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Behavioural mechanisms of invasion and displacement in Pacific island geckos (*Hemidactylus*)

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The house gecko *Hemidactylus frenatus* is currently displacing an ecologically similar, all-female parthenogenetic gecko *H. garnotii* on a global scale. We tested the previously proposed hypotheses that resource competition is responsible for this displacement, and that competitive interference occurs through male aggression. We quantified consumption of insect resources and behavioural interactions in dyads and triads composed of different combinations of sexes and species. Geckos consumed fewer insects when in pairs than when they were alone, indicating general evidence of resource competition. However, resource consumption of parthenogenetic *H. garnotii* was not negatively affected by the presence of invasive *H. frenatus*, suggesting that resource competition is not the primary mechanism of displacement. Males were aggressive towards conspecific males, but showed little aggression towards conspecific females and parthenogenetic females; females and parthenogens displayed little aggression. Male *H. frenatus* courted and copulated with both conspecific and heterospecific females in dyads and in triads and, by some measures, showed a preference for larger *H. garnotii* females. When paired with females or parthenogens, males consumed fewer resources because they turned their attention to courtship. Evidence of interspecific courtship suggests that sexual interference may be a more likely mechanism of displacement. Our results exclude the possibility that courtship decreases resource consumption in *H. garnotii*, but further study is required to determine whether interspecific mating disrupts parthenogenetic reproduction. This study demonstrates the importance of testing commonly invoked mechanisms of invasion and displacement by quantifying individual behaviour in an experimental setting.

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Increased travel and trade have led to a heightened spread of alien species, a leading anthropogenic disturbance with far-reaching implications (Naeem et al. 1995). About one-fifth of invasive species may cause extensive economic and ecological damage, with unpredictable negative effects on native populations that are second only to habitat destruction (Vitousek 1992; Jenkins 1996). Invasive species can alter successional patterns, mutualistic relationships, community dynamics, ecosystem function and resource distributions (Mooney & Cleland 2001). Invasive species that cause extinction of native species will ultimately reduce local and global species diversity (Vitousek et al. 1996; Mooney & Cleland 2001; Collins et al. 2002).

Invasive animals can negatively affect residents through ecological interactions such as competition or predation (Shea & Chesson 2002). Competition can occur through many processes that are often broadly categorized as exploitation or interference (Case & Gilpin 1974). These broad categories can be further reduced to mechanisms that stem from behavioural differences between competitors that affect foraging efficiency, aggression or social dominance. Behaviour can affect a wide variety of species interactions in sometimes surprising and nonintuitive ways (Werner & Peacor 2003; Sih et al. 2003, 2004), and it has become evident that many animal invasions can be fully understood only if individual behaviour is considered (Petren et al. 1993; Petren & Case 1996, 1998; Holway et al. 1998; Holway & Suarez 1999). It follows that understanding the behavioural interactions of invaders and residents will lead to better predictive ability and more effective control of invasive species.

Ecological interactions among species, such as resource competition, may be mimicked by other processes that involve shared predators or parasites (Holt 1977). Processes involving reproduction may also mimic competition. Within species, reproductive (or sexual) interference refers to the negative fitness consequences

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of behaviour that disrupts reproduction (Sparreboom 1996; Waights 1996) or reproductive behaviour that negatively affects fitness in other ways (Magurran & Seghers 1994; McLain & Pratt 1999). Reproductive interference may also occur between species if they have incompletely isolated mate recognition systems. Hybridization is the most commonly identified mechanism that falls under the broader category of reproductive interference (e.g. Kuno 1992; Hettyey & Pearman 2003). Interspecific reproductive interference also includes reduced female reproduction due to mating with heterospecific males (the 'satyr effect'; Ribeiro & Spielman 1986), fertilization and aborted development, sperm competition, mate guarding or sexual behaviour that negatively affects resource acquisition or survival of another species (Lynch 1984; Rhymer & Simberloff 1996; Takafuji et al. 1997; Westman et al. 2002). An effective way to distinguish among the potential mechanisms of resource competition and alternative processes, such as reproductive interference, is to quantify behavioural interactions among individuals.

The common house gecko, *Hemidactylus frenatus*, is rapidly expanding its range and displacing a number of other species, including a native parthenogenetic (all-female, clonally reproducing) gecko, *Hemidactylus garnotii*, on a global scale. Substantial evidence indicates that the decline of *H. garnotii* throughout the Pacific basin is coupled with the introduction of *H. frenatus* (Kluge & Eckardt 1969; Bolger & Case 1992; Moritz et al. 1993; Case et al. 1994). The broad geographical pattern, the rapid rate of often complete displacement, the similarity of species and their relatively simple ecological requirements offer a rare opportunity to quantify the behavioural mechanisms of invasion and displacement in a terrestrial vertebrate.

