

Lekking in marine iguanas: female grouping and male reproductive strategies

MARTIN WIKELSKI*†, CHRIS CARBONE‡ & FRITZ TRILLMICH*

*Lehrstuhl für Verhaltensforschung, Universität Bielefeld

†Max-Planck Institut für Verhaltensphysiologie, Abt. Wickler, Germany

‡Department of Biological Sciences, University of Zimbabwe

(Received 10 May 1995; initial acceptance 6 July 1995;
final acceptance 20 December 1995; MS. number: 4930)

Abstract. The breeding and non-breeding distributions of male and female marine iguanas, *Amblyrhynchus cristatus*, and their mating behaviour were analysed. The population size was low because of a long lasting El Niño. The distribution of female-sized iguanas was more clumped during the mating season than before and afterwards. Model iguanas placed outside territories attracted more females during the breeding season than during the non-breeding season. The majority (75%) of large males established clustered territories while the remainder established single territories. The locations of the clusters were not related to physical characteristics of the habitat and were only partially related to non-breeding female densities. Non-territorial ‘sneaker’ males, similar in size to females, attempted copulations inside territories when territorial males were absent. Moderate sized, non-territorial males remained in the vicinity of territories and attempted to copulate forcefully with female-sized iguanas. This form of harassment was much higher outside territories, but levels did not differ between lek and single territories. Therefore, while harassment may lead to an increase in grouping among female-sized iguanas, it probably does not influence the type of territory visited. Females preferentially mated with the largest territorial males and reproductive success for these males was independent of lek size. The reproductive success of smaller territorial males, however, increased with lek size. Lekking in marine iguanas, therefore, may represent a ‘hotshot’ phenomenon where small territorial males associate with large males to increase reproductive success. The likely mechanism behind clustering appeared to be a greater propensity for females to mate in leks where stimulation rates were higher.

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Marine iguanas, *Amblyrhynchus cristatus*, live in large aggregations on the coastline of the Galapagos Islands (Darwin 1883; Carpenter 1966; Trillmich & Trillmich 1984) and feed exclusively on macrophytic marine algae in the inter-tidal zone during low tide (Trillmich & Trillmich 1984; Wikelski et al. 1993; Wikelski & Hau 1995). Iguanas use rocks with interspersed crevices or bushes as resting sites. Shuttling between resting and foraging sites creates areas with a high density

of female traffic (Trillmich & Trillmich 1984; Wikelski & Trillmich 1994).

The males defend small mating territories. Receptive females normally copulate only once during the mating season and leave these areas at the end of the season to lay eggs (Trillmich 1983; Rauch 1985; Laurie 1990). This mating pattern was previously described as resource defence polygyny (Trillmich 1983; Trillmich & Trillmich 1984). Large males were thought to defend territories (only during the reproductive season) in areas that are micro-climatically more suitable for females than surrounding areas at the coast. Consequently, females were supposed to congregate within male territories more in response to the habitat than to the male (Trillmich & Trillmich 1984; Rauch 1985). However, all studies on marine iguanas thus far have been conducted at sites with extremely high animal densities

Correspondence and present address: M. Wikelski, Department of Zoology, Box 351-800, University of Washington, Seattle, Washington 98195, U.S.A. (email: wikelski@zoology.washington.edu). C. Carbone is at the Department of Biological Sciences, University of Zimbabwe, MB 167, Mount Pleasant, Harare, Zimbabwe. F. Trillmich is at the Lehrstuhl für Verhaltensforschung, Universität Bielefeld, Postfach 100131, D-33501 Bielefeld, Germany.

(>2000 individuals/km coastline). It was unclear whether changes in animal distribution had actually occurred during the reproductive period. Similarly, owing to high population densities male territories were expected to be clustered in any case. A population crash caused by El Niño conditions in 1991 (cf. Laurie 1989; Laurie & Brown 1990a, b; Kerr 1993) reduced the population at the Genovesa study site by more than half (Wikelski 1994). This allowed us to analyse the distributions of iguanas well below habitat saturation.

A central characteristic of lek mating patterns is that one sex, usually males, form clustered non-resource based territories (Bradbury 1977, 1981; Emlen & Oring 1977; Wiley 1991; for sex role reversed leks, see Svensson & Petersson 1988). In many lekking species the location of the lek is associated with a number of environmental factors or with female densities, or both (Bradbury 1985). In the Uganda kob *Kobus kob thomasi*, for example, lek sites are associated with areas of high visibility and little vegetation (Deutsch & Weeks 1992; Deutsch 1994a). Some *Drosophila* species require certain types of vegetation for display sites (Parsons 1977; Shelly 1987), pinnipeds need beaches (Gisiner 1993) and kakapos, *Strigops habroptilus*, need grass bowls (Merton et al. 1984). To distinguish these mating patterns, which lack obvious direct benefits to females, from resource defence polygyny it is important to ask whether the clustering of territories is the result of the resource distribution or whether it occurs for purely reproductive purposes (M. Taborsky, M. Wikelski & C. Carbone, unpublished data; lekking is also discussed as a special case of a suite of strategic adaptations by Bradbury 1985). In addition, a major factor leading to the clustering of territories in ungulate lekking systems is thought to be harassment of females from non-territorial males (Clutton-Brock et al. 1992, 1993; Stillman et al. 1993; see also Foster 1993). Considerable levels of harassment have been noted in previous studies on marine iguanas (Trillmich & Trillmich 1984).

In this paper we investigate whether resources are important for the mating strategies of marine iguanas and whether the distribution of the resources can explain the clumping of male territories (Trillmich 1983; Trillmich & Trillmich 1984; Rauch 1985). We also examine the possible influence of harassment on the movements of

female-sized iguanas and female mating patterns. In addition, we outline the reproductive tactics of males of different size classes.

METHODS

Study Site and Animals

We studied marine iguanas on Genovesa island (89°59'W, 0°19'N). The study site consisted of a long beach flanked by rocky areas, with a long lava flow used as a resting site and nearby intertidal zones as the foraging sites, totalling approximately 1 km of coastline. The iguana population at the study site, estimated from mark-recapture, declined from 2647 individuals in March 1991 to 403 in December 1993 (see below). The mating season began each year in early December and continued until early January. We conducted the study during the three reproductive periods in 1991–1992, 1992–1993 and 1993–1994 and made a final check during January 1995. We measured and weighed about a third of the entire population at the study site prior to the mating season. We calculated body condition from the ratio of body mass (g) $\times 10^6$ divided by the (snout to vent length)³ (see Laurie 1989). We were unable to distinguish young males from adult females reliably by external morphology; however, we determined the sex of these animals by probing the depth of the cloacal pouch (Dellinger & von Hegel 1990). We use the expression 'female-sized iguanas' for all individuals of female size. 'Females' is used only for individuals whose sex was clearly determined.

