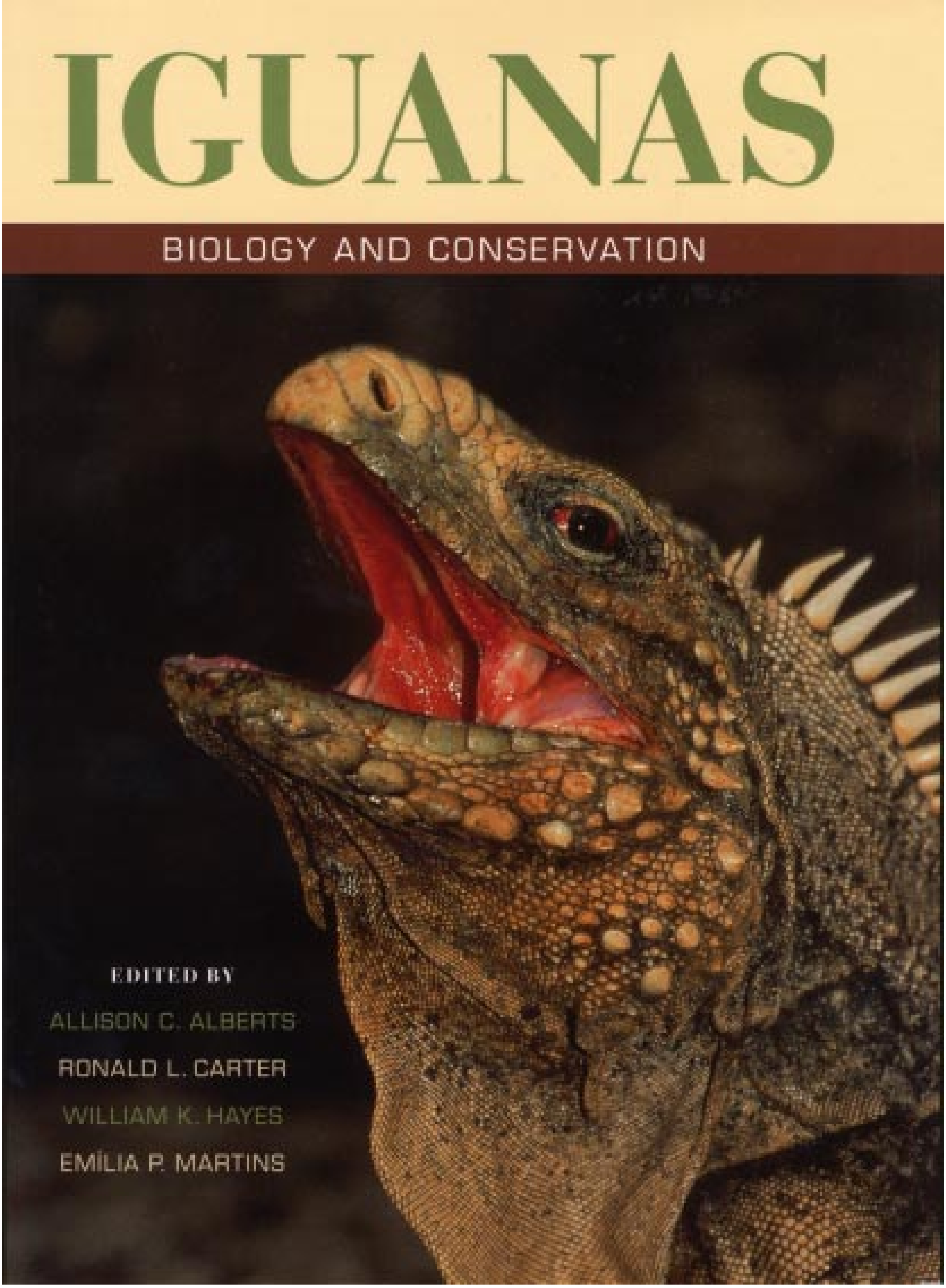
Excerpted from



IGUANAS

BIOLOGY AND CONSERVATION

EDITED BY

ALLISON C. ALBERTS

RONALD L. CARTER

WILLIAM K. HAYES

EMÍLIA P. MARTINS

©2004 by the Regents of the University of California. All rights reserved.
May not be copied or reused without express written permission of the publisher.

click here to
BUY THIS BOOK

10

Determinants of Lek Mating Success in Male Galápagos Marine Iguanas

BEHAVIOR, BODY SIZE, CONDITION, ORNAMENTATION, ECTOPARASITE LOAD, AND FEMALE CHOICE

William K. Hayes, Ronald L. Carter,
Martin Wikelski, and Jeffrey A. Sonnentag

MARINE IGUANAS *(Amblyrhynchus cristatus)* live in large aggregations along the rocky coastlines of the Galápagos Islands. They are unique among reptiles in that they forage almost exclusively on macrophytic algae in the intertidal and subtidal zones (Trillmich and Trillmich, 1986; Wikelski et al., 1993; Wikelski and Hau, 1995). They exhibit a lek mating system in which males cluster during the mating season and defend small, symbolic territories devoid of material resources other than sperm (Wikelski et al., 1996, 2001). These leks (clusters of territorial males) occur in the supratidal zone of the rocky coastline, where females also aggregate, presumably to select a male to mate. Sexual dimorphism, which is often exaggerated in species exhibiting lek mating (e.g., Höglund and Alatalo, 1995), is substantial in marine iguanas. Males attain a body mass that is severalfold greater than that of females (Trillmich, 1983; Laurie, 1989; Wikelski and Trillmich, 1997) and acquire richly colored hues on the dorsum during the mating season, as do females during the egg-laying season (Carpenter, 1966).

BODY SIZE, ALTERNATIVE MATING TACTICS, AND FEMALE CHOICE

Alternative mating tactics often evolve in polygynous (e.g., Taborsky, 1994) and lek-mating (e.g., Höglund and Alatalo, 1995; Lanctot et al., 1998) species and are well developed in the marine iguana. Body size is an important determinant of the mating tactics employed by male marine iguanas, and may also be an important criterion for female choice (Trillmich, 1983; Trillmich and Trillmich, 1984; Rauch, 1985; Wikelski and Bäurle, 1996; Wikelski et al., 1996, 2001). Only the largest males in good condition become territorial (lekking) males, which establish and defend territories within clusters of other males (leks). Satellite males of intermediate size roam near these territories, but are excluded from them. Satellite males, therefore, court and seek to copulate with females outside of the territories. Sneaker males are smaller yet, resembling females in size. They frequently intrude on territories and are generally inconspicuous unless they display to females or attempt copulations in the presence of the territorial male. Whereas the larger territorial males are slow and deliberate when copulating, satellite and sneaker males appear to use force to achieve copulations. Because territorial males quickly disrupt copulations by sneaker males within their territory, the sneaker males often utilize sperm stored in their hemipenis pouches via precopulatory masturbation to more quickly inseminate females (Wikelski and Bäurle, 1996). So strong is sexual selection on male body size in this species that it frequently drives body size beyond naturally selected limits, at which, during unfavorable environmental conditions (such as El Niño events), males become too large to survive (Laurie, 1989; Laurie and Brown, 1990a; Wikelski and Trillmich, 1997; Wikelski and Carbone, this volume).

There is substantial skew in mating success among male marine iguanas, with the largest individuals achieving the greatest number of copulations (Trillmich, 1983; Wikelski et al., 1996). However, the extent to which male-male competition (intrasexual selection) or female choice (intersexual selection) leads to the size-related skew in male mating success is unclear for lizards in general (Olsson and Madsen, 1998) and difficult to ascertain. Although females of lek-mating species are widely assumed to exercise a degree of female choice, it remains unclear how a female would benefit by choosing particular males at a lek. The notion that benefits must exceed the costs associated with female choice has become recognized as the "paradox of the lek" (Wiley, 1991; Williams, 1992; Kotiaho et al., 2001). Because males of lek-mating species offer females no material benefits (such as a high quality territory that is rich in resources), one resolution of the paradox is that females obtain higher quality offspring by preferentially mating with males with higher quality genes (Höglund and Alatalo, 1995). Even if the genetic benefits are small, the paradox can be resolved if the costs of female choice are especially low (Kotiaho et al., 2001).