Adult *H. frenatus* and *H. garnotii* are comparable in size, appearance, diet and activity patterns, and they occupy similar ecological niches (Meshaka 2000). This ecological similarity suggests that resource competition may be the mechanism of displacement. Field experiments have revealed that *H. frenatus* displaces a smaller asexual gecko, *Lepidodactylus lugubris*, primarily through resource exploitation (Petren et al. 1993; Petren & Case 1996), and alternative processes of apparent competition have been ruled out (Hanley et al. 1998). The displacement of *H. garnotii* by *H. frenatus* has been attributed to behavioural interference from aggressive males based on observation (Hunsaker 1966; Hunsaker & Breese 1967) and laboratory experiments (Bolger & Case 1992). Social dominance in lizard communities is frequently attributable to asymmetry in aggression or body size, and this asymmetry often leads to differential resource acquisition (Case & Gilpin 1974; Stamps & Krishnan 1994; Calsbeek & Sinervo 2002; Downes & Bauwens 2002). Agonistic interactions among individual *H. frenatus* and *H. garnotii* have been quantified, but only after short acclimation times (1–2 days) and in the absence of food and shelter (Bolger & Case 1992). Behavioural interactions, such as male territoriality, may operate very differently in the presence of resources such as food, shelter or mates (Parker 1974).

Our approach was to quantify intraspecific and interspecific behavioural interactions of *H. frenatus* and *H. garnotii* in dyads and triads in the presence of food and shelter and after extended acclimation periods. We tested the hypothesis that competition occurs between these species by monitoring food resource consumption. This hypothesis predicts that the presence of the successful sexual invader, *H. frenatus*, will cause the resident parthenogenetic *H. garnotii* to consume fewer resources. We also tested the hypothesis that the mechanism of displacement is direct behavioural interference due to male aggression. This hypothesis predicts that *H. frenatus* males will respond to *H. garnotii* much like they respond to conspecific males. One alternative prediction is that *H. frenatus* males will respond to *H. garnotii* much as they respond to conspecific females, resulting in the potential for reproductive interference.

METHODS

Subjects

Forty-nine mature *H. frenatus* (26 males and 23 females) collected from Oahu, Hawaii, U.S.A. and 19 mature *H. garnotii* collected from Fort Myers, Florida, U.S.A., were housed at the University of Cincinnati under IACUC protocol no. 00-04-28-02. Invading male *H. frenatus* had a mean ± SE snout–vent length (SVL) of 57.7 ± 0.39 mm (range 50.5–66.0 mm) and a mean ± SE mass of 4.3 ± 0.07 g. Female *H. frenatus* were smaller (SVL = 52.9 ± 0.25 mm, range 47.0–66.0 mm; mass = 3.1 ± 0.06 g). The prior resident, parthenogenetic *H. garnotii* were considerably larger than female *H. frenatus* (SVL = 60.8 ± 0.43 mm, range 55.0–69.0 mm; mass = 3.5 ± 0.08 g). Resident parthenogens were longer but not heavier than invading male *H. frenatus*. Both species are highly variable in coloration (dark/light), patterning and size. Variation in appearance occurs in parallel within each species, making them indistinguishable to an untrained observer, but a trained observer can distinguish them by sight. Geckos were housed separately in clear plastic 5.4-litre boxes exposed to a 12:12 h light:dark cycle and 40–60% humidity at 26–29 °C temperature. Partitions prevented visual contact among individuals, and each received approximately four small live crickets and water every 3 days. Individuals were acclimatized to the laboratory at least 1 month prior to experimental testing. Upon completion of the experiment, all geckos were adopted out as pets.

Experimental Procedures

Experimental enclosures (15 × 15 × 45 cm) were paired, oriented vertically and divided by opaque, plastic, removable dividers (Fig. 1). The front of the enclosure was made of clear acrylic to permit observation. A plastic shelter (11.5 × 6.5 cm) was attached to the upper part of the opaque vertical back wall of each subunit to serve as a hiding place. A lamp with a 15-W bulb provided dim illumination simulating dusk for the entire room. This experimental design mimics conditions typically found near human structures in the tropics where the natural invasion and displacement is most evident (Case et al. 1994).

