AN EXPERIMENTAL DEMONSTRATION OF EXPLOITATION COMPETITION IN AN ONGOING INVASION

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Abstract. A native asexual gecko, Lepidodactylus lugubris, declines numerically when the sexual gecko Hemidactylus frenatus invades urban/suburban habitats throughout the Pacific. Previous studies showed that the competitive displacement occurs rapidly and is facilitated by clumped insect resources. Five lines of evidence suggest that the mechanism of displacement is primarily due to differences in the ability of each species to exploit insect resources. (1) These species show nearly complete diet overlap. (2) Insects are a limiting resource for both geckos as evidenced by positive demographic effects with increased insect abundance. (3) Hemidactylus frenatus depletes insect resources to lower levels than L. lugubris, which results in reduced rates of resource acquisition in L. lugubris. (4) This reduced resource acquisition translates into significant reductions in the body condition, fecundity, and survivorship of L. lugubris individuals. (5) Evidence for interference (and other) mechanisms does not account for these negative demographic effects on L. lugubris.

Interspecific competition is stronger than intraspecific competition for L. lugubris, with increasing L. lugubris density having negligible effect on H. frenatus, mirroring the asymmetry of the large-scale displacement. The superior harvesting ability of H. frenatus is most pronounced when insects are clumped spatially and temporally, and is attributable to a variety of species-specific traits such as their larger body size, faster running speed, and reduced intraspecific interference while foraging. We conclude that clumped resources can increase interspecific exploitation competition, and this mechanism may contribute to species turnover when human environmental alterations redistribute resources.

Key words: clumped resources; competition; exploitation; geckos; Hemidactylus frenatus; human impact; insect predation; interspecific competition; intraspecific competition; invasion; Lepidodactylus lugubris; mechanism.

INTRODUCTION

Extinctions of native species, whether in prehistory or in more recent periods, are increasingly being traced to human activities including hunting, habitat destruction, and the introduction of exotic predators or large herbivores that disrupt habitats (Simberloff 1981, Casseils 1984, Diamond 1984, Olson and James 1984, Ebenhard 1988, Olson 1989, Steadman 1989, Case et al. 1992, Henderson 1992, North et al. 1994). The importance of competitive interactions in causing native species extinctions is thought to be minimal (Simberloff 1981). However, invaders could have significant effects on native competitors without necessarily causing extinctions, and without producing obvious evidence of negative effects. Competition for food is not a direct interaction between two competitors but is only manifested through the dynamic effects on shared food resources.

From a theoretical perspective, it is crucial that we understand how invaders drive competitors extinct. This is because we are prone to underestimating the impact of competition if we simply examine existing static communities, since competition is expected to decrease over time as species coevolve or disappear from areas of sympathy by local extirpation (Brown and Wilson 1956, MacArthur and Levins 1967, Grant 1972, Schoener 1975, Birch 1979, Roughgarden 1983a, Taper and Case 1992). Experiments measuring competition between long coexisting species may underestimate the role of competition in structuring communities. In contrast, communities undergoing recent invasions will provide ideal situations to evaluate experimentally the role of competition in altering community composition, and to unravel the mechanisms by which invaders gain their competitive advantage (Diamond and Case 1986, Brown 1989, Case and Bolger 1991, Case et al. 1992).

We have been studying competition between two nocturnal insectivorous geckos in urban/suburban habitats across the Pacific basin (Petren et al. 1993, Case et al. 1994; D. Bolger and T. Case, unpublished manuscript). The competitive dominance of the invader, Hemidactylus frenatus, over the resident, Lepidodactylus lugubris, is manifested most strongly when insects are abundant and clumped around lights. One would expect that increasing the degree of resource clumping would increase the potential for competitive interference while foraging. Although we had expected to find

1 Manuscript received 24 July 1994; revised 18 April 1995; accepted 21 April 1995.
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direct interference interactions in this system, our earlier studies found little if any direct agonism between the two species while they foraged syntopically (Petren et al. 1993). Nevertheless, we did detect short-term shifts in the local spatial distribution of *L. lugubris* when in the presence of *H. frenatus*. Subordinate *L. lugubris* moved away from lights when in the presence of *H. frenatus*. We could not rule out the possibility that these shifts occurred for reasons other than agonistic encounters (e.g., avoidance behavior or resource depletion).

In general, interference competition is more easily detected than exploitation because of the more direct nature of the interaction (Case and Gilpin 1974, Schoener 1977, 1983, Roughgarden 1983b, Maurer 1984). To demonstrate conclusively interspecific exploitation competition for food resources, a number of factors must be established (Birch 1957, 1979, Schoener 1977, 1983). (1) Two (or more) species must share a resource; (2) survivorship and/or reproduction of the competing species must be limited by the availability of this resource. (3) The presence of one species must negatively affect the acquisition of this resource by the other. (4) This reduced resource acquisition must translate into reduced demographic parameters such as survivorship or fecundity of the inferior competing species, causing a change in its distribution or abundance, or other long-term evolutionary change. (5) Interference mechanisms and other processes (Holt 1977) must be ruled out.

We present experimental results that establish the importance of exploitation competition in the displacement of *L. lugubris* by *H. frenatus* in the urban/sub-urban environment. We discuss species-specific traits that produce differences in harvesting ability, enabling the invader to succeed. Factors that may enhance these differences include: clumping of food resources, high resource levels, and reduced structural complexity of the urban environment. Our results implicate human activity as largely responsible for facilitating this invasion and the resulting competitive displacement. Humans created urban habitats, producing favorable situations for population growth and range expansion of the invader. The human-aided dispersal of the invader to these habitats in turn resulted in the competitive displacement of *L. lugubris* and probably other gecko species from these habitats (e.g., *Hemidactylus garnotii*, *Gehyra mutilata*, *G. oceanica*; see Case et al. 1994).

**Methods**

**Experimental enclosures**

Experimental enclosures are contained within aircraft hangars (revetments) built during World War II and located on the grounds of Barbers Point Naval Air Station on Oahu, Hawaii (Petren et al. 1993). Each hanger is a concrete half-dome with an asphalt floor similar in size and shape to a concert shell (17 m wide \( \times \) 14 m deep \( \times \) 6 m high). Insects can fly freely in and out of the large open end. Twelve hangars with identically constructed interiors were each divided into two enclosures yielding 24 experimental units (Fig. 1). Geckos are confined within hangars by the use of Fluon AD-1 (Northern Products, Woonsocket, Rhode Island), a teflon-based paint that geckos cannot walk across. Fluon was painted in stripes on the wall, as well as on aluminum barriers on the floor to keep experimental geckos in, and local geckos out. Potential mammalian predators (feral cats and mongooses) were deterred by placing a 0.5 m high fence in front of each hangar and periodic trapping and patrolling. Fig. 1A shows the general design of enclosures modified from previous experiments (Petren et al. 1993). The walls of all units near the light were coated with a thin layer of linoleum paste, which dries to a hard slick surface. This equalizes gecko clinging ability across hangars since imperfections in the surface texture of the walls caused by old paint and water marks can affect gecko clinging ability.

