

# The need for enemy-free space: The impact of an invasive gecko on island endemics

Nik C. Cole <sup>a,\*</sup>, Carl G. Jones <sup>b</sup>, Stephen Harris <sup>a</sup>

<sup>a</sup> School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK

<sup>b</sup> Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey JE3 5BP, Channel Islands, UK

Received 6 January 2005

Available online 13 June 2005

## Abstract

How introduced reptiles cause the loss of endemic reptiles is poorly understood and currently there are no available techniques for dealing with this major conservation issue. We addressed both these problems by investigating the role of the introduced house gecko *Hemidactylus frenatus* in causing the catastrophic decline and extinction of the endemic night gecko *Nactus* populations of the Mascarene Islands and how this introduced species can be excluded from habitats on the basis of morphology. Competition for enemy free space was tested in experimental enclosures and showed that *H. frenatus* displace the endemic *Nactus coindemirensis* and *Nactus durrelli* from favoured positions close to and from refugia, thus increasing the risk of predation and exposure to stochastic events. The ability of *H. frenatus* to grip substrates with their pad-bearing toes was examined, and we demonstrated that naturally occurring substrates with a greater amount of loose surface material of a higher particulate concentration and size excludes *H. frenatus*, but not *Nactus*. These findings support the hypothesis that *H. frenatus* led to the fragmentation and extinction of the endemic *Nactus* populations and demonstrate that artificial refugia made of a crumbly substrate may be used to limit future disturbances by this gecko and others like it in the Mascarene Islands and elsewhere.

© 2005 Elsevier Ltd. All rights reserved.

**Keywords:** Invasion; Competition; Exclusion; Gecko; Mascarenes

## 1. Introduction

The mechanisms promoting the co-existence of species are a major issue in ecology, as these fundamental processes affect community structure and organisation (Tokeshi, 1999). The introduction of alien species into established assemblages typically has the effect of disrupting these processes, frequently leading to the extinction of native species. For example, three-quarters of all recorded animal extinctions in the last 400 years have occurred on small remote islands rich in endemic species, and two-thirds of these have been attributed to intro-

duced species (World Conservation Monitoring Centre, 1992).

Reptile extinctions, in particular, have occurred exclusively on islands leading to a significant, but largely unpublicised, decline in global biodiversity (Case et al., 1992; Gibbons et al., 2000). The major process contributing to this decline is believed to be predation by introduced mammals (Case and Bolger, 1991), as exemplified in the decline of New Zealand reptiles (Townsend et al., 2001). However, the introduction of non-native reptile species can have equally dramatic impacts upon island reptile assemblages (Case and Bolger, 1991; Rodda and Fritts, 1992). Yet, unlike predation, there are few documented cases where competition has been implicated as the causal mechanism underlying the extinction of reptile species in particular, or endemic species generally

\* Corresponding author. Tel.: +44 177 928 8918; fax: +44 117 925 7374.

E-mail address: [nik.cole@bristol.ac.uk](mailto:nik.cole@bristol.ac.uk) (N.C. Cole).

(Case and Bolger, 1991; Mooney and Cleland, 2001). Competition between species can occur where an introduced species occupies the same microhabitat, operates along the same temporal niche and utilises the same resource(s) as resident species (Pianka, 1973). Competitive interactions are also thought to be most intense between morphologically similar species, but with larger species generally at a competitive advantage over smaller species (Pacala and Roughgarden, 1982; Losos, 2000; Melville, 2002). The paucity of evidence for competition as a causal mechanism for extinction may possibly be because interactions between invasive and native competitors can occur without any obvious direct negative effects, thereby making long-term deleterious effects difficult to measure (Crawley, 1986; Petren and Case, 1996). However, given the increasing rate at which reptiles are being introduced around the world, and increasing evidence that they may have significant competitive impacts on resident species, we need to understand the role of competition in driving extinction events (Rodda and Fritts, 1992; Losos et al., 1993; McCoid, 1993; Case et al., 1992, 1994; Petren and Case, 1998; Losos and Spiller, 1999; Brown et al., 2002). From a conservation perspective, a thorough understanding of these processes is also a fundamental requirement before management protocols can be applied successfully.

