not differ between male and female *Hf* (*t*-test, $n = 108$, $P = 0.32$) or between gravid and non-gravid females of either *Hf* (*t*-test, $n = 74$, $P = 0.34$) or *Ll* (Mann-Whitney *U*-test, $n = 127$, $P = 0.9$). Corticosterone levels did not vary with snout-vent length (Spearman rank correlation, *Hf*: $P = 0.26$; *Ll*: $P = 0.95$) or body condition [measured as the residual deviation from a linear regression of log weight versus snout-vent length (Petren et al. 1993); Spearman rank correlation, *Hf*: $P = 0.25$; *Ll*: $P = 0.40$]

Corticosterone levels did not differ among experimental treatments in either of the gecko species. A two-factor ANOVA revealed no effect of either intraspecific density or the presence of *Hf* on the corticosterone level of *Ll* ($P > 0.35$ for both factors and for the interaction between factors). Because *Hf* treatments were incompletely crossed for the presence of *Ll*, we used a one-factor ANOVA to compare the four *Hf* treatments; again there was no difference among treatments in corticosterone levels ($P > 0.85$). We repeated each of these analyses using only geckos which had been in the enclosures for more than 60 days but in no case did we detect any significant differences among treatments ($P > 0.4$). Figure 3 shows the mean corticosterone value per replicate for each treatment in each species.

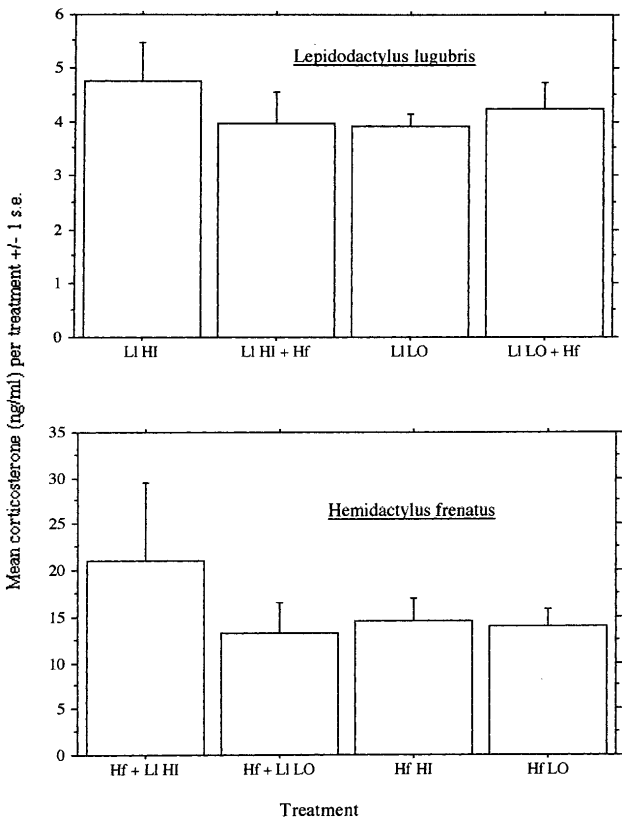

Fig. 3 Mean (±1 SE) corticosterone concentration per replicate for *L. lugubris* and *H. frenatus* separately in each experimental treatment. Note that the scale for corticosterone concentration (*y*-axis), and the treatments (*x*-axis) differ between the two species

Parasites

The identity, prevalence, and mean intensity of endoparasites infecting both *Ll* and *Hf* are listed in Table 1. With one exception [*Pharyngodon lepidodactylus* n. sp. (Bursey and Goldberg 1996)] the endoparasites infecting *Ll* were a subset of those infecting *Hf*. *Ll* and *Hf* were infested by different species of ectoparasitic mites.