Differences in wind exposure can affect insect abundance and gecko water balance. Wind exposure was measured by hanging a 50-mL conical plastic tube (with 5 mL increment divisions) filled with water in the center of each enclosure (two per hangar, one on each side) at a height of 2 m. Wire mesh was placed over each tube to prevent geckos from drinking the water. Sun exposure was limited by the roof of the hangar, but tubes in south-facing hangars received some direct sunlight near dawn or dusk. The amount of water evaporated after each interval was measured over two sampling periods: 14 June 1993 to 1 July 1993 (17 d) and 1 July 1993 to 8 July 1993 (7 d).

**Experiment 1**

Our primary experiment (from 10 February 1993 to 7 July 1993) tested the effects of competition on *L. lugubris* using a two-way factorial design, with completely crossed factors of intraspecific and interspecific density. The factors of intraspecific density (7 or 14 individuals) and presence/absence of competitor (*7 H. frenatus* individuals) were completely crossed in hangars 5–12, providing four replicates of four treatments: *L. lugubris* at low density alone, *L. lugubris* at low density with *H. frenatus*, *L. lugubris* at high density alone, and *L. lugubris* at high density with *H. frenatus*. Hangars 1–4 contained four replicates of *H. frenatus* only treatments at densities of 7 and 14 individuals for comparative purposes (Fig. 1B). Each hangar contained two enclosures, and assignment of treatments to enclosures was not random. The four replicates of each of the six treatments are balanced for neighboring treatment (all replicate units share a hangar with the same treatment type), and facing direction (units differ in orientation to the prevailing trade winds and amount and timing of direct sunlight). This produced three types of hangar, labeled A, B, and C (Fig. 1B). Experimental gecko densities were chosen to bracket nat-
urally observed densities, although there are currently few lighted places left where *L. lugubris* exists without *H. frenatus* in Hawaii.

All experimental geckos were collected from buildings on Oahu where lights and both species of gecko are present. Geckos about to lay eggs or appearing unhealthy were excluded. All geckos were measured, marked, and introduced into the experiment directly into a wall refuge the day after capture. Marking consisted of clipping the tip of one toe on each of three feet in a unique pattern, and marking the dorsal surface of the gecko with one to three stripes in a coded pattern with water-based acrylic paint. Painted patterns were unique to each unit and toe clip patterns were unique to each hangar. *Hemidactylus frenatus* were stocked at a ratio of three males to four females. When geckos died (or occasionally disappeared), they were restocked in the few days following each major census to maintain densities. All units were restocked to bring the total number of individuals up to 7 or 14 individuals, depending on the treatment.

Daytime censuses (seven in all, plus a closing census where only eggs were scored) were conducted every 14 d except for censuses 4–7 where the interval was =21 d. Geckos were processed and released sequentially to minimize handling stress, and the location of each was recorded. Each census consisted of recording the presence/absence, mass, snout–vent length (svl), egg presence and size (visible through the semitransparent ventral abdominal skin), and tail length of each gecko. Mass was measured to the nearest 0.1 g, and snout–vent length was measured to the nearest 0.5 mm. Body condition was calculated as the residual deviation of a regression of the log of body mass on snout–vent length for each species in a given census. One value was obtained for each individual by averaging residuals across all censuses. We assessed tail condition by judging the proportion of tail present (by mass). All individuals having <50% of their tail were excluded from statistical analyses on condition.

In order to reduce the effect of previous environment and handling stress, only established individuals (defined as those who were alive for at least 23 d in the enclosure, the maximum interval between stocking and first census) were included in analyses (except where explicitly noted). Thus geckos that were subsequently introduced to replace mortalities (i.e., after the initial stocking) are excluded from analyses until they have been in a hangar for at least 23 d.

Many geckos started and finished the experiment with eggs. Fecundity was therefore measured as the total number of egg state changes per individual during

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**FIG. 1.** Design and locations of experimental enclosures. The interior of each hangar (A) was divided into two enclosures. A number of additions made the hangar walls more suitable for geckos, including daytime refuges, plastic tubing to facilitate horizontal travel of geckos, water supplied ad libitum in aluminum pans, and lights to attract insects. Teflon paint (Fluon) barriers prevented experimental geckos from escaping, and local geckos from entering the enclosure. The 8-W fluorescent lights were controlled by photo-sensitive switches that automatically turned the lights on at dusk and off at dawn. An observation blind (1.5 m high) was placed in each hangar =2.5 m away from lights. The design of experiment 1 is shown in (B). The density of each species is manipulated to produce four focal “competition” treatments, and two “*H. frenatus* only” treatments, each with four replicates. Systematic pairing of treatments produces three types of hangars (A–C). Replicates of each treatment are balanced for the effect of facing direction.
the entire course of the experiment. Eggs were counted and egg state was scored as none, small (< 5 mm), medium (5–8 mm), or large (> 8 mm). A state change implies growth between consecutive categories. Some laying events were inferred after having seen only small or medium eggs. Reabsorption of visible eggs happens infrequently, and egg states seldom remain unchanged over the intercensus interval (Petren et al. 1993). Hatching success of eggs was not measured.

Survivorship was calculated simply as the proportion of all established individuals (from the initial introduction and restockings) who survived until the last two censuses. We also calculated the cumulative survival of all individuals from the initial introduction. The presence of scavengers (i.e., centipedes; K. Petren, personal observation) hampered complete recovery of corpses, although we found many identifiable corpses during the study.

**Measurement of insect abundance**

We refer to insect abundance rather than arthropod abundance because nearly all the recorded foraging attempts by geckos were for insects. Natural insect abundance was measured in all experimental units by counting the number of insects caught in sticky traps (ABEPCO Mfg. Inc., Orange, California) over 14 d. Two pairs of traps (24 cm × 12 cm each) were hung back-to-back on the center line dividing units within a hangar. These traps were placed 2 m high and 0.5 m away from the wall, and faced toward the light, perpendicular to the wall, =1 m from the center of the light (Fig. 1A). An additional pair of traps was placed at a height of 2 m, 0.25 m from the wall, and 9 m from the light, facing away from the wall, near the open end of each unit. Traps were replaced every other insect census (28 d).

