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Temporary alteration of local social structure in a threatened population of Cuban iguanas (*Cyclura nubila*)

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Abstract In small, insular populations, behavioral patterns that lead to increased variance in individual reproductive success can accelerate loss of genetic variation. Over a 1-year period, we documented behavior and hormone levels in a breeding group of adult Cuban iguanas (*Cyclura nubila*) at Guantánamo Bay. Male dominance was associated with body and head size, display behavior, testosterone levels, home-range size, and proximity to females. Based on their success in agonistic encounters, we ranked males in a linear dominance hierarchy. During the subsequent breeding season, we conducted a removal experiment in which the five highest-ranking males were temporarily relocated from the study site. Although we were unable to assess reproductive success directly, previously lower-ranking males assumed control of vacated territories, won more fights, and increased their proximity to females in the absence of the dominant males. When it results in greater mating opportunities for otherwise socially suppressed individuals, temporary alteration of local social structure may help limit erosion of genetic variation in small, insular populations.

Keywords Iguana · *Cyclura* · Behavior · Reproduction · Conservation

Introduction

Small populations are more prone than larger ones to chance fluctuations in birth and death rates which, when extreme, can lead to local extinction (Wilson and Willis 1975; Shaffer 1981). In addition, small populations lose genetic variation as a consequence of genetic drift more rapidly than large populations (Wright 1931; Franklin 1980; Lacy 1987). Loss of genetic variation can result in higher levels of homozygosity, which have been associated with retarded growth, lowered fecundity, reduced competitive ability, shifted sex ratios, increased frequencies of disease, and decreased survival during periods of stress (Garten 1976; Soulé 1980; Ralls and Ballou 1983; Soulé and Simberloff 1986). Over the long term, depletion of genetic variation in small populations can lead to an inability to adapt to changing environmental conditions, and ultimately to population extinction (Lacy 1987; Lande and Barrowclough 1987; Frankham and Ralls 1998; Saccheri et al. 1998).

Effective population size (Crow and Kimura 1970) can strongly influence a population's ability to maintain genetic variability over time (Franklin 1980). Factors producing greater than random variation in lifetime reproductive success among individuals, including skewed sex ratios, variable offspring survival, and unequal mating success, all tend to lower effective population size (Lande and Barrowclough 1987; Harris and Allendorf 1989; Creel 1998; Anthony and Blumstein 2000). Numerous modelling studies indicate that mating systems characterized by dominance polygyny, in which a limited number of dominant males mate disproportionately with many females, can result in significantly smaller effective population sizes (Harris and Allendorf 1989; Nunney 1993; Mills and Smouse 1994; Parker and Waite 1997). For small, isolated populations such as those on islands, the impact of social behavior on population dynamics can be particularly strong (Komdeur and Deerenberg 1997; Vucetich et al. 1997; Peterson et al. 1998).

West Indian rock iguanas (genus *Cyclura*) are among the most critically endangered lizards in the world, primarily as a result of habitat degradation and the devastating effects of invasive species on insular communities (Case and Bolger 1991). Two of 8 extant species of rock iguanas have declined to 200 individuals, and 9 of 16 subspecies number fewer than 1,500 (Alberts 2000). Like other iguanid lizards (Dugan 1982; Rodda 1992;

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Wikelski et al. 1996), social systems of rock iguanas are generally characterized by strong competition among males for mates and high variability in male mating success (Wiewandt 1977; Iverson 1979), factors that can act to exacerbate vulnerability to extinction under certain conditions by lowering effective population size. While it is clear that demographic factors are often paramount in determining the viability of small populations such as these (Lande 1988; but see Vucetich and Waite 1999), management strategies that integrate demographic and genetic considerations are likely to have the greatest success (Lande 1999).

Among lizards, insular populations often exhibit lower genetic diversity than their mainland counterparts, with the most marked reductions occurring on the smallest islands (Gorman et al. 1975; Soulé 1980). Among rock iguanas, heterozygosity and allelic diversity estimated through microsatellite analyses are generally lower in smaller populations, an effect exacerbated by prolonged bottlenecks (Malone 2000). The Jamaican iguana (*Cyclura collei*), currently estimated at no more than 100 individuals remaining in the wild, has been rare since the introduction of the Indian mongoose to the island in 1872 (Vogel et al. 1996). In this species, heterozygosity averages only 35% (S.K. Davis, personal communication), notably lower than that reported for other vertebrates (DeWoody and Avise 2000).

Promoting conditions under which otherwise nonbreeding individuals potentially contribute to the gene pool can help equalize genetic representation within a population, increase effective size, and decrease risk of extinction in predictable environments (Ebenhard 1995; Lande and Shannon 1996). Because relatively healthy populations of Cuban iguanas (*C. nubila*) still exist in the wild, this species provides a model for developing conservation strategies that can be applied to other more endangered forms. Over the course of a breeding season, we conducted a preliminary removal experiment in which dominant male Cuban iguanas were temporarily relocated. Effects of the removal on the behavior, hormones, and home-range dynamics of subordinate males and females were assessed and compared with baseline data from the previous breeding season, during which no manipulation occurred. The potential ramifications of utilizing temporary alteration of local social structure as part of an integrated conservation strategy for countering loss of genetic diversity in small, insular populations are discussed.

Methods

Study animals

We studied a breeding group of adult Cuban iguanas from April 1993 to July 1994, at a coastal site on the U.S. Naval Base at Guantánamo Bay, Cuba (19°54′06.43”N, 75°05′51.09”W). We captured all resident adults using hand nets, permanently marked them with unique crest scale clips, and temporarily marked them with a painted number on the flank for visual identification from a distance. The density of iguanas at coastal sites on the base (7.8±1.6 inds./ha; unpublished survey data) is comparable to estimates for healthy populations elsewhere in Cuba (Perera 1985). The adult sex ratio of 1.2:1.0 at our study site was slightly, but not significantly, male-biased (χ^2=0.22, *df*=1, *P*=0.64).