Several features of the lek mating system of marine iguanas suggest that this species is an ideal organism for the study of female choice. To our knowledge, female choice has been demonstrated in only four species of lizards, including *Eumeces laticeps* (Cooper and Vitt, 1993), *Ameiva plei* (Censky, 1997), *Psammodromus algirus* (Martín and Forsman, 1999), and the marine iguana (Wikelski et al., 2001). Female choice is apparently rare in lizards because: (1) males of most taxa are dispersed and occupy relatively large home ranges (or defend relatively large territories) containing resources beneficial to females; (2) home ranges of females typically overlap with only a few males, which limits opportunities for and elevates the cost of comparison of males; (3) female choices for mating are usually based on male territory attributes rather than phenotypic qualities; (4) male phenotypic traits, such as coloration, are often unreliable indicators of male quality; and (5) many females seek multiple copulations by which they can gain genetic benefits without incurring the cost of female choice (see, e.g., Stamps, 1983; Hews, 1993; Olsson et al., 1994; Olsson and Madsen, 1995; Baird et al., 1996; Abell, 1997; Gullberg et al., 1997; Zamudio and Sinervo, 2000; LeBas, 2001). For these reasons, differences in male mating success are usually best explained by male-male competition. However, circumstances are very different within the lek mating system of marine iguanas. Because the largest males are clustered and occupy small, symbolic territories that lack material resources, females that visit leks have ample opportunity to sample a number of males at relatively low cost (Wikelski et al., 2001). Moreover, female options for seeking multiple paternity are limited because their clutch size is comparatively small (one to six), they become unreceptive after mating, they appear to mate only once during the season, and they do not store sperm between seasons (Carpenter, 1966; Boersma, 1983; Wikelski and Bäurle, 1996; Wikelski et al., 1996). Consequently, sperm competition and multiple paternity may be negligible.

If female choice exists in marine iguanas, what criteria might females use to evaluate male quality? Because so many possible criteria exist, it is challenging to identify those that are most relevant. The existence of alternative mating tactics suggests that size is important, but male quality could be assessed by females in a variety of ways. In addition to the overall appearance of size (e.g., body mass and/or snout-vent length), certain male characters such as head width, size of limbs, or tail length may be reliable indicators of male fitness. The lengths of nuchal and dorsal spines are associated with body size, but they could be regarded as ornaments and therefore subject to evaluation by females. Several factors other than size might also reflect male quality. The vigor or frequency of courtship behavior, including headbobbing displays, may be evaluated. Because body coloration is at least partially dependent on diet (M. Wikelski, unpubl. data) and may be indicative of feeding success, certain qualities of male coloration may be assessed. Level of ectoparasite infestation may also be a useful indicator of male fitness, especially if it reflects a level of genetic resistance that can be conferred upon offspring (Hamilton and Zuk, 1982).

The primary objective of this study was to evaluate the contribution of multiple characters (behavior, body size, condition, ornamentation, ectoparasite load) to relative mating success (inferred from association with females) in a large population of male Galápagos marine iguanas. We also inferred those criteria by which females potentially assess male quality and choose with whom to mate.

METHODS

FIELD SITE

The study was conducted during the mating season of January 1997, on the 4.3 ha islet of Caamaño, just off the southern shore of Isla Santa Cruz, Galápagos. Up to several thousand iguanas reside along the 880 m of coastline, although numbers decline subsequent to El Niño events. During 1997, the population size was unusually large (more than one thousand adults). To facilitate our studies, thirteen sectors were marked along the shoreline, each roughly 60–80 m in length. Iguanas in this population were studied previously by Trillmich (1983), who described additional features of the islet and its ecology.

A unique aspect of this population is that the majority of territorial male iguanas do not reside permanently on Caamaño, but instead swim to the islet from the coastline of Santa Cruz over 500 m or more of open sea. Large males begin to arrive on Caamaño in November and December, several weeks or more in advance of the breeding season, and promptly displace the smaller males of the local population to establish their own lek territories (Trillmich, 1983). Once the breeding season ends in early February, these large males swim back to the coast of Santa Cruz.

MORPHOLOGICAL AND ECTOPARASITE MEASUREMENTS

We captured by noose or hand nearly all of the large male marine iguanas that were observed displaying territorial behavior along the coastline ($n = 234$). For each male, we measured snout-vent length (SVL; nearest mm), head width (widest point of head behind the eyes; nearest 0.1 mm), length of left hindleg (from mid-sagittal ventral plane to base of second toe with leg held perpendicular to body; nearest mm), tail length (from cloaca to tip; nearest mm), and length of longest nuchal and dorsal spines (nearest 0.1 mm). Body mass was determined from Pesola scales to the nearest 0.01 kg. Body condition, a relative measure of fatness, was later calculated from the ratio of body mass ($g \times 10^6$) divided by SVL^3 (see Laurie, 1989). Although this variable relates two interdependent variables and therefore is mathematically equivocal (Krebs and Singleton, 1993), it has been shown to make biological sense in marine iguanas (Laurie, 1989; Wikelski et al., 1996; Wikelski and Trillmich, 1997). We use it here, despite its problems, to make our results comparable with previous publications. We also recorded the number of ticks (presumably *Amblyomma* spp.; Wikelski, 1999) counted on the entire body, and the relative density of mites (undetermined species) using a scale of one to four, with four representing the highest level of mite infestation. Additionally, we collected blood samples from each male for future paternity evaluation of offspring. Unfortunately, because of the unexpectedly large number of adult iguanas (more than one thousand) and hatchlings captured subsequently (490), paternity analyses were not completed.

Each iguana was assigned a number and marked permanently on the chest and both sides of the dorsum by heat branding (Wikelski et al., 1996). To facilitate behavioral observations, we also wrote the number on each side of the dorsum with enamel paint and dabbed additional paint on the crown and nuchal spines. These temporary markings did not appear to influence iguana behavior and gradually wore off within several months (Hayes et al., 2000).

Although most territorial males were captured in the first week of January, others were captured during the following weeks, when we observed additional unmarked males exhibiting territorial behavior. We assumed the latter males were more recent arrivals from the mainland of Santa Cruz (compare Trillmich, 1983). We estimate that we captured 90% or more of the territorial males present on Caamaño during the month of January.

During the month of February, as lekking activities quickly declined, a number of males began to depart Caamaño. Some were observed from a boat as they swam across the channel to Santa Cruz. By March, most marked males were gone. When we returned to Caamaño in May, we recaptured nearly all of the remaining marked males (during the period 20 May–11 June) and resampled their body mass and ectoparasite infestations. Several marked males, whose identities were uncertain, eluded recapture. We assumed that all males recaptured in the May/June period were residents of Caamaño and that all nonrecaptured males were from Santa Cruz.

SCAN SURVEYS OF LEKKING ACTIVITIES AND PROXIMITY TO FEMALES

In this study, the large sample of marked territorial males allowed us to evaluate the complex relationships between male body size, male territorial behavior, association with females, body condition, ornamentation, and ectoparasite infestation.

Up to five times per day, usually at mid-morning or mid-afternoon, we employed momentary behavioral scans to survey the behavior of the entire population of marked male iguanas. Multiple surveys on a single day were conducted by up to four independent observers or were separated by several hours. For each marked iguana sighted during a survey, we recorded (1) the proximate behavior exhibited by the male (i.e., the first behavior observed), and (2) the number of females counted within a 1 m radius of the male (territories on Caamaño vary from 1.2 to 38.8 m^2, with a median of 10.5 m^2 at the height of mating season; Trillmich, 1983). To help us ascertain departures from the lek area, we also recorded the sector along the beach for each observation.

Male behaviors were ranked according to relative level of territorial activity as follows:

1. Rest (supine or supine with head up);
2. Headbobbing, headbobbing with mouth open, or walking;
3. Copulatory attempt (a side-walking approach toward a female to bite and grasp her by the neck) or agonistic behavior toward other males (chases and fights); and
4. Copulation with a female (which commences after a female has been grasped by the neck).

Time allocated to each of these behaviors was inversely proportional to the rank score, that is, rest was exhibited most often (75.5% of 5115 observations in the final data set) and copulations least often (0.5%). The natural sequence of behavioral acts corresponds to levels 1–3 for intrasexual (agonistic) interactions, and 1–4 for intersexual (courtship) interactions. We gave equal weight to agonistic behavior and copulatory attempts (a score of 3) because both are preceded by headbobbing and/or walking, and our momentary scans generally did not allow us to determine outcomes in either case (e.g., successful defense of territory or successful copulation).

