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The effect of anthropogenic habitat usage on the social behaviour of a vulnerable species, *Cyclura nubila*

Kathryn E. Lacy[1] and Emília P. Martins[2]

[1]Department of Biology, University of Oregon, Eugene, Oregon, 97405, USA; kitlacy@qwest.net
[2]Department of Biology, Jordan Hall, Indiana University, Bloomington, Indiana, 47405, USA.

Abstract

With the increasing human population world-wide, animals and humans are sharing more habitat. In this study, we consider the consequences of this habitat usage overlap on the behaviour patterns and social structure of a threatened species. Specifically, we used focal animal samples to collect data on the Cuban rock iguana, *Cyclura nubila*, in six field sites. Three of these sites are subject to considerable anthropogenic habitat usage, whereas three are in relatively low anthropogenic usage areas. Individuals in high anthropogenic usage sites were more closely assembled, with more males and females sharing a smaller amount of space. These animals exhibited even more aggressive behaviour and social interactions than expected when taking into account the larger number of possible interactants. High anthropogenic usage sites also had more male–male interactions and fewer males interacting with females. We suggest that social and mating system changes have occurred. Ramifications of these recent changes in the behavioural repertoires on the long-term survival of the species are discussed.

INTRODUCTION

With an ever increasing human population, more people are sharing habitat with wild animal populations. Yet, anthropogenic disturbance is a primary cause of decline in wild animal populations world-wide (e.g. Mace, 2000). Usage overlaps between non-human and human habitat have the potential to influence not only the density but also the behaviour, demographics and long-term survival of many animal species (e.g. Travis, Slobodchikoff & Keim, 1995; Sutherland, 1996; Beissinger, 1997; Nunney, 1999). In most cases, human habitat usage will affect animal populations through shifts in animal behaviour. Whether those sorts of changes will have an impact on population demographics and long-term survival depends on the exact types of behavioural shifts that are produced. In the current study, we compare the social behaviour of Cuban rock iguanas, *Cyclura nubila*, in areas that have relatively high human habitat usage with animals that are located in areas that are relatively underexploited by humans. Instead of trying to identify exactly which aspects of anthropogenic disturbance (habitat changes, supplemental feeding, actual visitation) caused changes in animal behaviour, our aim is to describe resulting differences in behavioural repertoire and types of social interactions in detail and to determine whether those differences are of

the sort that could lead to major changes in population demography.

How differences in human habitat usage translate into changes in social system, mating system or other components of demography is an important aspect of conservation biology that has only rarely been examined in studies of animals living in environments that overlap with humans. Shifts in density, sex ratio and mating system can lead to changes in how many and which individuals are actually mating in a small population, thus resulting in major changes in the genetic health of animal populations and their long-term survival (Lande & Barrowclough, 1987). In this study, we explore these behavioural details in *Cyclura* iguanas, a group in which cohabitation with humans is an important factor to consider for conservation management purposes.

All eight species of Caribbean rock iguanas (genus *Cyclura*) are threatened or endangered according to IUCN Red List criteria (Alberts, 2000*a*; Hilton-Taylor, 2000). Iguana conservation efforts in many cases have been concentrated on translocation of animals from sub-standard habitat to more suitable locations; head-starting programmes where animals are removed from the wild as juveniles, allowed to reach maturity in captivity and then re-established in the wild (Alberts, 2000*a*); and finally ecotourism used for educational purposes in order to focus human disturbance to only a few areas (Alberts, 2000*b*). Because so much of these species' habitat is shared with humans the possibility for habitat usage overlap influencing the behaviour of these species is great.

All correspondence to: Dr. Emília P. Martins. Tel: 812–856–5840;
Fax: 812–855–6705; E-mail: emartins@indiana.edu.

Cyclura is an excellent group for this type of study because of the complex social behaviour found within many species in the genus. Whereas many iguanian lizards have primarily been categorized as territorial (Carpenter, 1967; Stamps, 1977; Martins, 1994), species of iguanas show a diversity of social structures (reviewed Dugan & Wiewandt, 1982). Also, comparative studies have shown that the *Cyclura* genus is capable of very rapid behavioural change (e.g. Martins & Lamont, 1998). Because of this behavioural plasticity, even a brief stay in close contact with humans may lead to changes in social behaviour, mating system and communicative displays, possibly making it difficult to reintroduce animals into less disturbed areas.