The nocturnal house gecko *Hemidactylus frenatus* has the widest non-native distribution of its genus and has displaced native gecko species on many islands where it has been introduced (Case et al., 1994; Perry et al., 1998), including the Mascarene Islands. These once contained one of the richest endemic reptilian assemblages known but, following the introduction of *H. frenatus*, night geckos of the genus *Nactus* have undergone a catastrophic reduction in distribution, with extinction events on the islands of Réunion, Rodrigues and mainland Mauritius (Arnold, 2000). Until this study, relict populations of *N. coindemirensis*, *N. durrelli* and *N. serpensinsula* were only known to persist on five Mauritian islets free of *H. frenatus* (Fig. 1). Given that these *Nactus* species coexisted with mammalian predators on some of these islets, it has been hypothesised that the presence of *H. frenatus* rather than predation by mammals has been the major determinant of their current distribution (Arnold and Jones, 1994; Arnold, 2000). Yet the process(es) underlying these impacts are unknown: one possible mechanism that may have led to the decline of the night geckos is competition for refugia, resulting in increased exposure to predation and risk from stochastic events, and the extirpation/extinction of native species (Holt and Lawton, 1994).

However, in 2003 a new night gecko population was discovered on Flat Island (253 ha) to the north of Mauritius (Fig. 1); individuals of this population bore similarities to *N. coindemirensis*, although their specific identity is under review (E.N. Arnold, Pers. Commun.). System-

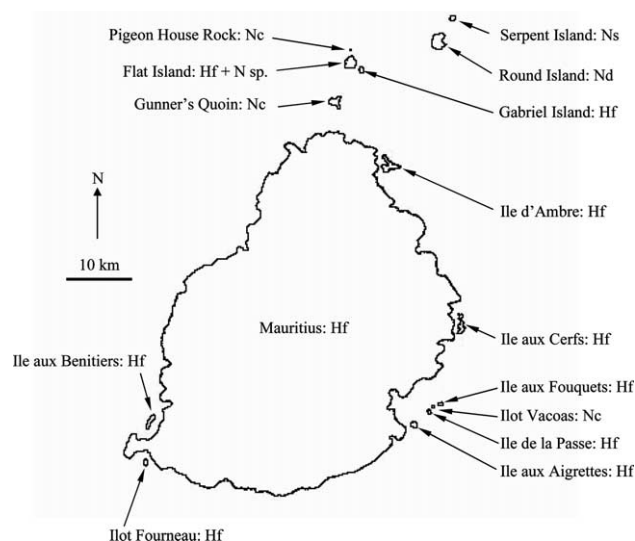


Fig. 1. Distribution of *Hemidactylus frenatus* (Hf), *Nactus coindemirensis* (Nc), *N. durrelli* (Nd), *N. serpensinsula* (Ns) and the newly discovered, as yet unidentified night gecko population (N sp.) of Mauritius.

atic nocturnal searches (>600 man-hours) revealed that *H. frenatus* was present across the islet, except for a single outcrop (<0.05 ha) of broken powdery tuff rock inhabited by the night gecko population. This is the only known location where a night gecko population survives in the presence of *H. frenatus*. Consequently, the mechanism(s) that allow these populations to exist in sympatry are of considerable theoretical and applied interest, as they may help identify a practical means for promoting the conservation of endemic reptile species in the presence of non-native competitors.

Given that *H. frenatus* have invaded the same microhabitats, operate along the same temporal niche and utilise the same resources as the night geckos (NCC, unpublished data), differences in morphology are possibly one factor promoting their co-existence on Flat Island. The greatest morphological difference between *H. frenatus* and the night geckos is foot morphology: night geckos grip with slender clawed toes whereas *H. frenatus* have toe pads that grip through van der Waals forces (Autumn et al., 2002), representing adaptations to climbing rough and smooth surfaces respectively (Zani, 2000). On Flat Island, these differences may, therefore, have enabled night geckos to survive in the presence of *H. frenatus* on the rough and crumbly surface of the powdery tuff rock. Those islands successfully colonised by *H. frenatus*, where night gecko populations no longer exist, are formed from basalt or are coralline islands and do not contain powdery tuff rock.

In this paper, we have used an experimental approach to test two key hypotheses. First, that competitive exclusion from refugia by *H. frenatus* is likely to have been responsible for the decline of the Mascarene night geckos. Second, that differences in foot morphology and

substrate structure have formed an ecological barrier allowing the co-existence of the Flat Island night gecko population and *H. frenatus*. Finally, we discuss the implications of this work for the conservation of reptile species.

## 2. Methods

### 2.1. Competitive exclusion experiments

Four experimental enclosures were constructed on Ile aux Aigrettes, a 26 ha nature reserve (Fig. 1), in terrain similar to habitats occupied by night geckos on other islets. Each enclosure consisted of a sheet of aluminium flashing (950 × 50 cm) cemented into the ground (depth = 10 cm) to create a circular arena (diameter Ø = 300 cm). Both sides of the arena were painted with lithium grease to prevent individuals entering or leaving (Rodda et al., 2001). At the centre of each enclosure we constructed a refugium by digging a pit (40 Ø × 30 cm) containing several layers of rock covered with leaf litter: concentric rings of polypropylene string were placed at 20 cm intervals from the centre so that the distance of geckos from the refugium could be quantified.