Cestodes, *Cylindrotaenia* sp., were the only parasites of Ll with a prevalence greater than 15%. A two-factor ANOVA revealed no effect of either the presence of *H. frenatus*, intraspecific density, or the interaction between the two factors on the cestode prevalence in *Ll* when all individuals were included in the analysis ($P > 0.4$ for all comparisons). Nor did cestode prevalences differ between experimental geckos and non-experimental geckos (unpaired *t*-test, $n = 20$, $P = 0.19$). Figure 4 shows the mean cestode prevalence per replicate in *Ll* in each treatment. Since the amount of time that individual geckos spent in the enclosures varied, and we expected that any effects of the treatments would not be manifested immediately, we limited the analysis of cestode prevalence in *Ll* to geckos that had occupied the enclosures for 60 days or longer (see section on Corticosterone for a discussion of time divisions in the data). However, this limitation did not qualitatively alter the results (two-factor ANOVA, $P > 0.4$ for all comparisons).

We tested for an association between cestode infection and body mass corrected for length (a measure of body condition) across all treatments in experimental *Ll*. An ANCOVA analysis using the log of snout-vent length as the covariate revealed no association between the log of body mass and the presence/absence of the cestode *Cylindrotaenia* sp. ($n = 129$, $P = 0.33$).

A MANOVA revealed no effect of treatment on the prevalence of gut and lung parasites of *Hf* (the parasites included in the analysis are listed in Table 2; Wilks' lambda $= 0.198$, $P = 0.34$), and these results were not qualitatively altered by limiting the analysis to geckos that had been in the enclosures for more than 60 days. The prevalence of *Skrjabinelazia machidai* was significantly greater among experimental geckos than among non-experimental *Hf* (unpaired *t*-test, $n = 20$, $P < 0.001$); the prevalence of the other parasites listed in Table 2 did not differ between experimental and non-experimental geckos ($P > 0.1$ for all comparisons). When coccidia results were divided into treatments, the prevalence was too low for statistical analysis.

We tested for an association between infection by particular parasites and body mass corrected for length.

Table 1 Identity, site of infection, prevalence (*P*: % infected individuals in the population) and mean intensity (*MI*: number of parasites per infected individual) (Margolis et al. 1982) of parasites infecting both *Hemidactylus frenatus* and *Lepidodactylus lugubris* across all treatments. No abundance data are available for cestodes or coccidia. Mite infestations are assigned to ranks (*1* = 0–10 mites, *2* = 10–100 mites, *3* = >100 mites) (*n* number of hosts surveyed for the corresponding parasite, – indicates that a measure of mean intensity is not applicable because prevalences is 0; *nm* prevalence or mean intensity was not measured)

Parasite	*H. frenatus*		*L. lugubris*		Site of infection
	P	MI	P	MI	
Pentastomids	*n* = 164		*n* = 169		Lungs
Raillietiella frenatus	27%	3.2	4%	1.1	
Nematodes	*n* = 164		*n* = 169		Gut
Spauligodon hemidactylus sp. n.[a]	21%	3.5	0	0	
Skriabinelazia machidai	24%	2.1	1%	1	
Pharyngodon lepidodactylus sp. n.[b]	0	–	1%	1	
Physocephalus sp.	1%	1	0	–	
Physaloptera sp.	1%	1	0	–	
Gongylonema sp.	1%	1	0	–	
Parapharynogodon sp.	1%	1	0	–	
Cestodes	*n* = 164		*n* = 169		Gut
Oochoristica sp.	31%	nm	2%	nm	
Cylindrotaenia sp.	5%	nm	19%	nm	
Coccidia	*n* = 85		*n* = 87		Unknown
Eimeria dixoni	12%	nm	1%	nm	
Eimeria furmani	8%	nm	1%	nm	
Eimeria frenatus	8%	nm	0	nm	
Eimeria rochalimai	19%	nm	0	nm	
Isopora schlegeli	8%	nm	0	nm	
Isopora frenatus	7%	nm	3%	nm	
Acarina	*n* = 158		*n* = 177		Epidermis
Geckobia keegani	nm	1.7	nm	0	
Geckobiella texana	nm	0	nm	1.0	