In the current study, we compare the social behaviour of Cuban rock iguanas in three sites that are relatively unused by humans and three sites where animals have high levels of human visitation and usage. Our high human usage sites were extremely disturbed, including picnic tables, paved parking lots, and daily visits from base residents and recreational users, whereas our low-usage sites were covered with native vegetation and experienced essentially no human visitation. Human base residents and visitors feed the iguanas at high-disturbance areas, and it was immediately obvious that high-disturbance sites had far higher densities of animals than did low-disturbance areas. Nevertheless, we began by comparing high and low anthropogenic usage sites in terms of number of nearest neighbours as a measure of local density. We then considered differences among sites in both the types and frequencies of behaviour produced and overall social organization.

METHODS AND MATERIALS

Study animal and site

The Cuban rock iguana, *Cyclura nubila nubila*, is a sexually dimorphic, large-bodied (maximum adult male snout–vent length (SVL): 74.5 cm; maximum adult female SVL: 62.3 cm), long-lived and primarily herbivorous lizard (Schwartz & Henderson, 1991; Schettino, 1999). This ground-dwelling species is found primarily on offshore islets and cays, and also in a few protected areas on the Cuban mainland. In other species of *Cyclura*, exotic predators such as feral cats, dogs and the Indian mongoose prey on juvenile iguanas (e.g. Iverson, 1978), and introduced mammals (e.g. goats and donkeys) compete with the iguanas for food (e.g. Mitchell, 1999). *Cyclura* iguanas were often the largest extant land animals on the islands that they inhabited and may be important seed dispersers for native vegetation (Iverson, 1985). *Cyclura* habitat is also being destroyed and fragmented through resort development and the increase in human population in the Caribbean (e.g. Estrada & Ruibal, 1999). In some areas, food resources have been temporally and spatially altered by the presence of non-native plants and other anthropogenic factors.

This study took place for 5 weeks from the end of April through May 2000 during the beginning of the *C. nubila* breeding season on the US naval base at Guantánamo Bay. The base is located on the southeastern coast of Cuba. Native vegetation primarily consists of coastal scrub forest that receives sporadic precipitation (350–500 mm annually) owing to the rain shadow of the surrounding mountain ranges (Borhidi, 1991). Tropical dry forests of the Caribbean, such as those that occur at Guantánamo Bay, are some of the most endangered ecosystems in the world, containing several endemics (Murphy & Lugo, 1986). The iguanas can be found throughout much of the approximately 117 km^2 of the base but are more numerous along the rocky coastal cliffs where shelter and basking locations are plentiful.

Guantánamo Bay offered an excellent opportunity to compare the influence of different levels of human habitat usage because of the regulated nature of the military base environment. Initially, we classified three sites that had high levels of human visitation with unlimited public access, where recreation facilities were present and where animals had been historically fed by visitors. These sites are referred to as high anthropogenic usage sites in the rest of this paper. All three areas contained some type of recreation structure, such as scuba dive ladders or picnic sites that were used by base residents in high numbers (visitors were seen on almost all research days). Considerable amounts of habitat in all of these sites had been altered for human use by the construction of roads and buildings, and much of the native vegetation had been removed. These sites were approximately 0.5 ha in area and contained approximately 15 male and ten female individuals per site (approximately 50 individuals/ha).

Second, three sites were identified that had little to no anthropogenic usage. These were classified as having low anthropogenic usage based on resident entry restrictions for most of them (two of the three sites were completely off-limits to base residents and special permission was needed to be able to observe lizards in those areas), the lack of any recreation structures and the extremely low occurrence of human visitors (only one visitor at one site seen during the entire study). All three of these sites retained most if not all of their natural vegetation, such as succulent groundcover, because no roads or buildings were found at any of them. These sites were also larger than high anthropogenic usage sites in area (approximately 1.0 ha) to ensure that they had roughly the same number of males and females (iguana density is approximately 25 individuals/ha at these sites).