In the first experiment, insect abundance is estimated by the number of insects caught on the sticky traps in each of seven 2-wk periods. Sticky traps were placed back-to-back in the center of each hangar, thus our measure of insect abundance is affected by the total number of geckos in a hangar, not solely by the number of geckos on a side. (In experiment 2, we measure insect depletion rates on a per-hangar basis.)

When calculating insect abundance we counted termite alates, moths, plant hoppers, leaf hoppers, flies, and roaches, because geckos were frequently observed attempting to capture them. Termites and large moths are given a numerical weight twice that of other insects in our calculations because they make up such a large proportion of the gecko diet. Insects <2 mm were excluded in an effort to reduce noise because of the infrequent foraging attempts for this abundant size class. Arthropods too large for geckos to ingest were excluded, as were many potentially consumable insects such as coleopterans, isopods, homopterans (other than leaf and plant hoppers), hymenopterans, and other taxa that the geckos generally ignored while foraging. Insect counts were log transformed prior to statistical analyses.

To measure directly insect landing rates on hangar walls near lights, two additional hangars were kept gecko-free (Fig. 1B: hangars 20 and 21). Each was equipped with two lights, and insect glue traps were placed directly on the walls near lights. Trap locations corresponded to regions used to record gecko foraging attempts (Fig. 2). Region 0 (directly on the light) was not sampled because the trap was opaque and blocked the light. Insect captures were recorded daily, and replaced at regular intervals or as needed. Seven censuses were taken from 30 June 1993 to 7 July 1993. For experiment 2 (below), insect density was monitored by placing three sticky traps 0.8 m above each light, flush to the wall (geckos were restricted from this area by an additional Fluon stripe). Insects were classified after a six-evening sample, at which time all traps were replaced.

**Foraging observations**

We conducted direct observations of geckos during peak gecko activity periods (the first 4 h following sunset) from the blind in each hangar. We report 110 hours of observational data on enclosures containing *L. lugubris* individuals alone and *L. lugubris* with *H. frenatus* (Fig. 1B: hangars 5–12). Two enclosures were viewed simultaneously, one with and one without *H. frenatus*, and all observations were taken by the same investigator (KP). All enclosures were observed an equal amount of time at regular intervals, however each
of the high density enclosures (Fig. 1B: hangars 5, 8, 9, and 12) was observed twice on different nights near the end of the experiment to gather-foraging data only. Enclosures were observed either one per night for ≈2.5 h, or four per night for 1 h each to minimize the effect of nightly variations in insect abundance.

Three types of data were recorded for each wall region (Fig. 2): all foraging attempts by all visible geckos; positions of all geckos in regions near the light at regular time intervals; and all dyadic agonistic interactions within and between species. For the position analysis, geckos not visible were assigned to region 8.

Pacific house geckos typically forage on vertical surfaces such as trees, leaves, and buildings. In foraging, geckos orient their body toward the insect, advance quickly at first, then more slowly, and then contract their bodies and lunge. We defined a foraging attempt as a movement toward an insect that is either landed or in constant contact with the wall. Strike distance was defined as the distance between the gecko and the insect at the beginning of a foraging attempt, and we classified attempts as short (< 20 cm) or long (> 20 cm). A foraging attempt was deemed successful once the insect was grasped in the jaws of the gecko. When insects were not observed directly, capture was inferred by mastication following a lunge. The region where the gecko commenced an attempt was noted as well as the type of insect (termite, moth, unknown small, unknown large).

Foraging success was measured as the proportion of all observed foraging attempts that were successful. To measure harvest rates we calculated the number of successful captures per gecko-minute for each species over all time point intervals. A per capita measure is used to reflect the large-scale pattern of a numerical displacement of L. lugubris by H. frenatus.

Dyadic agonistic interactions while foraging were recorded as described in Bolger and Case (1992) and Petren et al. (1993). All interactions included an approach and a retreat by one of the participants, except in rare instances when a display or physical contact ensued without an approach or retreat (see Results). The retreating gecko was taken to be the loser of the encounter. Details concerning the nature of interactions and social structure are reported elsewhere (K. Petren, M. Hetland, and T. Case, unpublished data).

**Experiment 2**

Because the split-hangar design of experiment 1 does not enable us to compare the insect depletion rates of both species directly, a second experiment was conducted after completion of the first. This experiment ran from 17 May 1994 until 26 July 1994, and used enclosures identical in construction to the first experiment. The experimental design is shown in Fig. 3. Each hangar was either left empty, or was stocked with an equal number of geckos of the same species on each side at either low density (7 per side), or at high density (14 per side). No mixed-species treatments were included, and three additional hangars were renovated for a total of 15 enclosures. Assignment of treatments to hangars was not random, but interspersed and balanced as much as possible with respect to facing direction (east/west). Within these constraints, we attempted to place H. frenatus treatments in hangars that had higher insect abundance in the first experiment. This was done to minimize the possibility that our results would reflect properties of individual hangars rather than the treatments inside. Geckos were obtained and maintained as described in the first experiment.

**Statistical analyses**

In assessing the effect of competition on L. lugubris in the following analyses, two comparisons are of primary interest: intraspecific density (7 or 14 individuals) and interspecific density (0 or 7 H. frenatus individuals), and the interaction of these factors. Table 1 shows the statistical model used to test our hypotheses. The model is a two-factor nested random-effect ANOVA,

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**Table 1. The ANOVA statistical model used to test competitive effects on L. lugubris. The model is a two-factor nested random-effect ANOVA.**

<table>
<thead>
<tr>
<th>Effects</th>
<th>df</th>
<th>F ratio test (mean squares)</th>
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<tbody>
<tr>
<td>A Interspecific density (7 or 14 L. lugubris)</td>
<td>1</td>
<td>A/C</td>
</tr>
<tr>
<td>B Intraspecific density (0 or 7 H. frenatus)</td>
<td>1</td>
<td>B/C</td>
</tr>
<tr>
<td>A-B Interaction of A and B</td>
<td>1</td>
<td>A-B/C</td>
</tr>
<tr>
<td>C(A-B) Replicate enclosures nested within (A and B)</td>
<td>12</td>
<td>Cle</td>
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<tr>
<td>e Residual error</td>
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* Total number of enclosures = 16. Replicate enclosures per treatment = 4.
in which the degrees of freedom used in the error term for $F$ tests is based upon the number of replicated enclosures instead of the total number of individuals, or residual degrees of freedom. The nested random effect refers to replicate enclosures within treatment types, and is incorporated only when multiple data per enclosure are used. When “nested random effect” or other design is not explicitly stated, a single value of each species within an enclosure is used.