Once per month during the breeding (April/June 1993) and nonbreeding (July 1993 to March 1994) seasons, we recorded the body mass and snout-vent length (SVL) of as many adult males (15.8±0.9, range 10–21 individuals) and females (7.1±0.5, range 5–10 individuals) as could be captured. In addition, we measured head width (distance across the jaw at the widest point) and maximum femoral gland size (diameter of the largest femoral pore). Although not previously examined in rock iguanas, both of these measurements are correlated with dominance status and androgen levels in other iguanid lizards, and probably represent important secondary sex characteristics (Alberts et al. 1992; Pratt et al. 1992). All research protocols were in accordance with the Zoological Society’s Institutional Animal Care and Use Committee and standard guidelines set by the National Institutes of Health.

Hormone assays

Each time an iguana was captured, we immediately collected a 1.0-ml blood sample from the caudal vein for hormonal analysis (Gorzula et al. 1976). Upon capture, all animals were placed in cloth bags to reduce stress during blood sampling. Handling time was generally no more than 3 min, such that the hormone levels measured should represent baseline values. Blood was collected into heparinized vacutainers and centrifuged at 2,000 rpm for 15 min to obtain plasma. All samples were transported to San Diego in a nitrogen vapor shipper for analysis. Steroids were extracted in ethyl acetate:hexane (3:2, v/v), snap-frozen in a dry ice-methanol mixture, and the organic phase decanted into glass culture tubes and dried under N_2. Steroids were redissolved in buffer, and radioimmunoassays carried out using testosterone, estradiol, and corticosterone antibodies obtained from ICN Biomedicals (Costa Mesa, Calif.) on 50-µl (estradiol) or 100-µl (testosterone, corticosterone) duplicate samples according to previously published methods for tritiated steroid assays (Lance and Lauren 1984). We measured testosterone in seven assays, with inter- and intra-assay coefficients of variation of 11.0% and 8.7%. We measured estradiol in four assays, with inter-and intra-assay coefficients of variation of 10.5% and 5.6%. We measured corticosterone in 16 assays, with inter- and intra-assay coefficients of variation of 10.5% and 3.6%.

Behavioral observations

Four observers collected weekly behavioral data on 23 males and 13 females in 160 focal animal observation sessions (3–4 sessions per animal), each lasting 30 min. We recorded two types of visual signals: shallow, rapid headnods typically observed among males courting females, and the species-typical headbob display utilized by adults of both sexes to advertise spatial position (Martins and Lamont 1998). We observed 935 agonistic interactions involving 18 different males and 84 agonistic interactions involving 9 different females. Male-male interactions were usually in the form of a chase, but occasionally consisted of prolonged stereotypical facial pushing matches, whereas female-female interactions consisted of chases only. If an animal succeeded in forcing an opponent to retreat at least 3 m, we considered it to have won the encounter. Although no tests of inter-observer reliability were conducted, the outcomes of all agonistic interactions were assessed on this quantitative basis.

We classified males winning more than 50% of their encounters as high ranking (*n*=7; mean % wins=81.7±7.2) and those winning less than 50% of their encounters as low ranking (*n*=11; mean % wins=24.2±5.2). The remaining males at the site never participated in agonistic interactions and were classified as nonranking (*n*=5). We determined ordinal dominance ranks of individual males using a computer program that created a win-loss matrix of paired encounters that minimized the number of times that a lower-ranking individual defeated one of higher rank (Boyd and

Silk 1983). Due to the extreme linearity of the hierarchy, cardinal dominance ranks were not determined. Because assignments of dominance status were not made until after the breeding season, observers were unaware of male rank at the time behavioral observations were made.

Home-range mapping

We recorded the position of each iguana on a map of the study site, constructed from aerial photographs in conjunction with ground measurements, twice per day throughout the study, once during the morning and once during the evening activity periods, weather permitting. We estimated home-range size using the convex polygon method (Rose 1982) with Wildtrak software (Todd 1993). We conducted an analysis of home-range size using chronologically increasing numbers of sightings for each of the adults on the study site. Home-range size initially increased with number of sightings, but ultimately revealed an asymptote at approximately 85% of the final estimated home-range size when 35 or more sightings were obtained (Fig. 1). Based on this analysis, the number of sightings obtained per individual during both the breeding (53.5±4.0) and nonbreeding (45.0±3.0) seasons was adequate to estimate home-range size accurately. We determined spatial proximity of males to females by analyzing the mean distance between simultaneously obtained pairs of coordinates for all possible male-female pairs.

Male removal experiment

During the subsequent breeding season, we temporarily removed the five highest-ranking males from the study site for a 6-week period (29 April to 11 June 1994). These males were housed in an outdoor holding pen equipped with shelters and climbing structures, with fresh produce and water provided daily. While the dominant males were absent from the study site, we monitored behavior, hormone levels, and home-range use as in the previous breeding season. Although behavioral observations and home-range mapping were continued for 5 weeks following the return of the dominant males to the study site (12 June to 19 July 1994), limited field personnel precluded collection of additional blood samples during this period. Unfortunately, we were unable to directly assess male reproductive success through paternity studies because of the unexpected influx of 50,000 Cuban and Haitian refugees to Guantánamo Bay in the autumn of 1994, which disrupted all nesting at the study site (Florin 1996).