The two types of area differed substantially in their three-dimensional environment structure as well as in their active human presence. Sites with high levels of anthropogenic usage were beach recreation sites with picnic tables and concrete shelters, and large patches of introduced grasses. Areas of low anthropogenic usage were primarily covered with coastal scrub plants, most of which are quite short (less than 1 m tall). Although no migrations were observed during the current study, each site was only 1 to 2 km away from the nearest neighbouring site and there has probably been considerable migration between sites by

individuals in the past. Thus, differences observed among animals at different sites are likely to be due to the recent impact of local environments rather than to genetic differences among populations. All six sites were marked with small flags every 10 meters in order to record animal location on the site.

Data collection

We made observations only during peak hours of iguana activity 0900–1230, 1330–1700 hours EST when animals are visible. We chose focal animals at random from a list and then observed each focal animal through binoculars from at least 10 m to avoid disrupting the animal's behaviour. Because females and juveniles are not easily distinguished from each other, data for these were combined into a single category for all statistical analyses. At the onset of each observation period, we recorded the number of neighbours within 5 and 10 m and the approximate distance to the nearest neighbouring individual (estimated visually using landmarks). We then recorded all behaviour (Table 1) continuously for up to 30 min on Tandy 100 portable computers using data collection software developed for this purpose. During social interactions, we recorded the body postures, communicative displays and behaviour of the interactant as well as the focal animal (Table 1). After each observation period, we splashed non-toxic paint from a water gun on the focal individual and recorded any morphological characteristics (e.g. scars, spine patterns) that could be used for subsequent identification of that individual. This was not necessary for one site, in which most animals had been individually marked with plastic beads. Both observers collected data at each site, and we used weekly reliability tests in which both observers recorded data for the same animals to ensure that data were identical for the two observers.

Statistical analyses

All data were transferred from the portable computer to personal computers using a Microsoft Excel macro designed to calculate frequency, duration and sequence of behaviour. Any observation period that lasted less than 10 min, usually because of the focal animal disappearing, was eliminated from the analyses to avoid biases due to our own presence disturbing the animal. We used least squared regression analyses to determine how much of the variation in number of neighbours and frequency of each behaviour at the sites was explained by the differences in anthropogenic usage (scored as high or low usage). In separate analyses, we also corrected behaviour frequency for differences in overall activity level among sites by regressing the frequency of each behaviour pattern (y) on the frequency of locomotion (x, a general indicator of activity level). We then regressed the residuals from this regression on anthropogenic usage. In each case, we began by fitting a full model, including individual identity, site identity (number 1–6), sex of the focal individual and interaction terms as predictor variables, and then used backwards elimination to remove these factors when they did not contribute significantly to the model. In analyzing social behaviour, we also included the number of neighbours as a possible explanatory variable. Residual plots showed that transformation of the data was not necessary; therefore, all analyses were conducted on the raw data. All analyses were run in SAS (Version 8.01, SAS Institute), using Type III sums of squares.

Finally, we tallied the number and types of social interactions individuals performed. The differences seen in social behaviour between low and high anthropogenic usage sites in terms of the number and type of social interactions were tested using χ^2 goodness of fit tests. This information was then used to create diagrammatic behavioural maps illustrating how many individuals were interacting, which animals had the greatest number of interactions and what types of interactions were performed most often.

Table 1. Behaviour categories for *C. nubila* recorded during focal animal samples

Behaviour	Description
Aggression	
Chase	Pursuit of another individual, usually until the other animal retreats
Bite	Open mouth contact with another individual
Lateral presentation	Compression of body trunk
Tail whip	Lashing of the tail, usually directed at another individual
Communication	
Head bob display	Relatively slow, stereotyped series of up-and-down motions of the head, including some horizontal motion (see Martins & Lamont, 1998 for description), often produced with no other animals in the immediate vicinity
Shudder bob	Rapid up-and-down movement of the head, usually produced by males while walking towards a female
Other social	
Approach	Locomotion towards another individual
Withdraw	Locomotion away from another animal, following an approach
Courtship	Male mounts a female
Other	
Number of neighbours	Number of iguanas within 5 m
Forage	Explore for and consume food
Tongue touch	Tongue extended to substrate or air
Head raise	Slow, single upward movement of the head
Locomotion	Running, walking or other movement between locations
Snort	Extrusion of salts from nostrils

RESULTS

We conducted a total of 254 focal observations ($N = 125$ high anthropogenic usage; $N = 129$ low anthropogenic usage) for all six sites, for a total of 107 hours of observations. Each of approximately 20 individuals was observed at each site in two separate observation sessions. More adult males were observed than females/juveniles, simply because there were more adult males in all six sites.