A total of forty scan surveys were conducted during the period 11–28 January. A small percentage of males was always missed during any given survey, especially those that were less aggressive and more often retreated to shade beneath the rocks. On occasion, a survey was interrupted and the entire coast was not covered. As the weeks passed, increasing numbers of males were also missed during surveys after they gave up their territorial behavior and began to wander along the coastline (where they were sometimes seen to forage) or into the interior of the island. Thus, sample sizes for repeated observations of individual males were variable.

Based on the behavioral scans, we derived two dependent measures that represented the relative quality and mating success of individual males. For territorial males represented by ten or more observations ($n = 213$), mean behavioral scores were computed to give each male a territorial behavior score that we interpreted to be indicative of male quality. Likewise, the mean number of females within a 1-m radius was also calculated for each male to assign a value for proximity to females. Because our island-wide surveys were unsuitable for quantifying copulations among individuals (no males were observed to copulate more than once during the momentary scans), we relied on the mean number of females in close proximity as an index of relative mating success. We also regarded association with females as an indicator of potential female choice. For many species, behavioral traits such as male display activity, display rate, aggression rate, and lek attendance are positively correlated with male mating success (e.g., Hews, 1993; Höglund and Alatalo, 1995; Fiske et al., 1998) and are therefore indicative of male quality. Wikelski et al. (2001) found that female marine iguanas in another study population (Isla Santa Fé) preferentially copulated with the male that had the highest display rate of all males visited. Because copulations are often difficult to observe in lizards, association with females is widely used as an index of probable mating success (e.g., Cooper and Vitt, 1993; Baird et al., 1996; Bull and Pamula, 1996; Abell, 1997; Gullberg et al., 1997; Salvador and Veiga, 2001).

ANALYSES

All statistical analyses were conducted using SPSS for Windows software (SPSS, Chicago, Illinois; release 8.0, 1997). Correlation analyses were performed for measures of relative male quality (mean behavioral score), relative mating success (mean number of females in close proximity), body size, body condition, ornamentation size, and ectoparasite infestation. Due to some missing values, bivariate correlations were based on varying sample sizes that ranged from 208 to 213. Pearson correlation coefficients (r) were calculated for all variables except those involving body condition and ticks. Because body condition and ticks were not normally distributed, Spearman correlation coefficients (rho) were calculated for these variables. Because of the large number of variables in the analyses and the consequent high experiment-wise error rate, we considered correlations at the 0.05 and 0.01 level of significance to be of marginal importance and used caution when making interpretations. However, correlations at the 0.001 level were regarded as highly meaningful (an adjustment of α for 66 tests gives a critical P of $0.05/66 = 0.00076$).

The correlation analyses raised important questions of cause and effect in the complex relationships between male behavior, number of nearby females, body size, body condition, ornamentation, and ectoparasite load. For example, do females prefer males because of their larger size, their more active behavior, their reduced ectoparasite load, or a combination of these characters? Is male territorial activity (behavioral score) related directly to body size or an indirect response to the number of females present? We used three approaches to tease apart these relationships. First, partial correlation analyses allowed us to evaluate certain relationships by controlling for one variable at a time. Second, multiple linear regression (using SPSS procedure STEPWISE, with probability of F to enter ≤ 0.05) was used to identify which set of independent variables best explains variance in the two dependent variables: male behavior and number of females in close proximity. In the first regression analysis, behavioral score was regressed against the full set of independent variables, including number of females in close proximity and measures of body size, body condition, ornamentation, and ectoparasite load. In the second regression analysis, number of females in close proximity was regressed against the full set of independent variables, including behavioral score and measures of body size, body condition, ornamentation, and ectoparasite load. Although we expected problems arising from multicollinearity in both regression analyses, body mass was the only variable in each analysis with a tolerance level < 0.20 (after head width was entered), and it was among the variables excluded by STEPWISE from the final regression models. Thus, we concluded that multicollinearity was minimal. Body condition and number of ticks were normalized by rank-transformation prior to partial correlation and regression analyses.

For the third approach, we used principal component analysis (PCA) in conjunction with regression analysis. This approach has been widely used for analysis of multiple phenotypic variables (e.g., Lande and Arnold, 1983; Hews, 1990; Abell, 1997; LeBas, 2001). It offers some advantages over inclusion of all variables in regression analysis, primarily by eliminating problems of multicollinearity (which did not plague our data set), by accommodating small samples relative to the number of independent variables (which was unnecessary with our data set), by pooling sets of related variables into common factors, and by avoiding the use of stepwise procedures (see comments below). We conducted two analyses to evaluate separately the two dependent variables. First, we regressed behavioral score against the factor scores from the four components extracted by PCA from a correlation matrix that included number of females, all measures of body size, body condition, both measures of ornamentation, and both measures of ectoparasite load. Second, we regressed number of females against the factor scores from the four components extracted by PCA from a correlation matrix that included behavioral scores, all measures of body size, body condition, both measures of ornamentation, and both measures of ectoparasite load. To extract the factors using SPSS, we applied the Kaiser criterion to decide the number of components to keep (those with eigenvalues ≥ 1.0) and used Varimax rotation to more clearly differentiate the factor loadings of each variable on a given factor. Following standard protocol (e.g., Lande and Arnold, 1983), variables were natural-log transformed prior to analyses; however, normality for body condition and longest nuchal spine was better achieved by square-root transformation. For these analyses, we entered all four principal components into each of the two regression models (i.e., we did not use stepwise procedures). Thus we used stepwise procedures for regression of the full set of independent variables but not for regression of the principal components.

We recognize that selection of a regression model based on theoretical reasons is generally preferred to reliance on a computer algorithm (stepwise procedures) for deciding which independent variables to include. However, we chose to use stepwise procedures for analyses of the full set of independent variables based on the following rationale. First, the inclusion of excessive independent variables usually results in a model trained to noise rather than to biological reality. Thus, a model must be subjectively chosen that includes only a subset of the independent variables. Second, with the sheer number of independent variables available for analysis, we wanted to use objective criteria (partial correlation values, as utilized by stepwise procedures) in the selection of a subset of independent variables to include in a model. Third, as one theoretical approach to selection of independent variables, we examined supplemental regression models that included the one independent variable within each category (behavior score or number of females, body size, body condition, ornamentation, ectoparasite load) that showed the strongest correlation with the dependent variable. In reality, our choice of independent variables was based on criteria similar to the stepwise procedures. The conclusions were identical to stepwise results, although the resulting models, which arbitrarily excluded some variables with high correlations and included more variables overall, did not provide significantly better fits. Finally, we concede that our analyses are exploratory in nature, regardless of the procedures used to select a model. At best, we can show associations between variables, from which we can only predict that a causal relationship exists.

Several tests were used to evaluate population changes in lekking activities as the season progressed. Linear regression allowed us to test for independent declines in behavioral scores, numbers of females in close proximity, and copulation rates (copulations observed per 100 behavioral observations). The relationship between body size (mass) and lek departure dates (the last day an iguana was recorded from the sector of its lek) was examined by Spearman correlation and by a Mann-Whitney *U* test comparing early (before 26 January, the last date on which multiple surveys were taken) versus late (after 26 January) departures, with the one-tailed hypothesis that early departing males had less body mass than did late departing males. Because cessation of lek behavior was difficult to detect unless the iguana left its sector, our estimates for departure dates were deemed conservative. For example, some iguanas may have given up lekking activities but remained in close proximity to their lek, thereby being recorded in the same sector. Moreover, many of the iguanas with fewer than ten observations had probably departed as well, either to the vegetation above the beaches, where many of the "bachelors" resided or perhaps back to Isla Santa Cruz, and these were excluded from our analyses.

We used two-tailed Mann-Whitney *U* tests to compare measures of body size and ectoparasite infestations of Caamaño versus Santa Cruz males. For resident males on Caamaño, which were captured and processed twice (in January and in May/June), we used two-tailed Wilcoxon matched-pairs signed-ranks tests to compare body mass and numbers of ectoparasites before and after the mating season. Territorial males are known to forego feeding during the entire mating season, which can be expected to have an impact on body mass (Trillmich, 1983) and may affect ectoparasite load as well.

RESULTS

LEKKING ACTIVITIES: CORRELATION ANALYSES

The correlation matrix of territorial activities (behavioral score), number of females in close proximity, body size (SVL, body mass, head width, hindleg length, tail length), body condition, ornamentation (lengths of nuchal and dorsal spines), and ectoparasite infestation (ticks and mites) indicated that most measures of body size, including ornamentation, showed high levels of covariance (table 10.1). SVL and body mass were significantly correlated not only with each other, but also with head width, hindleg length, tail length, and length of longest dorsal and nuchal spines (all $P < 0.01$). Although body condition was negatively correlated with SVL ($P < 0.01$) and positively correlated with body mass ($P < 0.01$), it was otherwise independent of all other morphological and ectoparasite measurements. Thus, body condition can be distinguished from all other measures of body size and ornamentation.