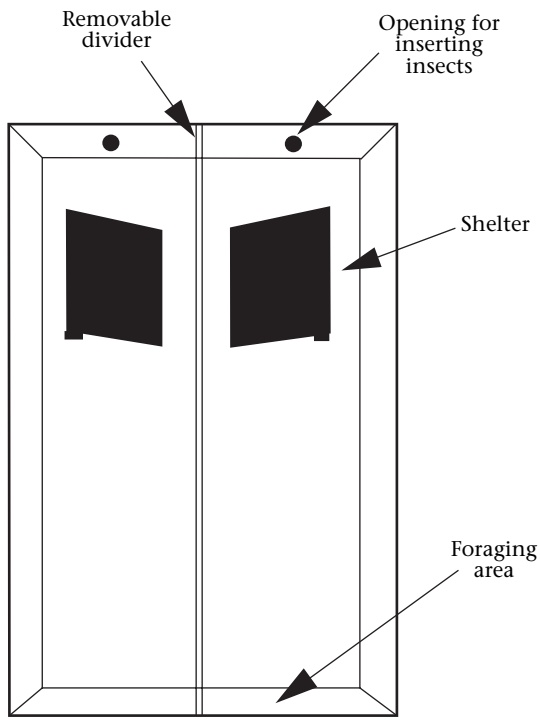

Figure 1. Experimental enclosures used for dyadic and triadic trials.

Geckos were acclimated in experimental enclosures for 5 days before testing in pairs or in triads. Acrylic paint was applied to the dorsum of each gecko for identification and snout–vent length, mass, tail condition and egg state were recorded (Petren & Case 1996). Most female *Hemidactylus* geckos in the tropics were found with developing eggs. Females with medium or large eggs were not used for experiments, except for one triad where females with equivalent egg state (large) were paired with a male. On the first and third day, each solitary gecko was given water (sprayed on the walls) and three small crickets at dusk (any remaining crickets were removed an hour later). The second feeding during acclimation was videotaped. On the fifth and sixth day at dusk, dividers were removed, six crickets were placed in the joint enclosure and interactions were recorded for 1 h. Thus, experimental trials were conducted in familiar surroundings and with the same per capita space and food resources that were available during acclimation. Dividers were replaced after videotaping. Two pairs of geckos were recorded simultaneously using a digital videotape recorder and tripod with no observers present.

Data Recorded

We recorded total foraging attempts, latency to first feeding, number of crickets eaten and position changes for each gecko in isolation. Latency was measured because it may more accurately reflect foraging success of geckos that cluster at resource clumps and often strike at the same insect (Petren & Case 1998). We expected that feeding on two consecutive nights left some geckos satiated, so we compared resource consumption only for the first night of paired or triadic interactions.

We quantified behavioural interactions similar to previous studies (Frankenberg 1984; Bolger & Case 1992), but we recorded more categories of behaviour (Table 1) and summed behaviour over both nights of observation. We recorded the frequency of visual displays (high, low, fast, and staccato tail wags and arches), vocalizations (clicks, growls, low clicks), approaches, retreats, lunges, bites, bite-holds, throws, wrestles, vent licks and copulations. Bites and bite-holds to the neck were distinguished from other bites and holds because they were primarily given by males towards females during copulation. Bites from males that were not delivered to the neck region of females were difficult to interpret and may indicate courtship instead of aggression. Social dominance among males was determined by the individual with more approaches and successful displacements (Frankenberg 1984; Bolger & Case 1992).

Experimental Design

Individuals of invasive *H. frenatus* (M = male, F = female) and prior resident *H. garnotii* (P = parthenogen) were paired in six combinations: three within sex (MM, FF, PP), one between sex within species (MF), and two between species (MP, FP). Pairings were temporally interspersed, individuals were used once in each type of pairing, and those used in more than one pairing were kept in isolation for at least 2 weeks between trials. Individual variation in body size was representative of natural populations, and individuals were randomly selected to represent natural encounters. After all dyadic pairings were completed, mate choice trials were conducted to determine whether pairwise behaviour translated to small groups. Triads with one male *H. frenatus*, one female *H. frenatus* and one parthenogenetic *H. garnotii* were used to determine male preference when females of both species were available.

Data Analysis

The experiment was designed to control for among-individual variation in foraging, aggression and courtship. We therefore used a within-subjects or repeated measures design to provide the most power for testing the most relevant a priori hypotheses regarding the negative effects on resident *H. garnotii*. Some individuals were used in multiple treatments, but because of the different pairings required, no individuals could be used in all treatments. Therefore, it was not possible to perform all hypothesis testings with a single statistical model. We protect against type I error by including global comparisons using ANOVA, repeated measures ANOVA, or MANOVA (Wilk's lambda) among all treatments (Scheiner 1993). Behaviour was classified as aggressive or courtship based on principal components analysis (PCA) using linear correlations among variables. Behaviours clustering with copulation were considered courtship, and behaviours clustering with obviously aggressive behaviours (bite-hold, wrestle) were considered aggression. We either treated behaviours as multiple dependent variables or summed categories of behaviour (aggression/courtship) within individuals for

Table 1. Frequency of all behaviours recorded (mean number per hour ± SE) during paired trials