We marked marine iguanas permanently by hot branding. To achieve this, the flank of an iguana was touched for about 0.5 s with a hot wire number 1 cm tall (wire diameter 1 mm). Marine iguanas do not react to this treatment. The resulting superficial skin damage heals within 1–2 weeks, leaving a permanent marking pattern. We chose this over alternative marking techniques (e.g. transponders, beads), because (1) it does not seem to hurt iguanas (the outer skin surface is dead tissue) and (2) readily visible brands enable selective recapture without disturbing unmarked animals to a large extent. We also painted numbers on their flanks using non-permanent paint. The numbers did not affect the behaviour of the animals, nor the reaction of other animals towards the painted iguanas (M. Wikelski,

unpublished data). A number of animals were measured and marked after being observed in a copulation sequence.

A long-term El Niño occurred throughout the study period (Kerr 1993; Pearce 1993) and as a result there was a complete failure of reproduction during 1991–1992, a ‘normal’ mating season during 1992–1993 and again an almost complete failure during 1993–1994, when out of 20 observed copulations only three females reproduced. Nevertheless, males established territories during all years of the study.

Thermal Measurements, Topography and Disturbance on Territories

We measured the effective environmental temperature using two thermo-transmitters contained in black copper bulbs (diameter 15 cm; cf. Bakken 1992; see also Bartholomew & Lasiewski 1965; Bartholomew 1966). The thermo-transmitters were calibrated before and after the field season in a laboratory water bath to the nearest 0.1°C. We used the thermo-transmitter bulbs to compare the thermal properties of four sites within four territories with each of four areas that contained high densities of females during the non-breeding season (on days 1, 5, 7, 9, 10, 12, 13, 15, 17, 18, 19, 21, 23, 26, 28 and 30 of December 1992 for sites 1–4 in Fig. 1). The bulbs were left for a minimum of 24 h, and temperature data were recorded every 2 min by an automatic receiver (Heinecke–Mohren-system, Seewiesen, Germany). The temperatures measured by this method were compared by Wilcoxon matched-paired tests (daytime as matched variable, comparison of mean hourly measured temperatures at both sites for 24 h at each site).

We classified the topography of territories into four categories: 0 for absolutely flat areas, 1 for flat areas with some rocks, 2 for mostly rocks with few flat areas, 3 for purely rocky areas. Disturbance on a territory by wave action was judged on a scale from 0 to 2: 0 for no disturbance by wave action during the entire reproductive season, 1 for disturbance for 1–2 days, 2 for disturbance for more than 2 days.

Observations of Territorial Sites

Four observers were trained by M.W. for 3 days to achieve inter-observer reliability at the

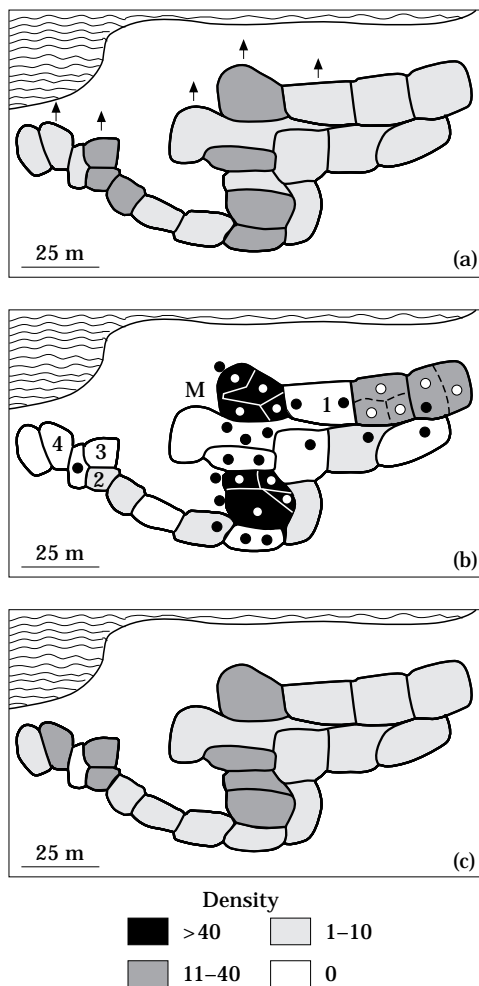


Figure 1. Density (iguanas/10 m²) of marine iguanas in the 1992–1993 season during counts in one part of the study area on 15 November 1992 (a, pre-mating), 15 December (b, mating season) and 15 January 1993 (c, post-mating). The connected polygons represent counting areas, the wave-line on top of each panel indicates the sea. Arrows show main travel routes of iguanas towards foraging areas. The open circles in (b) represent territorial males, filled circles marginal males. Neither was included in the counts. Broken or white lines indicate territory boundaries, M gives the location of model iguanas (see text) and the numbers (1–4) show where effective environmental temperatures were measured to compare with the four lek areas (dark shading).

beginning of each season. We divided the study area into two sections with two observers assigned to each section allowing for continuous

observation during daylight hours. The observers walked along a fixed circular route and used four observation locations. We made 15-min focal observations at each location, with a 5-min time-interval between each observation allowing for change of location. Focal observations were interrupted when copulations occurred and the observation was skipped; only the occurrence of the copulation was noted while behavioural data during this observation were dropped.

We observed territorial activity during the entire reproductive season (beginning of December to 5 January). We calculated the total number of copulation attempts, copulations, chases, fights and head-bobs from time sampling over the entire season. We also monitored the number of female-sized animals present on each territory in order to calculate male activity per female-hour. One section of the study site was divided into subregions in order to calculate the densities of female-sized individuals within each region (see Fig. 1). On 3 days (1 month prior to, during and 1 month after the breeding season) in the 1992–1993 season, we counted the total number of these animals present in the above subregions (Fig. 1).

Male Categories

We divided males into three categories according to their territorial and reproductive behaviour. Sneaker males (see also below) resembled females in size. Marginal males (after Trillmich & Trillmich 1984) were mostly of intermediate size. They were excluded from territories and were not able to gain territories by themselves. Most of them roamed around territories and attempted to gain copulations outside territories. Several marginal males showed signs of territorial behaviour in the vicinity of territories, but only in the absence of territorial males. Marginal males did not remain at any one site for longer than 12 daylight h. Territorial males were males that occupied and defended a particular area for more than 5 consecutive days. They were generally larger than the other two male categories (see Table I for comparison). For a comparison within territorial males, we divided this group of males again into 'large territorial' and 'small territorial' males (see below).