Statistics

We used Kruskal-Wallis nonparametric ANOVA followed by nonparametric multiple comparison tests (Dunn 1964) to compare morphology and home-range parameters among males and females, as well as to compare behavior and hormones among the three classes of males, during the breeding and nonbreeding seasons. We used one-tailed Wilcoxon paired-sample tests to test the directional hypothesis that, in the absence of the dominant males, the behavior and hormone levels of subordinate males would change to resemble those of the dominant males whose home ranges they assumed. Mann-Whitney *U*-tests were used to test for differences in behavior and hormone levels of the dominant males and the subordinate males that replaced them during the removal experiment. Finally, we used two-tailed Wilcoxon paired-sample tests to: (1) compare the behavior and hormone levels of females during the initial breeding season and subsequent removal experiment; (2) examine changes in testosterone levels in subordinate males just prior to and during the removal experiment; and (3) test for effects of the removal experiment on the behavior of dominant males following their return to the study site.

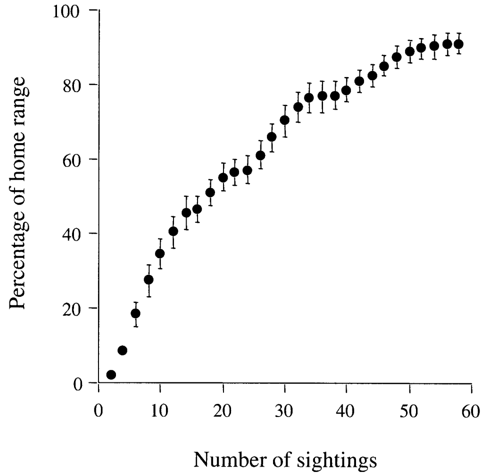

Fig. 1 The relationship between number of sightings and mean (±SE) percent of total convex polygon home-range size for 42 adult Cuban iguanas

Results

Morphology

We found differences in body mass (H=20.05, df=3, P=0.0002), SVL (H=18.99, df=3, P=0.0003), head width (H=23.33, df=3, P=0.0001), and femoral gland size (H=17.98, df=3, P=0.0004) among females and high-, low-, and nonranking males during the 1993 breeding season (Table 1). High-ranking males were larger in

Table 1 Morphological, behavioral, home-range, and hormonal data (mean±SE) for female and high-, low-, and nonranking male Cuban iguanas during the 1993 breeding season. *Asterisk* indicates a significant difference at P≤0.05

	Females *n*=10	High-ranking males *n*=7	Low-ranking males *n*=11	Nonranking males *n*=5
SVL (mm)*	355.8±13.7	482.9±6.8	440.5±11.7	407.0±30.8
Mass (kg)*	3.0±0.3	6.0±0.1	5.1±0.3	3.9±0.7
Head width (mm)*	55.3±3.4	104.8±2.4	86.3±3.6	76.6±7.5
Gland diameter (mm)*	1.0±0.1	3.2±0.4	1.7±0.2	2.1±0.4
% Wins*	42.1±11.3	81.7±7.2	24.2±5.2	–
Displays/30 min*	4.4±1.0	59.0±13.1	11.6±3.3	14.3±6.7
Courtship/30 min*	–	0.9±0.5	0.1±0.1	0.0±0.0
Home-range size (m^2)	274.2±53.5	262.5±51.0	510.3±72.5	302.8±93.0
Testosterone (ng/ml)*	–	58.3±6.7	32.0±6.4	28.9±8.2
Estradiol (pg/ml)	218.7±88.1	–	–	–
Corticosterone (ng/ml)	–	9.6±2.7	5.5±1.6	4.1±1.0

Table 2 Morphological, behavioral, home-range, and hormonal data (mean±SE) for female and high-, low-, and nonranking male Cuban iguanas during the 1993 nonbreeding season. *Asterisk* indicates a significant difference at $P \leq 0.05$

	Females *n*=13	High-ranking males *n*=7	Low-ranking males *n*=11	Nonranking males *n*=5
SVL (mm)*	375.5±10.5	493.6±6.3	469.0±11.4	386.7±48.1
Mass (kg)*	2.7±0.2	6.4±0.2	5.7±0.2	3.5±0.9
Head width (mm)*	56.1±2.1	99.8±1.9	86.2±3.7	70.4±11.1
Gland diameter (mm)*	1.0±0.1	3.4±0.2	1.7±0.2	1.6±0.3
% Wins	42.1±14.0	67.7±9.6	20.0±7.1	–
Displays/30 min*	33.3±15.2	34.4±6.9	7.5±5.0	9.0±9.0
Home-range size (m^2)	365.1±80.1	346.6±69.8	534.1±45.0	229.2±146.9
Testosterone (ng/ml)	–	10.1±1.4	6.2±1.5	4.8±2.1
Estradiol (pg/ml)	143.8±33.2	–	–	–
Corticosterone (ng/ml)	–	5.6±1.3	4.0±0.6	9.7±3.8

SVL, head width, and femoral gland size than both low- and nonranking males (all $P<0.02$), but there were no significant differences in these measurements between low- and nonranking males (all $P>0.20$). Both low- and nonranking males exceeded females in SVL, head width, and femoral pore diameter (all $P<0.05$). High-ranking males also exhibited greater body mass than low- and nonranking males ($P<0.02$ for both). However, in contrast to the other morphological measurements, body mass in nonranking males was significantly lower than in low-ranking males ($P=0.05$) and did not differ from that of females ($P>0.10$).