	Within sex			Between sex	Between species	
Behaviour	M–M (*N*=13)	F–F (*N*=10)	P–P (*N*=9)	M–F (*N*=18)	M–P (*N*=15)	F–P (*N*=10)
Movement/visual displays						
Approach: movement towards an individual that retreats	2.31±0.71	3.42±1.46	2.30±1.20	1.69±0.62	2.92±1.09	1.70±0.57
Retreat: movement away from an approaching individual	2.31±0.71	3.42±1.46	2.30±1.20	1.69±0.62	2.92±1.09	1.70±0.57
Arch: posture with raised back and extended legs	2.44±0.69	1.58±0.70	0.45±0.24	0.26±0.14	0.57±0.22	0.26±0.14
High wag: slow, sinuous, lateral movement of tail perpendicular to substrate	1.34±0.43	0.40±0.24	1.05±0.43	2.13±0.85	1.41±0.53	1.27±0.16
Low wag: slow, sinuous, lateral movement of tail parallel to substrate	0.06±0.06	0.42±0.26	0.24±0.22	0.49±0.46	0.26±0.19	0.15±0.09
Fast low wag: fast, lateral movements of stiff tail parallel to substrate	0	0.08±0.08	0.58±0.41	0.81±0.35	1.47±0.48	0.12±0.07
Vocalizations						
Clicks: high-frequency, high-amplitude clicks repeated slowly 3–8 times	0.31±0.09	0.10±0.07	0	3.33±1.32	1.53±0.59	0
Growl: low-frequency, rapidly repeated, glottal grating sound	0.12±0.08	0	0	0	0	0
Low click: low-frequency, very low-amplitude click with intermediate repeat rate	0	0	0.06±0.06	0	0	0
Aggression						
Lunge: jump towards an individual without contact	0.15±0.07	0	0	0.14±0.07	0	0.06±0.06
Bite: brief mouth contact to body	0.45±0.11	0.05±0.04	0	0.02±0.02	0.45±0.28	0.03±0.12
Bite-hold: extended mouth contact to another's body	0.64±0.18	0.15±0.08	0.06±0.04	0.09±0.03	0.03±0.03	0.03±0.03
Wrestle: prolonged body contact between individuals	1.18±0.36	0	0	0	0.10±0.05	0
Throw: one individual hurls another off the substrate	0.18±0.10	0	0	0	0	0
Courtship						
Staccato wag: high tail wag with frequent stutter-stops	0.33±0.33	0	0	4.14±1.69	9.49±2.65	0
Neck bite: brief mouth contact posterior to the head	0	0	0	0.02±0.02	0.25±0.15	0
Neck hold: extended mouth contact posterior to the head	0	0	0	0.09±0.06	0.51±0.16	0
Vent lick: mouth contact to individual's own cloaca	0	0	0	0.20±0.11	0.51±0.22	0
Copulation: cloacal contact, with the female's tail raised	0	0	0	0.12±0.05	0.20±0.09	0

M = male *H. frenatus*, F = female *H. frenatus*, P = parthenogenic *H. garnotii*.

hypothesis testing using repeated measures. Click vocalizations were not included with courtship behaviour because of the difficulty of distinguishing separate occurrences. Data were inspected for normality and nonparametric statistics were used when clear deviations from normality were present (Siegel & Castellan 1988). Analyses were conducted with SYSTAT (v. 10.2, SPSS, Chicago, Illinois, U.S.A.) or JMP (v. 5.2.1, SAS Institute, Cary, North Carolina, U.S.A.). An alpha of 0.05 was used for all statistical tests.

RESULTS

Body size (SVL) differences between paired geckos paralleled those observed in nature. Parthenogenetic *H. garnotii* were on average 2.6 mm longer than male *H. frenatus* and 6.4 mm longer than female *H. frenatus*. Male *H. frenatus* were, on average, 5.0 mm longer than female *H. frenatus*, and mean length differences for the remaining treatments were less than 3.0 mm. Resource consumption overall declined by 19% on the second night of observation. This probably reflected satiation; thus, we confined foraging comparisons to the first night of interaction. Latency to consume the first insect was highly correlated with total resource consumption across all pairings (Spearman rank correlation: $r_S = 0.81$, $N = 75$, $P < 0.0001$); thus, we report only total cricket consumption.

Resource Competition within Species

A comparison of resource consumption across all treatments revealed general evidence of resource competition. Resource consumption was significantly lower in pairs than when alone (repeated measures ANOVA, blocked by trial, effect of pairing type: $F_{1,127} = 7.03$, $P < 0.01$; Fig. 2). Consumption differed between the three pairings and three acclimation sessions for a set of male *H. frenatus* (repeated measures ANOVA: $F_{5,9} = 15.78$, $P < 0.001$) and parthenogens ($F_{5,4} = 7.00$, $P < 0.05$) but not female *H. frenatus* ($F_{5,3} = 1.32$, $P < 0.6$); however, sample sizes for this test were small.