Territorial Behaviour and Territory Boundaries

Territorial behaviour consisted of head-bobbing sequences and posturing towards adjacent territorial males. Fights were defined as encounters that resulted in the physical contact of two animals for longer than 10 s. Chases sometimes also involved contact between opponents, but for shorter periods. We monitored the duration of territory tenure for every territorial male during the entire reproductive season. Territorial boundaries were determined by observing conflicts with neighbouring males. The boundaries of single territorial males were estimated from territorial chases against smaller non-territorial males. We mapped the territory boundaries by triangulation with metric tape after the reproductive season. We estimated the centres of each territory by eye, and the distance between centres from a map of the region. The projected surface area of each territory was determined by weighing the paper-sheets of territorial maps against sheets of standard size. We refer to males as being clustered when their territory boundaries were adjacent to neighbouring territorial males. All single male territories were at least 14 m away from the next closest territory. Single territories were included in the comparison of leks of different sizes.

Reproductive Strategies

There were a number of distinctly different types of copulatory modes observed which were predominantly determined by the body size and territorial status of the male. Territorial males attempted to copulate with females by approaching slowly while using side-step-head-bob display (Trillmich 1980). We define this as a 'slow' copulation attempt. Marginal males usually chased after female-sized iguanas and attempted to bite their neck spines and mount them. We defined this type of copulatory approach as a 'chase' copulation attempt. The latter mode of copulatory behaviour appeared to occur frequently and probably caused considerable energetic and time costs to the recipient. Sneaker (small, female-sized) males within male territories were observed to attempt copulations while the territorial male was absent. Copulation attempts in this group often began by the male piling on top of others (a common non-reproductive behaviour) and then

attempting to bite the neck spines and mount. We defined this as a sneaker attempt after for example Taborsky (1994; see also Crews 1983). Because all modes of copulation attempts made females move at least temporarily and thus incurred at least thermal opportunity cost (cf. Sinervo & Adolph 1994), we use the occurrence of copulation attempts as a measure of harassment (after Clutton-Brock et al. 1992).

We observed the behavioural reaction of female-sized iguanas after copulation attempts by males, namely whether female-sized iguanas (1) 'stayed', that is did not move away from the male for more than three body lengths, or (2) moved into small crevices, for example between stones, rocks or under bushes, where only a single iguana fitted, which stopped males from approaching further. A group was defined as two or more iguanas that remained within one body length of each other. We also noted the occurrence of interrupted copulations where males approached and physically separated the couple. We assume that a copulation had taken place when we witnessed the joining of the two cloacal regions of the iguanas. It was not always clear, however, whether intromission had taken place, although in some cases intromission clearly did not occur. We captured both animals immediately after the copulation and then measured, weighed and painted them (cf. Wikelski & Bäurle 1996).

Manipulation of Female Groups

To test whether iguanas tended to group together, we constructed model iguanas and placed them in areas that were not normally frequented by iguanas. The six models consisted of black plastic bags filled with sand, with 'head' and 'tail' sections separated by constrictions. While these models were of simple construction, iguanas were attracted to them. We assumed, therefore, they were sufficiently realistic to test grouping behaviour in this species. Marine iguanas do not usually approach new objects out of pure curiosity. We counted the number of females that came closer than one body length to the models and stayed longer than 30 s. There was no obvious qualitative difference in this behaviour between females during reproductive and non-reproductive seasons. The experiments with the models were performed at the same locations during the reproductive season

and a month afterwards for each of 6 days (see Fig. 1).

Statistical Analysis

Data were processed with SPSS (1991) for Windows. Two-tailed test statistics were used. The distribution of data was inspected for normality by Kolmogorov–Smirnov one-sample tests. Regression lines were drawn according to the best fit between linear and exponential models. Data are given as $\bar{X} \pm \text{SD}$ if not otherwise indicated, except for regression equations (given as $\bar{X} \pm \text{SE}$).

RESULTS

Iguana Distributions

Iguanas were more clumped and confined to fewer clusters during than before and after the breeding season (Fig. 1). This difference was reflected when we analysed the frequency distributions of iguana densities before, during and after the mating season in counting areas in one part of the observation area (Fig. 2). The distribution of numbers of female-sized iguanas among these counting areas was close to a Poisson distribution before and after the mating season, as expected (test for difference from Poisson distribution, before: Kolmogorov–Smirnov $z=0.90$, $P=0.39$; after: $z=0.70$, $P=0.76$; Fig. 2a, b, respectively). However, the frequency distribution was bimodal during the mating season and differed significantly from a Poisson distribution, as female-sized iguanas clustered into a few territories (Figs 1b and 2b; $z=1.50$, $P=0.02$).

During three mating seasons large males (Table I) established territories, three-quarters of which (30 of 41) were in clusters of two to six males (Fig. 1b for the 1992–1993 season). A number of marginal males were distributed in the vicinity of these clusters. The mean number of males in territory clusters was 3.75 ± 1.19 ($N=8$ clusters with a total of 30 males). The mean distance between centres of adjacent clusters was 77.3 ± 71.8 m. The mean distance between centres of territories within clusters was 8.3 ± 1.5 m ($N=8$).

Female-sized iguanas tended to group together more during the breeding season. In the immediate post-mating season (6 January 1993), the

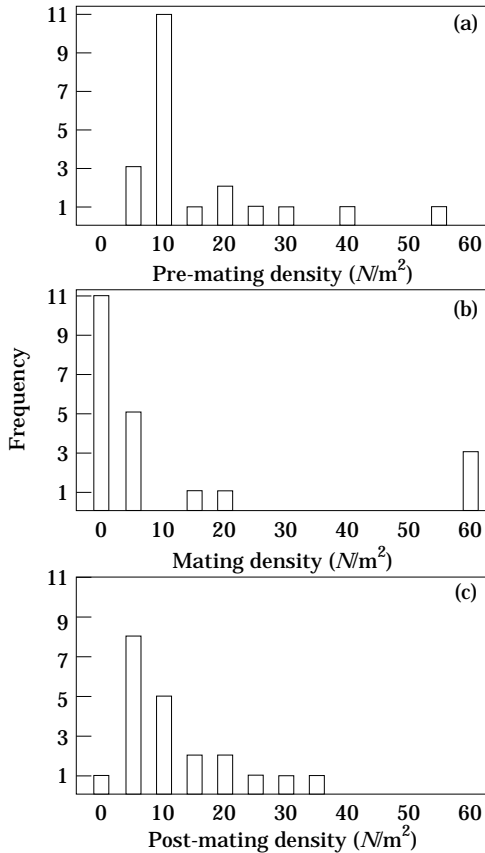


Figure 2. The densities (female-sized marine iguanas/10 m²) shortly before (a), during (b) and immediately after (c) the 1992–1993 mating season. The coefficients of dispersion were 12, 41 and 10, respectively. The bimodal distribution indicates a clustering of female-sized iguanas into territories during mating seasons.

plastic model iguanas (put out on area M in Fig. 1b) attracted 1.0 ± 0.9 females per day compared with 9.2 ± 5.7 females per day during the breeding season (17 December 1993; Mann–Whitney *U*-test: $z = -2.7$, $N_1 = N_2 = 6$, $P < 0.01$).