Animals in high anthropogenic usage areas usually had one neighbour within 5 m, whereas animals in low anthropogenic usage areas had no neighbours within 5 m (Table 2). Thus the number of near neighbours corresponds well with the density of animals at each site (50 animals/ha at high anthropogenic usage areas versus 25 animals/ha at low anthropogenic usage areas). This difference in number of neighbours was significantly greater than zero ($F_{1,248} = 33.10$, $P < 0.0001$) in a multiple regression including site identity ($F_{4,248} = 5.01$, $P < 0.001$). Factors for individual identity and sex (adult male versus female/juvenile) of the individual did not explain a significant amount of the variation and therefore were removed from the model.

Individuals in high anthropogenic usage sites moved more, produced more tongue touch behaviour and produced fewer head raises than in low anthropogenic usage sites (Table 2). Adult males had a higher rate of locomotion than did female/juveniles ($F_{2,248} = 3.20$, $P < 0.05$) but site identity and individual identity did not explain a significant portion of the variation. This difference in locomotion was significant ($F_{1,246} = 13.2$, $P < 0.001$) in a multiple regression including sex (adult male versus female/juvenile) as a factor in the model. Even after taking this difference in activity into account, the difference in tongue touch behaviour between sites was also significant in a multiple regression ($F_{1,252} = 8.32$, $P < 0.05$). Site identity, sex and individual identity were

removed from the model because they did not explain a significant amount of the variation. Iguanas in low anthropogenic usage sites used head raise behaviour more often than those in high anthropogenic usage sites (Table 2). This difference was significant ($F_{1,252} = 6.04$, $P < 0.01$) in a multiple regression taking differences in locomotion into account but removing individual identity, sex of the individual and site from the model. The frequency of head bob displays was not significantly different between low anthropogenic usage and high anthropogenic usage sites once locomotion had been taken into account. However, adult males displayed (mean = 15.91 displays/hr, SE = 0.086) more often than female/juveniles (mean = 4.65 displays/hr, SE = 0.052) and this difference was significant regardless of the human usage of the site ($F_{1,251} = 7.30$, $P < 0.05$).

Despite having obtained 55 hours of observations at the low anthropogenic usage sites, we observed a total of only 20 social encounters. In the 52 hours of observation at the high anthropogenic usage sites we observed 79 social
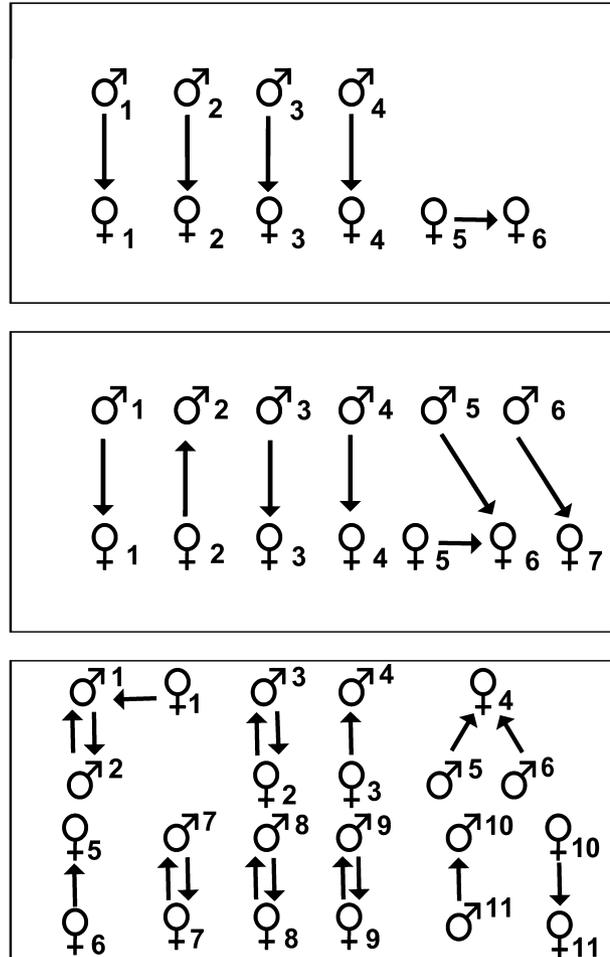
Table 2. Differences between behaviour patterns used at high and low anthropogenic usage sites. Number of neighbours is the total number of individuals within 5 m of the focal individual. All other behaviour patterns are measured as the mean frequency produced by the focal animal per hour. Means (SE) for each behaviour pattern and the corresponding F value from the least squared regression are given.