The dependent measures of relative male quality (behavioral score) and relative mating success (number of females) were positively correlated with each measure of body size and ornamentation (all $P < 0.01$; table 10.1). Behavioral

TABLE 10.1

Correlation Matrix for Lekking Male Marine Iguanas on Caamaño, Galápagos

	BEHAVIORAL SCORE	NUMBER OF FEMALES	SVL	MASS	HW	HLL	TL	BODY CONDITION	NSL	DSL	TICKS	MITES
Behavioral score	—											
Number of females	0.55[3]	—										
Snout-vent length (SVL)	0.39[3]	0.41[3]	—									
Body mass	0.43[3]	0.46[3]	0.90[3]	—								
Head width (HW)	0.48[3]	0.50[3]	0.88[3]	0.91[3]	—							
Hindleg length (HLL)	0.44[3]	0.43[3]	0.88[3]	0.89[3]	0.86[3]	—						
Tail length (TL)	0.35[3]	0.35[3]	0.79[3]	0.78[3]	0.76[3]	0.79[3]	—					
Body condition	0.10	0.10	–0.20[2]	0.20[2]	0.08	0.05	0.03	—				
Nuchal spine length (NSL)	0.19[2]	0.26[3]	0.44[2]	0.43[3]	0.44[3]	0.37[3]	0.38[3]	0.03	—			
Dorsal spine length (DSL)	0.24[3]	0.25[3]	0.46[3]	0.47[3]	0.49[3]	0.37[3]	0.39[3]	0.10	0.67[3]	—		
Number of ticks	–0.16[1]	–0.16[1]	0.03	0.02	0.01	0.02	0.03	0.04	0.05	0.07	—	
Number of mites	–0.16[1]	–0.14[1]	–0.19[2]	–0.15[1]	–0.17[1]	–0.13	–0.13	0.04	–0.07	–0.07	0.25[3]	—

Note: Sample size for each bivariate correlation ranges from $n = 208$ to $n = 213$.

[1] $P < 0.05$.

[2] $P < 0.01$.

[3] $P < 0.001$.

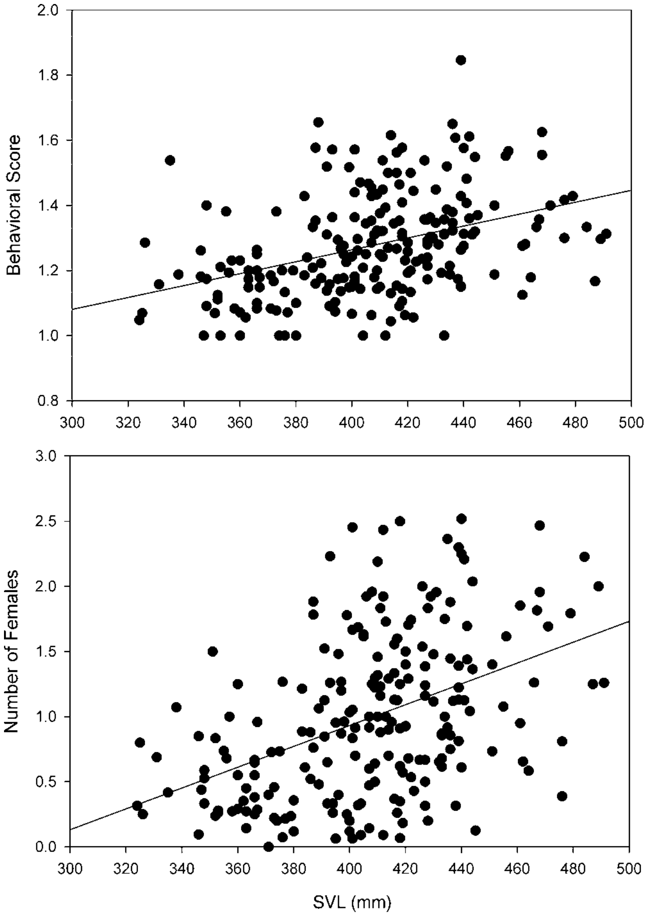


FIGURE 10.1. Relationships between male body size (snout-vent length [SVL]) and measures of relative mating success in male marine iguanas exhibiting territorial behavior. Larger males exhibited higher territorial (behavioral) scores and had more females in close proximity than did smaller males.

score and number of females were highly correlated (all *P* < 0.001; table 10.1; compare Trillmich, 1983). In contrast to measures of body size and ornamentation, body condition was not associated with either dependent measure (*r* ≤ 0.103 for both). Body mass and head width explained the greatest proportion of variance in behavioral score and number of females, although SVL and hindleg length were also highly correlated with these dependent measures. Scatterplots of SVL versus each of the dependent measures are shown in figure 10.1.

Numbers of ticks and relative numbers of mites were highly correlated (*P* < 0.001; table 10.1). However, whereas mites were negatively but weakly associated with iguana body size (*P* < 0.01 for SVL; *P* < 0.05 for body mass and head width), tick numbers were independent of body size. Neither ticks nor mites were associated with body condition. There was a negative but weak association of both ticks and mites with behavioral score and number of females (*P* < 0.05 for both).

Partial correlation analyses allowed us to examine associations among the variables apart from the potentially confounding influence of male behavior and number of females present. When controlling for number of females present (i.e., comparing males with similar numbers of females in close proximity), male behavioral scores remained highly correlated with a number of body size measures, including SVL, body mass, head width, hindleg length, and tail length (all *P* < 0.001). Hence, the higher levels of territorial activity exerted by larger males was intrinsically related to body size and not merely a

TABLE 10.2

Coefficients and Their Significance for Independent Variables in the Final Stepwise Regression Models

	COEFFICIENTS			
	B	BETA	*t*	*P*
Behavioral score = Number of females × Head width				
Number of females	0.105	0.410	6.43	0.000
Head width	0.009	0.296	4.64	0.000
Number of females = Behavioral score × Head width × Number of ticks				
Behavioral score	1.548	0.395	6.06	0.000
Head width	0.034	0.280	4.35	0.000
Number of ticks	–0.001	–0.126	–2.22	0.028

Note: Excluded from the final models were other measures of body size (SVL, mass, hindleg length, tail length, body condition, ornamentation, and number of mites).

consequence of having more females nearby. When controlling for male behavior (i.e., comparing males that exhibited similar behavioral scores), significant correlations of head width and body mass with number of females in close proximity ($P < 0.001$ for both) suggested that more females were found in the territories of larger males. Hence, the intrinsic qualities of male size were preferred by females regardless of the behaviors exhibited by males. Thus, territorial activity and number of females in close proximity were independently associated with male body size, rather than one being a consequence of the other.

LEKKING ACTIVITIES: REGRESSION ANALYSES OF RELATIVE MALE QUALITY AND MATING SUCCESS

Multiple regression analyses with inclusion of all independent variables allowed us to evaluate select male attributes that might be associated with male quality or preferred by female iguanas. The final models and their coefficients are summarized for each of the two dependent variables in table 10.2. For behavioral score, the final model included two variables—number of females and male head width ($F_{2,200} = 59.1$, $P < 0.001$)—which explained 36.5% of the variation. For number of females in close proximity, the final model included three variables—behavioral score, head width, and number of ticks ($F_{3,199} = 39.8$, $P < 0.001$)—which also accounted for 36.5% of the variance. In addition to supporting the relationship between male behavior and number of females in close proximity, these results identify male head width as the primary character of body size associated with each of the dependent variables and reveal that females associated more with males having fewer ticks (note the negative coefficient for ticks in table 10.2).