Resource Distributions

There were no differences between the thermal properties of areas defended by males during the breeding season and other areas, which contained moderate to high female densities during the non-breeding season. Hourly means of effective temperatures were not different between leks and formerly occupied areas except for one daily

comparison (Wilcoxon tests for 24-h periods for a comparison of the four leks with areas 1–4 in Fig. 1b: top left lek: $P_1 = 0.10$, $P_2 = 0.56$, $P_3 = 0.13$, $P_4 = 0.16$; top middle lek: $P_1 = 0.86$, $P_2 = 0.34$, $P_3 = 0.47$, $P_4 = 0.38$; top right lek: $P_1 = 0.79$, $P_2 = 0.23$, $P_3 = 0.17$, $P_4 = 0.04$; lower lek: $P_1 = 0.09$, $P_2 = 0.35$, $P_3 = 0.28$, $P_4 = 0.19$; each $N_1 = N_2 = 24$). There were also no obvious differences in rock structure as all measured areas had similar values on the flatness scale.

Male Mating Tactics and Reproductive Success

Male mating tactics varied in relation to body size (Table I). Large males established territories in mid-November, approximately 2 weeks before the first copulation attempt was observed. They chased medium-sized males off territories. The latter then became marginal males if they could not establish territories themselves. Individual males that were territorial in 2 consecutive years (1992–1993 and 1993–1994) showed high site fidelity between years (11 of 12 males). Males were not observed to herd females into their territories. However, territorial males attempted copulation at a higher rate when outside than when on territory (26.4 ± 20.4 versus 6.4 ± 5.7 copulation attempts/female-hour; Wilcoxon test: $T = 0$, $N = 6$ males, $P < 0.05$). We saw 16 slow copulation attempts by territorial males where the sex of the recipient was subsequently verified. Of these, 15 (93.8%) were directed towards females (Table I).

Several marginal males attempted to establish territories away from territory clusters (e.g. in counting area 3, Fig. 1b) and remained in these areas for an average of 2.25 ± 1.03 days ($N = 8$). Females did not settle on these territories, nor did other males establish adjacent territories. Marginal males appeared unable to distinguish the sex of the female-sized individuals with which they attempted to copulate. Of 43 chase copulation attempts 23 were directed towards males (Table I).

Territorial males appeared unable to distinguish female-sized sneaker males from females but chased these individuals when they saw them displaying inside territories (head-up position, body elevated, head bob). Sneaker males were often approached by displaying large males. However, like females, these males were able to reject slow copulation attempts by moving away.

Table I. Male mating pattern of marine iguanas at Genovesa island during the 1992–1993 season

	Territorial males	Marginal males	Small males	<i>P</i>
Body size (SVL mm)	243 ± 22 (41)	228 ± 17 (15)	210 ± 7 (16)	<0.001*
Body mass (g)	657 ± 183	503 ± 131	424 ± 44	<0.001†
Condition (kg/m ³)	44.5 ± 5.2	41.6 ± 4.1	46.6 ± 4.5	0.01‡
Copulation mode	Gentle	Forced	Forced	
			54% males,	
Copulation attempts§	94% females (16)		46% females (43)	<0.01
Copulation attempts/female-hour	3.8 ± 1.16 (17)	34.1 ± 7.5 (23)	21.2 ± 5.9 (5)**	<0.001††
Size of copulated female	190 ± 16 (14)	186 ± 12 (8)	188 ± 19 (9)‡‡	>0.05§§
Total copulations***	129	6	6	
Copulations per male	3.1 ± 5.1	0.4 ± 0.8	0.3 ± 0.6	0.01†††
Maximum no. of fast days	36	8	4	

Data represent $\bar{X} \pm SD$ (total *N*). SVL: snout–vent length.

*Kruskal–Wallis test: $\chi^2=30.0$, $df=2$, total *N*=72.

†Kruskal–Wallis: $\chi^2=28.5$, $df=2$, *N*=72.

‡Kruskal–Wallis: $\chi^2=7.9$, $df=2$, *N*=72.

§Percentage of copulation attempts directed against females versus males (sex known from previous recapture), of *N*=17 males (large versus other males) during 9 days in December 1992, $\chi^2=0.78$, $df=2$, *N*=59.

**In territories when large territorial males were absent.

††Friedman test: $\chi^2_1=3.9$, $df=2$, total *N*=45 males.

‡‡Females grow up to 240 mm snout–vent length, but only small females were in condition to reproduce.

§§Unreceptive females also frequented the leks.

¶¶Females that could be captured immediately after copulation, Friedman test: $\chi^2_1=2.3$, $df=2$, total *N*=31.

***Calculated from focal animal sampling.

†††Calculated from focal animal sampling, Kruskal–Wallis: $\chi^2=8.9$, $df=2$, total *N*=141 copulations.

Table II. Multiple regression model on factors influencing male mating success at Genovesa island during the 1992–1993 mating season

	<i>B</i>	Beta	<i>T</i>	<i>P</i>
Body size (SVL, mm)	0.08	0.32	2.2	0.03
Condition (kg/m ³)	0.41	0.41	3.0	0.005
Topography	–1.37	–0.33	–2.6	0.01
Disturbance	–1.93	–0.29	–2.3	0.03
Mean female-sized iguanas/territory (<i>N</i>)	0.19	0.29	1.8	0.08
Days of territory tenure	0.04	0.08	0.6	0.57
Lek versus single	–1.45	–0.13	–1.0	0.32

SVL: snout–vent length.

Male Mating Success

We tried to elucidate possible factors responsible for differences in territorial male success, including physical properties (body size, condition), territorial properties (topography, mean number of female-sized iguanas, days of territory tenure and lek versus single territory) and chance flooding frequency. A significant multiple regression model ($F_{7,32}=8.53$, $P<0.001$; Table II) of reproductive success as a function of the above

listed variables explained 75% of the variance. Mating success significantly increased with the factors ‘body size’ and ‘body condition’ (Fig. 3), whereas ‘territory topography’ and ‘degree of environmental disturbance’ significantly decreased the mating success, that is, flatter and less disturbed territories were better. The factors ‘mean number of female-sized iguanas’, ‘days of territory tenure’ and ‘lek versus single territory’ were not significant (Table II; for scattergrams

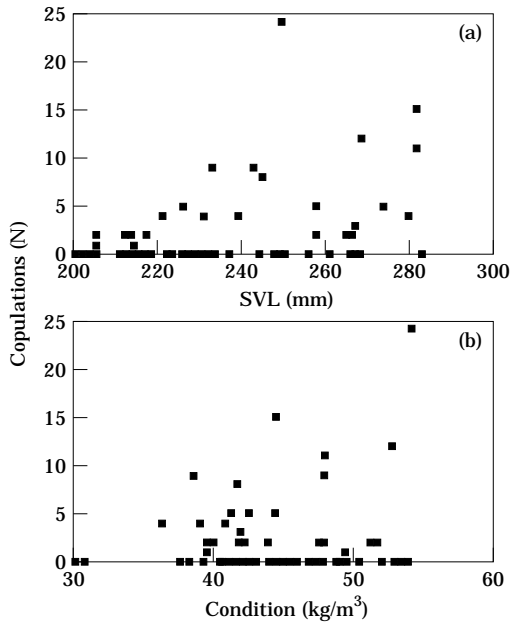


Figure 3. Relationship between (a) body size (snout-vent length, SVL) and (b) condition, and numbers of copulations achieved by individual marine iguana males during the mating season 1992-1993 on Genovesa island.