If our experimental design was effective at revealing the effects of social dominance on resource acquisition, social dominance should be related to resource access in males.

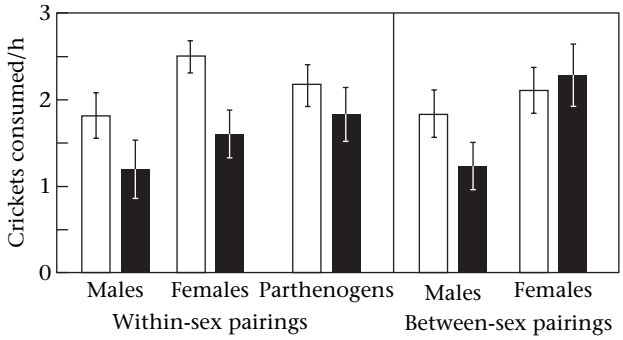

Figure 2. Mean ± SE number of crickets consumed per gecko in within-species paired treatments. □: consumption while each gecko was alone immediately before removal of a divider separating two geckos. ■: consumption in the presence of the other gecko after dividers were removed.

This prediction was supported in *H. frenatus* male–male dyads, where dominant males consumed more crickets than did subordinate males (binomial test: df = 10, $P = 0.021$). Male size (SVL) was not related to social dominance (binomial test: df = 11, $P = 0.41$), but sample sizes and body size differences were limited. When paired with conspecific females, male *H. frenatus* consumed fewer insects than when they were alone (paired *t* test: $t_9 = 2.535$, $P = 0.032$). In contrast, female *H. frenatus* consumed significantly more resources in the presence of a conspecific male ($t_9 = -2.333$, $P = 0.045$).

Resource Competition between Species

The resource competition hypothesis predicts that the parthenogenetic resident *H. garnotii* will consume fewer resources in the presence of the successful invader, *H. frenatus*. In contrast, insect consumption for parthenogens did not differ for parthenogens when they were alone and when they were paired with heterospecific *H. frenatus* males (paired *t* test: $t_9 = 0.452$, $P = 0.662$; Fig. 3). Female *H. frenatus* also had little effect on parthenogenetic *H. garnotii* consumption (paired *t* test: $t_9 = 1.408$, $P = 0.322$). The power to detect a consumption difference of 0.5 was 40%, and the power to detect a difference of 1.2 (the difference observed in males, below) was 96%. Contrary to expectations, invasive male *H. frenatus* ate significantly less when paired with resident parthenogenetic *H. garnotii* (paired *t* test: $t_9 = 3.857$, $P = 0.004$) than when they were alone, thus mirroring the response of males to conspecific females. Furthermore, when paired with the successful invader, parthenogens consumed almost the same amount as female *H. frenatus* (mean consumption was 2.0 for females and 1.9 for parthenogens; $t_{19} = 0.18$, $P = 0.86$). Parthenogens consumed significantly more than did males ($t_{28} = 4.28$, $P < 0.001$). Latency to consume the first insect revealed similar patterns (data not shown). On average, males delayed foraging for 26 min in the course of a 60-min trial when in the presence of heterospecific females. In summary, patterns of interspecific resource consumption were in the opposite direction to that predicted by our main hypothesis of competitive displacement. When paired, the successful invader consumed less and the displaced resident consumed more.

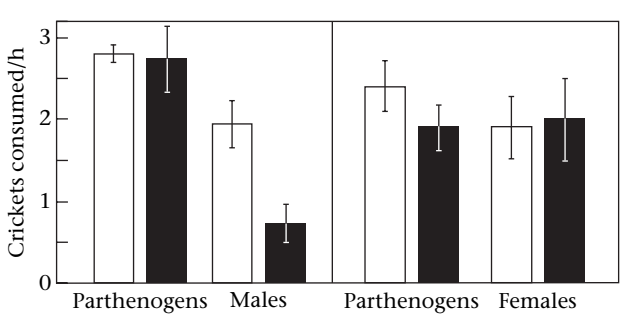

Figure 3. Mean ± SE numbers of crickets consumed per gecko in between-species paired treatments. □: consumption while each gecko was alone immediately before removal of a divider separating two geckos. ■: consumption in the presence of the other gecko after dividers were removed.

Social Behaviour

Pairings showed significant differences when all behaviours were subjected to MANOVA analysis with trial as a blocking factor ($F_{95,534} = 2.88$, $P < 0.0001$). Most of these differences were attributable to males, who typically initiated aggressive and courtship interactions. When analysed in separate MANOVA models, males showed distinct differences between treatments ($F_{38,42} = 4.56$, $P < 0.0001$), females showed marginal differences ($F_{38,20} = 2.00$, $P = 0.0501$), and parthenogens showed no differences ($F_{38,20} = 0.73$, $P = 0.79$). Thus, we focus our analysis on male behaviour.