Initially each enclosure was stocked with 12 adult individuals (six male, six female) of a single species (Table 1): *H. frenatus* snout vent length (SVL) = 50.0 mm (±3.0 SD), mass = 3.0 g (±0.6 SD); *N. coindemirensis* SVL = 30.8 mm (±2.3 SD), mass = 0.7 g (±0.2 SD); *N. durrelli* SVL = 49.4 mm (±2.6 SD), mass = 3.5 g (±0.5 SD); *N. serpensinsula* was excluded because of the problem of obtaining specimens from their remote location and the possible impact upon the currently unknown population size. After a five-day habituation period, we recorded the mean distance of the 12 geckos from the refugium 8 h after sunset, when geckos start to move closer to and enter diurnal refugia, for eight consecutive days.

After eight days we removed six individuals (three males, three females) from each enclosure, and placed endemic and introduced species in sympatry in each of two enclosures (Table 1): for both endemic species, one enclosure had previously been occupied by *H. frenatus* and one by the corresponding native species. We then recorded the mean distance from the refugium of the six individuals of each species in each enclosure for a further eight days. In addition, we recorded the number of toes

and tails lost by individuals during the experiment as a measure of the pattern of intra- and inter-specific interaction.

The mean distance from the refugium in each enclosure across the eight-days of each experiment was analysed separately for each species using repeated-measures analysis of variance (ANOVA) followed by Tukey's post hoc comparisons. Models included the following terms: "night" was used to determine whether the distance from refugia was consistent between nights of observation throughout the experiments; "presentation" was used to determine whether prior occupancy of the enclosure by a species affected the distance from refugia; and "isolation/sympatry" was used to test for the treatment effects of *H. frenatus* being added to *N. coindemirensis* and *N. durrelli* and vice versa. We added a further "group" factor when analysing distances for *H. frenatus* to determine if the two sets of 12 individuals (Table 1) reacted consistently to treatments.

### 2.2. Substrates, surfaces and gripping ability

Flat Island is low-lying with a raised ridge (summit 102 m) along the south-western coast and is classified as a volcanic tuffaceous island topped with a basaltic layer covering most of the low-lying area (Saddul, 2002); most of the ridge remains as exposed tuff with very little vegetation. The newly discovered night gecko population occupies the small patch of weathered scree of powdery tuff rock at the base of the ridge. This scree is surrounded by compacted tuff rock, basalt rock and sparsely vegetated *Casuarina equisetifolia* tree trunks, all of which are occupied by *H. frenatus*.

We used a spring scale attached to a nylon noose fastened around the body behind the forelegs of 20 adult *H. frenatus* to determine the maximum force required to displace individuals from each of the four substrates: *Casuarina* tree trunks, basalt rock, compacted tuff rock and powdery tuff rock. Each individual underwent three trials in each substrate; the maximum force required to dislodge each individual was used for analyses: the site of attachment and order of presentation to each substrate was undertaken at random. To prevent loose particles adhering to the feet, we allowed individuals to lick their feet clean for at least 2 h between trials.

To obtain the mass of loose material on each substrate, a 90 cm<sup>2</sup> strip of heavy-duty adhesive tape was stuck adjacent to each attachment site ( $n = 80$ ), ensuring

Table 1  
Stocking arrangements of geckos in four enclosures for isolated and sympatric species enclosures

Enclosure	"Isolation" enclosures	"Sympatric" enclosures
1	6♂:6♀ <i>Nactus coindemirensis</i>	3♂:3♀ <i>Nactus coindemirensis</i> + 3♂:3♀ <i>Hemidactylus frenatus</i> Group 1
2	6♂:6♀ <i>Hemidactylus frenatus</i> Group 1	3♂:3♀ <i>Hemidactylus frenatus</i> Group 1 + 3♂:3♀ <i>Nactus durrelli</i>
3	6♂:6♀ <i>Nactus durrelli</i>	3♂:3♀ <i>Nactus durrelli</i> + 3♂:3♀ <i>Hemidactylus frenatus</i> Group 2
4	6♂:6♀ <i>Hemidactylus frenatus</i> Group 2	3♂:3♀ <i>Hemidactylus frenatus</i> Group 2 + 3♂:3♀ <i>Nactus coindemirensis</i>

full contact between tape and substrate. Adhering material was then removed with white spirit, dried and weighed. Differences between substrates with respect to dislodging forces and mass of loose material were analysed using Friedman and Kruskal–Wallis tests respectively, with appropriate post hoc comparisons (Siegel and Castellan, 1988).