[a] S.R. Goldberg and C.B. Bursey, personal communication
[b] Goldberg and Bursey (1996)

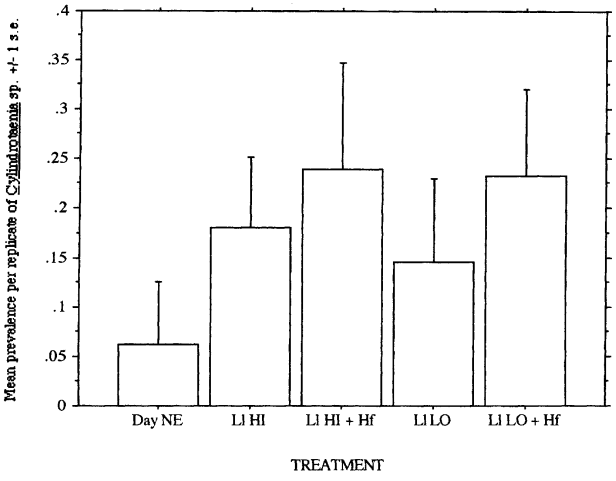

Fig. 4 Mean (±1 SE) prevalence per replicate of *Cylindrotaenia* sp. in *L. lugubris* in each experimental treatment

An ANCOVA analysis using the log of snout-vent length as the covariate showed no association between body mass and infection by any of the parasites listed in Table 2 ($P > 0.15$ for all comparisons).

Table 2 Mean prevalence per replicate (or for *Geckobia keegani* proportion of individuals with infestation rank >1) of five species of parasites in *H. frentaus* hosts in each of five treatments (described in the text). In no case did parasite prevalence differ among experimental treatments. The prevalence of *S. machidai* was significantly lower among non-experimental geckos (in italics) than experimental geckos; the prevalence of the other four parasites did not differ between experimental and non-experimental geckos. Statistics are listed in the text

Parasite	Day NE	*Hf*-hi	*Hf*-lo	*Hf* + *Ll*-hi	*Hf* + Ll-*lo*
Oochoristica sp.	0.36	0.41	0.15	0.39	0.11
R. frenatus	0.17	0.33	0.29	0.42	0.16
G. keegani	0.39	0.77	0.81	0.73	0.46
S. hemidactylus	0.10	0.30	0.26	0.15	0.23
S. machidai	*0.00*	0.28	0.30	0.26	0.34

Parasites and corticosterone

Finally, we tested whether parasitic infection was associated with changes in circulating corticosterone. Because corticosterone increased with captivity, we divided geckos of each species into two groups based on their mean corticosterone levels: (1) non-experimentals and enclosure occupancy categories that did not differ from non-experimentals and (2) enclosure occupancy catego-

Table 3 Mean corticosterone concentrations of *H. frenatus* and *L. lugubris* infected with a variety of parasites (see text for criteria for inclusion of hosts in this table). *P*-values are the results of *t*-tests comparing the log of the corticosterone concentrations of hosts infected versus uninfected by the parasite in each row; *P*-values are corrected for multiple comparisons (Rice 1989). *H. frenatus* collected at night are analyzed separately from those collected during the day; all *L. lugubris* were collected during the day. The values in italics is statistically significant

Host	Parasite	Mean corticosterone (ng/ml)		*n*	*P*
		Infected	Uninfected		
H. frenatus (daytime)	*Oochoristica sp.*	8.7	2.5	13	0.08
	G. keegani	3.7	6.8	15	0.44
H. frenatus (nightime)	*Oochoristica sp.*	26.7	8.0	18	0.20
	G. keegani	21.8	13.8	18	0.32
	R. frenatus	24.4	14.7	18	0.38
	S. hemidactylus	7.6	21.1	18	0.15
L. lugubris	*Cylindrotaenia sp.*	7.3	3.5	46	*0.03*

ries that did differ from non-experimentals. Among *Hf*, group 1 was composed of non-experimentals (day and night analyzed separately), and group 2 was composed of all experimental geckos. Among *Ll*, group 1 was composed of non-experimentals and experimental geckos with very short or short enclosure occupancy and group 2 was composed of geckos with medium or long enclosure occupancy. Only parasites that infected five or more individuals in the specified group were considered.