Regression analyses of the principal components gave somewhat different results. The factor loadings for each of the two dependent variables (behavioral score, number of females in close proximity) are summarized in table 10.3. In each case, four variables were extracted, and these gave components that corresponded to body size (PC1), ornamentation (PC2), ectoparasite load (PC3), and body condition (PC4). That nuchal and dorsal spines loaded independently of body size (body mass and length measurements) supports the interpretation that spines can be regarded as ornaments apart from body size. The first regression model, with behavioral score as the dependent variable, provided a significant fit ($F_{4,197} = 21.5$, $P < 0.001$) and accounted for 29.0% of the variance (table 10.4). Three of the four components were significant,

TABLE 10.3

Factor Loadings of Each Trait for Four Principal Components

TRAIT	FACTOR LOADINGS			
	PC1	PC2	PC3	PC4
PCs extracted for analysis of behavioral scores				
Number of females	0.440	0.132	–0.469	0.296
SVL	**0.929**	0.222	–0.082	–0.167
Mass	**0.912**	0.226	–0.033	0.246
Head width	**0.910**	0.265	–0.123	0.103
Hindleg length	**0.935**	0.134	–0.034	0.025
Tail length	**0.848**	0.161	0.008	–0.054
Body condition	0.047	0.028	0.095	**0.936**
Longest nuchal spine	0.232	**0.877**	–0.015	0.039
Longest dorsal spine	0.273	**0.862**	0.010	0.012
Ticks	0.106	0.041	**0.839**	–0.037
Mites	–0.153	–0.011	**0.625**	0.308
Variance explained (%)	40.7	15.9	12.3	10.6
PCs extracted for analysis of number of females				
Behavioral score	0.492	0.084	–0.370	0.330
SVL	**0.929**	0.224	–0.062	–0.178
Mass	**0.909**	0.231	–0.003	0.241
Head width	**0.910**	0.267	–0.094	0.102
Hindleg length	**0.935**	0.136	–0.020	0.029
Tail length	**0.846**	0.165	0.008	–0.046
Body condition	0.040	0.036	0.120	**0.943**
Longest nuchal spine	0.231	**0.879**	0.008	0.025
Longest dorsal spine	0.275	**0.860**	–0.005	0.035
Ticks	0.093	0.032	**0.823**	–0.068
Mites	–0.158	–0.020	**0.688**	0.232
Variance explained (%)	41.0	15.8	12.0	10.6

Notes: The four principal components (PC) were extracted (with Varimax rotation) from each of the two analyses. For each component, the traits with the highest factor loadings (> 0.6) are shown in bold, giving components that correspond to body size (PC1), ornamentation (PC2), ectoparasite load (PC3), and body condition (PC4). For both analyses, 79.4% of total variance was extracted.

including those for body size, ectoparasite load, and body condition. In this analysis, the number of females as an independent variable loaded moderately on PC1, PC3, and PC4, and poorly on PC2; therefore, it was not well represented by any one component. The second regression model, with number of females in close proximity as the dependent variable, also provided a significant fit ($F_{4,197} = 21.6$; $P < 0.001$) and explained 29.0% of the variance (table 10.4). All four components were significant, including those for body size, ornamentation (which was weaker than the others), ectoparasite load, and body condition. In this second regression, behavioral score as an independent variable was moderately loaded on PC1, PC3, and PC4, but was poorly represented by PC2; therefore, it was not well represented by any one component. Results from the two regression analyses suggest that ornamentation and body condition, in addition to body size and male behavior, contribute to male mating success and may be discriminated by females. Both regression models using principal components explained less variance

TABLE 10.4

Coefficients and Their Significance for the Principal Components of Table 10.3 Used as Independent Variables in Regression Models

	COEFFICIENTS			
	B	BETA	*t*	*P*
Behavioral score = PC1 × PC2 × PC3 × PC4				
PC1 (body size)	0.071	0.443	7.45	0.000
PC2 (ornamentation)	0.018	0.111	1.86	0.064
PC3 (ectoparasite load)	–0.041	–0.258	–4.34	0.000
PC4 (body condition)	0.028	0.172	2.89	0.004
Number of females = PC1 × PC2 × PC3 × PC4				
PC1 (body size)	0.260	0.429	7.22	0.000
PC2 (ornamentation)	0.074	0.123	2.07	0.040
PC3 (ectoparasite load)	–0.160	–0.263	–4.43	0.000
PC4 (body condition)	0.119	0.194	3.26	0.001

than the regression models based on data. The likely reason is that in each model with principal components, variance accounted for by an important independent variable (number of females in the first model, behavioral score in the second model) was poorly resolved and therefore loaded on more than one principal component.

LEKKING ACTIVITIES: SEASONAL CHANGES

By the time we ended the behavioral surveys (28 January), it was clear that lekking activities had declined and a number of males were departing the leks. Regression analysis revealed that mean daily behavioral scores declined during the study ($F_{1,12} = 23.15$, $P < 0.001$, $r^2 = 0.660$), averaging 1.25–1.42 between 11 and 17 January, but declining to 1.08 by 28 January. The copulation rate also declined ($F_{1,12} = 5.10$, $P = 0.043$, $r^2 = 0.298$) from a peak of 1.24 copulations per one hundred observations on 15 January to zero on each day after 23 January. In contrast to male behavior, the number of females in close proximity to males remained constant during the study period ($r^2 < 0.001$). By 26 January (the last day with multiple surveys), forty-four (20.7%) of the 213 males had departed from the sector in which they were lekking. The relationship between departure date and body mass approached significance (Spearman's rho = 0.129, $P = 0.061$), suggesting that smaller males gave up lekking activities earlier than did larger males. A one-tailed Mann-Whitney *U* test indicated that males that remained longer averaged significantly greater body mass (mean ± standard error) than those that departed earlier (3260 ± 67 g and 3012 ± 99 g, respectively; $P = 0.046$). Many of the males that gave up lek tenure wandered along the beach and continued courting females outside of the lekking male territories (i.e., as satellite males). Informal observations confirmed that several such males achieved copulations.

RESIDENT VERSUS MIGRATORY MALES: BODY SIZE AND ECTOPARASITE INFESTATIONS

In May and June, we recaptured thirty-eight males on Caamaño that were assumed to be permanent residents of the island. Thus, approximately 84% of the 234 territorial males on Caamaño in January had returned to Santa Cruz. Based on capture data in January, territorial male iguanas that were residents of Caamaño were significantly smaller in length and body mass than males that swam to Caamaño from Santa Cruz ($P < 0.001$ for both; table 10.5). Although numbers of ticks did not vary between the two groups, males from Caamaño had sig-

TABLE 10.5

Comparison of Body Size and Ectoparasite Infestations of Lekking Marine Iguanas from Caamaño and Santa Cruz

DEPENDENT MEASURE	CAAMAÑO MALES (N = 38)			SANTA CRUZ MALES (N = 196)			
	MEAN ± SE	MIN	MAX	MEAN ± SE	MIN	MAX	*P*
SVL (mm)	363 ± 3	325	414	413 ± 2	289	491	0.001
Mass (g)	2220 ± 70	1180	3200	3368 ± 53	975	5750	0.001
Ticks (number)	2.2 ± 0.3	0	8	3.9 ± 0.4	0	42	0.390
Mites (scale)	2.7 ± 0.1	1	4	2.3 ± 0.1	1	4	0.034

Notes: Caamaño males are resident males; Santa Cruz males are migrants. Probability levels indicate the results of two-tailed Wilcoxon matched-pairs signed-ranks tests. SE = Standard error.

nificantly higher levels of mite infestation than did Santa Cruz males ($P = 0.034$; table 10.5).

EFFECTS OF FOOD DEPRIVATION AND CHANGES IN ECTOPARASITE INFESTATIONS

The effects of food deprivation on territorial male iguanas during the mating season are evident from the significant loss of body mass ($P < 0.001$) shown in table 10.6. Caamaño males lost 13% of their body mass on average during the period from early January to May/June, despite having the opportunity to forage for several months following the end of the mating season in February. These same males suffered an increase in numbers of ticks during the period, whereas mite infestations showed a significant decline ($P \leq 0.001$ for both). Foraging conditions were good in 1997, which was not an El Niño year.

DISCUSSION

Bivariate and multivariate analyses of 213 territorial (lekking) male marine iguanas identified a number of male qualities that appear to be important determinants of male quality and mating success, including body size, behavior, body condition, ornamentation, ectoparasite infestation, and probable female choice. We discuss each of these variables—and others not considered in our study—in the sections that follow. Although multiple determinants of mating success are typical of lek-mating species (Höglund and Alatalo, 1995; Fiske et al., 1998; see also Johnstone, 1995; Ord et al., 2001), the number of potential factors we have identified exceeds that of any other lizard species examined to date. We attribute this to a lek-mating system that affords efficient female choice and reproductive attributes (relatively small clutch size, brief period of receptivity, lack of multiple mating) that limit the option of obtaining genetic benefits by multiple paternity. Our detection of these factors depended on two regression approaches that included as independent variables either all traits or just the principal components extracted from the correlation matrix. Despite being complementary, the two approaches yielded different conclusions. Although many authors seem to prefer exclusive use of principal components in regression analyses involving multiple phenotypic traits (Hews, 1990; Abell, 1997; LeBas, 2001), we believe that regression including all variables is also valid, provided the sample size is sufficient, multicollinearity is minimal, and other parametric assumptions are reasonably met.