The concentration of material adhering directly to gecko toe pads was quantified using a further six adult *H. frenatus*. Each animal was placed on a randomly selected site on each substrate in a random order; immediately after attachment, the front right foot was placed onto a segment of gelatine. A further sample was then obtained by pressing gelatine directly onto the substrate adjacent to the point of attachment. We calculated the concentration of particles from gel samples as the number of particles within 1 cm<sup>2</sup> at 100× magnification. The mean particulate size of samples was calculated by measuring the surface area of ten randomly selected particles ( $n = 180$ ) from each sample to the nearest 10 μm. Loose particles were not obtained from the *Casuarina* tree trunks using the gelatine sampling protocol; consequently, this substrate was excluded from this analysis. Differences between root-transformed particulate concentrations of each substrate surface and adhering to gecko feet were tested using one-way and repeated-measures ANOVA respectively. Differences in root-transformed particulate size between the substrates were tested using one-way ANOVA. Differences between substrates were identified using Tukey's post hoc comparisons.

In all statistical analyses, variables and residuals met the underlying assumptions for each respective test. Analyses were conducted using Minitab (Release 13.31, 2000). Results were considered significant where  $\alpha < 0.05$ .

### 3. Results

#### 3.1. Competitive interactions

For both endemic species, the pattern of presentation of species and the night on which observations were made did not affect distance from refugia (Table 2(a) and (b)): mean distance from refugia increased when in sympatry with *H. frenatus* (Fig. 2). Conversely, for *H. frenatus*, the mean distance from refugia did not differ significantly between the two groups of individuals, or when in sympatry with either night gecko species (Fig. 2): the pattern of introduction did not significantly affect distance to refugia, but there was a significant difference between the night of observation (Table 2(c)), with individuals being closer to the refugium on the one night when it rained. Interactions between *H. frenatus* and both *N. coindemirensis* and *N. durrelli* were mostly

Table 2

Repeated measures ANOVA of the distances from the refugium for *N. coindemirensis* (a), *N. durrelli* (b) and *H. frenatus* (c)

Source	SS	d.f.	MS	F	p
<i>(a) Nactus coindemirensis</i>					
Night	1743.5	7	249.1	2.06	0.119
Presentation	1556.4	1	8.5	0.07	0.795
Isolation/sympatry	3905.9	1	3905.9	32.27	<0.001
Error	1694.6	14	121.0		
Total	8900.4	23			
<i>(b) Nactus durrelli</i>					
Night	712.1	7	101.7	0.57	0.766
Presentation	2361.5	1	291.8	1.64	0.221
Isolation/sympatry	2500.4	1	2500.4	14.08	0.002
Error	2485.7	14	17.5		
Total	8059.7	23			
<i>(c) Hemidactylus frenatus</i>					
Night	9823.4	7	1403.3	11.46	<0.001
Presentation	114.8	1	312.5	2.55	0.119
Isolation/sympatry	407.4	2	203.7	1.66	0.203
Group	107.0	1	107.0	0.87	0.357
Error	4424.5	36	122.9		
Total	14877.2	47			

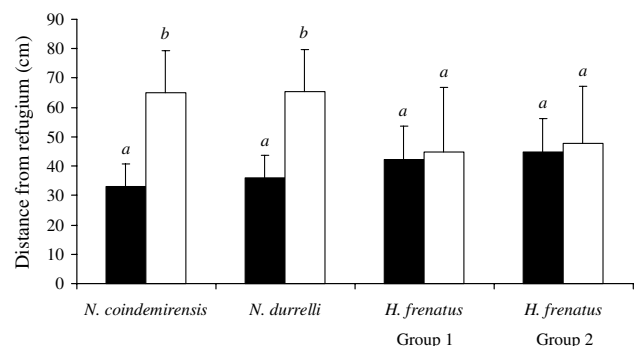


Fig. 2. Gecko distances (means + SD) from refugia in “isolation” enclosures (closed columns) and in “sympatric” enclosures (open columns). Significant differences between treatments for each species/group are indicated by different italicised letters.

aggressive, with the former frequently observed stalking, lunging towards and biting the latter, e.g., two individual *N. coindemirensis* lost toes, a further two individuals lost their tails and one male was predated.