Table 3 shows the results for group 1. Corticosterone is significantly higher in *Ll* infected with the cestode *Cylindrotaenia* sp. than uninfected *Ll*. Corticosterone is also higher, though not significantly higher after correction for multiple tests, in *Hf* (both day and night) infected with the cestode *Oochoristica* sp. Comparisons for group 2, the geckos whose corticosterone had increased during captivity, showed no difference in corticosterone between infected and uninfected geckos of either species for any of the parasites listed in Table 3 (Mann-Whitney *U*-test, $P > 0.8$ for both *Hf* and *Ll*).

Discussion

Corticosterone, parasites, and competition

Contrary to our initial hypothesis, we found no evidence in this study that interaction between *H. frenatus* and *L. lugubris* influences levels of circulating corticosterone and/or parasite prevalence in either species. We did not detect any significant changes in circulating corticosterone or in parasite prevalence in either gecko species in response to an increase in either interspecific (competitor) density or a twofold intraspecific density increase.

Corticosterone occurs in two states: (1) free and biologically active or (2) bound to corticosterone-binding protein (CBP) and biologically inactive (Wingfield et al. 1984). If levels of CBP change, the amount of biologically active corticosterone may also change without any change in overall corticosterone levels. Due to the small amount of plasma produced by each gecko, we were unable to measure CBP. However, we did detect changes in total corticosterone level in association with parasites (see below) and length of enclosure occupancy in both species and we found evidence that corticosterone levels follow a circadian cycle in *H. frenatus*. Thus we believe we are justified in calling the lack of difference in total corticosterone levels between treatments a true negative result rather than a failure to detect differences in levels of CBP.

There were significant declines in body condition, fecundity, and survivorship of these *L. lugubris* individuals as a response to these density increases (Petren and Case 1996). Some previous studies have shown that high density and starvation can increase corticosterone secretion (e.g., Elsey et al.1990; Astheimer et al. 1992) and that poor nutrition can increase host susceptibility to helminths (Slater and Keymer 1986; Bundy and Golden 1987; Michael and Bundy 1992). Other studies, however, have shown that food limitation does not necessarily increase corticosterone production (reviewed in Maxwell 1993) and that chronic social stress does not necessarily impair immune function (Klein et al. 1992). In this study *L. lugubris* followed the latter pattern, even while undergoing severe reductions in demographic parameters.

Our results are not consistent with the biogeographic pattern documented by Hanley et al. (1995) of higher cestode prevalence in *L. lugubris* that are sympatric with *H. frenatus*. Parasite prevalence did not differ among experimental treatments in either gecko species. Captivity did not appear to affect parasite distribution among the experimental geckos since, with the exception of the nematode *S. machidai*, parasite prevalence did not differ between experimental and non-experimental geckos.

We can think of three possible explanations for the discrepancy between the biogeographic and experimental distribution of cestodes. First, we may have failed to detect differences in parasite prevalence due to relatively high mortality among infected geckos. If cestode-infected *L. lugubris* had higher rates of mortality than

uninfected conspecifics, then measurements of parasite prevalence at the end of the experiment could underestimate overall rates of infection across all treatments. If this were the case, then differences in survivorship among treatments, such as the significantly lower survivorship of *L. lugubris* stocked with *H. frenatus* (Petren and Case 1996), may have biased estimates of parasite prevalence. Conversely, replacement of mortalities might have increased parasite prevalence if parasites were transported into the enclosures with new individuals and spread through the population. Second, the biogeographic pattern may occur due to some subtle difference between sympatric and allopatric islands in climate or habitat rather than to the presence of *H. frenatus* itself.