Behavior and hormones

High-, low-, and nonranking males also differed in display rate ($H=7.87$, $df=2$, $P=0.02$), frequency of courtship ($H=7.07$, $df=2$, $P=0.03$), and testosterone levels ($H=6.19$, $df=2$, $P=0.05$), but not corticosterone levels ($H=2.76$, $df=2$, $P=0.25$), during the breeding season (Table 1). High-ranking males exceeded low- and nonranking males in rates of headbob display ($P<0.005$ for both), but there was no difference in this behavior between low- and nonranking males ($P>0.50$). Courtship was performed significantly more often by high- than by nonranking males ($P<0.01$), but the difference in courtship rates between high- and low-ranking males did not achieve statistical significance ($P<0.10$). Courtship rates did not differ significantly between low- and nonranking males ($P>0.50$). Copulation was not observed, possibly because it may occur underground in spacious rocky crevices, which serve as overnight retreats and refuges from predators. Although corticosterone levels did not differ significantly among males, high-ranking males exhibited higher testosterone levels than both low- and nonranking males ($P<0.05$ for both). No differences in testosterone levels were observed between low- and nonranking males ($P>0.50$).

Home range

High-ranking males defended relatively small territories that each overlapped the ranges of one to four females. All territories were situated in rocky, coastal terrain containing no significant food resources, and defense was restricted to morning and evening hours when social interactions were at their peak. At midday, these territories were temporarily abandoned when iguanas of all age and size classes migrated into nearby areas of dry tropical forest to feed. Low-ranking males did not defend territories at any time, instead moving extensively throughout large, loosely defined home ranges while being constantly chased by high-ranking males. Nonranking males, which resembled females in appearance and behavior, occupied peripheral home ranges with very limited access to females, tending to avoid movement to escape aggression. Although differences in home-range size during the breeding season among females and high-, low-, and nonranking males did not achieve statistical significance ($H=7.44$, $df=3$, $P=0.06$), home ranges of low-ranking males tended to exceed those of high- and nonranking males, as well as those of females (all $P<0.02$) (Table 1).

Nonbreeding season

Differences between females and high-, low-, and nonranking males in body mass ($H=26.06$, $df=3$, $P=0.0001$) and femoral pore diameter ($H=23.64$, $df=3$, $P=0.001$) persisted during the nonbreeding season (Table 2). As during the breeding season, femoral pore diameter of high-ranking males exceeded that of low- and nonranking males ($P<0.001$ for both). During the nonbreeding season, body mass decreased in all groups except low-ranking males, such that there was no longer a significant difference in body mass between high- and low-ranking males ($P>0.20$). Both high- and low-ranking males continued to exceed nonranking males in body mass at this time of year ($P<0.001$ for both).

Although lower among all classes of males during the nonbreeding season, rates of headbob display continued to differ among high-, low-, and nonranking males ($H=6.99$, $df=2$, $P<0.03$), with high-ranking males performing significantly more displays than low-ranking males ($P<0.02$). No courtship was observed outside the breeding season. While corticosterone levels remained relatively constant, testosterone levels in males and estradiol levels in females decreased during the nonbreeding season (Fig. 2). Neither testosterone ($H=4.74$, $df=2$,

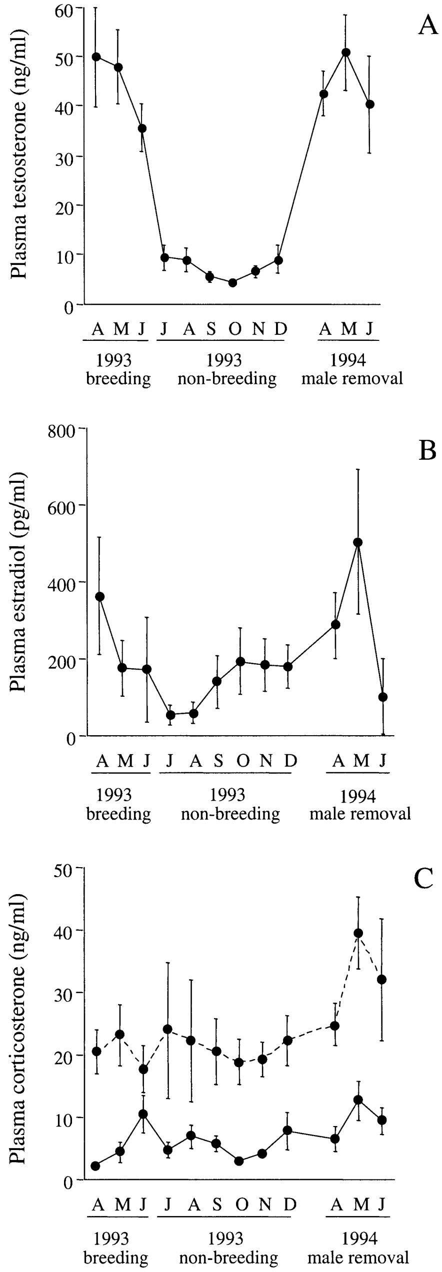

Fig. 2 Seasonal variation in mean (±SE) monthly plasma testosterone levels of 23 adult male Cuban iguanas (**A**), plasma estradiol levels of 19 adult female Cuban iguanas (**B**), and plasma corticosterone levels of 23 male (*solid line*) and 19 female (*dashed line*) adult Cuban iguanas (**C**)

P=0.09) nor corticosterone (*H*=3.53, *df*=2, *P*=0.17) levels varied among high-, low-, and nonranking males at this time of year (Table 2).

Whereas low- and nonranking males retained their breeding-season home ranges, home-range size among high-ranking males and females expanded by 32% and 33%, respectively, during the nonbreeding season, resulting in greater home-range overlap. We found no differences between females and high-, low-, and nonranking males in home-range size during the nonbreeding season (*H*=5.89, *df*=3, *P*=0.12).