#### 3.2. Surfaces and gripping ability

The force required to dislodge *H. frenatus* differed significantly between the four substrates (Friedman test:  $\chi^2 = 60.0$ , d.f. = 3,  $n = 20$ ,  $p < 0.001$ ), and there was also a significant difference in the mass of loose material obtained from each substrate surface (Kruskal–Wallis test:  $\chi^2 = 59.45$ , d.f. = 3,  $n = 80$ ,  $p < 0.001$ , adjusted for ties). Post hoc comparisons indicated that dislodging force decreased as the mass of loose material increased (Fig. 3(a)). There was a significant difference between



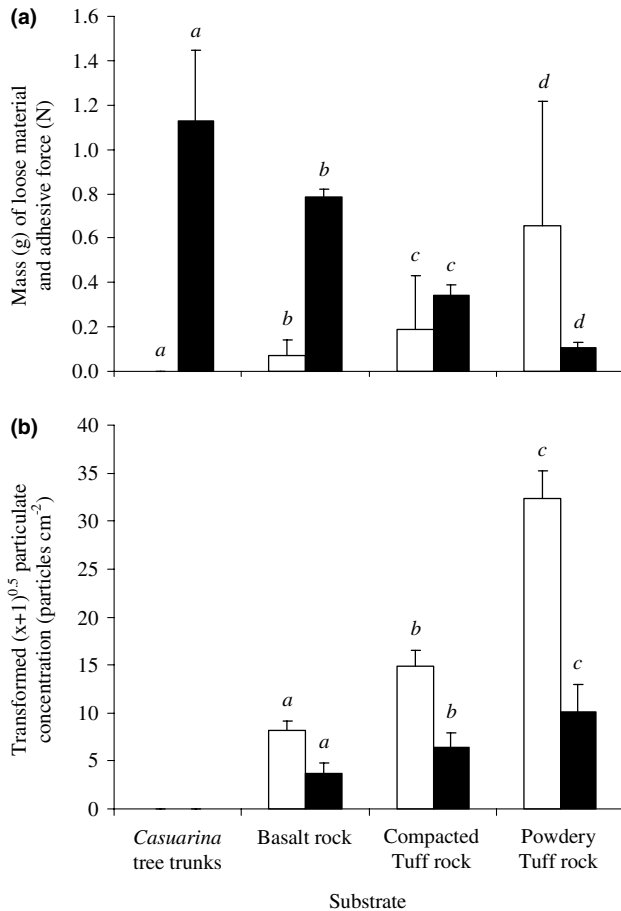


Fig. 3. The median + upper quartile mass of loose material (open columns) and adhesive force of gecko attachment (filled columns) for each substrate (a), and the means + SD particulate concentrations obtained from substrate surface (open columns) and gecko toes (filled columns) for each substrate (b). Significant differences between each independent variable are indicated by different italicised letters.

substrates with respect to particulate concentration from the substrate surface (oneway ANOVA:  $F_{2,15} = 236.65$ ,  $p < 0.001$ ) and that adhering to geckos' feet (repeated-measures ANOVA:  $F_{2,10} = 80.42$ ,  $p < 0.001$ ): particulate concentration increased on both substrate surface and feet in tandem (Fig. 3(b)). Particulate sizes obtained from the three substrates were significantly different (ANOVA:  $F_{2,177} = 14.20$ ,  $p < 0.001$ ), with particles from the powdery tuff rock having a larger surface area. Overall, therefore, powdery tuff rock had a significantly greater mass of loose material and particulate concentration than the other substrates, resulting in larger particles adhering to the feet of *H. frenatus* and significantly reducing the force required to dislodge them.

#### 4. Discussion

The spatial segregation of *H. frenatus* and the night geckos throughout the Mascarene islands is reflected in

an analogous situation in the Mediterranean where the lacertid lizard, *Podarcis sicula* has spread and replaced the native *P. melisellensis* throughout coastal areas and numerous islands (Nevo et al., 1972). Following experimental introductions of *P. sicula* to islands inhabited by *P. melisellensis* it was suggested that the former species were competitively excluding the natives (Radovanovic, 1965). However, the causal mechanism of this putative exclusion has only recently been demonstrated using experimental enclosures to show that juvenile *P. sicula* outcompete juvenile *P. melisellensis* for microhabitats of preferred thermal properties through asymmetric aggressive interactions, thus affecting growth and fitness of *P. melisellensis* (Downes and Bauwens, 2004). In this study, we also demonstrate that in experimental enclosures asymmetrical aggressive interactions are responsible for the competitive exclusion of both *N. coindemirensis* and *N. durrelli* from daytime refugia by *H. frenatus*, such that individuals of native species were forced to occupy areas approximately twice as far from refugia in the presence of *H. frenatus* versus its absence (Fig. 2). For ethical reasons, the number of night geckos used was kept to a minimum and therefore replicates of the experiment with different groups of geckos were not performed. It was also deemed unethical to test directly whether the pattern of exclusion increased the rate of predation of endemic species through experimental introductions of *H. frenatus* to night gecko-populated islands, as conducted for the lacertids in the Mediterranean (Radovanovic, 1965). However, being pushed further from the safety of refugia is certainly likely to increase the risk of being predated and increases vulnerability to adverse weather conditions, such as cyclones (Schoener et al., 2001). Furthermore, the loss of toes and tails has been shown to reduce locomotion and gripping ability: tail loss decreases growth, reduces fecundity, reduces home range size and enhances loss of territories in other lizard species (Mahendra, 1941; Ballinger and Tinkle, 1979; Dial and Fitzpatrick, 1981; Salvador et al., 1996; Martin and Avery, 1998). Tail regeneration in females of some gecko species can also inhibit reproduction (Henle, 1990). Therefore, in addition to the likely increased mortality risk arising from exclusion from refugia, the injuries sustained by night geckos through direct aggressive interactions with *H. frenatus* are likely to have a further direct impact upon the survival of individuals, especially the smaller *N. coindemirensis*.