Finally, the biogeographic pattern in cestode prevalence may be attributable to an effect of *H. frenatus* on the distribution of *L. lugubris* in the habitat rather than to an effect on susceptibility. The mechanism for such an effect would depend on the route of transmission of the cestode. Prudhoe and Bray (1982) suggest that the genus *Cylindrotaenia* may have two alternate pathways for transmission, both of which may operate concurrently. In the first, the cestode is transmitted directly from gecko to gecko via coprophagy, the larval stages of the parasite develop in a cyst in the host's intestinal wall, and the adults then excyst and take up residence in the intestine. If this route of transmission is common in this system, then any effects of *H. frenatus* on levels of coprophagy in *L. lugubris*, due for example to crowding, social interactions, or changes in substrate, might create the observed biogeographic pattern. In the second, more usual route of transmission for this order of cestodes (Cyclophyllidea), the parasite passes from one gecko to another via an invertebrate intermediate host, most likely an insect. If this route is important, then changes in the diet of *L. lugubris* in response to *H. frenatus* could result in changes in cestode distribution. We did not examine the intestines of the geckos in this study for cysts and so cannot say whether both or only one of these types of transmission occur in this system.

The experimental enclosures mimicked the environmental conditions under which *Cylindrotaenia* sp. is normally transmitted among *L. lugubris*. In the biogeographic study, many of the cestode-infected *L. lugubris* were collected from concrete buildings equipped with electric lights. These were the habitats on which the experimental enclosures in the current study were modelled. Geckos in this study had free access to normal prey items and behaved in a manner similar to free-living geckos in this type of habitat. Nonetheless, it is possible that the expression of interspecific effects on cestode transmission depends on some type of variation in the habitat that was not present in the enclosures. For example, water dishes provided in the enclosures may have differentially affected transmission, as *L. lugubris* appeared to use them more often than *H. frenatus*; however, containers did not appear to be very different from naturally occurring puddles of water.

The higher parasite diversity and prevalence among *H. frenatus* relative to *L. lugubris* found in this study was consistent with previous studies (Brown et al. 1995; Hanley et al. 1995). Brown et al. (1995) have attributed this difference in parasite load to differences in susceptibility between the two species; the larger and more rapid corticosterone response of *H. frenatus* to captivity (discussed below) might seem to provide a mechanism for such a difference in susceptibility. However, it is important to note that despite the rapid elevation of corticosterone in experimental *H. frenatus*, we detected a difference in parasite prevalence between experimental and non-experimental geckos in only one of five parasite species. Additionally, other factors including larger body size (Guegan et al. 1992; Guegan and Hugueny 1994) and higher insect harvesting rates of *H. frenatus* may offer a simpler explanation for the observed trend in parasite load . Asymmetries in parasite load may not affect the relative competitive ability of the two species if the larger-bodied *H. frenatus* is able to support more parasites than its smaller competitor at the same relative cost (discussed in Hanley et al. 1995).

Other factors influencing corticosterone

Interspecific interactions, body condition, and parasitic infection did not explain the observed variation in corticosterone levels in the geckos used in this experiment. Elevated corticosterone was associated with infection by cestodes among geckos whose corticosterone was not affected by captivity. Along similar lines, Dunlap and Schall (1995) have shown that fence lizards infected with malaria show an elevated corticosterone surge in response to handling stress relative to uninfected animals. However, we did not detect a difference between the corticosterone levels of cestode-infected and cestode-free experimental geckos.

Corticosterone levels did increase with time spent in the experimental enclosures, an effect which has been documented in other lizards (Moore et al. 1991). Our stocking density bracketed the natural densities of both geckos and their invertebrate prey, and many individuals in all treatments increased in mass, produced eggs, and survived the duration of the experiment. There are however a number of factors that differed between the natural and experimental setting that may have produced the pattern of higher corticosterone levels in individuals which had been in enclosures for longer periods of time. One of these is that geckos in the enclosures were handled approximately every 2 weeks to collect census data. Handling is known to cause increased corticosterone secretion in other lizards (Moore et al. 1991).