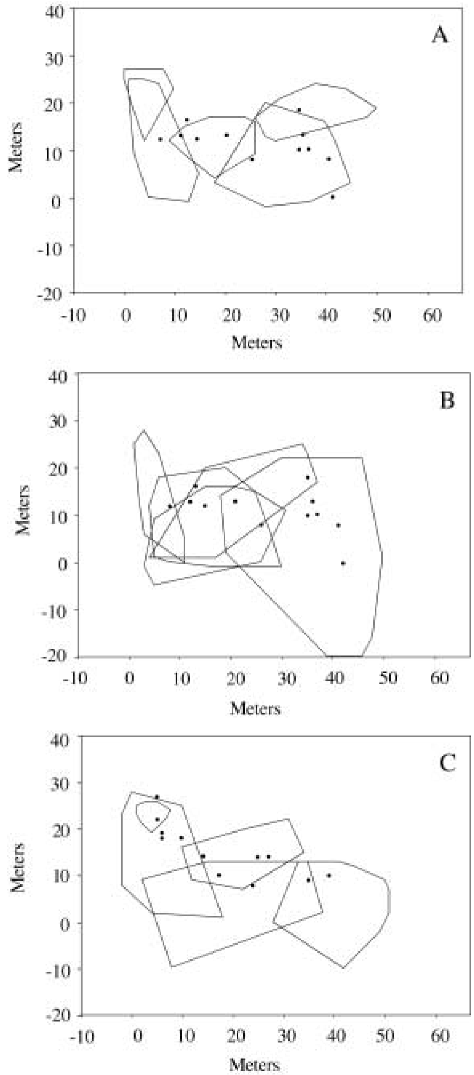

Fig. 3 Home-range maps of five dominant male Cuban iguanas during the 1993 breeding season (**A**), five subordinate male Cuban iguanas during the 1993 breeding season (**B**), and five subordinate male Cuban iguanas during the 1994 breeding season (**C**), when the five dominant males were removed from the study site. *Points* indicate arithmetic mean centers of the home ranges of females

Removal experiment

Effect on subordinate males

Removal of high-ranking males during the 1994 breeding season produced dramatic changes in male social structure. Within a few days, the five largest previously subordinate males began to actively defend territories, winning more than 50% of their encounters (mean % wins=74.8±10.1), and could be classified as high ranking. All of the previously nonranking males began to move throughout the study site and engage in agonistic interactions with other males, and could be classified as low ranking (mean % wins=27.8±10.4). Territories of the five highest-ranking males during the 1993 breeding season (Fig. 3A) were oriented such that they each overlapped the home ranges of several females. Once these males were removed from the study site in 1994, the five males that achieved higher rank in their absence each defended territories that were spatially similar to those vacated by the removed males (Fig. 3C). This represented a departure from the large, overlapping home ranges these five individuals had occupied in 1993 as subordinate males (Fig. 3B).

In addition to spatial orientation of home ranges, we observed several other behavioral and physiological changes among the five males that achieved high-ranking status in the absence of the dominant males. Compared to the previous year, these newly dominant males increased their percentage of encounters won (t=0.49, n=5, P=0.02; Fig. 4A) and proximity to females (t=0.95, n=5, P=0.05; Fig. 4B). Although they changed in the expected direction, increases in testosterone levels (t=1.51, n=5, P=0.06; Fig. 4C) and display rates (t=1.51, n=5, P=0.06; Fig. 4D) fell short of achieving statistical significance. Testosterone concentration in these males showed a significant increase relative to levels measured just prior to removal of dominant males from the site (t=0.49, n=5, P=0.02), suggesting that the observed change was not due to developmental variation. Although not statistically significant, the rate of courtship by these males was higher (t=5.02, n=5, P=0.30; Fig. 4E) and their home-range size was lower (t=4.50, n=5, P=0.25; Fig. 4F) during the removal experiment than during the previous year. For all variables examined, we found no significant differences between the behavior and hormone levels of dominant males in 1993 and the lower-ranking males that replaced them in 1994 (all P>0.40; Fig. 4A–F).

Effect on females

We assessed effects of the removal experiment on females by comparing their behavior and hormone levels during the male removal with those observed during the previous year (Table 3). Resident females did not alter the size of their home ranges in response to removal of the high-ranking males (t=13.50, n=7, P>0.90). For those females that participated in agonistic interactions, we found no significant difference in percentage of encounters won during the removal experiment (t=1.5, n=3, P>0.30). However, we did observe a significant increase in female display rate compared to the previous breeding season (t=0.50, n=7, P<0.03). There were no significant differences in either mean estradiol (t=11.50, n=6, P>0.60) or mean corticosterone (t=2.50, n=6, P<0.10) levels during the1993 breeding season and the 1994 removal experiment.

Effect on dominant males

At the close of the breeding season, four of the five previously dominant males were returned to the study site.

