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## **Why is Female Choice not Unanimous? Insights from Costly Mate Sampling in Marine Iguanas**

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### **Abstract**

Females do not unanimously choose the single ‘best’ male, even when female choice is strong, such as in leks, or in polygynous mating situations. A possible explanation is that females base their choices on limited information, perhaps because gathering information is costly. We tested this hypothesis by continuously observing individual female marine iguanas throughout the mating period in order to document the information they gathered about each potential mate. Females actively visited approximately five additional males during the 3 d prior to copulation, compared to the males seen on their normal foraging routes. Females were more likely to visit large-bodied males, but preferentially copulated with the male that had the highest display rate of all males they visited. Females that mated on a dense territory cluster mated with more active males than did those that mated on dispersed territories. However, females on a dense cluster also lost more body mass, potentially as a consequence of high rates of interaction with males. This mass loss may represent an important cost and result from postural changes in response to male attention. Such costs may explain why females only gather a certain amount of information and why females on dispersed territories choose less active mates. Lack of complete information introduces subjectivity into female choice: what is perceived as best by one female may not be perceived as best by another. Thus, lack of complete information may prevent unanimity of female choice.

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## Introduction

Female choice may lead to high mating skew, especially in leks, but choice is never unanimous (Bradbury et al. 1985; Clutton-Brock et al. 1988; Wiley 1991; Jennions & Petrie 1997; Kokko & Lindström 1997). This lack of uniformity of mate choice has attracted considerable attention because one would expect that only the single 'best' male should be selected in each mating cluster (Queller 1987; Keller & Krieger 1996). To account for the lack of uniformity of mate choice, several possible explanations have been investigated: (i) dominant females may prevent other females from mating with the 'best' male (Jennions & Petrie 1997; Rintamäki et al. 1998); (ii) particularly good males may become physically exhausted by mating with too many females in a very short time (cf. Rosenqvist 1990) – such behaviour could potentially even lead to sperm depletion (Birkhead 1991); (iii) some males may try to cheat and pretend that they are much better than others even if 'objectively' they are not – to achieve this, males may try to exploit the sensory systems of females (Ryan 1998); (iv) females may select a variety of fathers for their offspring if they aim at increasing offspring genetic diversity or quality (Petrie 1994).

Here we focus on an alternative explanation for variation in mate choice: females may make mistakes in their choice because they do not have complete information about potential mates (Johnstone & Earn 1999). Thus, females may prefer different males because each female perceives the quality of each male differently. Females may be unable to gather complete information if collecting such information is costly (Reynolds & Gross 1990). If information gathering is expensive, then females should choose only from a subset of potential mates and choose with incomplete, subjective information (Kokko 1997). Another factor contributing to a lack of complete, 'objective' information about mates is that each female may sample a male under different circumstances (Gibson 1996). For example, a male may be highly active during the visit of one female, but may be largely inactive if another female is around.

We took advantage of an exceptional opportunity to test this hypothesis in Galápagos marine iguanas. Here we were able to continuously follow 12 receptive female marine iguanas (*Amblyrhynchus cristatus*) throughout the mating period and record how males behaved in their presence. Thus, we gauged the males through the eyes of individual females (Trail & Adams 1989; Rintamäki et al. 1995). This measure represents a 'subjective' criterion that may vary from female to female. At the same time, we determined the overall characteristics of the males as complete, 'objective' information from an observers point of view using scan sampling of males (Mackenzie et al. 1995). The latter method is commonly used in behavioural ecology because it is largely impractical if not impossible to follow individual females in sufficient detail throughout the entire mating season (Kirkpatrick 1987).

Marine iguanas offer an ideal system to study how individual females gather information about mates because female movements can be observed practically all of the time, or at least whenever they visit males on territories (Trillmich 1983;

Rauch 1985; Wikelski et al. 1996). Furthermore, because females usually only mate once during a particular season, every copulation results in a fertilization (Trillmich 1983). Marine iguanas do not have predators and therefore decision making is largely governed by energy optimization. Thus, 'activity induced by males' represents a good currency with which to measure the cost of female mate choice because it may significantly impact female energetics (Laurie 1990; Wikelski & Trillmich 1997). Moreover, iguanas mate in territorial clusters (Trillmich & Trillmich 1984), which on some islands resemble leks (Deutsch 1994; Höglund & Alatalo 1995; Wikelski et al. 1996; Wikelski & Baurle 1996; see also Dugan 1982; Dugan & Wiewandt 1982). The mating skew in those leks can be very high, although one male never gets more than about 35% of all copulations in a lek (Wikelski et al. 1996). Thus, this highly skewed and energy-limited polygynous mating system lends itself to studying the costs of female choice.

We predict that females will choose males according to which male is 'best' in their eyes. However, males chosen according to these subjective criteria may not necessarily be the globally best males in a mating cluster.