**RESULTS**

**Resource overlap between H. frenatus and L. lugubris**

Diet overlap was nearly complete between $L. lugubris$ and $H. frenatus$. Winged termite alates comprised 63% of all $L. lugubris$ captures and 63% of all $H. frenatus$ captures. Moths accounted for 17% of the diet of each species. Other diet items included house flies, roaches, plant and leaf hoppers, and small flies. Large roaches were taken by both species, however male $H. frenatus$ are much more capable of this than $L. lugubris$. In the absence of geckos, 35% of insects over 2 mm in length were termites, while 30% were moths. When compared to diet composition, this suggests that both species are preferentially foraging for termites, although this assumes that the relative proportions of these insects remained similar throughout the experiment.

Practically all alates captured were West Indian drywood termites (Isoptera: Cryptotermes brevis). Alates are destined to found new colonies and may carry higher levels of nutrients than other insects. They appear to be poor fliers and are presumably easy for geckos to capture. Geckos often ignored other insects, especially small ones flying around the light when termite alates were available. On many occasions, geckos resting on or near lights in low density $L. lugubris$ treatments (hangars 6, 7, 10, and 11) did not make capture attempts for termites that were within striking range.

This was never observed in high density treatments, suggesting that geckos in the low density treatments were sometimes satiated and thus not always foraging at maximum rates.

Fig. 4 shows the high degree of insect clumping around lights, and the spatial foraging patterns of each species. Insect landing rates decline significantly as one moves a short distance from the light (one-factor ANOVA, $P < 0.0001$, Fisher’s PLSD (Protected Least Significant Difference) $< 0.0001$ for region 1 compared pairwise to all other regions). Differences in landing rates between region 1 (edge of fixture to 11 cm) and region 2 (11 cm to 31 cm from light) are significant, and more insects land below the light than above the light (two-factor ANOVA, for region 1 vs. 2, $F_{1,13} = 17.2, P < 0.001$; for above or below light, $F_{1,13} = 54.3, P = 0.007$).

The most productive foraging occurs very close to the light (Fig. 4). The number of captures per square metre for geckos in each region decreases as the distance from light increases (one-factor ANOVA, $F_{7,13} = 19.5, P < 0.0001$. Fisher’s PLSD is significant at $P < 0.0001$ for region 0 compared to all other regions). Both species show very similar distributions of successful captures in the regions around the light ($G$ test, regions 5–7 pooled, $P > 0.2$). Because the viewing area around the light represents less than one-fifth of the wall area available in the enclosure, and 40–50% of all geckos were routinely seen in this area, it is apparent that geckos actively seek to forage near the light.

Fig. 5 shows temporal patterns of gecko activity and gecko harvesting for the 4-h period after sunset. Gecko activity (Fig. 5A) was measured as the mean proportion of all geckos in each enclosure seen near the light (in regions 0–7). Gecko harvest rate (Fig. 5B) is measured as the mean number of captures per minute for each species in each enclosure over the same time intervals.
Geckos forage near the light throughout the evening, however insect resources are temporarily clumped, as harvest rate is highest in the 1st h after dusk (one-factor ANOVA, \( F_{3,15} = 17.1, P < 0.0001 \), Fisher's PLSD shows all pairwise comparisons are significant at \( P < 0.0001 \), except for hour 1 to hour 2, \( P = 0.056 \), and hour 3 to 4, \( P < 0.04 \). Many geckos remained on or near the light for long periods of time with no insect activity. *Hemidactylus frenatus* and *L. lugubris* show much temporal overlap in harvesting (*G* test on relative proportions for hours 1–3, \( P > 0.5 \)).

**Environmental effects alter insect availability and gecko condition**

Wind produced a systematic pattern of differences in insect abundance between enclosures. The prevailing trade winds coming out of the northeast created counter-rotating eddies of wind within the hangars, such that for each pair of treatments, wind moved from the north-facing unit to the south-facing unit (Fig. 1B). Fig. 6 shows the relationship between wind exposure, insect abundance, condition, and fecundity of *L. lugubris*. Each enclosure faced one of four compass points: northeast, northwest, southeast, and southwest. Units differing with respect to north/south facing direction had significantly different rates of water evaporation over a 17-d interval, while the east/west component differed, but not significantly (two-factor ANOVA, north/south \( F_{3,21} = 8.3, P < 0.01 \); east/west \( F_{3,21} = 2.2, P > 0.15 \)). Similar results were obtained when this experiment was repeated over a 7-d interval. Evaporation due to sun exposure cannot account for these differences.

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**Fig. 5.** Temporal activity patterns of geckos and insects near experimental lights. Foraging activity patterns (A) of *H. frenatus* and *L. lugubris* over the first 4 h after dusk as reflected in the mean proportion (±1 se) of geckos for each enclosure recorded near the light. (B) Mean (±1 se) harvest rate (insects-gecko⁻¹-min⁻¹-enclosure⁻¹) for each species in each enclosure over 15-min and 30-min sampling periods. Geckos were active throughout the 4 h after dusk, however insect activity was concentrated in the 1st h. The species show a high degree of overlap in temporal patterns of foraging.

**Fig. 6.** The facing direction of experimental enclosures determines exposure to trade winds as evidenced by mean (±1 se) amount of water evaporated (mL) in all experimental enclosures, and mean insect abundance (insects-trap⁻¹-night⁻¹) is inversely related to the amount of wind exposure (A). Southwest-facing units had the least wind and most insects, and northeast-facing units had the most wind and fewest insects. The relative body condition and fecundity (±1 se) of *L. lugubris* show a similar pattern according to facing direction (B). NE = northeast facing, NW = northwest facing, SE = southeast facing, SW = southwest facing.
results because south-facing units received more sun exposure and retained more water.

Fig. 6A shows insect abundance as measured directly on walls near lights in the absence of geckos (summed over all light regions in the gecko-free hangars 20 and 21). In this analysis, both north/south and east/west factors were significant (two-factor ANOVA; for north/south $F_{1,21} = 6.9, P < 0.02$; east/west $F_{1,21} = 5.3, P < 0.04$). In addition, facing direction significantly affected insect abundance at traps near the light across all experimental units containing geckos (two-factor ANOVA with factors of treatment type with six levels, and facing direction with four levels. For facing direction $F_{3,21} = 8.266, P < 0.001$). Wind exposure systematically affects insect abundance such that south-west facing units had the least evaporation and the most insects, and northeast-facing units had the highest evaporation and the fewest insects.