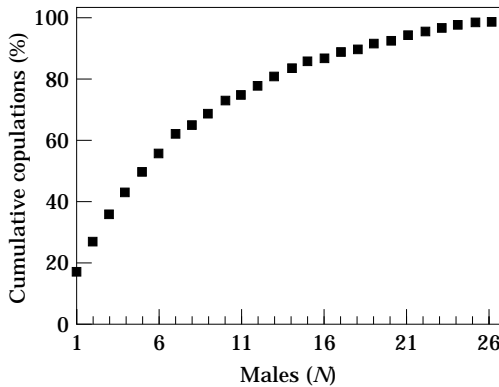


Figure 4. Cumulative percentage of copulations during the 1992-1993 season for male marine iguanas. The most successful male gained approximately 20% of all copulations.

of male success versus snout-vent length and condition see Fig. 3).

Male mating success was highly skewed (Fig. 4). Large territorial males gained more copulations than small territorial males (Table I). Large

territorial males had approximately the same mating success on single and lek territories (Table III). However, when we corrected for chance events, physical properties within groups and territorial differences, small territorial males copulated at a higher rate on leks than on single territories. The opposite was true for large territorial males, which had higher adjusted copulatory success in single territories (Table III).

Marginal males copulated at a rate one-tenth that of territorial males (Table I) and were observed to copulate only in the vicinity of lek clusters. The success of marginal males was about a third of that of small territorial males (Tables I, III). Sneaker males achieved a mating success similar to marginal males by copulating inside territories when the territorial males were absent (Table I).

Comparison of Differently Sized Leks

The mean distance (m) between territory centres (a measure of territory size) decreased with lek size (distance = $12.09 [\pm 1.0] - 1.0 [\pm 0.25] \times$ clustered-males, $F_{1,6} = 15.6$, $P = 0.007$, $r^2 = 0.72$; Fig. 5a). The number of female-sized iguanas per male tended to decrease with increasing lek size, but this relationship was not significant ($F_{1,7} = 5.1$, $P = 0.057$, $r^2 = 0.42$; Fig. 5b). The number of copulations per male did not vary significantly with lek size ($F_{1,7} = 1.7$, $P = 0.23$, $r^2 = 0.19$; Fig. 5c). However, the same relationship was significant with single territories excluded from the analysis ($Y = -1.59 [\pm 1.44] + 1.07 [\pm 0.36]X$, $F_{1,6} = 8.54$, $P = 0.02$, $r^2 = 0.58$).

We subdivided territorial males into two size classes ('large' >240 mm and 'small' <240 mm) according to the frequency distribution of snout-vent lengths in the population of territorial males (Fig. 6). We analysed the number of copulations per male against lek size separately for the two size classes of territorial males. The average mating success for large territorial males did not change with lek size (Fig. 7a; $F_{1,5} = 1.3$, $P = 0.37$), nor did it change for the most successful territorial male (linear regression: $F_{1,7} = 2.0$, $P = 0.20$, $r^2 = 0.22$). However, small territorial males had higher average mating success on larger leks (Fig. 7b; $Y = 3.3 [\pm 2.8] - 2.8 [\pm 1.6]X + 0.6 [\pm 0.2]X^2$; $F_{2,4} = 9.8$, $P = 0.02$, $r^2 = 0.83$).

Table III. Comparison between single territories and leks (two to six clustered territories)

	Single territories	Leks	<i>P</i>
Total number of territorial males	11	30	
Mean body size (SVL, mm)	243.6	242.5	0.88
Median body size	244	238	
Body mass (g)	647 ± 212	660 ± 175	0.73
Condition (kg/m ³)	43.6 ± 4.1	44.8 ± 5.6	0.53
Mating success per territorial male	4.0 ± 5.4	2.8 ± 5.0	0.64
Total number of copulations	44	85	
Mean number of female-sized iguanas per lek	7.7 ± 6.3	10.1 ± 8.3	0.38
Territory size (m ²)	35.0 ± 23.8	39.8 ± 32.5	0.93
Harassment rate (copulation attempts/female-hour)	0.149 ± 0.08 (4)	0.178 ± 0.11 (13)	0.49
Total number of fights	3.7 ± 4.5 (9)	24.7 ± 26.6 (8)	0.002
Number of fights/male	4.0 ± 4.6 (9)	5.9 ± 5.8 (8)	0.23
Territory tenure (days ± SD)	37.7 ± 13.4	34.7 ± 10.5	0.63
Adjusted mean copulatory success per large territorial male (>240 mm SVL)	6.5 ± 1.6 (6)	4.0 ± 1.1 (15)	0.01
Adjusted mean copulatory success per small territorial male (<240 mm SVL)	0.07 ± 1.4 (5)	1.5 ± 0.82 (13)	0.01

SVL: snout-vent length. Significances are given for two-tailed Mann-Whitney *U*-tests. The adjusted mean copulatory success represents the success of males when keeping the factors 'body size', 'condition', 'territory topography', 'degree of environmental disturbance', 'mean number of female-sized iguanas' and 'days of territory tenure' constant (see text and Table II; ANOVA: $F_{3,39}=4.4$, $P=0.01$). Numbers represent $\bar{X} \pm SD$ (N , if different from total number of territorial males).

Harassment and Responses to Copulation Attempts

Variation with lek size

Between leks of different size, there were no differences in harassment rates (i.e. copulation attempts per female-hour, regression: $F_{1,7}=0.05$, $P=0.82$, $r^2=0.0$) or in average morphological characteristics of territorial males (condition: $F_{1,7}=1.0$, $P=0.35$, $r^2=0.15$; body size: $F_{1,7}=0.38$, $P=0.56$, $r^2=0.06$). However, the number of slow copulation attempts per female, a measure of the stimulation or attention males provide for females, did increase with lek size ($Y=0.11[\pm 0.02]+0.02[\pm 0.007]X$, $F_{1,7}=6.5$, $P=0.04$, $r^2=0.48$; Fig. 8a). Similarly, the mean number of copulations per male per mean number of females, a measure of the readiness of females to mate, increased with lek size ($Y=-0.68[\pm 0.60]+0.49[\pm 0.16]X$, $F_{1,7}=9.3$, $P=0.02$, $r^2=0.57$; Fig. 8b). These two factors were positively correlated with each other ($Y=-1.81[\pm 1.18]+16.17[\pm 6.64]X$, $F_{1,7}=5.9$, $P=0.04$, $r^2=0.46$; Fig. 8c). Finally there was no significant variation in the sex ratio among female-sized iguanas found on lek and single territories during the 1994–1995 breeding season (data from four leks and two single territories, $P>0.05$).