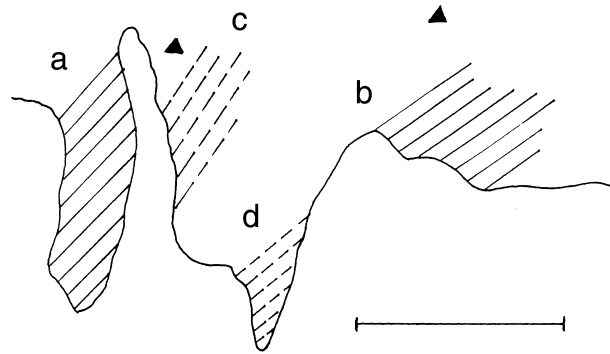
## Methods

### Study Site

Marine iguanas (*Amblyrhynchus cristatus*) were studied during Dec. 1994 at the 'Miedo' study site on Santa Fé island, Galápagos archipelago, Ecuador (90°02' W, 0°50' S). The area consists of some steep cliffs and adjacent inter-tidal foraging areas, as well as several hundred meters of shallow inter-tidal areas (for detailed descriptions see Wikelski et al. 1997). During the course of a research project begun in 1981, several hundred iguanas at this site had been permanently marked by small brandings on the flanks. Two sites in this area containing leks were chosen for observations: a site with a high density of territories (high density territorial site), and another with a low density of territories (low density territorial site). This was an important distinction because mating patterns may differ in interesting ways in relation to animal density (see Balmford et al. 1993). The high density territorial site was enclosed within a peninsula (see Fig. 1). The low density territorial site was separated from the high density site by about 250 m coastline (130 m straight line). There were two other leks between the two sites. The overall population density of iguanas at our study site was very high (about 8000 individuals per km coastline).

### Study Animals

We captured 78 male and 62 female marine iguanas at the beginning of the mating season (first week of Dec.) and measured snout-to-vent length (SVL), tail length, spine length, head width and body mass (for methods see Wikelski & Trillmich 1997). This included all territorial males in the two study sites, but not all females that copulated. Thus, matings with unmarked females were included



*Fig. 1:* Map of the coastline at Miedo study site, Santa Fé, showing the high (a) and the low density (b) territorial site in shading, while two other leks are shown in broken lines (c, d). Triangles indicate observation sites. The horizontal bar represents 50 m. Map redrawn from Laurie (unpublished report)

in the mating success of males. We recaptured and re-weighed as many of the marked animals as possible at the end of the mating season. The mass change was calculated as the difference in body mass between initial and final recapture. The sex of individuals was determined by external morphology and was verified, whenever necessary, by probing the depth of the cloacal pouch (Von Dellinger & Hegel 1990). Numbers were painted on the flanks using non-permanent paint for identifications during behavioural observations. These markings did not affect the behaviour of the animals, or other animals' reactions towards them (Wikelski, unpubl. data; see also Watkins 1997).

#### Observations of Territorial Sites

Five observers practised observations for 2 d at the beginning of the field season to achieve inter-observer reliability. Subsequently, each of the two territorial sites was continuously monitored by an observer during daylight hours throughout the mating season, from Dec. 5 to Dec. 30 1994. Marked males and females were observed using 15 min focal animal samples. Male behaviour recorded during these samples included: all courtship displays and copulation attempts towards females; aggressive displays towards females; aggressive displays towards other males; and unsuccessful copulation attempts. Female behaviours recorded include: all movements between territories; and reactions to male copulation attempts. We also noted all copulation attempts that occurred on the study site. Copulations lasted between 5 and 23 min and were very conspicuous. We are confident that we witnessed all copulations that occurred in the two study areas during the study period.

#### Territorial Behaviour

The mating season, defined as the time of high territorial activity (see Trillmich 1983; Laurie 1990), began in early Dec. and continued until the end of

Dec. Territorial behaviour consisted of head-bobbing sequences and posturing towards adjacent territorial males (Trillmich 1983; Wikelski et al. 1996). Short bouts of head-bobs performed within 3 s of each other were considered part of the same sequence. Fights were defined as encounters that resulted in the physical contact of two animals for longer than 10 s. Chases sometimes also involved brief periods of contact. A male was defined as a territorial male if he remained in an area and defended it for at least 5 consecutive days (cf. Wikelski et al. 1996). Territorial boundaries were determined by observing conflicts with neighbouring males. A number of males were transient and did not establish territories and so were defined as non-territorial (cf. Wikelski et al. 1996).