Demographic indicators of body condition and fecundity for L. lugubris show a similar pattern of differences according to facing direction (Fig. 6B), as geckos in south-facing enclosures had higher relative body condition and greater fecundity. Differences in body condition were not significant (nested random-effect ANOVA with factors of treatment, density, north/south facing $F_{1,11} = 2.7, P = 0.1$, east/west facing $F_{1,11} = 1.3, P = 0.26$). However the effect of north/south facing direction had a significant effect on fecundity (nested random-effect ANOVA with factors of treatment, density, north/south facing $F_{1,11} = 8.36, P = 0.02$, east/west $F_{1,11} = 2.4, P = 0.15$). Differences in survivorship did not show a pattern with respect to facing direction.

Geckos deplete available insects, and H. frenatus depletes insects to lower levels than does L. lugubris

Gecko density and species composition affected insect abundance as reflected in the number of insects caught in traps (Fig. 7). The three hangar types differed significantly in insect abundance (one-factor nested random-effect ANOVA, log-transformed, three levels, $F_{2,21} = 11.6, P < 0.005$). Because all hangars in the first experiment contained 7 H. frenatus, this effectively amounts to a comparison of 14 H. frenatus (type A), to 14 L. lugubris (type B), and 28 L. lugubris (type C). Type A hangars had 65% fewer insects than type B hangars, suggesting that H. frenatus has a substantially larger per capita impact on insect abundance than L. lugubris. The greater impact of H. frenatus is evident even in terms of gecko biomass. In this study, H. frenatus is on average ($\pm$ 1 se) nearly twice as massive as L. lugubris (3.06 $\pm$ 0.02 g vs. 1.60 $\pm$ 0.02 g). Hangars A and C harbor a similar biomass of H. frenatus and L. lugubris, respectively, yet type A hangars, with more of that mass in the form of H. frenatus, show substantially greater insect depletion rates. A twofold increase in L. lugubris density (hangar types B and C) had a large impact on insect abundance (36% fewer insects), but this difference is not significantly different when type A hangars are omitted from the analysis ($F_{1,7} = 3.4, P > 0.1$).

This experiment has been interpreted with caution for two reasons. First, hangars occupied solely by H. frenatus (type A) are not interspersed with the two-species treatments (types B and C), thus a degree of pseudoreplication exists for these comparisons (this problem is corrected in experiment 2). Additionally, this experiment was designed primarily to compare demographic effects of H. frenatus on L. lugubris, and to measure L. lugubris foraging side-by-side with and without H. frenatus. Thus the effect of each species together and in isolation was not measured in a similar manner for each species; half of all L. lugubris in a hanger were foraging with H. frenatus.

Experiment 2 allowed between-species comparisons without pseudoreplication, and also enabled comparison of empty hangars with those containing geckos.
(Fig. 3). Fig. 8 shows that both *H. frenatus* and *L. lugubris* deplete insects compared to background levels in gecko-free hangars (nested random-effect ANOVA, one factor, *H. frenatus* presence: $F_{1,7} = 13.1, P < 0.01$; nested random-effect ANOVA, one factor, *L. lugubris* presence: $F_{1,7} = 5.56, P = 0.05$). We compared the insect depletion ability of each species directly by excluding the empty hangars from the analysis. *H. frenatus* depleted insects to lower levels than *L. lugubris*, which was marginally significant (nested random-effect ANOVA, two factors of species and facing direction, for species: $F_{1,9} = 4.72, P = 0.058$). Facing direction of each hangar was included as a factor in this analysis because of the strong pattern of differences in wind exposure between east- and west-facing hangars, and is significant ($F_{2,9} = 13.3, P < 0.005$). Increasing gecko density did not have the expected negative effect on insect abundance (Fig. 8).

**Hemidactylus frenatus negatively impacts *L. lugubris* foraging ability**

Foraging success of *L. lugubris* was dramatically reduced from 65 to 39% at low density, and from 56 to 38% at high density in the presence of *H. frenatus* (Fig. 9A, left side; two-factor ANOVA on angularly transformed proportions, for *H. frenatus* presence $F_{1,12} = 24.2, P < 0.0005$). Intraspecific density had little effect ($F_{1,12} = 1.18, P > 0.2$). The interaction term was also not significant ($F_{1,12} = 0.9, P > 0.3$).

To see if *L. lugubris* were being denied access to preferred prey items by *H. frenatus*, we asked whether the proportion of termite alates (the preferred food item of both species) differed between treatments (Fig. 9B). The proportion of termite captures for *L. lugubris* was reduced by *H. frenatus* presence, although this effect was not quite significant (two-factor ANOVA; $F_{1,12} = 4.24, P > 0.06$). There was no interaction of *H. frenatus* and *L. lugubris* density ($F_{1,12} = 0.37, P > 0.5$). Increasing *L. lugubris* intraspecific density caused a reduction in the percentage of termites in the *L. lugubris* diet from 80 to 61% without *H. frenatus* present, and from 66 to 53% with *H. frenatus* present ($F_{1,12} = 8.68, P < 0.02$; Fig. 9B).

The presence of *H. frenatus* did not have a significant impact on the strike distance of *L. lugubris* (Fig. 9C). *Hemidactylus frenatus* had a larger proportion of long strikes than *L. lugubris* overall ($F_{1,22} = 7.75, P < 0.01$), suggesting there are consistent differences in foraging style between species.

The presence of *H. frenatus* reduced *L. lugubris* harvest rates from 0.17 to 0.10 captures-gecko$^{-1}$-min$^{-1}$ in low density *L. lugubris* treatments, and from 0.12 to 0.09 captures-gecko$^{-1}$-min$^{-1}$ at high density (Fig. 10), however this effect was not statistically significant (two-factor nested random-effect ANOVA: for *H. frenatus* presence $F_{1,12} = 2.0, P > 0.15$). Although the effect of *H. frenatus* on *L. lugubris* harvest rate appears to be large in magnitude (a reduction of 42% at low density and 25% at high density), harvest rates were highly variable due to nightly and seasonal fluctuations in insect abundance. Also, foraging effort of geckos in low density treatments was not always maximal, as evidenced by occasions when geckos did not attempt to forage on the most preferred prey item: termite alates.