Comparison of territories and non-territorial areas

Female-sized iguanas appeared to move freely between male territories within leks. They were, however, more likely to experience copulation attempts outside territories (65% of 153 copulation attempts) than inside (10% of 264 copulation attempts; $\chi^2=138$, $df=1$, $P<0.001$). Receptive and unreceptive females (determined by whether or not they mated and nested) and female-sized sneaker males always attempted to escape and usually freed themselves from chase copulation attempts. In the 1992–1993 season, chase copulation attempts were significantly less successful (cloacal contact) (12 of 664, 1.8%) than sidewalk copulation attempts (129 of 1698, 7.5%; $\chi^2=25.25$, $df=1$, $P<0.001$, total $N=2362$).

Single female-sized iguanas outside territories always moved at least five body lengths away from a male after a copulation attempt, whereas female-sized iguanas on territories retreated less often (Table IV). Female-sized iguanas adjusted their reaction to the mode of copulation attempts: 75% moved away after chase copulation attempts ($N=24$), but only 32% after slow copulation attempts ($N=44$; $\chi^2=11.6$, $df=1$, $N=68$, $P<0.001$).

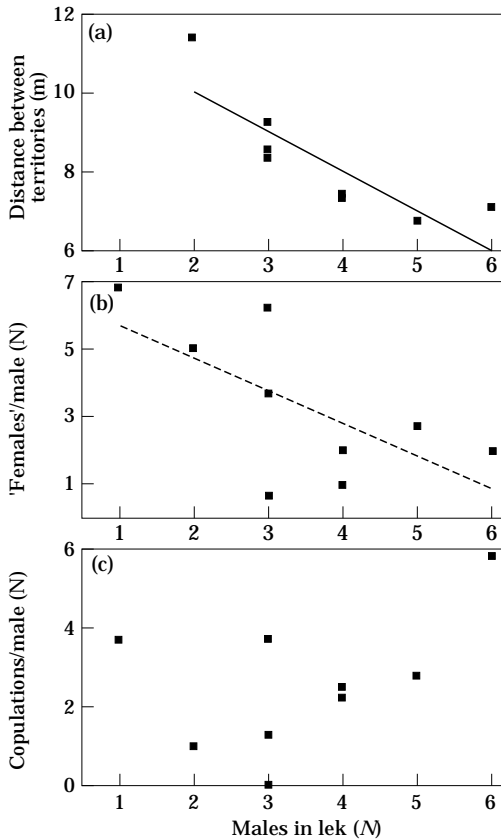


Figure 5. Comparison of (a) distance between territories, (b) female-sized iguanas per male and (c) copulations per male for different-sized leks of marine iguanas on Genovesa island during the 1992–1993 mating season. Males occupying single territories were included as ‘leks of size 1’ except in (a). Lines represent regression lines (dashed line indicates a close to significant relationship). Each point represents the mean for one lek.

DISCUSSION

Previous studies have suggested that marine iguana males defend rocky areas which are micro-climatically suitable for females and, therefore, the mating system should be described as resource defence polygyny (Trillmich 1983; Trillmich & Trillmich 1984; Rauch 1985). However, these studies were conducted near maximal animal densities and this limited the potential to assess male distributions with respect to differences in micro-climate.

After a dramatic decline in population size, we examined the factors leading to an observed

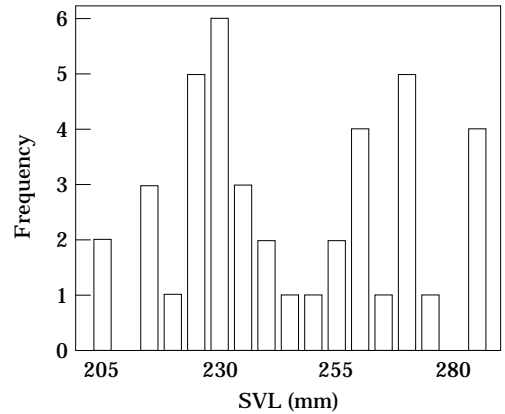


Figure 6. The distribution of body sizes of territorial males during the 1992–1993 mating season on Genovesa island. Territorial males could be separated into large (snout-vent length, SVL > 240 mm) and small territorial males (SVL ≤ 240 mm). The bimodal distribution is probably due to a different representation of age cohorts in the population.

clustering of male territories and the aggregation of females on these areas, both for mating purposes. This phenomenon is generally viewed as lekking (Bradbury 1981; Kirkpatrick & Ryan 1991; Williams 1992). The clustering of territorial males did not appear to be determined by the thermal properties of these areas. During the onset of the mating season iguanas abandoned several formerly occupied areas that had similar micro-climates to the sites containing clusters of territories. To explain the processes that result in clustering, we pose four questions. (1) Why are females more gregarious during the mating season? (2) Why do males hold small resource territories rather than maximize resource coverage (the latter would be expected from a resource-defence polygyny)? (3) Why do these territories become clustered? (4) What are the mechanisms behind clustering and how do females influence the mating pattern? Finally, we place this first reptilian lek in the framework of lek evolution by discussing its peculiarities.

Female Gregariousness during the Mating Season

Female distributions were more clustered during the breeding season than before and afterwards. After the mating season, clusters dispersed and the post-mating distribution closely matched

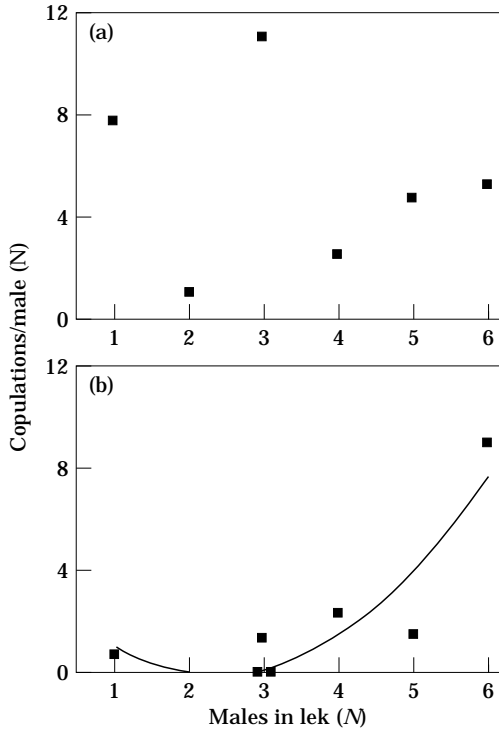


Figure 7. The mean number of copulations per male in leks of different size separated for (a) large and (b) small males.

that during the pre-mating season (Figs 1, 2). We demonstrated the seasonal change in the tendency to cluster by manipulating the location of groups of female-sized individuals through the use of model iguanas (cf. Clutton-Brock & McComb 1993; McComb & Clutton-Brock 1994). The number of individuals settling near the models was significantly higher during the breeding season than afterwards.