The synergistic effects of exclusion from refugia and mammalian predation are evident from the known pattern of extirpation and extinction of *Nactus* species in the Mascarenes. For example, the presence of brown rats *Rattus norvegicus* on Gunners Quoin (Fig. 1) from the mid 19th Century until their eradication in 1995 (Bell, 2002) undoubtedly led to the localized extinction of several larger endemic reptiles (Cheke, 1987), but did not lead to the extirpation of the population of

*N. coindemirensis* (Bullock et al., 1985); following the removal of rats, this population has since increased in abundance and distribution (NCC, unpublished data). The presence of predatory mammals alone did not, therefore, lead to the extirpation of this population. Yet, islands colonized by both *H. frenatus* and predatory mammals, including cats *Felis catus*, ship rats *R. rattus* and musk shrews *Suncus murinus* (Bell, 2002; Varnham et al., 2002) no longer support night gecko populations (Fig. 1). These data are, therefore, consistent with the hypothesis that competition with *H. frenatus* in conjunction with predation by introduced mammals has been responsible for the loss of endemic night geckos from islands in this archipelago. It is also likely that, in the presence of *H. frenatus*, some avian and reptilian predators may have been just as important, if not more important in determining the current distribution of the night geckos due to exclusion from refugia.

Further support for the hypothesis of the parallel roles of predation by and competition with introduced species in driving *Nactus* population changes is apparent with the discovery of the new night gecko population on Flat Island. In this instance, this population appears to have survived in the presence of both a substantial *H. frenatus* population and a history of colonization by cats and ship rats (Cheke, 1987; Bell, 2002) because of the spatial segregation between native and non-native gecko populations afforded by their morphological differences. *H. frenatus* is able to colonize locations outside its natural range successfully because of its small size and aggressive, anthropophilic and generalist nature. In part, however, its ability to saturate an environment is due to its highly specialized scansorial toes, which are adapted for gripping smooth surfaces through dry adhesion provided by van der Waals forces (Zani, 2000). The mean force ( $\pm$ SD) required to pull *H. frenatus* from clean flat surfaces in laboratory conditions is 1.00 ( $\pm$ 0.31) N (Irschick et al., 1996). In this study, a similar force was required to dislodge individuals from smooth *Casuarina* tree trunks ( $1.21 \pm 0.24$  N), but this decreased as the amount of loose material on substrate surfaces increased (Fig. 3a).

The decreased ability of *H. frenatus* to grip a crumbly surface on Flat Island is not a failure of the van der Waals forces, but a failure of the substrate surface. As the setae bond to a surface covered with a high concentration of loose particles, they become saturated, leaving only small areas for secure attachment, and this is made worse by particles with a large surface area adhering to larger numbers of setae. For these reasons, powdery tuff rock is a most undesirable surface for *H. frenatus* to climb and is a likely explanation for the observed distribution of this gecko on Flat Island. Powdery tuff rock is therefore acting as an ecological barrier preventing the colonisation of this microhabitat by *H. frenatus*, thus creating a competitor-free space for the night geckos,

which are able to penetrate the loose material and grip fine rugosities in the underlying stable rock with their slender clawed toes. Given that the night geckos have substantial populations on their few remaining islands, their restricted distribution on Flat Island is most likely a response to asymmetrical aggressive interactions with *H. frenatus*. These interactions would have enhanced predation by the now eradicated cats and ship rats.

This is the first instance where *H. frenatus* has been directly implicated in the extinction of endemic gecko populations. This study also alludes to a likely mechanism underlying the decline of the Mascarene night geckos: without the interactions of an introduced competitor, predation alone cannot always explain extinction events of island reptiles. Therefore, in the light of current reptilian declines, further attention must be paid to the impact of competitors in combination with predators in altering community composition.