### **Male Behaviour**

Copulation attempts by territorial males consisted of head-bobs accompanied by a slow side-walk approach (Trillmich 1980; 'slow' copulation attempts, Wikelski et al. 1996). Non-territorial males chased females and attempted to forcibly mount them ('chase' copulation attempts, cf. Wikelski et al. 1996). For each male, we scored activity based on all observations of that male. Male activities were separated into those directed at other males (activity against males) and those directed at females (activity against females). Activity scores against males were based on rates of head-bobs, chases and fights – although fights occurred infrequently and contributed little to these scores. Activity scores towards females were based on rates of head-bobs towards females and copulation attempts. To test whether the male behaviour influenced mating patterns of females, we ranked all males visited by an individual female by: (i) male activity towards the females in the territory; and (ii) the time a female spent with the male prior to copulation. We contrast this 'individualistic' (female-centred) score against the overall 'objective' activity score as determined by scan sampling (see below). Thus, for example, a male could have a subjective score of 1 (best male in a female's view), whilst overall the male would have an objective score of 3 (compared to all other males at all times). To standardize the score for different numbers of males visited by different females, we used the percentage of this score (e.g. 100% for the best male vs., for example, 50% if the male was the 5th best of 10 males).

### **Scan Samples, Female Movements and Associations with Males**

Every 30 min, we recorded the locations of all visible marked females and, when appropriate, the territorial male. Three times per day, we scanned the entire study site (07:00 h, 11:00 h, 15:00 h) and recorded the territorial males present and the number and identity of females within each male's territory.

We monitored all marked females and only females that were observed mating were described as 'receptive'. Non-receptive females included all females not seen mating. It is possible that we missed copulations in these females, e.g. when they moved between lek areas. However, non-receptive females were never

observed to head-bob against males, which is usually a clear sign that a female has copulated previously (Wikelski et al. 1996). For an analysis of daily patterns of movement, we used 12 females for which we knew the time of copulation and had a complete record of movements before and after copulation. Patterns of movements of these females were then compared 2 d before and on the day of copulation with the pattern 3 d after copulation. We favoured an interval of 3 d for this comparison because it provided sufficient time for a female to visit several males. Our results, however, would have been qualitatively the same had we chosen 5 d or 2 d for each interval. The receptive window of marine iguana females is presently unknown, thus we could not choose our observation interval accordingly. However, this is not a major concern because females can also gather information about males outside their 'reproductive window'. For each day, we subdivided movements into two categories: (i) 'feeding movements', or direct routes from the resting place to the feeding area; and (ii) 'detour movements', or movements that deviated from the direct route by an angle of more than 60 degrees. Detour movements were unrelated to feeding activities (cf. Wikelski & Hau 1995) and may represent a form of mate sampling behaviour. To examine possible seasonal effects on patterns of movement, we subdivided the breeding season into early and late periods (based on the mean date of copulation of all marked females; Dec. 17). We then compared the number of males visited during these two periods by females who were not seen to mate.

### Statistical Analyses

Data were analysed with SPSS for Windows (SPSS Inc. 1991) and means are given  $\pm$  SD if not noted otherwise. Two tailed tests were used and the  $\alpha$ -level was set at 5%. Bonferroni adjustments were performed as indicated in the results. Non-parametric tests were used when the distributions of variables differed from random.

## Results

### Male Densities and Female Numbers

During the mating season, the high density site was occupied by a mean of  $22 \pm 5$  territorial males, the low density site by  $19 \pm 6$  territorial males ( $\chi^2 = 0.22$ ,  $df = 1$ ,  $p = 0.68$ ). The mean territory size was approximately 2.5 times larger in the low density area than in the high density area ( $32.2 \pm 11.4$  m<sup>2</sup> vs.  $13.2 \pm 7.4$  m<sup>2</sup>, Mann-Whitney U-test,  $n_1 = 27$ ,  $n_2 = 25$ ,  $p = 0.008$ ). As a consequence, the mean density of territorial males was about 2.5 times higher in the high density area than in the low density area (0.75 vs. 0.31 animals/10 m<sup>2</sup>, respectively). The number of females present did not differ between the two sites ( $76 \pm 32$  vs.  $58 \pm 20$  high density vs. low density, respectively,  $\chi^2 = 2.4$ ,  $df = 1$ ,  $p > 0.28$ ). Consequently, the number of females per male was not different

between the two sites (high density site: 3.45, low density site: 3.01;  $\chi^2 = 0.03$ ,  $df = 1$ ,  $p = 0.75$ ).

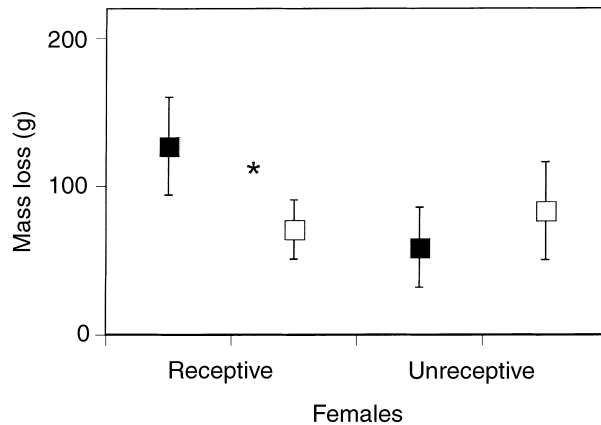
### Male Mating Success and Female Mating Tactics

Mating success was highly skewed, as indicated by the fact that three out of 56 males gained nearly half (45%) of all copulations. To understand the variance in male success, we analysed female mating decisions as a two-stage process. First, we analysed which factors contribute to the number of females that were attracted to territorial males, using a multiple regression model. It appeared that only body size was important for female visitation rate (Table 1a), while activity, condition, spine length and territory attendance did not affect female visitation rate to territories. Next, we determined what influenced the number of copulations a male achieved, again using a multiple regression model. The two factors 'activity towards females' and 'territory attendance' were most important (Table 1b). This confirmed earlier analyses that male display is most important in mate choice.