Principal components analysis allowed us to distinguish which of the 19 behaviours recorded (Table 1) were related to aggression and courtship (Fig. 4). Principal component axes 1 and 2 accounted for 16.0% and 14.7% of behavioural variation, respectively, with corresponding eigenvalues of 3.0 and 2.9. Axis 1 appeared to distinguish social behaviour from courtship, and axis 2 generally distinguished aggressive and submissive behaviour.

Aggression

Aggressive behaviour differed between the three conspecific pairings (ANOVA: $F_{2,61} = 11.41$, $P < 0.001$; Fig. 5). Aggression was higher among male–male *H. frenatus* pairings than among female–female *H. frenatus* pairings and *H. garnotii* parthenogen–parthenogen pairings (Tukey test: $P < 0.001$). Individual *H. frenatus* males directed more aggressive behaviour towards other conspecific males than towards conspecific females (Wilcoxon matched-pairs test: $T = 99$, $N = 14$, $P = 0.002$). Individual *H. frenatus* males directed more aggressive behaviour towards other conspecific males than towards parthenogenetic *H. garnotii* females (Wilcoxon matched-pairs test: $T = 70$, $N = 12$, $P = 0.012$). In summary, male *H. frenatus* were aggressive towards other males, but displayed

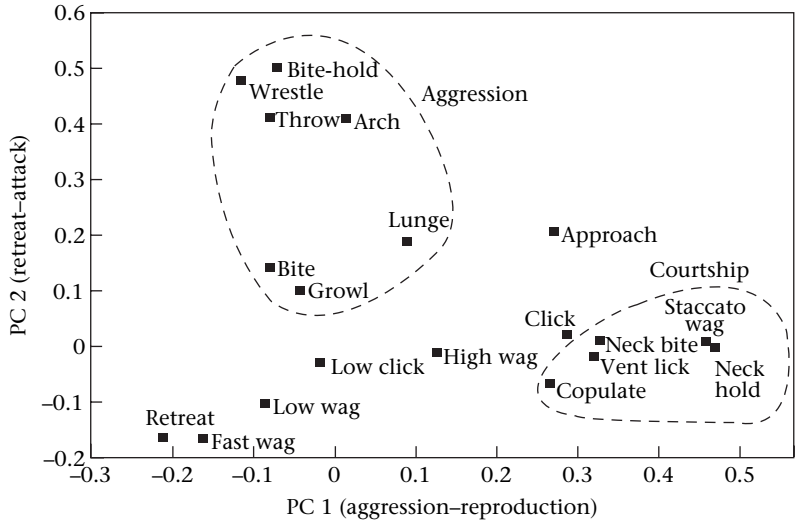

Figure 4. Factor loadings for the first two principal component axes for all behaviours recorded. Circles enclose behaviours considered to indicate aggression and courtship.

similarly low levels of aggression towards conspecific and heterospecific females, so we rejected the hypothesis that male aggression is a factor in the displacement of the resident parthenogen *H. garnotii*.

Courtship

Courtship interactions occurred in 66.7% of all male *H. frenatus*–female *H. frenatus* pairings ($N = 18$). Interspecific courtship occurred in 93.3% of all pairings of male *H. frenatus* and parthenogenetic *H. garnotii* ($N = 15$). Individual male *H. frenatus* displayed more courtship behaviour when paired with the larger parthenogenetic females than when paired with conspecific *H. frenatus* females (Wilcoxon matched-pairs test: $T = 92.5$, $N = 14$, $P = 0.009$; Fig. 6). Both female *H. garnotii* and female *H. frenatus* appeared to be receptive to male courtship. Of the 10 male *H. frenatus* that were paired both with *H. frenatus* females and parthenogens, two copulated successfully with a female *H. frenatus*, and four copulated with parthenogenetic *H. garnotii*.

Resource Consumption in Triads

Male *H. frenatus*, female *H. frenatus* and female *H. garnotii* differed in cricket consumption in triads (ANOVA: $F_{2,33} = 8.694$, $P = 0.001$). Parthenogens consumed more crickets than did *H. frenatus* males (Tukey test: $P = 0.003$) and females ($P = 0.003$), and consumption by parthenogenetic *H. garnotii* was higher in the presence of two potential *H. frenatus* competitors than when they were alone (alone: 2.33 insects/h; in triads: 2.67 insects/h; paired *t* test: $t_{11} = -0.842$, $P = 0.417$). On average, *H. garnotii* consumed insects 10 min sooner than did *H. frenatus*. Patterns of resource consumption in triads mirrored those of dyads, and were in the opposite direction predicted by the resource competition hypothesis.