Furthermore, food resources were aggregated by lights in the experimental setting, whereas there were no lights, and consequently no resource clumping, in the areas outside of the enclosures from which most of the non-experimental geckos were collected. This difference

in resource distribution may have affected geckos in two ways. First, as food resources become more aggregated, intraspecific interactions in lizards increase, creating dominance hierarchies when none are evident if resources are more dispersed (Brattstrom 1974; Stamps 1977). Several studies have shown that social status can influence corticosterone levels, with subordinate animals having higher corticosterone concentrations (e.g., Greenberg et al. 1984; Greenberg and Wingfield 1987; Sapolsky and Ray 1989). Examining 15 *L. lugubris* from two of the enclosures, we found that, as in the studies mentioned above, individuals which fought and won aggressive encounters did have lower levels of corticosterone than those which fought but never won an encounter. However, *L. lugubris* individuals which were never observed to fight at all had significantly lower levels of corticosterone than those which had fought and won an encounter (K.A. Hanley, unpublished data). If the observed difference in corticosterone between experimental and non-experimental animals is attributable to differences in intraspecific social interactions, then we would expect to see higher levels of circulating corticosterone in the highly aggregated geckos found in lighted, urban settings which were the model for our experimental conditions, compared to the widely spaced geckos in unlit rural areas and forests.

A second possible explanation for the increase in corticosterone over time stems from previous studies which suggest that elevated corticosterone can trigger an increased feeding rate (e.g., Asteheimer et al. 1992). Aggregations of insects in our enclosures enabled geckos to feed at increased rates compared to environments which have more dispersed food resources. We may have selected for the most efficient foragers over the course of the experiment by replacing mortalities. If corticosterone is positively correlated with foraging rate, individuals which survive the longest may have higher corticosterone levels, or may be more capable of increasing their corticosterone levels. However, the relationship between corticosterone and activity is complex (Gray et al. 1990; Astheimer et al. 1992), and elevated corticosterone can decrease home-range size and overall activity (DeNardo and Sinervo 1994 a, b).

One intriguing result is that *H. frenatus* and *L. lugubris* had similar corticosterone levels under completely natural conditions, but *H. frenatus* had higher corticosterone levels than *L. lugubris* in the enclosures and showed a more abrupt increase in corticosterone levels after introduction. *H. frenatus* also showed the ability to increase foraging rates in the presence of its competitor, whereas *L. lugubris* foraging rates declined in the presence of *H. frenatus* (Petren and Case 1996). Although it is risky to compare corticosterone levels across species, such comparisons have been made in previous studies. For example, Wingfield et al. (1992) compared the corticosterone response to capture stress among five species of desert and riparian birds under different levels of environmental stress. More experiments are needed to test the hypothesis that corticosterone is linked primarily to foraging rates in these species, and to discriminate this from the many other stress-based hypotheses for corticosterone function which have been proposed.

Conclusions for competition

The interaction between *H. frenatus* and *L. lugubris* has become a model system for the study of competitive displacement (e.g., Petren et al. 1993; Case et al. 1994; Hanley et al. 1995; Petren and Case 1996; D.T. Bolger and T.J. Case, unpublished manuscript). In this system, exploitation competition with *H. frenatus* (Petren and Case 1996) has a significant impact on *L. lugubris* populations while direct interference and apparent competition seem to have little or no role in the interaction between the two species. Rarely have so many facets of competition been studied in a single system.

However, one aspect of competition remains poorly understood in this and other animal species. The proximate, physiological bases for competition have yet to be thoroughly investigated. This study raises the intriguing possibility that corticosterone may mediate competition between the two gecko species not through its effect on immune function but rather through its effect on feeding behavior. Additionally, our limited behavioral data suggest that corticosterone may respond more strongly to intraspecific interactions than to interspecific interactions. Considerably more information is needed to test these speculations; future investigation of the interaction between competition and corticosterone should focus on the association between corticosterone and individual behavior.