Out of the 62 marked females, 17 visited both the low density and high density territorial areas (11 females went from the low to the high density site, while six females went the other way). Those females which visited both areas were assigned to the area where they spent the most time. Females at both sites were similar in size, initial body mass and initial body condition (comparing high vs. low density, respectively: SVL:  $275 \pm 16$  mm,  $271 \pm 14$  mm; mass:  $1196 \pm 180$  g,  $1150 \pm 132$  g; condition:  $60.2 \pm 4$  kg/m<sup>3</sup>,  $60.1 \pm 5$  kg/m<sup>3</sup>; all Mann–Whitney U-tests  $p > 0.05$ ,  $n_1 = 32$ ,  $n_2 = 18$ ). Receptive females who spent most of their time in

*Table 1:* (a) Multiple regression models on factors influencing the number of females that visit territorial male marine iguanas (the model was significant;  $F_{6,25} = 2.5$ ,  $p = 0.04$ ,  $r^2 = 0.38$ ). (b) Multiple regression models on factors influencing the number of copulations achieved by territorial male marine iguanas (the model was significant;  $F_{6,27} = 3.5$ ,  $p = 0.01$ ,  $r^2 = 0.44$ )

	Beta	t	p
Part (a)			
Activity towards females (n/15 min)	0.05	0.2	0.82
Activity towards males (n/15 min)	0.30	1.2	0.30
Condition (kg/m <sup>2</sup> )	0.01	0.1	0.96
Body size (SVL, mm)	0.65	3.8	0.002
Spine length (mm)	0.23	1.1	0.27
Territory attendance (%)	0.02	0.1	0.90
Part (b)			
Activity towards females (n/15 min)	0.54	2.9	0.007
Activity towards males (n/15 min)	-0.30	-1.6	0.13
Condition (kg/m <sup>2</sup> )	-0.09	-0.5	0.61
Body size (SVL, mm)	-0.17	-0.9	0.39
Spine length (mm)	0.06	-0.4	0.72
Territory attendance (%)	0.45	2.7	0.01



*Fig. 2:* Mass loss of receptive vs. unreceptive females in the two territorial areas. Filled symbols, high density area. Open symbols, low density area. All animals lost some mass due to seasonal changes in food abundance, but receptive females in the high density area experienced twice the mass loss of other females. Data show mean  $\pm$  95% confidence interval; the star indicates a significant difference (see text). Samples sizes from left to right: 17, 13, 15, 5, respectively

the high density area lost more mass during the mating season than receptive females in the low density area. The loss of body mass of unreceptive females was comparable to that of females in the low density area (Fig. 2; receptiveness was a bivariate variable distinguishing receptive from non-receptive females; two-way ANOVA,  $F_{3,46} = 6.0$ ,  $p = 0.02$ ; for receptiveness  $p = 0.3$ ; for area  $p = 0.5$ ; for receptiveness  $\times$  area  $p = 0.04$ ). The difference in mass loss between receptive females on the high vs. the low density area was not the result of a difference in foraging duration (Mann–Whitney U-tests  $p > 0.05$ ,  $n_1 = 14$ ,  $n_2 = 12$ ).

The total number of female movements between territories on the high density area was about 50% higher than for females on the low density area: on the high density area, females stayed on average 0.95 h basking at one spot, while females on the low density area stayed for 1.55 h (Mann–Whitney U-test,  $n_1 = 62$ ,  $n_2 = 35$ ,  $z = 4.9$ ,  $p < 0.001$ ).

On average, there were no major morphological or behavioural differences between low density and high density territorial males except that high density males showed a higher rate of copulation attempts and were more active even without females present on their territories (Table 2). Interestingly, the coefficient of variation in morphological and behavioural traits was always higher for high density territorial males, indicating that the differences between males are more extreme in high density areas. It also indicates that males with extremely good traits are more likely to be found in high density areas. Our data indicate that females make the most of this situation because in the high density area females mated with more active males than in the low density area (Fig. 4, two-way ANOVA,  $F_{3,47} = 4$ ,  $p = 0.01$ ; for activity  $p = 0.08$ ; for area  $p = 0.6$ ; for activity  $\times$  area  $p = 0.03$ ).