There are several non-exclusive explanations for this phenomenon. First, although there was no measurable thermal resource on clusters, female decisions may still have been somehow influenced by ‘resources’ (e.g. by territory topography or environmental disturbance). Second, reduced harassment might explain clustering. Outside territories, females were exposed to a high frequency of chase copulation attempts by marginal males and this suggests that female-sized individuals may use male territories as a place of refuge (Clutton-Brock et al. 1992, 1993; Clutton-Brock & McComb 1993, McComb & Clutton-Brock 1994).

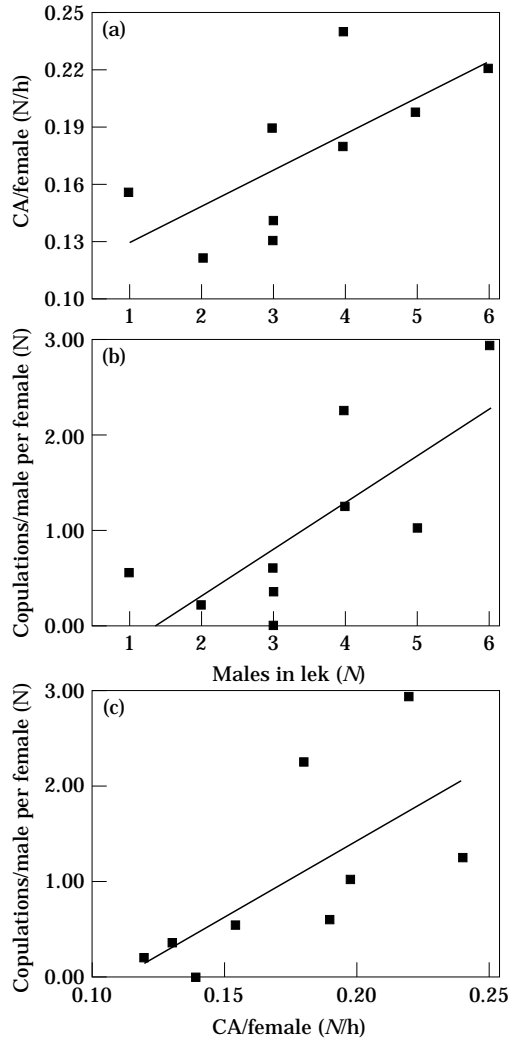


Figure 8. Comparison of (a) rate of copulation attempts (CA) per female, (b) number of copulations per male per mean number of females, for different-sized leks of marine iguanas on Genovesa island during the 1992–1993 mating season; (c) shows the relationship between both dependent variables from (a) and (b). Males occupying single territories were included as ‘leks of size 1’ in (a) and (b). Each point represents the mean for one lek. (a) can be interpreted as ‘male attention towards females’, (b) as ‘female readiness to mate’; (c) shows that both are interrelated.

However, as there was no difference in the levels of harassment in lek and single territories, harassment per se cannot be the mechanism behind the clustering of male territories in this species

Table IV. Comparison of reproductive behaviour of female-sized iguanas on Genovesa island during the 1992–1993 mating season

	Single females	Females in groups	<i>P</i>
Copulation attempts/(female-hour)	1.75 ± 0.44 (153)	0.15 ± 0.26 (264)	<0.001
Move after copulation attempt	97% (33 of 34)*	2% (2 of 87)†	<0.001 for both
Disruption of copulation	54% (22)	2% (49)	<0.001

*Following copulation attempts, single female-sized iguanas most often moved away from the male; they moved equally likely into crevices or joined groups ($\chi^2=15.7$, $df=2$, $P<0.001$, $N=34$).

†Females in groups hardly ever moved out of groups after a copulation attempt ($\chi^2=75.8$, $df=2$, $P<0.001$, $N=87$), but sometimes joined larger groups.

(Carbone & Taborsky, in press; but see also Clutton-Brock & McComb 1993; Clutton-Brock et al. 1993). Finally, females might be attracted to, and thus congregate because of, certain qualities of territorial males (Bradbury & Gibson 1983; Bradbury & Andersson 1987). This might explain the high skew in mating success, characteristic of all lek mating species, which we also found in marine iguanas (cf. Wiley 1991; MacKenzie et al. 1995). Male body size and condition seemed the predominant factors determining mating success (Fig. 3), although it is usually difficult to separate the influence of several factors on individual success in leks (Apollonio et al. 1989; McKaye et al. 1990; Balmford et al. 1992). We discuss the female decisions in more detail below.

Resource Territories, Display Territories and Mating Tactics

Thermal resources seemed to be relatively uniformly distributed throughout the suitable habitat so that there was no need for males to defend a specific area within this habitat. Rather, males congregated around some, but not around all, of the 'hotspot' routes towards the feeding areas (Bradbury et al. 1986; but see Balmford et al. 1993). These areas might be important as initial nuclei at which males, especially those that seasonally migrate from very distant foraging areas towards these leks, are more likely to gather or meet.

Once in the mating area, mating tactics depended on the size and territory status of the individual male (as in many other lekking species, Clutton-Brock et al. 1988, 1992; Wiley 1991). Males established territories and defended these sites against intruding males (Table I). During the

mating season, territorial males seldom left their territories and so fasted for long periods (Trillmich 1983; Dellinger 1991). Territorial males predominantly approached females slowly and the females usually terminated the display. Marginal males occasionally established temporary territories away from territorial males, but did not succeed in attracting other iguanas to these sites. They mostly stayed near territorial males and frequently chased females in an attempt to mount them (chase copulation attempts). Female-sized sneaker males attempted to sneak copulations with similarly sized individuals within territories (cf. Crews 1983; Taborsky 1994). The iguanas seemed unable to distinguish the sex of female-sized individuals and both sexes were subjected to slow and chase copulation attempts. The inability to distinguish female-sized males from females was an important factor limiting the success of males using sneak and chase copulation attempts.

Marginal and female-sized males nevertheless achieved some copulations (as in most species, Thirgood 1991; Wiley 1991). In years of high population density, when all suitable mating areas are occupied by territorial large males, marginal males may experience lower copulatory success (see e.g. Trillmich 1983; Rauch 1985; Laurie 1990; Dellinger 1991; Wikelski & Bäurle 1996).

Clustering of Territories

Why do the display territories become clustered in a habitat where space would clearly allow the separation of all territories? To answer this question, we compared the properties of single territories with those of lek territories. There was no difference in the size of lek and single territories but territories in larger leks were smaller (cf.