Although we did not measure mating success directly (the unexpectedly large number of adults and hatchlings made paternity analysis unfeasible), the number of females in close proximity corresponds to opportunities for mating. Thus, as in other studies of lizards (e.g., Cooper

TABLE 10.6

Comparison of Body Mass and Ectoparasite Infestations of Male Marine Iguanas Residing on Caamaño at the Start of the Mating Season and Several Months Afterward

DEPENDENT MEASURES	JANUARY	MAY/JUNE	*P*
Mass (g)	2221 ± 70	1941 ± 54	0.001
Ticks (number)	2.2 ± 0.3	4.6 ± 0.9	0.001
Mites (scale)	2.7 ± 0.1	1.5 ± 0.1	0.001

Notes: Means ± standard errors are given; $n = 38$. January is the start of the mating season. Probability levels indicate the results of two-tailed Mann-Whitney *U* tests.

and Vitt, 1993; Baird et al., 1996; Bull and Pamula, 1996; Abell, 1997; Salvador and Veiga, 2001), we regard this as a measure of relative mating success. Spatial proximity corresponds reasonably well with actual paternity in nonlekking lizards (e.g., Abell, 1997; Gullberg et al., 1997; LeBas, 2001), and appears to hold true for lek-mating marine iguanas (Trillmich, 1983; Wikelski et al., 2001; authors' pers. obs.). We also recognize that the analyses of association we used are limited in that they do not confirm causation, but association is a necessary requirement of a causal relationship.

BODY SIZE

Correlation analyses indicated that a strong relationship exists between body size and relative male quality (behavioral score) and between body size and relative mating success (number of females in close proximity). Larger males exhibited significantly higher levels of territorial activity (behavioral scores) and were in close proximity to significantly more females. These relationships were evident regardless of the measure of body size (SVL, body mass, head width, hindleg length, tail length). The partial correlation coefficients revealed that the two dependent measures (behavioral score, number of females in close proximity), although highly correlated, were independent of each other. Thus, larger males exhibited higher levels of territorial activity regardless of the number of females nearby, and females associated more with larger males regardless of their behavior. Size-related differences in male mating success are widespread in lizards (Stamps, 1983; Olsson and Madsen, 1998) and other animals (Höglund and Alatalo, 1995), and have been documented previously for marine iguanas. Wikelski et al. (1996) showed that larger male marine iguanas on Isla Genovesa secured more copulations than did smaller males, but contrary to the present results, the number of copulations achieved was independent of the number of female-sized iguanas in close proximity. This difference may be the result of the smaller sample size compared with our study or to differences in the density of females at the leks (see also Wikelski et al., 2001).

Regression analyses identified male head width as the primary measure of body size associated with male quality and mating success. Sexual dimorphism of head size is common in lizards and exists among many iguanids (e.g., Dugan and Wiewandt, 1982; Carothers, 1984), including marine iguanas (M. Wikelski, unpubl. data). Head size dimorphism in lizards may arise from four primary causes (see Bull and Pamula [1996] for another cause): (1) intrasexual selection (via male-male interactions; e.g., Carothers, 1984; Anderson and Vitt, 1990; Mouton and Van Wyk, 1993; Bull and Pamula, 1996; Censky, 1996); (2) intersexual selection (via female choice; in Herrel et al. [1999], note the lack of evidence for this in lizards); (3) differential allocation of energy for reproduction (Cooper and Vitt, 1989; Mouton and Van Wyk, 1993); and (4) resource partitioning (e.g., sex-based differences in food size; Schoener, 1977; Stamps, 1977; Best and Pfaffenberger, 1987; Herrel et al., 1999). For marine iguanas, we suggest that selection for larger male head size is most likely to arise from sexual selection. Resource partitioning is not evident, as both sexes graze on algae, and foraging strategies are size-related rather than sex-specific (Trillmich and Trillmich, 1986; Wikelski et al., 1993; Wikelski and Trillmich, 1994). Sex-related differences in allocation of energy for reproduction contribute to body size dimorphism (Wikelski and Trillmich, 1997), but the extent to which this influences head size dimorphism remains uncertain. However, head width may be particularly important during pre-mating territory establishment and, therefore, subject to intrasexual selection. Males at this time engage in escalated contests with rival males involving head bobs, head pushing duels, and biting (Trillmich, 1983). Individual fights may last for several hours and, with many interruptions, may continue for several days (Trillmich, 1983). Males in our study with wider heads also attracted more females, suggesting that head width may be an important attribute of female choice and therefore subject to intersexual selection.

Prior studies have identified specific head dimensions as targets of sexual selection in lizards. In each case, the resulting dimorphism was attributed to male-male competition (intrasexual selection). In *Uta palmeiri,* head depth was identified as a direct target of selection, apparently through male-male interactions and a biomechanical advantage in grasping females during mating (Hews, 1990). Other traits (including SVL, body mass, jaw length, and head width) that Hews examined in a linear selection-gradient hypothesis appeared to be under indirect selection through correlation with head depth and territory quality—the direct targets of selection. In staged aggressive interactions between males similar in SVL and body mass, winning was associated with greater head depth and not with head width or jaw length. In staged interactions of male *Gallotia galloti,* head length but not head width influenced the outcomes (Molina-Borja et al., 1998). In *Ctenophorus ornatus,* male head depth (by virtue of more females in territories) and body size (by virtue of more extraterritorial copulations) were independently related to the number of offspring sired (LeBas, 2001). Among smaller male *Tiliqua rugosa,* those with wider heads were more likely to be paired with females (Bull and Pamula, 1996). Although head size dimorphism in marine iguanas may result largely from intrasexual selection, our findings suggest potential involvement of female choice. Females might be able to assess head width directly or through some correlated aspect of headbobbing behavior. In fruit flies, male head and face dimensions appear to be direct targets of mate choice by females (Norry et al., 1995, 1999).

In the marine iguana, sexual selection on body size is opposed by natural selection during periods of low resource availability, such as El Niño events, when the largest iguanas starve to death (Wikelski and Trillmich, 1997). At present, the possibility that head width (or mouth width) is the “real” target of natural selection, arising from constraints on grazing the depleted algal beds, remains untested (Wikelski and Trillmich, 1997). Remarkably, marine iguanas have the capacity to shrink their body length and presumably their skeletal structure by up to 20% during El Niño events (Wikelski and Thom, 2000). It would be interesting to examine plasticity of head width in particular.

BEHAVIOR

Results from the bivariate and multivariate analyses indicated that significantly more females were in close proximity to lekking males that exhibited higher levels of territorial activity. When either male behavior or number of females was controlled for, a significant relationship between body size and the other dependent measure still existed, which suggests that male behavior and female association were independent of and not a consequence of each other. Accordingly, females may be able to choose males on the basis of their behavior, either by their display rate, their copulatory rate (after grabbing a female by the nape, a male typically lifts her and may ambulate or turn around several times before mounting her, perhaps to display his success), or finer motor details that we did not measure (e.g., headbobbing characteristics). Wikelski et al. (2001) found that whereas females were attracted to male territories largely on the basis of male size, the decision to mate was influenced most by level of activity towards females and lek attendance.

Females of many lekking animals can rely on behavioral cues, such as display rates, to select a quality mate (Höglund and Alatalo, 1995). However, the ability of female lizards to assess male behavior remains unclear. In a review of the evidence for mate choice in lizards, Tokarz (1995) pointed out that most studies of headbobbing, push-up, dewlap, and other displays have focused on questions regarding communication theory, species-isolating mechanisms, and the evolution of display behavior. Studies of anoline lizards suggest that the capacity to display and courtship frequency may be important for attracting females, but the evidence is limited and in some cases contradictory (see Tokarz, 1995). In *Crotaphytus collaris,* male mating success was associated with frequency of lateral displays, push-up displays, and initiation of social interactions, but the differences were age related and probably permitted tolerance of younger males within territories of the larger, more successful males (Baird et al., 1996). Our own study suggests that female marine iguanas may assess the behavior of males. Recent consideration suggests that headbob walking may be the cue females use most for mate selection (M. Wikelski et al., unpubl. data).