**Negative effects on foraging ability are asymmetric**

Increasing *L. lugubris* density had a small negative impact on *H. frenatus* foraging, as seen in the right-hand column of Figs. 9 and 10. *Hemidactylus frenatus* had a success rate ($\pm$ 1 SE) of 56.2 $\pm$ 7.6% in low density *L. lugubris* treatments, and 48.9 $\pm$ 2.6% success with *L. lugubris* at high density, although this difference was not significant (unpaired $t$ test: $F_{1} = 0.82, P = 0.4$). *Hemidactylus frenatus* also showed little change in diet as a response to increased *L. lugubris* density (Fig. 9B, right side). Termites comprised 66% of *H. frenatus* diet when *L. lugubris* were at low density compared to 61% at high density.

When *H. frenatus* and *L. lugubris* harvest rates (Fig.
in high density *L. lugubris* treatments are considered, when insects were most abundant and *H. frenatus* were foraging closer to maximal rates (one-factor nested random-effect ANOVA, \( F_{1,10} = 13.9, P < 0.004 \)).

When harvest rates for *H. frenatus* only were considered, over all time points there was no difference between *H. frenatus* rates in low density or high density *L. lugubris* treatments. However in the 1st h after dusk, *Hemidactylus frenatus* per capita harvest rates (± 1 SE) nearly doubled as a response to increased *L. lugubris* density from 0.013 ± 0.003 to 0.026 ± 0.005 captures/gecko-minute (one-factor ANOVA, \( F_{1,6} = 9.83, P < 0.02 \)).

*Reduced resource acquisition leads to negative demographic consequences in* *L. lugubris*

Fig. 11 shows the effect of *H. frenatus* presence and intraspecific density on condition, fecundity, and survivorship of *L. lugubris*. *Hemidactylus frenatus* consistently depressed the mean body condition of *L. lugubris* (Fig. 11A; two-factor nested random-effect ANOVA; \( F_{1,12} = 40.4, P < 0.0001 \)). The effect of increasing intraspecific *L. lugubris* density also had a significant negative impact (\( F_{1,12} = 6.6, P < 0.03 \)), however the interaction of *H. frenatus* presence and intraspecific *L. lugubris* density was not significant (\( F_{1,12} = 0.25, P > 0.6 \)). The effect of *H. frenatus* at low density translates into an 8.4% reduction in mass for the average-sized *L. lugubris* (SVL = 44.0 mm, mass = 1.6 g), compared to a 3.6% reduction in mass in the presence of an equal number of *L. lugubris* individuals.

Interspecific and intraspecific effects on fecundity were similar (Fig. 11B). For *L. lugubris*, the number of egg transitions per week was significantly reduced in the presence of *H. frenatus* by 26.3% (two-factor nested random-effect ANOVA; for *H. frenatus* presence: \( F_{1,12} = 6.2, P < 0.03 \)). The effect of doubling intraspecific *L. lugubris* density was similar to the interspecific effect, with a 28.8% reduction in fecundity (effect of density: \( F_{1,12} = 8.0, P < 0.02 \); for the interaction of *H. frenatus* presence and density: \( F_{1,12} < 0.1, P > 0.9 \)).

*Hemidactylus frenatus* presence significantly reduced survivorship of all established *L. lugubris* from 79.5 to 61.5% (Fig. 11C; two-factor ANOVA, arcsine-transformed proportions for each enclosure, effect of *H. frenatus* presence: \( F_{1,12} = 15.73, P < 0.002 \), but increasing intraspecific density did not significantly affect survivorship (\( F_{1,12} = 0.87, P > 0.3 \)). The interaction of intraspecific density and *H. frenatus* presence was also not significant (\( F_{1,12} = 0.05, P > 0.8 \)). Similar results are obtained if the cumulative survival until the final census of all initial introductees is considered (two-factor ANOVA, arcsine-transformed proportions for each enclosure, effect of *H. frenatus* presence: \( F_{1,12} = 7.4, P < 0.02 \); intraspecific density: \( F_{1,12} = 0.6, P > 0.4 \); interaction test: \( F_{1,12} = 0.4, P > 0.5 \)).

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**Fig. 9.** Foraging success, diet, and strike distance of *L. lugubris* (LI) and *H. frenatus* (HF). Foraging success (A) is the proportion (± SE) of successful captures per attempt for all individuals of a given species within an enclosure during experiment 1. *Hemidactylus frenatus* had a large negative impact on the foraging success of *L. lugubris*. Both species preferentially foraged on termite alates, which accounted for 63% of all successful captures in both species. For *L. lugubris*, the proportion (± SE) of successful captures that were termites (B) declined as a response to *H. frenatus*, but not significantly. However the proportion of termites in *L. lugubris* diet occurred in response to increased intraspecific density. Strike distance (C), measured as the proportion of foraging attempts <20 cm (± SE), was not altered significantly for *L. lugubris* in the presence of *H. frenatus*, however *H. frenatus* had a greater proportion of longer strikes than *L. lugubris*. An increase in *L. lugubris* density had little effect on *H. frenatus* foraging (right-hand side). The magnitude of interspecific competition on *L. lugubris* (shown by lines) can be compared directly to intraspecific competition (left and center columns).

10) were compared directly over all treatments, we did not find significant differences (one-factor nested random-effect ANOVA; \( F_{1,22} = 1.4; P = 0.25 \)), but *H. frenatus* had a significantly higher harvest rate compared to *L. lugubris* when only the 1st h of foraging...
Negative demographic effects are asymmetric

In contrast to the strong impact *H. frenatus* had on *L. lugubris*, there was little effect of increasing *L. lugubris* density on the condition, fecundity, and survivorship of *H. frenatus* (Fig. 11, right-hand side).

Interference mechanisms are minimal

While foraging near lights, *L. lugubris* show much higher levels of intraspecific agonism than *H. frenatus* (Fig. 12). *Hemidactylus frenatus* displayed little direct agonism toward *L. lugubris*: displays, vocalizations, charges, lunges and bites which characterized intraspecific interactions of both species were not observed. Most interactions were passive approaches by foraging *H. frenatus*, followed by short retreats (avoidance) by *L. lugubris*. However on three occasions foraging strikes were made toward exposed body parts of partially concealed *L. lugubris*. Conversely, on a number of occasions *L. lugubris* directed attacks accompanied by vocalizations, charges, and bites toward *H. frenatus*. These attacks provoked little response from *H. frenatus*.