Gosling & Petrie 1990). The number of fights per male was not affected by lek size. However, there was a non-significant tendency for the number of females per male to decline with increasing lek size (Fig. 5b). Large territorial males occupying single or lek territories had similarly high mean mating success. In contrast, the number of copulations for small territorial males increased with lek size (Fig. 7). A similar effect was recently found in ruffs, *Philomachus pugnax* (Widemo & Owens 1995). The fact that small territorial males had higher per male mating success in larger leks could be explained in two ways.

(1) Males of higher competitive ability are associated with large groups, which in turn leads to higher reproductive success, as found in several other lekking species (e.g. black grouse, *Tetrao tetrix*: Alatalo et al. 1992, ruff: Höglund et al. 1993; Hovi et al. 1994). In this model, females select not for male characteristics, but for larger clusters of males, thereby gaining access to males of higher quality as a side-effect. Under this scenario, males might arrange themselves in a manner reminiscent of an ideal free distribution for unequal competitors (Parker & Sutherland 1986). However, the ideal free model would predict that large males would also do better in clusters than alone, which was not supported by our data. Several other studies also did not find this effect (Lill 1976; van Rhijn 1983; Bradbury et al. 1989; Deutsch 1994b).

(2) Females preferred to mate with large territorial males, but small territorial males in clusters got some accidental matings. This finding, that large males do well regardless of lek size, but small males do well only on large leks supports Beehler & Foster's (1988) hotshot model of lek evolution. One should, however, bear in mind that the sample size for comparing leks was low, which reduces the power of statistical tests.

Female Mating Decisions and Mechanisms of Clustering

Does the mating success of small territorial males on larger leks increase because they are more able to procure these copulations or do females induce this effect? It appeared that females had a high degree of control over paternity, suggested by the fact that most chase copulations by marginal males failed (see also Gowaty 1994). Females rejected such copulation attempts by

struggling free or by resisting cloacal contact. A female's ability to resist such copulation attempts may also be related to the morphology of the hemi-penis which is not well suited for forceful intromissions (Arnold 1984; Tokarz & Slowinski 1990; Tokarz & Kirkpatrick 1991). Females seemed to prefer matings with large (territorial) males and responded to their copulation attempts more often than to those of non-territorial males (Bradbury et al. 1985). As yet we do not have the data to determine whether the age of the males or the behaviour of individual males towards individual females might affect the female's decision to mate (cf. McDonald 1989).

While mating success was highest in large territorial males, the number of copulations per male was not affected by lek size in these males (Fig. 7). This was surprising in light of the fact that the proportion of female-sized iguanas tended to decline with lek size. The decline in the relative number of female-sized individuals, however, was compensated by an increase in the tendency of females to mate on large leks, a situation similar to black grouse leks (Alatalo et al. 1992). As the sex ratio of female-sized iguanas did not seem to vary with lek size, this may be due to an increase in the frequency of slow copulation attempts. Among small territorial males, copulatory success was low for all lek sizes, but the increase in mating success with lek size overcompensated for the reduction in relative number of female-sized individuals. This suggests that small territorial males may benefit from clustering because females are more likely to mate with them under these conditions, while large males perform roughly the same for all lek sizes (Beehler & Foster 1988).

Reptilian Lek

The marine iguana lek on Genovesa island shares a number of characteristics with leks of different taxa: single matings of females (e.g. fallow deer, *Dama dama*: Clutton-Brock et al. 1988; Apollonio et al. 1989), (terrestrial) ectotherm limitations on performance during certain (e.g. day-) times (Svensson & Petersson 1987, 1988; Bourne 1992), intense harassment of females by marginal males (e.g. fallow deer: Clutton-Brock et al. 1993; Kafue lechwe, *Kobus leche kafuensis*: Nefdt 1995) and the existence of single territories in addition to clustered territories (e.g. kob: Leuthold 1966; topi: Gosling & Petrie

1990; lechwe: Schuster 1976; Nefdt 1995; fallow deer: Apollonio et al. 1992). This system is also characterized by a long territory tenure of a month or more (see also lechwe: Nefdt 1995), the absence of predation (e.g. Balmford & Turyaho 1992; Deutsch & Weeks 1992) and the failure of males to distinguish (visually) female-sized males from females and unreceptive from receptive females (Table I, cf. Trail 1990; for a possible role of chemoreception in reptiles see Alberts & Werner 1993; Schwenk 1993; Cooper 1994). In other studies predation risk may have led to clustering of territories (cf. Balmford & Turyaho 1992) but there is (and was) no predation on marine iguanas in Genovesa.

It seems likely that the following scenario for the evolution of leks applies in marine iguanas. Males defend territories in areas where females rest, which is usually close to inter-tidal feeding resources. Therefore, territories can be small since they do not contain resources such as food. Females prefer to mate and probably also to rest in territories rather than outside them because they are not harassed in territories. They also prefer large males, perhaps because these harass them less, keep out juveniles more effectively or have better genes. Large males might also be a more sure bet, because they are usually very old and thus tested by time. The main cause of territory clustering seems to be that smaller, less preferred males establish territories nearer to larger males to enhance their mating success, which supports the hotshot model (Beehler & Foster 1988). Our results suggest females might drive clustering because the high frequency of slow copulation attempts on leks makes them more ready to mate. The intricacies of female mating decisions still remain to be determined.

ACKNOWLEDGMENTS

We thank A. Türk, A. Sanchez, B. Gall, D. Schütz, G. v. Hegel, G. Betzl, J. Guayman, J. Garcia, K. Ueberscheer, M. Oltrogge, M. Hau, S. Bäurle and T. Wikelski for invaluable field assistance. Special thanks to E. Connors, P. Whelan, F. Walsh, V. Carrillo and J. Partecke for field assistance and saving M.W.'s life during a cholera epidemic. We thank the Galápagos National Park Service (A. Izurieta and F. Cruz), the Charles-Darwin Research Station (D. Evans,

C. Blanton, L. Chellis), Metropolitan Touring through the yacht Isabela II and TAME for enabling this work; E. Ott and S. Layer for providing communication; S. Emlen, R. Alatalo, J. Höglund, S. Daan, H. Hofer, M. East, M. Hau, M. Taborsky, R. Weinzierl, R. Diesel, T. Mejer, N. Michiels, R. Bshary, P. Bednekoff, S. Choudhury, S. Tebbich and especially J. Deutsch, R. Dunbar and an anonymous referee for comments on the manuscript; B. Knauer and H. Geissler for preparing figures. Special thanks to W. Wickler for continuous moral and financial support and the 'WC'-round for discussions. This is contribution no. 528 of the Charles-Darwin-Foundation and was supported by the Deutsche Forschungsgemeinschaft grant Tr 105/7 and the European Capital and Mobility grant 'Ecology and Evolution of Mating Aggregations' to F.T., a Royal Society grant to C.C. and a Feodor-Lynen and a Smithsonian fellowship to M.W.

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