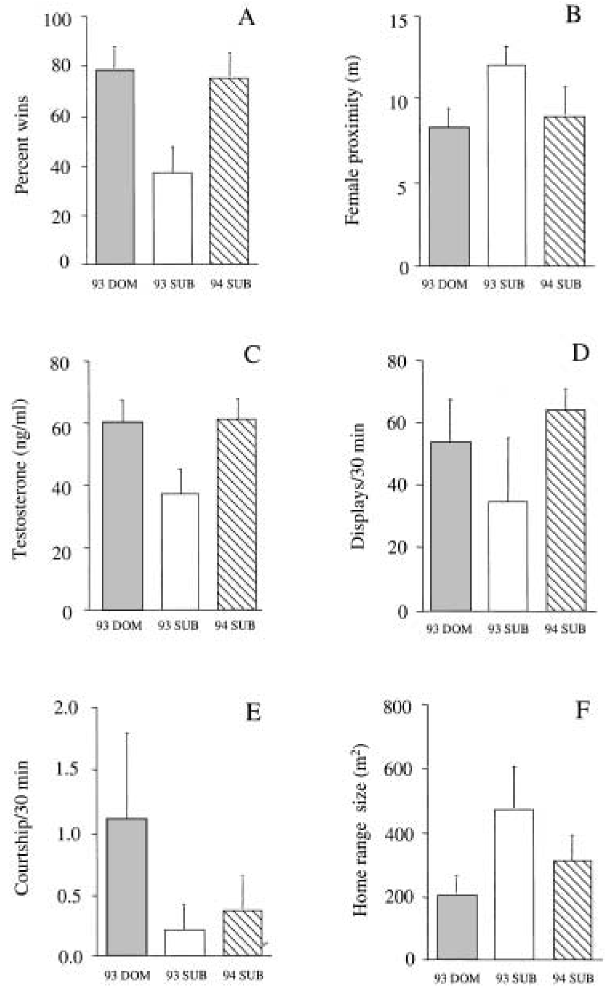

Fig. 4 Success in agonistic encounters (**A**), proximity to females (**B**), testosterone levels (**C**), display rate (**D**), courtship rate (**E**), and home-range size (**F**) (mean±SE) for five dominant male Cuban iguanas during the 1993 breeding season (*93 DOM*; *shaded*), five subordinate male Cuban iguanas during the 1993 breeding season (*93 SUB*; *unfilled*), and five subordinate male Cuban iguanas during the 1994 breeding season, when the five dominant males were removed from the study site (*94 SUB*; *hatched*)

Table 3 Effect of temporary removal of five dominant male Cuban iguanas for the duration of the 1994 breeding season. For females, behavior and hormones during the 1994 removal experiment are compared with the same 6-week period (29 April to 11 June) in 1993. For dominant males, behavior following return to the study site in 1994 is compared with the same 5-week period (12 June to 19 July) in 1993. *Asterisk* indicates a significant difference at P≤0.05

	1994 Male removal	1993 Control
Females		
%Wins	39.2±14.1	25.0±11.2
Displays/30 min*	20.6±6.6	3.9±1.3
Home-range size (m^2)	276.9±62.4	243.0±55.7
Estradiol (pg/ml)	204.2±98.5	543.4±348.3
Corticosterone (ng/ml)	17.4±3.3	33.7±6.4
Dominant males		
%Wins	53.0±13.2	87.3±7.2
Displays/30 min	37.6±13.8	71.5±29.1
Home-range size (m^2)	111.8±30.1	155.6±50.0

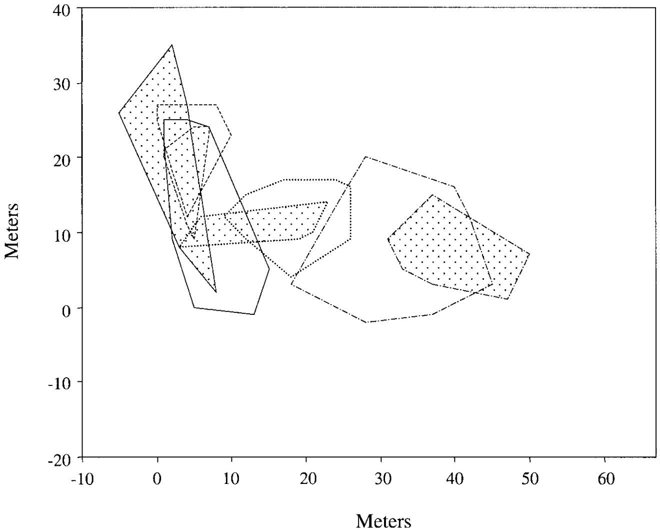

Fig. 5 Home-range maps for four dominant male Cuban iguanas during the 5-week post-removal monitoring period (*stippled*) compared with their home-range maps for the previous breeding season (unfilled)

Unfortunately, one individual escaped from the holding pen during the 6-week period and could not be retrieved. The other four males each regained their previous territories within 48 h, although the aggressive interactions required for re-establishment were among the longest and most intense observed during the entire study. The previously low-ranking male who assumed the territory of the escaped male retained that territory, together with his high-ranking status, throughout the post-removal monitoring period.

Behavioral observations and home-range mapping for 5 weeks following the return of the dominant males indicated no significant changes in their behavior from that observed during the previous year (Table 3). Percent wins (t=0.50, n=4, P>0.2), display rates (t=1.50, n=4, P>0.30), and home-range size (t=2.60, n=4, P>0.60) for the dominant males were not significantly different from that recorded in 1993. Although only a rough approximation due to a restricted number of sightings (29.3± 3.6), home-range mapping during the post-removal period showed that the dominant males returned to defend territories that overlapped those they had occupied in the previous year (Fig. 5).

Discussion

Natural mating system

The high-, low-, and nonranking male social classes identified in our study appear to be functionally equivalent to the territorial male, peripheral/marginal male, and pseudofemale/sneaker male categories previously documented for green (*Iguana iguana*) and marine (*Amblyrhynchus cristatus*) iguanas (Dugan 1982; Rodda 1992; Wikelski et al. 1996), and may be a common feature of iguanid social systems. Similar to other iguanid lizards, dominance status in male Cuban iguanas was associated with large body size, enlarged jaw musculature, and well-developed femoral glands (Wiewandt 1977; Carothers 1981; Dugan and Wiewandt 1982; Alberts et al. 1992). Our morphological findings for high-, low-, and nonranking males suggest that body length, together with secondary sex characteristics, may be important in mediating success in agonistic interactions between males, while body mass may be a key determinant of a male's willingness to participate in such interactions.