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References

Astheimer LB, Buttemer WA, Wingfield JC (1992) Interactions of corticosterone with feeding, activity and metabolism in passerine birds. Ornis Scand 23: 355–365

Birch LC (1957) The meaning of competition. Am Nat 91: 5–18

Brattstrom BH (1974) The evolution of reptilian social behavior. Am Zool 14: 35–49

Brown SG, Kwan S, Shero S (1995) The parasitic theory of sexual reproduction – parasitism in unisexual and bisexual geckos. Proc R Soc Lond B 260: 317–320

Bundy DAP, Golden MHN (1987) The impact of host nutrition on gastrointestinal helminth populations. Parasitology 95: 623–635

Bursey CB, Goldberg SR (1996) *Pharyngodon lepidodactylus* sp. n. (Nematoda: Pharyngodonidae) from the mourning gecko, *Lepidodactylus lugubris* (Lacertilia: Gekkonidae), from Hawaii. J Helminthol Soc Wash 63: 51–55

Case TJ, Gilpin ME (1974) Interference competition and niche theory. Proc Nat Acad Sci USA 71: 3073–3077
Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the tropical Pacific. Ecology 75: 464–477
DeNardo DF, Sinervo B (1994a) Effects of corticosterone on activity and home-range size of free-ranging male lizards. Horm Behav 28: 53–65
DeNardo DF, Sinervo B (1994b) Effects of steroid hormone interaction on activity and home-range size of male lizards. Horm Behav 28: 273–287
Dunlap KD, Schall JJ (1995) Hormonal alterations and reproductive inhibition in male fence lizards (*Sceloporus occidentalis*) infected with the malarial parasite *Plasmodium mexicanum*. Physiol Zool 68: 608–621
Elsey RM, Joanen T, McNease L, Lance V (1990) Stress and plasma corticosterone levels in the American alligator – relationships with stocking density and nesting success. Comp Biochem Physiol 95A: 55–63
Gray JM, Yarian D, Ramenofsky M (1990) Corticosterone, foraging behavior and metabolism in dark-eyed juncos (*Junco hymenalis*). Gen Comp Endocrinol 79: 375–384
Greenberg N, Wingfield JC (1987) Stress and reproduction: reciprocal relationships. In: Norris DO, Jones RE (eds) Hormones and reproduction in fishes, amphibians and reptiles. Plenum, New York, pp 461–505
Greenberg N, Chen T, Crews D (1984) Social status, gonadal state and the adrenal stress response in the lizard, *Anolis carolinensis*. Horm Behav 18: 1–11
Guegan JF, Hugueny B (1994) A nested parasite species subset pattern in tropical fish: host as major determinant of parasite infracommunity. Oecologia 100: 184–189
Guegan JF, Lambert A, Leveque C, Combes C, Euzet L (1992) Can host body size explain the parasite species richness in tropical fishes? Oecologia 90: 197–204
Hanley KA, Vollmer DM, Case TJ (1995) The distribution and prevalence of helminth and coccidial parasites of two competing species of gecko: implications for apparent competition. Oecologia 102: 220–229
Holt RD (1977) Predation, apparent competition and the structure of prey communities. Theor Popul Biol 12: 197–229
Holt RD (1984) Spatial heterogeneity, indirect interactions and the structure of prey communities. Am Nat 124: 377–406
Klein F, Lemaire V, Sandi C, Vitiello S, Van der Logt J, Laurent PE, Neveu P, Le Moal M, Mormede P (1992) Prolonged increase of corticosterone secretion by chronic social stress does not necessarily impair immune function. Life Sci 50: 723–731
Lance VA (1990) Stress in reptiles. Progr Clin Biol Res 342: 461–466