BODY CONDITION

In the present study, there was a weak but significant association between number of females in close proximity and body condition. This was evident only from regression analysis of principal components. However, body condition was similarly associated with number of copulations achieved by male marine iguanas on Isla Genovesa (Wikelski et al., 1996). Although covariance might be expected, no association between body condition and ectoparasite load was detected. Ectoparasite load was also independent of body condition in *Lacerta agilis* (Olsson et al., 2000). As an index of relative fitness, body condition can probably be perceived by visual cues. Alternatively, body condition may be assessed indirectly by cues that we did not examine, such as coloration (see below). In contrast to our findings, multiple regression analysis showed that in *Psammodromus algirus,* the number of females associating with a male was explained by the emergence from hibernation date and SVL, but not by body condition (Veiga and Salvador, 2001).

ORNAMENTATION

The regression analysis of principal components indicated that females associated preferentially with males having longer nuchal and dorsal spines. To our knowledge, this is the first study to suggest that male ornamentation in the form of a physical structure (apart from coloration, equated with ornamentation by Salvador and Veiga [2001]) may influence mating success in lizards, in this case via possible female choice. However, spines and other elaborate structures are well represented among lizards (e.g., horned lizards [*Phrynosoma* spp.], chameleons [Chamelionidae], basilisk lizards *[Basiliscus]*), and females of such taxa may also be attentive to ornamentation.

ECTOPARASITES

Our data suggest that marine iguanas having lower parasite loads—especially reduced numbers of ticks—had higher relative mating success and may have been preferred by females. This finding is consistent with recent theory regarding the influence of parasites on mating decisions. Hamilton and Zuk (1982) proposed that individuals that mate most successfully are those that possess genes for resistance to parasites. They also suggested that individuals resistant to pathogens could signal their quality by development of extravagant ornamentation or brighter coloration. Indeed, there is some empirical evidence (although mixed) to support the relationship between parasite load, male phenotypic traits, and female choice in some species (Hamilton and Poulin, 1997). However, in lizards that have been examined, the relationship between parasite load and coloration is either absent or negative (e.g., brightly colored lizards have more parasites), contradicting the Hamilton-Zuk hypothesis (reviewed by Tokarz [1995]; see also Olsson and Madsen [1995]). In our study, we could not evaluate the relationship between coloration and ectoparasite load. However, the absence of a correlation between ectoparasites and ornamentation (table 10.1) suggests that if females do indeed discriminate among males based on parasite loads, it is independent of their ornamentation. In contrast with marine iguanas, there was no relationship between mite load and any measure of fitness in *Sceloporus virgatus,* including mating success, survival to the following year, and relative weight loss (Abell, 2000). Further, female *Lacerta agilis* do not reject males on the basis of their parasite load (Olsson and Madsen, 1995).

The relationship between ectoparasite load and male phenotypic characters is further complicated by the interplay between androgen-dependent male characters and immune function, which could explain why some studies fail to find a relationship between parasite load and mating success. According to the immunocompetence handicap hypothesis, males having superior immunocompetence are able to allocate more resources to development of costly ornament traits, but in doing so, they compromise their immune system and end up with a parasite load similar to less immunocompetent males (Folstad and Karter, 1992). Thus, for example, males with higher testosterone levels responsible for brighter coloration or exaggerated ornamentation will compromise their immune system and remain susceptible to parasites or suffer a disproportionate increase in parasites during the mating season. Olsson et al. (2000) showed that mating success in *Lacerta agilis* was associated with brighter coloration and greater mobility, that testosterone increased mobility (mating opportunities) and caused immune suppression (as reflected by a gain in tick loads), but that testosterone did not change coloration. Increased testosterone similarly resulted in higher ectoparasite loads in *Psammodromus algirus* (Salvador et al., 1996, 1997). In our study, we were unable to evaluate changes in ectoparasite loads during the mating season. However, several months after mating had ended, the lekking males resident on Caamaño had suffered an increase in ticks and a decrease in mites compared with their status early in the mating season (table 10.6). The ticks apparently remain affixed to their host for days, if not weeks, and can locomote quickly enough to switch hosts and therefore make contagious infection possible (Wikelski, 1999).

Differences in exposure to ticks, rather than variation in male phenotypic quality, may instead explain variation in ectoparasite burden. The distribution of iguanas in the supratidal zone may have led to differences in exposure to ticks. For example, males that are more sought out by females hold drier territories (Trillmich, 1983; Wikelski et al., 1996), in which larval ticks may be less likely to survive while searching for a host. Clearly, the interactions between ectoparasites, testosterone, and fitness consequences need further study in the marine iguana.

OTHER FACTORS

In addition to the factors already discussed, there are others we did not consider that may be associated with male mating success and potential female choice. These include coloration, chemical signals, lek attributes (spatial and territorial features within and between leks), harassment of females by nonterritorial males, female copying, postfertilization consequences, and alternative mating tactics. We discuss each of these here (see Olsson and Madsen [1998] for further discussion).

COLORATION

Although we did not evaluate differences in coloration, the extent or intensity of dichromatic male coloration (or "badges") can be a reliable signal of status in some lizards and may be an important cue for male-male interactions or female choice in marine iguanas. In marine iguanas, male coloration becomes more pronounced (reddish flanks) during the mating season (Trillmich and Trillmich, 1984) and may correspond to feeding success (M. Wikelski, unpubl. data). However, the greenish dorsal spine coloration is apparently related to testosterone levels and might be used by females in mate choice (K. Nelson et al., unpubl. data). Because differences in male coloration are often associated with territory size and fighting success in lizards, sexual dichromatism is generally attributed to the outcome of intrasexual selection (Thompson and Moore, 1992; Diaz, 1993; Olsson, 1994; Martín and Forsman, 1999; Olsson et al., 2000; LeBas, 2001). Male coloration is typically correlated with body condition (Olsson, 1994; LeBas, 2001) and hormone levels (Cooper et al., 1987; Pratt et al., 1994; Salvador et al., 1996). Color dichromatism could also result from differential habitat selection (Vial and Stewart, 1989), but this clearly is not the case for marine iguanas. A number of studies have sought to find evidence that female lizards prefer males with more extensive or intense coloration, but with few possible exceptions (see Tokarz, 1995), the investigators show absence of female mating preferences (e.g., Cooper and Vitt, 1993; Olsson and Madsen, 1995; Abell, 1997; Martín and Forsman, 1999). We suggest that the marine iguana would be an ideal candidate for further study of female preferences for male color.

CHEMICAL CUES

Iguanids produce secretions from femoral glands that may contribute in some way to mating success. In the green iguana, activity of the glands varies seasonally and the secretions are involved in communication and male dominance relationships (e.g., Cole, 1966; Alberts et al., 1992a; Phillips et al., 1993). Whether marine iguanas attend to or communicate via chemical signals remains to be examined.

LEK ATTRIBUTES

Wikelski et al. (1996) showed that certain attributes within or between leks were associated with copulatory success of male marine iguanas. Territorial males had similar success at leks and on single territories. However, small territorial males achieved more copulations at leks than on single territories, whereas large territorial males did better at single territories. The mean number of copulations per male did not vary with lek size, but again, small territorial males did better at larger leks. These findings suggest that smaller males benefit most by establishing lek territories. In addition, territory topography and degree of environmental disturbance were negatively associated with mating success (i.e., flatter territories that were less disturbed by extreme tides were better). In another study, Wikelski et al. (2001) determined that male quality (both behavior and morphology) varied more in a high-density lek than in a low-density lek. As a presumed consequence, females in the high-density area mated with males exhibiting higher activity levels than females in the low-density area, but females in the high-density area also lost more body mass, suggesting a cost associated with assessment of potential mates.

The position within a lek is important for many lekking taxa, with central positions often being advantageous (Höglund and Alatalo, 1995). Although central versus peripheral territories have not been compared in marine iguanas, Trillmich (1983) observed stratification of mating success within the intertidal zone. Males with territories higher above the water had more females resting in their territories and achieved more copulations than males lower in the intertidal zone, whose territories were used largely by females during transit to and from foraging sites at low tide. She also noted that territory size was associated with male body size, number of females on the territory, and number of copulations achieved.