Table 2: Male characteristics. Data show mean  $\pm$  SD. CV (coefficient of variance) is given for behaviours which females can see (thus, we did not include the CV for 'activity without females'). CVs were always higher for the high density males. Bonferroni adjustments for multiple comparisons revealed significant  $\alpha$ -levels at  $p < 0.003$

	High density site (n = 27)	Low density site (n = 25)	p	CV high density	CV low density
Body size (mm SVL)	349 $\pm$ 22	355 $\pm$ 13	0.41	6.3	3.4
Head width (mm)	51.6 $\pm$ 3.3	51.8 $\pm$ 1.8	0.96	6.9	3.6
Tail length (mm)	518 $\pm$ 54	528 $\pm$ 30	0.97	11.8	6.2
Body mass (g)	2144 $\pm$ 353	2147 $\pm$ 165	0.92	16.1	3.6
Mass loss (g)	100 $\pm$ 10	80 $\pm$ 20	0.66	124.3	47.4
Spine length (mm)	19.8 $\pm$ 4.9	19.1 $\pm$ 2.9	0.61	25.5	15.8
Body condition (kg/m <sup>3</sup> )	50.4 $\pm$ 6.2	48 $\pm$ 2.6	0.57	12.1	5.3
Color index	1.84 $\pm$ 0.8	1.92 $\pm$ 0.52	0.64	44.2	36.2
Head bob to male (n/min)	0.122 $\pm$ 0.11	0.111 $\pm$ 0.08	0.15	98.1	72.9
Head bob to female (n/min)	0.041 $\pm$ 0.06	0.043 $\pm$ 0.05	0.82	146.8	116.3
Number of females on territory	4.0 $\pm$ 3.0	3.7 $\pm$ 2	0.73	75.4	54.1
Copulation attempts (n/min)	0.074 $\pm$ 0.038	0.052 $\pm$ 0.021	0.03	51.4	40.0
Activity without females (n/min)	0.17 $\pm$ 0.15	0.03 $\pm$ 0.05	0.002	—	—

### Female Mate Choice

Receptive females visited, on average, 4.5 more males during the 3 d prior to mating than they did 3 d after mating (Fig. 3; Wilcoxon test,  $z = -2.9$ ,  $n_{1,2} = 12$ ,  $p = 0.003$ ). This was not caused by seasonal changes in patterns of movement in general, because unreceptive females did not vary in the number of males visited before and after the mean mating date (Dec. 17; Fig. 3; Wilcoxon test,  $z = -0.55$ ,  $n_{1,2} = 15$ ,  $p = 0.58$ ). Receptive females also made more detour movements during the 3 d before copulation ( $5.1 \pm 3.7$ ) than the 3 d after copulation ( $1.0 \pm 1.2$ ; Wilcoxon test,  $n = 12$ ,  $z = -3.06$ ,  $p = 0.002$ ). Receptive females spent more time with the chosen male before than after copulation (visitation rank of chosen male before copulation:  $74 \pm 23\%$ ; after copulation  $44 \pm 35\%$ ; Wilcoxon test,  $n = 12$ ,  $p < 0.05$ ).

Only two out of 12 females copulated with the male with whom they spent the most time. Instead, females on average copulated with males of score 2.38, or the male they visited approximately the second most frequently. A randomization test showed that females spent more time on territories of males they mated with than would be expected by chance ( $n = 12$ ,  $p < 0.05$ ).

### Subjective and 'Objective' Male Quality

Females chose males that were objectively not quite the best, because the female's subjective view of those males tended to overestimate male quality. Females were more likely to copulate with the male that showed the highest

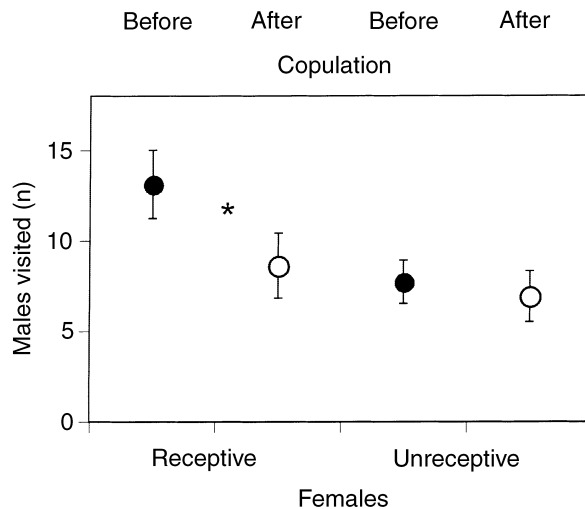


Fig. 3: Males visited by receptive ( $n = 12$ ) vs. unreceptive ( $n = 15$ ) females in the two territorial areas. Filled symbols, before copulation; open symbols, after copulation. For the unreceptive females, we used the median days of all copulations to separate the time before and after copulation. Data show mean  $\pm$  95% confidence interval; the star indicates a significant difference (see text)

display rate of all the males that a given female visited. The score for the chosen male was  $1.22 \pm 0.44$  (for  $n = 12$  females; this score was significantly higher than random, randomization test  $p < 0.01$ ). This contrasted with the fact that females did not choose males that had the overall highest display rate in a comparison among all males each female visited, as determined from an observer's point of view (average objective score for all males visited by each female:  $1.89 \pm 0.78$ ). The two scores were significantly different, suggesting that subjective (female-centred) and objective (observer-determined) male display rate differed (Mann-Whitney U-test,  $z = -2.12$ ,  $n_{1,2} = 12$ ,  $p = 0.03$ ).