Passive interactions were few, however *L. lugubris* may still be displaced from the light to avoid foraging *H. frenatus*. We tested this by comparing access to the light (mean position by region) for *L. lugubris* with and without *H. frenatus*. *Lepidodactylus lugubris* were on average farther from the light when *H. frenatus* were present, but this difference was not significant (two-factor nested random-effect ANOVA, for *H. frenatus* presence, $F = 2.77, P > 0.1$; for intraspecific density, $F = 0.05, P > 0.8$; interaction of intraspecific density and *H. frenatus* presence, $F = 1.53, P > 0.2$). Generally, many *L. lugubris* foraged side-by-side with *H. frenatus* throughout the course of the experiment. The difference in light access (mean position of all geckos, by region) was greater in high *L. lugubris* density treatments (mean $\pm 1 \text{ se}$, $6.37 \pm 0.9$ with *H. frenatus*, $5.59 \pm 0.2$ without) than at low density ($5.98 \pm 0.3$ with *H. frenatus*, $5.96 \pm 0.2$ without). Given the magnitude of interspecific competition at high and low *L. lugubris* density, passive interference cannot be the main mechanism of competition.

**DISCUSSION**

**Evidence for exploitation competition in house geckos**

When taken in the context of related research on this system, a cohesive picture emerges of exploitation competition being the key factor causing the numerical decline of *L. lugubris*. We review these results following the five criteria set forth in the Introduction.

1) There is high spatial and temporal overlap in foraging behavior and extensive diet overlap between the species. Both species use the concentrated insect resources near lights, and competition is strongest when lights are present. This is evident in the current study, but also in previous experimental (Petren et al. 1993) and broad geographical surveys (Case et al. 1994). On the scale of neighborhoods, light rearranges existing insect distributions, yet compared to the home range of an individual gecko, the effect of light is to create an overall increase in abundances as well as an increase in spatial aggregation.

2) Evidence that insects are a limiting resource for geckos comes from three sources. Large-scale natural surveys demonstrate an increase in gecko density and biomass in lighted environments (Case et al. 1994). Manipulative experiments show both species achieve higher body condition when lights are present (Petren et al. 1993). Finally, in the current experiment, differences in insect abundance (created by differences in wind exposure) lead to parallel differences in the body condition and fecundity of *L. lugubris*. Differences in body condition translate into differences in fecundity and survivorship, which are closely related to the short-term population trajectory.

3) Evidence that the presence of *H. frenatus* causes reduced resource availability for *L. lugubris* comes from a number of sources. First, both species depleted insect resources, and *H. frenatus* depleted insects to lower levels than *L. lugubris*. Perhaps the most convincing evidence comes from direct foraging obser-
FIG. 11. The demographic effects of competition on *L. lugubris* (LI) and *H. frenatus* relative body condition, fecundity, and survivorship. A single value was obtained for each enclosure, and mean values (±1 se) between replicates are shown. Relative body condition (A) is the arithmetic mean condition (see Methods) for all established individuals over all censuses during experiment 1. Fecundity (B) is the number of egg transitions (egg production) per week for all established individuals. Survivorship (C) is calculated as the proportion of successfully introduced individuals present at the end of the study for each species. For *L. lugubris*, interspecific competition was detected (and is asymmetric) for all three responses measured, however intraspecific competition is of similar magnitude only for fecundity. An increase in *L. lugubris* density had little effect on *H. frenatus* (right-hand side). The magnitude of interspecific competition on *L. lugubris* (shown by lines) can be compared directly to intraspecific competition (left and center columns).

**vations. Lepidodactylus lugubris** had reduced foraging success per foraging attempt, and reduced harvest rates overall in the presence of *H. frenatus*. Conversely, *H. frenatus* responded to an increase in *L. lugubris* density by increasing harvest rates in the 1st h after dusk when insects are most abundant.

4) The reduced access to resources translated into negative demographic effects for *L. lugubris*. Body condition, fecundity, and survivorship were significantly depressed by the presence of *H. frenatus*, and interspecific competition was more severe than intraspecific competition.

5) Contrary to our initial expectations, *H. frenatus* do not actively exclude *L. lugubris* from lights. “Active” interference in the form of directed agonistic attacks (Maurer 1984) was observed on fewer than five occasions over the course of the present and previous (Petren et al. 1993) studies. All of these attacks could be attributed to an *H. frenatus* mistaking an *L. lugubris* body part for an insect. The contrast between this pattern and earlier behavioral studies (Bolger and Case 1992) may be due to longer habituation times, and/or the presence of foraging and sheltering sites in the present study.

We previously determined a passive interference mechanism (Maurer 1984) whereby subordinate *L. lugubris* avoid *H. frenatus* foraging near the light (Petren et al. 1993). However the experiment was followed only for a matter of days after initial introduction of *H. frenatus*. Over the extended observation time in the current study, displacement of *L. lugubris* from the light was subtle and not significant. The reduction in foraging success of *L. lugubris* corroborates the assertion that indirect interference is minimal, because it shows that *L. lugubris* in the presence of *H. frenatus* had foraging opportunities, attempted to forage (and thus were not curtailing foraging effort), and were in regions where insects were landing. Interference during foraging may have some effect, but it simply cannot explain the magnitude of the demographic impact under these conditions.

Interference competition was not detected in daytime.
refuges. Both species shared shelters during the day, often at high densities, suggesting that neither “active” (Maurer 1984) nor “preemptive” (Schoener 1983) interference was acting (K. Petren and T. Case, unpublished data). We have not directly tested the possibility that H. frenatus may actively exclude L. lugubris from shelters when they are severely limited. The density of all geckos is extremely low on some recently constructed buildings, possibly due to a lack of adequate shelter (K. Petren and T. Case, personal observations). However, most older buildings (which comprise the majority of the urban Pacific basin) appear to have abundant suitable shelter.

The possibility of apparent competition (Holt 1977) through differential parasite susceptibility has also been investigated in this experiment (K. Hanley, K. Petren, and T. Case, unpublished manuscript) and on a larger geographic scale (Hanley et al. 1995). Although some parasites are shared between H. frenatus and L. lugubris, an extensive survey of internal and external parasites across many islands does not support this hypothesis.

We have not eliminated the possibility that predation mechanisms contribute to the displacement, however in our experiments large predators are excluded by fences, yet we still see the competitive displacement at this mesoscale. Although numerous birds, insects, and mammals are known to eat geckos, we know of no predators that regularly rely on geckos as a food source where the displacement is observed. Domestic cats are the most likely predator to impact geckos, as they often kill geckos and they also occur in urban environments where gecko competition is strongest. However, because the regional pattern of L. lugubris decline is closely tied to the invasion of H. frenatus (Case et al. 1994), if predators play a role at all, it must be in an interactive way with the presence of H. frenatus. One possibility is that H. frenatus may force L. lugubris to move to the ground where predators could more easily capture them. As discussed above, there was little indication that L. lugubris become more vulnerable to predators in the presence of H. frenatus. Direct predation of H. frenatus on L. lugubris hatchlings may occur under extreme circumstances (Bolger and Case 1992), but was not observed in this study.