	Anthropogenic usage		
	High	Low	F value
Headbob display[+]	11.4 (0.30)	8.6 (0.20)	0.6[b]
Number of neighbours	1.1 (0.01)	0.0 (0.01)	33.1 ***[a]
Tongue touch[+]	4.4 (0.20)	1.4 (0.20)	8.3*[a]
Head raise[+]	0.5 (0.10)	3.3 (0.20)	6.0 **
Locomotion	21.3 (0.30)	11.5 (0.20)	13.2*[b]
Combined behaviour patterns:			
Aggression[†]	0.7 (0.04)	0.1 (0.09)	7.0 **[b]
Communication[†]	8.4 (1.50)	1.4 (0.50)	16.6 ***
All social[†]	8.4 (0.10)	1.4 (0.30)	20.2***

[+] indicates that locomotion frequency (index of activity level) was included in the model.
[†] indicates that number of neighbours was included in the model.
[a] indicates that individual site contributed significantly to the least squared regression model.
[b] indicates that the sex of the individual contributed significantly to the least squared regression model.
* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fig. 1. Diagrammatic behavioural maps of each low anthropogenic usage site. Only individuals that participated in social interactions are shown; other individuals have been omitted for clarity. Arrows indicate interactions between individuals and the direction of the arrows represents the performer and the recipient. One arrow may represent more than one interaction between two individuals.
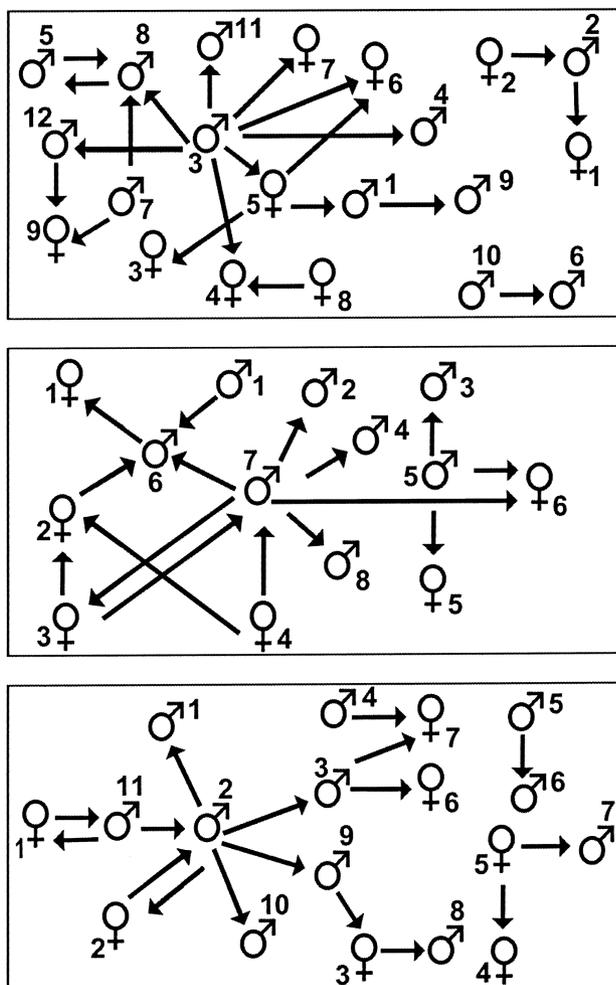
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Table 3. The percentage of focal individuals that interacted with 1–3 individuals or 4+ individuals and the percentage of males that interact with 0, 1 or 2 female/juveniles during the course of the study.