As in many lizard species, the largest, most dominant male Cuban iguanas were responsible for the majority of advertisement displays and courtship attempts during the breeding season (Carpenter 1960; Stamps 1977a; Tokarz 1985; Cooper and Guillette 1991; Pratt et al. 1992; Baird et al. 1996). Among iguanas, high-ranking males probably have better access to females and higher mating success than lower-ranking males as a result of their large body size and behavioral dominance (Wiewandt 1977; Iverson 1979; Dugan 1982; Rodda 1992; Wikelski et al. 1996). In both green and marine iguanas, male mating success is highly skewed toward the largest males, which perform 80–90% of observed copulations (Dugan 1982; Wikelski et al. 1996). Both the number of females associated with a male and the frequency of inter-sexual encounters are important predictors of mating success in many lizard species (Rauch 1985; Hews 1993; Baird et al. 1996). Nevertheless, without genetic studies, it is difficult to draw firm conclusions about the relative mating success of dominant and subordinate males.

Among reptiles, corticosterone is the major adrenal glucocorticoid hormone (Sandor et al. 1976), and is known to increase in response to a broad array of social and environmental stressors (Lance 1990; Moore et al. 1991). Although testosterone levels were positively correlated with social status of male Cuban iguanas during the breeding season, corticosterone levels were similar regardless of rank. This contrasts with other studies showing an inverse correlation between corticosterone levels and male dominance status (Greenberg et al. 1984), aggression (Tokarz 1987; DeNardo and Licht 1993), sexual behavior (Moore and Miller 1984), and home-range size (DeNardo and Sinervo 1994) in a variety of species. In these studies, however, a laboratory environment and/or exogenous administration of corticosterone may have produced acute, relatively short-term effects that would be less evident in unmanipulated, natural populations.

The observed association between elevated testosterone levels and frequency of display behavior in high-ranking male Cuban iguanas during the breeding season is consistent with studies on many vertebrates (Wingfield and Marler 1988), including reptiles (Marler and Moore 1988; Greenberg and Crews 1990; Pratt et al. 1992), and may be a prerequisite for successful acquisition and maintenance of a territory (Tokarz 1995). In our study, only the largest, most dominant male Cuban iguanas defended territories during the breeding season, which they abandoned during feeding bouts. Although neutral feeding areas have been described for the Anegada iguana (*C. pinguis*) (Carey 1975), the Turks and Caicos iguana (*C. carinata*) generally feeds within defended areas, perhaps accounting for the unusual pattern of year-round territorial defense in this species (Iverson 1979). Among iguanid lizards in general, territorial defense of food may be rare as a result of shifting availability of high-quality plant resources in space and time (Stamps 1977a; Dugan and Wiewandt 1982). As in the Mona Island iguana (*C. stejnegeri*), patterns of home-range overlap among male Cuban iguanas suggest they probably defend areas based on the local density and distribution of females, while site fidelity and consistent use of preferred refuges indicate that female home ranges are centered primarily around favored retreats (Wiewandt 1977).

Unlike many lizards in which male home ranges are significantly larger than those of females (Ferner 1974; Ruby 1978; Smith 1985; Baird et al. 1996), home ranges of male and female Cuban iguanas were generally similar in size, with only low-ranking males exceeding females in home-range size during the breeding season. Although large home-range size resulted in high overlap of female home ranges by low-ranking males, this did not translate into greater association with females. Virtually all available females at the site were overlapped by at least one high-ranking male who vigorously defended females from intruding males. Low-ranking males spent a great deal of time fleeing from the periphery of one territory to another, while non-ranking males moved through territories cautiously, rarely approaching females and exhibiting subordinate behavior, including the raised tail posture typically employed by females to reject courtship attempts (Wiewandt 1977). The modest territory sizes observed in high-ranking male Cuban iguanas relative to many smaller, insectivorous species (Turner et al. 1969) probably reflect energetic constraints on the ability of dominant males to detect and respond effectively to continuous intrusion by lower-ranking males.

During the nonbreeding season, home ranges of females and high-ranking males increased by approximately 30%, leading to greater overlap with conspecifics. Although high-ranking males continued to display at a higher rate than lower-ranking males, the frequency of displays was reduced by almost half and territorial defense was abandoned. Even among the highest-ranking males, testosterone levels showed a dramatic decline at this time of year. Apparently, as in many lizard species, territoriality and concomitant aggressive behavior are only observed among dominant male Cuban iguanas during the breeding season, when they presumably enhance access to potential mates (Stamps 1977b; Ruby 1978; Rodda 1992; Hews 1993).

Male removal experiment

Although removal experiments have been used extensively to study spacing behavior and territorial dynamics in vertebrates (Davies 1978), most of these studies have been with birds and have occurred over appropriately short time scales, usually hours or days. Those that have been conducted with reptiles (Boag 1973), amphibians (Mathis 1990), and fish (Clarke 1970) have generally taken place over weeks to months, time frames more suited to the protracted periods over which territorial establishment usually occurs in ectotherms. That abandoned territories are rarely left vacant by birds implies that resident territory holders are actively excluding settlement of those areas by conspecifics (Davies 1978). Once residents are removed, their territories are generally rapidly occupied by new, previously non-territorial males, or annexed by neighboring territorial males (Beletsky and Orians 1987a; Sherry and Holmes 1989).

Two non-exclusive hypotheses, one based on differences in resource-holding potential and the other based on asymmetries in the value of territories to different individuals, have commonly been invoked to explain why some individuals are able to successfully defend territories from conspecifics while others are not (Rohwer 1982; Beletsky and Orians 1987a). The resource-holding potential hypothesis maintains that residents hold territories primarily because they are physically superior fighters, while the value asymmetry hypothesis predicts that residents hold territories because they fight harder than nonresidents to defend areas that are disproportionately valuable to them as a result of prior familiarity (Maynard Smith and Parker 1976; Parker and Rubenstein 1981). The lack of a relationship between size or other morphological characters with status and fighting ability (Eckert and Weatherhead 1987; Jakobsson 1988; Shutler and Weatherhead 1991), and the inverse correlation between time held off the territory and the resident's probability of regaining it (Krebs 1982, but see Shutler and Weatherhead 1992), support the importance of value asymmetries in territory maintenance among birds.