Lepidodactylus lugubris has an innate demographic advantage because it is parthenogenetic whereas H. frenatus is sexual. Egg production rates are similar in the two species but all eggs of L. lugubris are female. Our experiments do not cross generations, so we cannot directly quantify how this female birth rate advantage translates into competitive success. However, the severe negative effect of H. frenatus on L. lugubris foraging that we have measured here combined with the observed geographical competitive displacement throughout many areas of the Pacific (Case et al. 1994) indicate that asexuality is not sufficient to compensate for the negative impact of H. frenatus on L. lugubris.

Mechanisms of exploitation

Biological differences between H. frenatus and L. lugubris create differences in their harvesting ability. First, H. frenatus are larger than L. lugubris, and their gut capacity is presumably larger as well, although this was not directly measured. Because insects are aggregated temporally and spatially, H. frenatus may be able to consume more insects during brief surges in abundance. H. frenatus are also faster than L. lugubris (Huey et al. 1989), and may move faster to an insect once it becomes available. This size and strike speed advantage may act to produce the observed increase in harvest rates shortly after dusk. Even if H. frenatus is unsuccessful at capturing an insect, by charging after it from a longer distance than L. lugubris on open surfaces, insects will take flight, becoming unavailable for a period of time for geckos. Thus insect depletion rates stem not only from insect consumption, but from increased local emigration away from the walls.

The greater strike distance of H. frenatus is consistent with its greater maximal velocity (Huey et al. 1989). Roughgarden (1995) predicted on theoretical grounds that strike distance and strike velocity in Anolis lizards should be related, which was borne out by experiment. Moreover, since velocity and body size are allometrically related in lizards (Huey and Hertz 1982, Huey et al. 1989), some of the species-specific foraging results that we find must stem in part from the body size differences of these two geckos.

Differences in intraspecific interference between these species may also affect maximum harvest rates. Hemidactylus frenatus females show little aggression while foraging, while L. lugubris (all female parthenogens) often engage in prolonged agonistic encounters while foraging (Fig. 12; Petren et al. 1993; K. Petren, M. Hetland and T. Case, unpublished data). The relative roles of size, speed, and intraspecific interference differences are being addressed with additional experiments. The degree to which these traits are found to be important in other successful invasions will determine their utility in predicting outcomes for biological control and conservation.

The pattern we suggest of increasing interspecific competition with increased resources is somewhat counterintuitive since one usually associates food limitation with low, not high, food levels. However, on theoretical grounds it is the differential between species in their resource usage that is important in setting the intensity and direction of interspecific competition. We suggest that this differential is often greater when food is common and spatially clumped compared to when it is rare and diffuse. This subject needs more theoretical attention. Lights increase total insect density, however lights also increase clumping of insects. We have not separated the relative contribution of each in facilitating competition.

Clumped resource distributions and elevated re-
source levels have been implicated as important factors in a well-known case of exploitation competition involving desert granivores (Reichman 1979, Brown and Munger 1985). In a number of other studies, concentrated food resources seem to intensify interspecific competition (chipmunks: Brown 1971; wasps: Moller and Tilley 1989, Harris et al. 1991; squirrels: Sexton 1990; birds: reviewed in Maurer 1984), suggesting that this may be a common phenomenon. Most of these studies either implicate interference competition, or do not present evidence as to the mechanism of competition. Maurer (1984) reasoned that clumped and more abundant resources should promote interference, while exploitation will generally prevail with lower, more dispersed resources. Our results suggest that to the contrary, exploitation may also be augmented when resources are abundant and concentrated.

The structural simplicity of the urban environment may enhance differences in exploitative ability. Urban buildings, where competition is strongest (Case et al. 1994), have broad flat walls, and insects and intruding geckos can be seen and pursued by resident geckos from long distances. The speed and strike distance advantage of H. frenatus is put to best advantage over the flat and open surfaces of building walls. If intra-specific interference is also an important factor determining harvesting ability in L. lugubris, then this effect may be ameliorated if lines of sight are reduced in structurally complex environments. Experiments are currently underway to address the importance of habitat structure and resource clumping in facilitating competition between these species.

When predators and prey are mobile, it is more difficult to garner unequivocal evidence for exploitation mechanisms than interference competition because the depletion of resources is spatially diffuse and the effects of one individual’s foraging efforts on another individual’s success requires careful experiments. (Case and Gilpin 1974, Schoener 1977, 1983, Roughgarden 1983b, Maurer 1984). Demonstrating that one species negatively affects consumption of a resource by the other is a central factor in demonstrating exploitation. However harvest rates are variable as individuals become satied during foraging, and resource fluctuate hourly, daily, and seasonally. These difficulties are multiplied when competition is temporally and spatially variable, as it appears to be in this system. Intensive experimental investigation on model systems may be the best approach toward understanding mechanistic details about competition (Gurevitch et al. 1992). Patterns and mechanisms uncovered in systems where competition is currently shaping communities through invasions can be used to formulate hypotheses and predict outcomes in systems where large-scale manipulations are simply not possible (Schoener 1986, Tilman 1987).

Human activity often results in habitat destruction, but more subtle changes can promote shifts in community composition. Humans have had a major impact on Pacific basin gecko communities by facilitating interisland colonization, and by creating new habitats with altered insect resources. Garbage dumps, agricultural fields, orchards, paved roads and water-warming power plants are but a few examples of other modifications that alter the distribution of resources, which can, in turn, change relative exploitation rates by various organisms. Smaller insect-sized species may perceive these altered environments as seas of superabundance (e.g., flies at a dump, termites in wooden buildings). However at higher trophic levels, insect predators perceive these alterations as resource clumps, and some species may be able to exploit these clumps to the detriment of other, possibly native species. More work is needed to assess the general importance of exploitation mechanisms and species turnover where human development alters the spatial distribution and abundance of resources.

ACKNOWLEDGMENTS

We are indebted to the Pacific Division of the U.S. Navy for permission to conduct this research, the staff at Barbers Point Naval Air Station, and the Barbers Point Riding Club. We thank M. Hetland, R. Raditkey, K. Hanley, J. Heyman and D. Bolger for assistance in the field. For insightful comments on the manuscript we thank P. Kareiva and three reviewers. This work was supported by NSF grants DEB-9220621, BSR-9107739, and NRSA training grant 5T32 GM 07240.

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