Lance VA, Lauren D (1984) Circadian variation in the American alligator, *Alligator mississippiensis*, and the effects of ACTH injections. Gen Comp Endocrinol 54: 1–7
Margolis L, Esch GW, Holmes JC, Kuris AM, Schad GA (1982) The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). J Parasitol 68: 131–133
Maurer BA (1984) Interference and exploitation in bird communities. Wilson Bull 96: 380–395
Maxwell MH (1993) Avian blood leucocyte responses to stress. World Poultry Sci J 49: 34–43
Michael E, Bundy DAP (1992) Nutrition, immunity and helminth infection: effect of dietary protein on the dynamics of primary antibody response to *Trichuris muris* (Nematoda) in CBA/Ca mice. Parasite Immunol 14: 169–183
Moore MC, Thompson CW, Marler CA (1991) Reciprocal changes in corticosterone and testosterone levels following acute and chronic handling stress in the tree lizard, *Urosaurus ornatus*. Gen Comp Endocrinol 81: 217–226
Morici LA, Elsey RM, Lance VA (1997) Effects of long-term corticosterone implants on growth and immune function in juvenile alligators, *Alligator mississippiensis*. J Exp Zool 279: 156–162
Petren KR, Case TJ (1996) An experimental demonstration of exploitation competition in an ongoing invasion. Ecology 77: 118–132
Petren K, Bolger DT, Case TJ (1993) Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science 259: 354–358
Prudhoe S, Bray RA (1982) Platyhelminth parasites of the amphibia. Oxford University Press, Oxford
Rice WR (1989) Analyzing tables of statistical tests. Evolution 43: 223–225
Saad AH, El Ridi R, El Deeb S, Soliman MA (1987) Corticosteroids and immune system in the lizard *Chalcides ocellatus*. Dev Comp Immunol 11: 141–151
Sapolsky RM, Ray JC (1989) Styles of dominance and their endocrine correlates among wild olive baboons (*Papio anubis*). Am J Primatol 18: 1–13
Schoener TW (1977) Competition and the niche. In Gans C, Tinkle DW (eds) Biology of the Reptilia, vol 7. Academic Press, New York, pp 35–124
Slater AGF, Keymer AE (1986) *Heligomosomoides polygyrus* (Nematoda): the influence of dietary protein on the dynamics of repeated infection. Proc R Soc Lond B 229: 69–83
Stamps JA (1977) Social behavior and spacing patterns in lizards. In Gans C, Tinkle DW (eds) Biology of the Reptilia, vol 7. Academic Press, New York, pp 265–334
Tenorio J (1985) Two new lizard mites from Hawaii. Proc Hawai Entomol Soc 25: 19–20
Upton SJ, Hanley KA, Case TJ, McAllister CT (1991) Description of *Isospora schlegeli* sp. nov. (Apicomplexa: Eimeriidae) from gekkonid lizards in the South Pacific. Can J Zool 69: 308–310
Upton SJ, Hanley KA, Case TJ (1994) *Eimeria frenatus* n. sp. and *Eimeria rochalimai* (Apicomplexa: Eimeriidae) from *Hemidactylus frenatus* in Hawaii, U.S.A. Trans Amer Microsc Soc 113: 390–394
Wilson BS, Wingfield JC (1992) Correlation between female reproductive condition and plasma corticosterone in the lizard *Uta stansburiana*. Copeia 1992: 691–697
Wingfield JC, Matt KS, Farner DS (1984) Physiologic properties of steroid hormone-proteins in avian blood. Gen Comp Endocrinol 53: 281–292
Wingfield JC, Vleck CM, Moore MC (1992) Seasonal changes in the adrenocortical response to stress in birds of the Sonoran desert. J Exp Zool 264: 419–428.
Zerani M, Gobetti A (1993) Corticosterone during the annual reproductive cycle and in sexual behavior in the crested newt, *Triturus carnifex*. Horm Behav 27: 29–37