	Anthropogenic usage		
	High	Low	χ^2 tests
Number of interactants			
1–3	93%	100%	$\chi^2_1 = 5.35$ *
4+	7%	0%	
Number of female/juvenile interactants per male			
0	42%	10%	$\chi^2_3 = 18.2$ ***
1	27%	90%	
> 2	31%	0%	

* $P < 0.05$, *** $P < 0.001$.

other individuals (Table 3). In contrast, about 7% of the animals (all adult males) in high anthropogenic usage sites frequently interacted with four or more individuals ($\chi^2 = 5.35$, d.f. = 1, $P < 0.02$) (Table 3). Male–male interactions were rare in the low anthropogenic usage sites and male–female/juvenile interactions were more common than at high anthropogenic usage sites ($\chi^2 = 12.71$, d.f. = 1 $P < 0.001$) (Table 4). Approximately 90% of the adult males in low anthropogenic usage sites interacted with exactly one female/juvenile individual. In contrast, roughly equal number of adult males in the high anthropogenic usage sites interacted with no female/juveniles, one female/juvenile or more than two female/juveniles ($\chi^2 = 18.2$, d.f. = 3, $P < 0.001$) (Table 3).

Table 4. Percentages of interactions involving different sex combinations in the high and low anthropogenic usage sites. Fem./juv. refers to animals in the female/juvenile category.

	Anthropogenic usage		
	High	Low	χ^2 tests
Male–male	27%	5%	$\chi^2_2 = 20.7$ ***
Fem./juv.–fem./juv.	21%	20%	
Male–fem./juv.	52%	75%	

*** $P < 0.001$.

DISCUSSION

Our results suggest that significant anthropogenic presence can result in differences not only in the overall density of animals at a site (i.e. the number of nearest neighbours), but also in the behavioural repertoire and social organization of a species in ways that could have considerable impact on the population genetics, demographics and long-term survival of endangered species. Although we cannot distinguish between the direct effects of anthropogenic disturbance (e.g. feeding) and longer-term effects such as the higher animal densities (probably also the result of anthropogenic disturbance), we found several patterns of interest. *Cyclura nubila* in our high anthropogenic usage sites were found in groups approximately three times bigger than the low anthropogenic usage sites, had more frequent social interactions and higher levels of aggression. More specifically, virtually all males in areas of low human impact interacted regularly with only a single female/

encounters. At the high anthropogenic usage sites the number of behavioural interactions per individual and the level of aggression were greater than for the low anthropogenic usage sites (Table 2). These differences were significant in a multiple regression even after including the number of neighbours as a predictor (interactions, $F_{1,252} = 20.28$, $P < 0.0001$; aggression, $F_{1,250} = 7.03$, $P < 0.01$) (Table 2). Adult males were also more likely to interact in an aggressive manner ($F_{1,250} = 6.53$, $P < 0.05$). Social interactions were also more likely to include visual displays (e.g. head bob displays) at the high anthropogenic usage sites than at the low anthropogenic usage sites (Table 2). This difference was significant in a multiple regression ($F_{1,252} = 16.57$, $P < 0.0001$) after individual identity, sex of the individual and site identity were removed from the model.

Lumping together data from all observation periods in our study (Figs 1 & 2), we found that no animal in the low anthropogenic usage sites interacted with more than three

juvenile. In high anthropogenic usage sites, there were several males who interacted with no females at all and a few who regularly interacted with more than four female/juveniles.

Individuals in high anthropogenic usage sites engaged in more frequent aggressive interactions than those in low anthropogenic usage sites. Although some increase in aggression can be explained by the increase in the number of animals, the observed difference was substantially greater than that expected based solely on the concurrent increase in the number of neighbouring individuals (i.e. possible interactants) at high anthropogenic usage sites. This extends the results of primate crowding studies in which aggression also increased more than expected given the number of animals (e.g. Wrangham, 1974; Hill, 1999). As with crowded captive green iguanas (Alberts, 1994), a few 'despotic' males seem to have emerged at high anthropogenic usage sites. Apparently instead of reducing aggression among male *C. nubila*, however, frequent aggressive encounters among males persist despite the change in social structure.