#### 4.1. Conservation implications

Preventing invasions of small anthropophilic reptilian species such as geckos is often very difficult to manage, and once established there are no known methods of eradication. However, the results of this study indicate that the specialized ability by which pad-bearing species can saturate environments can also be exploited to exclude them: replicating habitats with artificial or naturally occurring substrates with a crumbly/highly concentrated particulate surface would be beneficial for claw-bearing species, such as *Nactus* spp., whilst excluding pad-bearing reptiles, such as *H. frenatus*, which are disrupting native reptile communities. Simple habitat modifications through the addition of artificial refugia have been proposed as a means to enhance populations of endangered reptiles (Milne and Bull, 2000; Souter et al., 2004). For example, the use of artificial rocks have previously been shown to enhance the number of some saxicolous lizards in Australia (Webb and Shine, 2000). It is therefore feasible to create habitats within the natural range of the night geckos for potential reintroductions.

#### Acknowledgements

The Mauritian Wildlife Foundation, National Parks and Conservation Service – Mauritius, A. Aumjaud, D. Bullock, L. Cole, L.J. Harmon, S. North and T. Ross helped with fieldwork. We are grateful for the comments of P.J. Baker and two anonymous referees in improving this manuscript and the support of E.N. Arnold throughout this project. This project was approved by Bristol University ethical review committee and funded by NERC Grant NER/S/A/2001/05996 and by the National Parks and Conservation Service – Mauritius.