### Discussion

Our observations suggest that female choice is costly in marine iguanas, and that females do not choose the single best male because they lack perfect (objective) information about the male's quality. Female marine iguana apparently chose mating partners as they actively visited males, and not while on daily foraging trips. Receptive females visited 4.5 more males before copulation compared to after copulation (as well as compared to unreceptive females in general). These additional visits to males increased the total amount of male attention to females, especially at high density territories. At the same time, these visits nearly doubled the total number of postural or site changes for females. During postural changes, female heart rate and energy expenditure increase dramatically (Wikelski et al., unpubl. data). This energy expenditure probably underlies the observed mass loss in receptive females on the high density lek. Our main question here is how such costs of mate choice contribute to the lack of unanimity of mate choice in marine iguanas.

#### Mate Choice in Marine Iguanas as a Two-Step Process

Marine iguana males cannot monopolize females (Wikelski et al. 1996), thus the high mating skew observed during our studies is probably the result of female choice (Rauch 1985; Wikelski & Bäurle 1996). Females also actively solicited male attention by laying down on the tail or leg of a temporarily inactive territorial male, only to become the immediate target of display by this male (pers. obs.). Because there are no resources on male territories, we concluded earlier that there is potential for direct choice of males (Wikelski et al. 1996; cf. Andrews 1985; Gibson 1992). This is not a common phenomenon in lizards, possibly due to the costs involved in mate searching (Carothers 1984; Cooper & Vitt 1993; Hews 1993; Olsson & Madsen 1995; Censky 1997). However, not all females choose the single best male as identified from an observer's point of view. To understand this variance in female choice, we studied the choice criteria that female marine iguanas use.

Among territorial males, large males attracted more females than small ones (Table 1; Olsson 1993). Once females were attracted to territories, they did not automatically mate (Gibson 1996; Wiley & Poston 1996; Kotiaho et al. 1996).

Receptive females freely roamed between territories and between leks. Among the males that a female visited, the best predictor of her mating decision was total display rate. These results are in agreement with a previous study, where we found that females were more likely to copulate when male display rates on a lek were higher (Wikelski et al. 1996).

### **Costs and Potential Benefits of Choice**

In response to the head-bob copulation approach of a male, females either move a few steps or stay put and allow subsequent mounting and copulation (Trillmich 1980; Trillmich 1983; Rauch 1985; Wikelski et al. 1996). Therefore, a female experiencing many copulation attempts will have to move more often than a female with less male attention (Saether et al. 1999). Although these movements of females are usually small, they may impair thermoregulation (Buttemer & Dawson 1993) and cause heart rates to increase dramatically (unpubl. data using heart-beat body temperature recorders). The body temperature of marine iguanas has been shown to react very rapidly to body adjustments, e.g. to push-ups (Bartholomew & Lasiewski 1965; Bartholomew 1966; White 1973; Wikelski & Trillmich 1994). These adjustments are necessary when females reject copulation attempts (cf. Watson et al. 1998). It is therefore likely that females with a high rate of male attention cannot achieve the high body temperatures necessary for fast digestion (Wikelski et al. 1993; Wikelski & Wrege 2000) or efficient foraging (Buttemer & Dawson 1993; Wikelski & Trillmich 1994).

Regardless of the exact details of the underlying mechanism (Wikelski et al., in prep.), receptive females experiencing high rates of male attention on the high density lek lost more mass than those with low male attention on the low density lek (cf. Stillman et al. 1993). The total difference in mass loss was about 55 g ( $\approx 8\%$  total body mass). Because this is equivalent to two-fifths of the total clutch mass, it appears to be a biologically significant cost, either by reducing clutch size or by reducing post-laying female survival (Laurie 1990). It should be emphasized here that marine iguana females do not suffer from dehydration because they forage in the sea almost every day (Drent et al. 1999). Thus, assuming that females are in water balance, mass loss indeed indicates loss of fat or muscle tissue. Two alternative hypotheses could explain this mass loss: (i) food quality, quantity, or availability differed between the two sites; and (ii) females simply foraged less at the high density lek. We can disprove the first hypothesis because unreceptive females lose mass at the same rate in both areas. Hypothesis two would be true if females were more choosy on the high density lek and fed less than females choosing on the low density lek. However, we could not detect any differences in foraging duration between those two groups of females.