Excessive aggression among adult males can lead to greater stress and inhibit the behaviour of smaller animals. This conclusion is reinforced by the observation of significantly more tongue touching in high anthropogenic usage sites. Tongue touching in lizards is thought to be related to stress commonly associated with exploratory behaviour (e.g., Greenberg 1985, 1993; Burghardt, Allen & Frank, 1986) and can keep small males from maintaining territories (e.g. as in collared lizards, *Crotaphytus collaris*, Baird & Timanus, 1998). Stress and inhibition can also increase the levels of stress hormones in the much smaller females, making it difficult for females to court, mate and lay their eggs successfully (Pottinger, 1999). Although both effects tend to reduce the overall number of iguanas in the population, they may persist even in very dense populations if anthropogenic usage also helps to recruit animals from neighbouring areas. Studies of the rate of turnover in particularly dense populations are clearly needed to explore this issue more directly.

The social organization in the high anthropogenic usage sites is also notably different from that in low anthropogenic usage sites, in that a greater number of males are interacting with no females. In low anthropogenic usage sites, each male regularly interacts with one female. In high anthropogenic usage sites more than 40% of males did not interact with any females. Access to females is required for mating, so this result suggests that many more males in the high anthropogenic usage sites are not mating. Dominant males in high anthropogenic usage sites may have more access to females and consequently sire more offspring, increasing the reproductive variance of males in these sites. If fewer males are responsible for offspring paternity, population viability may be reduced through inbreeding or the accumulation of deleterious alleles through genetic drift in a small population (Lande & Barrowclough, 1987). This result points to the importance of linking behaviour and the demographic consequences of that behaviour for the conservation of endangered animals. A behavioural shift of the sort observed in this study could have profound effects on the genetic health and long-term survival of iguana populations.

Cyclura iguanas are behaviourally complex, and among species and populations there are considerable differences in *Cyclura* displays (Martins & Lamont, 1998; Bissell & Martins, in press). Other species have also evolved unique functions for the head bob display (Martins & Lacy, in press). With such rapid change in behaviour, considerations for future conservation efforts for any *Cyclura* species must consider possible behavioural isolation of populations exposed to different levels of human habitat usage. Of course, if human influence is removed from an area, the once influenced populations may revert somewhat quickly to normal behavioural patterns. This study also demonstrates that detailed examination of a species in a portion of their habitat that has already been compromised or destroyed may not yield the most accurate results for demographic model predictions, especially if their social organization has changed. Therefore, careful consideration must be made when choosing populations on which to base demographic data for viability analysis. It is also important to consider behavioural ecology in the design and implementation of recovery, reintroduction and relocation programmes. The potential for behavioural changes needs to be considered for head starting and reintroduction plans because of the chances of aberrant behaviour developing (Dodd & Seigel, 1991).

REFERENCES

Alberts, A. C. (1994). Dominance hierarchies in male lizards: implications for zoo management programs. *Zoo Biol.* **13**: 479–490.

Alberts, A. C. (2000*a*). Overview of West Indian iguana populations. In *Status survey and conservation action plan: West Indian iguanas*: 10–14. Alberts, A. C. (Ed.). Gland, Switzerland: IUCN – World Conservation Union.

Alberts, A. C. (2000*b*). Education and ecotourism. In *status survey and conservation action plan: West Indian iguanas*: 95–96. Alberts, A. C. (Ed.). Gland, Switzerland: IUCN – World Conservation Union.

Baird, T. A. & Timanus, D. K. (1998). Social inhibition of territorial behaviour in yearling male collared lizards, *Crotaphytus collaris*. *Anim. Behav.* **56**: 989–994.

Beissinger, S. (1997). Integrating behaviour into conservation biology: potentials and limitations. In *Behavioral approaches to conservation in the wild*: 23–47. Clemmons, J. R. & Buchholtz, R. (Ed.). Cambridge: Cambridge University Press.