HARASSMENT OF FEMALES

Recent studies primarily involving ungulates (e.g., Carbone and Taborsky, 1996) suggest that female movements and mate selection may result more from harassment by nonterritorial males than from female choice. Wikelski et al. (1996) showed that female marine iguanas suffer less harassment when in territories of males, but there was no difference in levels of harassment between lek and single territories. Thus, harassment does not favor the clustering of males and probably contributes minimally to mating variance. Reduction in harassment, however, may result in less energy expenditure by resting marine iguanas (Wikelski et al., 2001) and more time for feeding in other lizards (e.g., *Ameiva plei;* Censky, 1997). Thus, reduced levels of harassment could be viewed by females as a nonmaterial resource.

FEMALE COPYING

Females of various lek-mating species appear to copy the mate choice of others (Höglund and Alatalo, 1995). By doing so, females can reduce the time required to sample prospective mates or increase the precision of assessment by relying on the assessment of other females. Wikelski et al. (1996) found that female marine iguanas aggregated in the vicinity of female-sized model iguanas, which suggests a degree of copying, although not necessarily at the level of copulation. That lekking iguanas often appear to display females between grasping them by the neck and copulating with them suggests that females might be attracted to a successful male. However, more careful observation is needed. The prevailing view is that female copying increases mating skew, but other explanations suggest the opposite (Höglund and Alatalo, 1995).

POSTFERTILIZATION CONSEQUENCES

Gullberg et al. (1997) point out three postfertilization consequences that are seldom considered in studies of reproductive success: (1) clutch size, which often covaries with female size and may promote preference for large females by males; (2) mating order (first or last male effects), important in those species with female promiscuity, sperm competition, and potential multiple paternity; and (3) sperm quantity and quality, which may influence not only sperm competition, but also constrain the number of females a male can fertilize. At present, we have not considered whether marine iguana males exercise mate choice. Although males seem incapable of reliably distinguishing between females and small males (Wikelski et al., 1996), selection might favor size discrimination if their sperm supplies are limited. Mating order, however, can probably be ignored, because females have small clutches, become unreceptive after mating, and apparently mate only once per season (Wikelski and Bäurle, 1996; Wikelski et al., 1996).

TERRITORY SAMPLING VERSUS MATE CHOICE

Wikelski et al. (2001) deduced that mate choice by females likely involves a two-stage process for marine iguanas, with different criteria assessed at each stage. Females on Isla Santa Fé visited a number of male territories prior to copulation and preferentially visited those held by the largest males. Thus, male size appears to be the most important criterion for visitation. However, females subsequently mated preferentially with males that exhibited the highest display rate of all males visited. Because there are costs involved in visitation of multiple territories (as evidenced by loss of body mass), females can gather only a limited amount of information. The lack of complete information introduces subjectivity into female choice, such that what is perceived as best by one female may be perceived differently by another female. Thus, lack of complete information may prevent unanimity of female choice.

ALTERNATIVE MATING TACTICS

Male marine iguanas exhibit several alternative mating tactics, the adoption of which appears to be largely size (or condition) dependent. In addition to the aforementioned tactics (large territorial lekkers, marginal-size satellite males, small sneaker males), we have studied a fourth tactic (marginal-size intertidal lekkers; W. Hayes et al., unpubl. data) that was first described by Trillmich (1983). These males establish temporary territories in the intertidal zone when females are foraging at low tide, exhibit reduced behavioral scores compared with stationary (large territorial) lekkers, and are in close proximity to fewer females. Alternative tactics are typically attributed to genetic differences that predispose males to use a particular tactic, environmental conditions that favor the use of one mating tactic over another by certain individuals, or phenotypic differences that arise from competitive differences (e.g., Lanctot et al., 1998). Although genetic-based alternative mating tactics have been reported in lizards (Zamudio and Sinervo, 2000), we have seen males switch tactics in a single season, suggesting that the alternative mating tactics in marine iguanas are condition dependent. Experimental data now support this view (M. Wikelski et al., unpubl. data).

LEK MATING IN REPTILES

Compared with other vertebrates (e.g., amphibians, birds, mammals), examples of lek mating in reptiles are exceptionally scarce. Although the marine iguana was the first reptile in which a lek mating system was described (Wikelski et al., 1996), there are reasons to suspect that lekking has evolved in other reptile species. For example, reconsideration of the mating system of green iguanas *(Iguana iguana)* suggests that, like marine iguanas, lek systems have evolved in at least some populations (Burghardt, this volume; see also Tokarz [1995], who anticipated this). Indeed, large, dominant males cluster together and defend small mating territories that do not seem to possess material resources useful to females or their offspring (Dugan, 1982a,b; Dugan and Wiewandt, 1982; Rodda, 1992). Similar to marine iguanas, green iguanas exhibit size-dependent alternative mating tactics, including (with increasing size) sneaking, peripheral courtship, and territoriality (Dugan, 1982a; Pratt et al., 1992). Most other iguanids, in contrast, appear to exhibit promiscuous or other forms of polygynous mating systems (e.g., Iverson, 1979; Christian and Tracy, 1982; Dugan and Wiewandt, 1982; Ryan, 1982; Werner, 1982; Hayes et al., this volume).

A number of reptiles likely satisfy the prerequisites for lek mating and exhibit life histories that promote male clustering. The prerequisites include (Höglund and Alatalo, 1995):

1. Lack of paternal care;
2. Inability of males to monopolize resources and thereby gain matings;
3. Internal fertilization;
4. Sufficient mobility to reduce costs for females to search for aggregations and for males to avoid predation; and
5. Female preference for mating at aggregations.

Examples of life histories that promote clustering include hibernation at dens (e.g., many temperate snakes), formation of mating aggregations (e.g., sea snakes, crocodilians), and dependence on ephemeral bodies of water (e.g., crocodilians, chelonians). As pointed out by Höglund and Alatalo (1995), leks may exist in close proximity to, or be dependent upon, limited resources, so long as males do not monopolize resources and females visit the clustered males largely for the purpose of fertilization. There are numerous examples of resource-based leks in insects, including sites where food is found or where females emerge (Höglund and Alatalo, 1995), and comparable examples may exist in reptiles. The potential for lek mating may be greatest among those reptiles that have high variance in male mating success, high density (particularly if patchy in space or time), reduced territoriality, traditional mating sites, high mobility for assessment of potential mates, and/or limited capacity for multiple paternity (e.g., small or few clutches, brief period of fertility, male mate-guarding). We urge those who study the sexual behavior of reptiles to be more alert for the possibility of a lek mating system in their subjects.

SUMMARY AND CONCLUSIONS

We studied the mating activities of 213 lekking male marine iguanas on the islet of Caamaño in the Galápagos Islands. We examined the influence of multiple traits on relative male quality (scores derived from courtship and agonistic behaviors) and relative mating success (quantified by number of females in close proximity). All measures of male body size (body mass, SVL, head width, hindleg length, tail length) and ornamentation (length of nuchal and dorsal crests) were positively correlated with territorial activity and number of females in close proximity. Partial correlation analyses indicated that territorial activity and number of females in close proximity were independently associated with male body size rather than one being a consequence of the other. Multiple regression analysis revealed that male head width was the primary character of body size associated with territorial activity, and that females associated more with males exhibiting higher levels of territorial activity, wider heads, and fewer ticks. Regression analysis of principal components suggested that body size, ornamentation, and ectoparasite loads were associated with male quality, and that body size, body condition, ornamentation, and ectoparasites all independently influenced relative mating success. Larger males also remained at their leks for a longer time than did smaller males. Although multiple determinants of mating success are typical of lek-mating species, the number of potential factors identified exceeds that of any lizard examined to date. We attribute this to the lek-mating system that affords relatively efficient female choice (males are clustered and therefore easily compared) and reproductive characteristics (small clutch size, brief period of receptivity, lack of multiple mating) that limit the option of obtaining genetic benefits by multiple paternity. Although some determinants are undoubtedly influenced by male-male competition, the data support the view that female choice exists in this species.

ACKNOWLEDGMENTS

Mónica Freire P., Franz Kümmeth, Sandra Orellana T., Jose Torres C., and Daniel Vergara G. kindly provided long hours of assistance in the field. Shelton Herbert and Shawn Fry compiled the data for statistical analyses. Shelton Herbert and Ivan Buchheim assisted with preparation of the figures. We thank the Parque Nacional Galápagos for granting permission to conduct the study and the Estación Científica Charles Darwin and Transporte Aereo Militare Ecatoriano (TAME) for enabling this work. We also thank Wolfgang Wickler, Max-Planck Institut für Verhaltensphysiologie, for continuous support. MW was supported by a Feodor-Lynen and a Smithsonian Tropical Research Institute fellowship. This chapter is contribution no. 503 of the Charles Darwin Foundation.