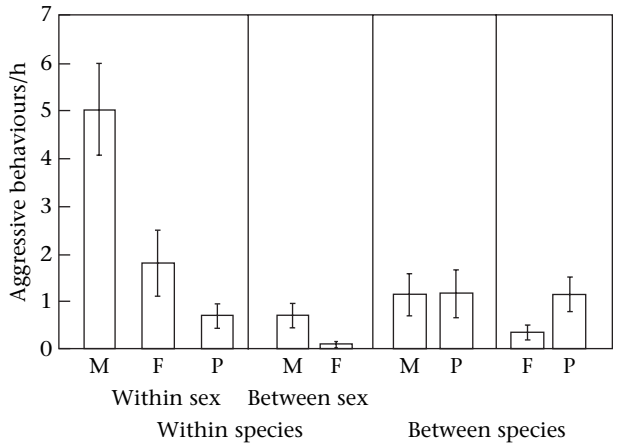

Figure 5. Mean ± SE number of aggressive behaviours displayed per gecko during paired trials. M = male *H. frenatus*, F = female *H. frenatus*, P = parthenogenic *H. garnotii*.

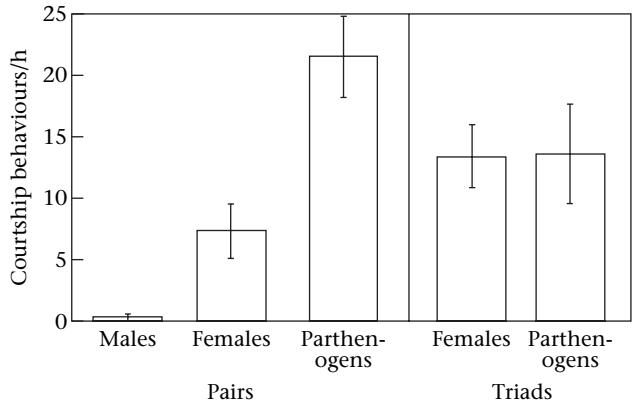

Figure 6. Mean ± SE number of courtship behaviours by invasive male *H. frenatus* directed towards males, female *H. frenatus* or parthenogenetic *H. garnotii*, in paired trials and in triads.

Male Mate Choice in Triads

Males did not reveal a preference for conspecific females or parthenogens, based on the number of courtship behaviours displayed by males in triads (paired *t* test: $t_{11} = 0.08$, $P = 0.93$; Fig. 6). Compared to male behaviour in dyads, males in triads increased their courtship towards conspecific females (from 7.3/h to 13.4/h) and decreased their courtship towards parthenogens (from 21.9/h to 13.7/h), resulting in very similar values and indicating no mate preference. Copulations occurred in three of 12 triads, and all were with female *H. frenatus*.

DISCUSSION

The hypothesis that resource competition is the mechanism of displacement of *H. garnotii* by *H. frenatus* received no support from our experiments. *Hemidactylus garnotii* did not consume fewer resources when in the presence of *H. frenatus* and, in both experiments, tended to consume more insects in the presence of the successful invader. The hypothesis that *H. frenatus* male aggression is responsible for the displacement of *H. garnotii* was also rejected. Male *H. frenatus* were not aggressive towards *H. garnotii* and instead courted and copulated with them. Male *H. frenatus* responded to heterospecific *H. garnotii* much as they responded to conspecific females.

Based on these results, we reject the hypothesis that male aggression is the primary mechanism of invasion of *H. frenatus* and displacement of *H. garnotii*. The lack of aggression displayed by *H. frenatus* towards parthenogenetic *H. garnotii* is unlikely to change fundamentally over longer intervals. These results differ qualitatively from those of previous studies of *Hemidactylus* geckos (Frankenberg 1984; Bolger & Case 1992) primarily because of the increased realism of our experimental setting. We incorporated shelter and food resources into the design to elicit more natural behaviour, which is an important consideration for experimental studies of behaviour (Parker 1974). The observation of several copulations suggests that these efforts were successful. We were also careful to quantify behaviour so that we could distinguish between aggressive behaviour and courtship interactions, which can appear superficially similar.

Ruling out competition and other alternatives is difficult in a laboratory setting. We can rule out resource competition as a mechanism of displacement under the specific conditions of our experiment. Different densities of competitors and levels of resources could produce a different result. However, several factors support the conclusion that experimental circumstances reflected the natural context of invasion. We found general evidence of density dependence during resource consumption. In this regard, experimental conditions reflected natural conditions where density-dependent depletion of insects by geckos has been measured (Petren & Case 1996). Only a subset of experimental treatments failed to reveal evidence of density-dependent resource consumption. However, these treatments were central to the hypothesis that competition drives the displacement, and the patterns were similar in dyads and small group (triadic) interactions. Experimental conditions were sensitive enough to show that male social dominance led to increased access to food resources, as is expected based on studies of other lizards (Case & Gilpin 1974; Bolger & Case 1992; Stamps & Krishnan 1994; Meshaka 2000). Furthermore, this experimental setting has successfully revealed exploitation competition in a different context. Dyads of *Lepidodactylus* geckos showed consumption differences that were predicted based on natural patterns of invasion (unpublished data). We conclude that resource competition among adults is unlikely to be the primary mechanism of invasion and displacement among the species studied here, but other viable mechanisms such as intraguild predation (Gerber & Echternacht 2000) and juvenile competition (Downes & Bauwens 2002) remain to be tested.