## References

- Arnold, E.N., 2000. Using fossils and phylogenies to understand evolution of reptile communities on islands. In: Rheinwold, G. (Ed.), *Isolated Vertebrate Communities in the Tropics*. Bonner Zoologische Monographien, pp. 309–323.
- Arnold, E.N., Jones, C.G., 1994. The night geckos of the genus *Nactus* in the Mascarene Islands with a description of the distinctive population on Round Island. *Dodo Journal of the Jersey Wildlife Preservation Trusts* 30, 119–131.
- Autumn, K., Sitti, M., Liang, Y.C.A., Peattie, A.M., Hansen, W.R., Sponberg, S., Kenny, T.W., Fearing, R., Israelachvili, J.N., Full, R.J., 2002. Evidence for van der Waals adhesion in gecko setae. *Proceedings of the National Academy of Sciences of the United States of America* 99, 12252–12256.
- Ballinger, R.E., Tinkle, D.W., 1979. On the cost of tail regeneration to body growth in lizards. *Journal of Herpetology* 13, 374–375.
- Bell, B.D., 2002. The eradication of alien mammals from five offshore islands, Mauritius, Indian Ocean. In: Veitch, C.R., Clout, M.N. (Eds.), *Turning the Tide: The Eradication of Invasive Species*. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union, Gland, Switzerland, pp. 40–45.
- Brown, S.G., Lebrun, R., Yamasaki, J., Ishii-Thoene, D., 2002. Indirect competition between a resident unisexual and an invading bisexual gecko. *Behaviour* 139, 1161–1173.
- Bullock, D.J., Arnold, E.N., Bloxam, Q., 1985. A new endemic gecko (Reptilia, Gekkonidae) from Mauritius. *Journal of Zoology* 206, 591–599.
- Case, T.J., Bolger, D.T., 1991. The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology* 5, 272–290.
- Case, T.J., Bolger, D.T., Petren, K., 1994. Invasions and competitive displacement among house geckos in the tropical Pacific. *Ecology* 75, 464–477.
- Case, T.J., Bolger, D.T., Richman, A.D., 1992. Reptilian extinctions: the last ten thousand years. In: Fiedler, P.L., Jain, S.K. (Eds.), *Conservation Biology: The Theory and Practice of Conservation, Preservation, and Management*. Chapman & Hall, New York, pp. 91–125.
- Cheke, A.S., 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. In: Diamond, A.W. (Ed.), *Studies of Mascarene Island Birds*. Cambridge University Press, Cambridge, pp. 5–89.
- Crawley, M.J., 1986. The population biology of invaders. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences* 314, 711–731.
- Dial, B.E., Fitzpatrick, L.C., 1981. The energetic costs of tail autotomy to reproduction in the lizard *Coleonyx brevis* (Sauria, Gekkonidae). *Oecologia* 51, 310–317.
- Downes, S., Bauwens, D., 2004. Associations between first encounters and ensuing social relations within dyads of two species of lacertid lizards. *Behavioral Ecology* 15, 938–945.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50, 653–666.
- Henle, K., 1990. Population ecology and life history of three terrestrial geckos in arid Australia. *Copeia* 1990, 759–781.
- Holt, R.D., Lawton, J.H., 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25, 495–520.
- Irschick, D.J., Austin, C.C., Petren, K., Fisher, R.N., Losos, J.B., Ellers, O., 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biological Journal of the Linnean Society* 59, 21–35.
- Losos, J.B., 2000. Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences of the United States of America* 97, 5693–5695.
- Losos, J.B., Marks, J.C., Schoener, T.W., 1993. Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions. *Oecologia* 95, 525–532.
- Losos, J.B., Spiller, D.A., 1999. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* 80, 252–258.
- Mahendra, B.C., 1941. Contributions to the bionomics, anatomy, reproduction and development of the Indian house-gecko, *Hemidactylus flaviviridis* Rüppel. *Proceedings of the Indian Academy of Sciences B* 13, 288–306.
- Martin, J., Avery, R.A., 1998. Effects of tail loss on the movement patterns of the lizard, *Psammodromus algirus*. *Functional Ecology* 12, 794–802.
- McCoid, M.J., 1993. The new herpetofauna of Guam, Mariana Islands. *Herpetological Review* 24, 16–17.
- Melville, J., 2002. Competition and character displacement in two species of scincid lizards. *Ecology Letters* 5, 386–393.
- Milne, T., Bull, C.M., 2000. Burrow choice by individuals of different sizes in the endangered pygmy blue tongue lizard *Tiliqua adelaidensis*. *Biological Conservation* 95, 295–301.
- Minitab, 2000. Minitab Statistical Software. Release 13.32.
- Mooney, H.A., Cleland, E.E., 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 98, 5446–5451.
- Nevo, E., Gorman, G., Soule, M., Yang, S.Y., Clover, R., Jovanovi, V., 1972. Competitive exclusion between insular *Lacerta* species (Sauria: Lacertilia). *Oecologia* 10, 183–190.
- Pacala, S., Roughgarden, J., 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. *Science* 217, 444–446.
- Perry, G., Rodda, G.H., Fritts, T.H., Sharp, T.R., 1998. The lizard fauna of Guam's fringing islets: island biogeography, phylogenetic history, and conservation implications. *Global Ecology and Biogeography* 7, 353–365.
- Petren, K., Case, T.J., 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* 77, 118–132.
- Petren, K., Case, T.J., 1998. Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Academy of Sciences of the United States of America* 95, 11739–11744.
- Pianka, E.R., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74.
- Radovanovic, M., 1965. Experimentelle beiträge zum problem der kompetition. *Zoologischer Anzeiger* 29, 534–539.
- Rodda, G.H., Campbell, E.W.I., Fritts, T.H., 2001. A high validity census technique for herpetological assemblages. *Herpetological Review* 32, 24–30.
- Rodda, G.H., Fritts, T.H., 1992. The impact of the introduction of the colubrid snake *Boiga irregularis* on Guam's lizards. *Journal of Herpetology* 26, 166–174.
- Saddul, P., 2002. *Mauritius: A Geomorphological Analysis*, revised ed. Mahatma Gandhi Institute, Mauritius.
- Salvador, A., Martin, J., Lopez, P., Veiga, J.P., 1996. Long-term effect of tail loss on home-range size and access to females in male lizards (*Psammodromus algirus*). *Copeia* 1996, 208–209.
- Schoener, T.W., Spiller, D.A., Losos, J.B., 2001. Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412, 183–186.
- Siegel, S., Castellan, N.J., 1988. *Nonparametric Statistics for the Behavioral Sciences*, second ed. McGraw-Hill Education, Singapore.
- Souter, N.J., Bull, C.M., Hutchinson, M.N., 2004. Adding burrows to enhance a population of the endangered pygmy blue tongue lizard, *Tiliqua adelaidensis*. *Biological Conservation* 116, 403–408.
- Tokeshi, M., 1999. *Species Coexistence, Ecological and Evolutionary Perspectives*. Blackwell Science, Oxford.

- Towns, D.R., Daugherty, C.H., Cree, A., 2001. Raising the prospects for a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles. *Biological Conservation* 99, 3–16.
- Varnham, K.J., Roy, S.S., Seymour, A., Mauremootoo, J.R., Jones, C.G., Harris, S., 2002. Eradicating Indian musk shrews (*Suncus murinus*, Soricidae) from Mauritian offshore islands. In: Veitch, C.R., Clout, M.N. (Eds.), *Turning the Tide: The Eradication of Invasive Species*. Invasive Species Specialist Group, Species Survival Commission, World Conservation Union, Gland, Switzerland, pp. 342–349.
- World Conservation Monitoring Centre, 1992. *Global Biodiversity: Status of the Earth's living resources*. Chapman & Hall, London.
- Webb, J.K., Shine, R., 2000. Paving the way for habitat restoration: can artificial rocks restore degraded habitats of endangered reptiles? *Biological Conservation* 92, 93–99.
- Zani, P.A., 2000. The comparative evolution of lizard claw and toe morphology and clinging performance. *Journal of Evolutionary Biology* 13, 316–325.