### **Why Choose Mates if it is Costly?**

If females suffer this cost of male attention, an important question emerges: why don't females move to the low density lek or to single territories, where male

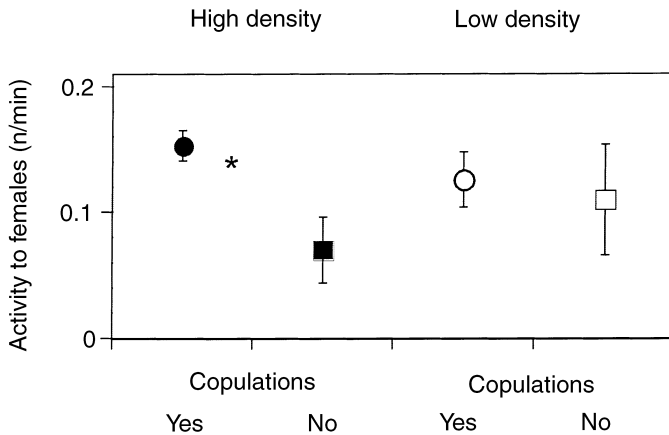


Fig. 4: Activity rates of successful and non-successful male marine iguanas on the high density (filled symbols,  $n = 10, 29$ , respectively) vs. the low density territorial site (open symbols,  $n = 7, 5$ , respectively). Data show mean  $\pm$  95% confidence interval. See text for differences between groups

attention is less frequent and thus choice less costly? Mate searching may bring benefits that outweigh this cost (cf. Reynolds & Gross 1990; Petrie 1994). Although we did not set out to study this question in particular, our data indicate that variance in male traits is higher on high density clusters. Thus choosing between lek males may allow females to pick the male with the most extreme traits. Indeed, males chosen by females in high density clusters were more active than males not chosen (Fig. 4 and Table 2). Whether such traits are important for the survival of hatchlings, and thus truly represent a benefit of choice, is presently under investigation.

#### Why is Mate Choice not Unanimous?

Male display, but not body size, appears to be used by females as final choice criterion. Display rate, however, is variable in time for each male. This behavioural variability may explain some variance in female mating decisions. A female copulated with the male that displayed strongest during the time she visited. But because every female saw a different set of males at different times, there is necessarily variance in the final mate choice. Thus, while for one female a particular male may reveal the highest display score, the same male may only be the second or third best for another female. We consider this distinction between complete, objective information and incomplete, subjective information highly important. We suggest that variance in mate choice in many animal mating systems can be partly or largely attributed to such incomplete information. Thus, even if each female makes the 'perfect' choice in her eyes, the cost of female choice will prevent females from gathering complete information to make the objectively 'perfect' choice.

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### Literature Cited

- Andrews, R. M. 1985: Mate choice by females of the lizard *Anolis carolinensis*. *J. Herpetol.* **19**, 284–289.
- Balmford, A., Bartos, L., Brotherton, P., Herrmann, H., Lancingerova, J., Mika, J. & Zeeb, U. 1993: When to stop lekking: density-related variation in the rutting behaviour of sika deer. *J. Zool. London.* **231**, 652–656.
- Bartholomew, G. A. 1966: A field study of temperature relations in the Galapagos marine iguana. *Copeia* **2**, 241–250.
- Bartholomew, G. A. & Lasiewski, R. C. 1965: Heating and cooling rates, heart rate and simulated diving in the Galapagos marine iguana. *Comp. Biochem. Physiol.* **16**, 573–582.
- Birkhead, T. R. 1991: Sperm depletion in the Bengalese Finch, *Lonchura striata*. *Behav. Ecol.* **2**, 267–275.
- Bradbury, J. W., Vehrencamp, S. L. & Gibson, R. 1985: Leks and the unanimity of female choice. In: *Essays in the Honor of John Maynard-Smith* (Greenwood, P. J., Harvey, P. H. & Slatkin, M., eds). Cambridge Univ. Press, Cambridge, pp. 301–314.
- Buttemer, W. A. & Dawson, W. R. 1993: Temporal pattern of foraging and microhabitat use by Galapagos marine iguanas, *Amblyrhynchus cristatus*. *Oecologia* **96**, 56–64.
- Carothers, J. H. 1984: Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.* **124**, 244–254.
- Censky, E. J. 1997: Female mate choice in the nonterritorial lizard *Ameiva plei* Teiidae. *Behav. Ecol. Sociobiol.* **40**, 221–225.
- Clutton-Brock, T. H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S. D. 1988: Passing the buck: Resource defense, lek breeding and mate choice in fallow deer. *Behav. Ecol. Sociobiol.* **23**, 281–296.
- Cooper, W. E. & Vitt, L. J. 1993: Female mate choice of large male broad-headed skinks. *Anim. Behav.* **45**, 683–693.
- Deutsch, J. C. 1994: Lekking by default. Female habitat preferences and male strategies in Uganda kob. *J. Anim. Ecol.* **63**, 101–115.
- Drent, J., Lichtenbelt, W. & Wikelski, M. 1999: Foraging mode and seasonality effects on the energetics of the marine iguana *Amblyrhynchus cristatus*. *Funct. Ecol.* **13**, 493–499.
- Dugan, B. 1982: The mating behaviour of the green iguana, *Iguana iguana*. In: *Iguanas of the World: Their Behaviour, Ecology, and Conservation* (Burghardt, G. M. & Rand, A. S., eds). Noyes Press, Park Ridge, pp. 320–341.
- Dugan, B. & Wiewandt, T. V. 1982: Socio-ecological determinants of mating strategies in Iguanine lizards. In: *Iguanas of the World: Their Behaviour, Ecology, and Conservation* (Burghardt, G. M. & Rand, A. S., eds). Noyes Press, Park Ridge, pp. 303–319.
- Gibson, R. M. 1992: Lek formation in sage grouse. The effect of female choice on male territory settlement. *Anim. Behav.* **43**, 443–450.
- Gibson, R. M. 1996: Female choice in sage grouse, the roles of attraction and active comparison. *Behav. Ecol. Sociobiol.* **39**, 55–59.