One general implication of this study is that interspecific ecological interactions may be affected by social interactions, and the latter should be quantified if the goal is to make relevant inferences about ecology. In our experiments, the presence of females affected foraging. Male *H. frenatus* consumed fewer resources and consistently turned their attention towards courtship when females were present. Over longer intervals, males may turn their attention away from courtship, but observations suggest that this is not the case. Dominant male *H. frenatus* routinely engage in courtship during peak foraging times in a natural setting (Petren & Case 1996, 1998; K. Petren, unpublished data). The reduced foraging effort by males probably led to increased foraging opportunities for females and parthenogens, who in some instances increased their resource intake, perhaps to increase provisioning of eggs in the advent of fertilization.

The patterns of courtship, copulation and mate preference demonstrate that reproductive interference is a viable alternative hypothesis to account for the displacement of *H. garnotii* by *H. frenatus*. In our dyadic experiments, male *H. frenatus* showed a greater response to heterospecific *H. garnotii* parthenogens than to conspecific females. The larger size of *H. garnotii* parthenogens compared to *H. frenatus* females may have provided a superstimulus and elicited more courtship from males. Both experimental evidence (Verrell 1990) and theoretical evidence (Pfennig 1998) suggest that closely related heterospecifics that resemble high-quality conspecifics may be perceived as especially attractive mates. Results of the mate choice experiments using triads showed that male *H. frenatus* courted both conspecific and heterospecific females equally; thus, the patterns observed in dyads was not due to a limited choice of mates.

Interspecific reproductive interference may take at least two forms relevant to geckos: the time and energy spent engaging in or avoiding courtship or direct interference with the production of viable offspring. Our results do not support a cost of harassment to *H. garnotii* parthenogens, because they generally consumed more resources in the presence of courting and copulating male *H. frenatus*. Observations of heterospecific copulations suggest that direct interference with asexual reproduction may be a more likely mechanism of sexual interference. In geckos,

hybridization is commonly observed among sexual species and parthenogens, and hybridization is the most likely origin of many parthenogenetic lizards (Case 1990; Hanley et al. 1994; Radtkey et al. 1995). However, *H. frenatus* and *H. garnotii* are not known to form hybrids. In the absence of hybridization, negative effects on parthenogenetic reproduction may still occur after copulation but before hatching (Ribeiro & Spielman 1986; Takafuji et al. 1997; Price et al. 2001). The effect of heterospecific mating on reproductive success has not been quantified in parthenogenetic *H. garnotii*. We were unable to compare egg hatching rates of mated and unmated *H. garnotii* because of limited sample sizes and low hatching rates of eggs of this species in captivity. In general, few data are available from nature quantifying negative effects of heterospecific mating that does not lead to the production of hybrids. This lack of data may reflect a low frequency of occurrence of this type of reproductive interference, or it may be attributable to the difficulties associated with demonstrating its presence, which requires control over mating and the measurement of hatching success. In *Hemidactylus* geckos, longer periods of isolation would be required to circumvent the additional complication of sperm storage, which can exceed 6 months (Murphy-Walker & Haley 1996).

Evidence of interspecific reproductive interference is confined largely to instances where hybrids are formed, and even this mechanism is thought to be an underappreciated factor in the displacement of native species by invasives (Huxel 1999). Hybridization with invasive species can result in the complete displacement of native species (Rhymer & Simberloff 1996; Dowling & Secor 1997; Mooney & Cleland 2001; Westman et al. 2002). Reproductive interference without hybrid formation occurs in arthropods (Takafuji et al. 1997) and may have a greater potential for exclusion than competition for resources (Kuno 1992). The cost of reproductive interference may change throughout the course of invasion (Hettyey & Pearman 2003), and may differ according to species and sex (Parker 1982; Pfennig 1998). Reproductive interference may be particularly costly for all-female parthenogens in taxa where reproductive investment is higher for females than males (Lynch 1984). The potentially dramatic impact of reproductive interference, combined with the difficulty of detecting it, suggests that it receive greater attention as a potential mechanism of invasion and displacement. Studies of individual behaviour in a laboratory setting will provide valuable information about the general importance of reproductive interference in nature, and will help to discriminate among alternative mechanisms of invasion and displacement.

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