In our study, dominant male Cuban iguanas were removed from their territories for a 6-week period. In each case, their territories were rapidly taken over by lower-ranking males, who successfully defended them for the remainder of the breeding season. Presumably, the replacement males would have had ample time to familiarize themselves with all relevant aspects of territory quality, including the location of stable refuges, as well as the behavior and habits of resident females and neighboring males (Beletsky and Orians 1987b; Eason and Hannon 1994). Despite the fact that previous value asymmetries were expected to be greatly diminished by the time the dominant males were returned to the site, replacement males were ousted within 2 days of their return. These results suggest that physical attributes, including larger body size and jaw musculature, played a key role in allowing the dominant males to regain control of their territories. Differences in resource-holding potential may have magnified importance for long-lived, slow-maturing species such as Cuban iguanas, where significant differences in body size between high- and low-ranking males exist.

Although replacement males were unable to defend territories successfully against the returned dominants at the close of the experiment, changes in their behavior and physiology suggest that their access to potential mates was enhanced during the removal. Compared to the previous breeding season, they won more fights and spent more time in close proximity to females, and showed a tendency toward higher testosterone levels and increased display rates. In birds and fish, replacement males are at least sometimes successful in attracting mates and inseminating females (Clarke 1970; Thompson 1977; Macdougall-Shackleton et al. 1996). Anecdotal data on the removal of a single adult male Mona Island iguana indicated that the resident female remained at the site and mated with the male replacing him (Wiewandt 1977). Despite suggestive evidence, definitive measures of male reproductive success require paternity analyses, which were precluded in our study.

We found little evidence that female reproductive cycling at the site was impaired as a result of the removal experiment. Although females displayed more often, possibly as a result of increased competition for access to limited high-quality males, they did not alter the size of their home ranges when dominant males were removed from the site. Peak estradiol levels did not differ significantly from those measured in the previous year. Although corticosterone levels in females showed a slight increase during the removal experiment, they were comparable to levels considered normal for female lizards undergoing vitellogenesis and possessing oviductal eggs (Wilson and Wingfield 1992, 1994). Both the number of post-ovipositional females observed at the study site at the close of the breeding season, as well as the dates when they were observed, were similar across years.

Conservation implications

Our experimental results suggest that temporary removal of dominant male Cuban iguanas may represent a viable conservation strategy for increasing individual genetic representation in local populations characterized by variable male mating success. It is important to note that our experiment was unreplicated and could not rule out the potentially confounding influence of annual variation, and also that small sample sizes limited the power of some of our statistical analyses. For these reasons, our results should be interpreted with caution. Future studies spanning multiple years are needed, in which the reproductive success of dominant and subordinate males both before and during removal experiments is measured.

Although modeling studies indicate that effective population size declines under polygynous mating systems, the magnitude of this effect may decrease with lengthening generation time because individual males experience more breeding seasons in which they potentially can breed successfully (Nunney and Campbell 1993). If lower-ranking male Cuban iguanas are younger individuals that eventually acquire the physical attributes necessary for dominance and territory acquisition, then they are expected to ultimately contribute to the population gene pool, thus diminishing the value of male removals as a management strategy. In addition, if dominant males possess “good genes” that translate into enhanced offspring survival and/or reproduction, then removals could potentially be disadvantageous to the population by promoting mating by suboptimal males. Finally, if the three male strategies observed in our study reflect a balanced polymorphism in which lifetime reproductive success is equivalent across males (e.g., Sinervo and Lively 1996), temporarily removing dominant males may do little to equalize genetic representation over the long term. Clearly, more information is needed on how dominance is attained and maintained, how social status translates into breeding success and offspring quality, and how these variables influence effective population size, before the utility of male removals for conservation purposes can be fully evaluated.

Despite these cautions, there appear to be circumstances under which temporary removal of dominant males may be warranted as an emergency short-term conservation measure. Among rock iguanas, the rapidity with which precipitous population declines can occur in the face of predation by introduced species is striking. On Pine Cay, the Turks and Caicos iguana decreased from an estimated population of 5,500 to near extirpation in less than 3 years as a result of predation by dogs and cats (Iverson 1978). Likewise, the population of San Salvador iguanas (*C. rileyi*) on White Cay in the Bahamas, estimated at 150–200 individuals, was reduced by more than 50% over approximately a year, probably because of predation by a single marooned raccoon (W.K. Hayes and R.L. Carter, personal communication). When populations fall below a critical threshold, where immediate loss of fitness due to inbreeding becomes a concern (Franklin 1980), even modest positive increments to effective population size achieved through temporary alteration of local social structure may help to forestall further loss of genetic variation. Such interim measures will be most effective when coupled with active intervention in the form of predator control and other programs aimed at reducing direct threats to population recovery.

Recently, there has been an increasing awareness that the field of animal behavior can make a valuable contribution to conservation in the wild (Clemmons and Buchholz 1997; Caro 1998; Sutherland 1998; Anthony and Blumstein 2000), especially when the consequences of particular behavioral patterns can be translated into genetic or demographic terms (Beissinger 1997; Reed 1999). Knowledge regarding relevant behavioral attributes, including the ramifications of different types of mating systems, can guide the design of creative management practices that counter the factors limiting population size in rare and endangered species (Komdeur and Deerenberg 1997). Given the flexibility of many vertebrate social systems, artificial manipulation of breeding structure may represent a valuable conservation strategy when conservatively applied to small, fragmented or insular populations at high risk for significant loss of genetic variation.

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