- Hews, D. K. 1993: Food resources affect female distribution and male mating opportunities in the iguanian lizard *Uta palmeri*. *Anim. Behav.* **46**, 279–291.
- Höglund, J. & Alatalo, R. V. 1995: *Leks*. Princeton University Press, Princeton.
- Jennions, M. & Petrie, M. 1997: Variation in mate choice and mating preferences: a review of causes and consequences. *Bio. Rev. Camb. Phil. Soc.* **72**, 283–327.
- Johnstone, R. & Earn, D. J. D. 1999: Imperfect female choice and male mating skew on leks of different sizes. *Behav. Ecol. Sociobiol.* **45**, 277–281.
- Keller, L. & Krieger, M. J. B. 1996: Mating success in male birds. *Nature* **380**, 208–209.
- Kirkpatrick, M. 1987: Sexual selection by female choice in polygynous animals. *Ann. Rev. Ecol. Syst.* **18**, 43–70.
- Kokko, H. 1997: The lekking game: Can female choice explain aggregated male displays? *J. Theoret. Biol.* **187**, 57–64.
- Kokko, H. & Lindström, J. 1997: Measuring the mating skew. *Am. Nat.* **149**, 794–799.
- Kotiaho, J., Alatalo, R. V., Mappes, J. & Parri, S. 1996: Sexual selection in a wolf spider – male drumming activity, body-size, and viability. *Evolution* **50**, 1977–1981.
- Laurie, W. A. 1990: Population biology of marine iguanas *Amblyrhynchus cristatus*. 1. Changes in fecundity related to a population crash. *J. Anim. Ecol.* **59**, 515–528.
- Mackenzie, A., Reynolds, J. D., Brown, V. J. & Sutherland, W. J. 1995: Variation in male mating success on leks. *Am. Nat.* **145**, 633–652.
- Olsson, M. 1993: Male-preference for large females and assortative mating for body size in the sand lizard *Lacerta agilis*. *Behav. Ecol. Sociobiol.* **32**, 337–341.
- Olsson, M. & Madsen, T. 1995: Female choice on male quantitative traits in lizards – why is it so rare? *Behav. Ecol. Sociobiol.* **36**, 179–184.
- Petrie, M. 1994: Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature* **371**, 598–599.
- Queller, D. C. 1987: The evolution of leks through female choice. *Anim. Behav.* **35**, 1424–1432.
- Rauch, N. 1985: Female habitat choice as a determinant of the reproductive success of the territorial male marine iguana *Amblyrhynchus cristatus*. *Behav. Ecol. Sociobiol.* **16**, 125–134.
- Reynolds, J. D. & Gross, M. R. 1990: Costs and benefits of female mate choice: Is there a lek paradox? *Am. Nat.* **136**, 230–243.
- Rintamäki, P. T., Alatalo, R. V., Höglund, J. & Lundberg, A. 1995: Mate sampling behaviour of black grouse females *Tetrao tetrix*. *Behav. Ecol. Sociobiol.* **37**, 209–215.
- Rintamäki, P., Lundberg, A., Alatalo, R. V. & Höglund, J. 1998: Assortative mating and female clutch investment in black grouse. *Anim. Behav.* **56**, 1399–1403.
- Rosenqvist, G. 1990: Male mate choice and female–female competition for mates in the pipefish *Nerophis ophidion*. *Anim. Behav.* **39**, 1110–1115.
- Ryan, M. J. 1998: Sexual selection, receiver biases, and the evolution of sex – differences. *Science* **281**, 1999–2003.
- Saether, S. A., Fiske, P. & Kalas, J. A. 1999: Pushy males and choosy females, courtship disruption and mate choice in the lekking great snipe. *Proc. Roy. Soc. Lond. B. Biol. Ser.* **266**, 1227–1234.
- SPSS Inc. 1991: *SPSS Statistical Algorithms*. SPSS Inc., Chicago.
- Stillman, R. A., Clutton-Brock, T. H. & Sutherland, W. J. 1993: Black holes, mate retention and the evolution of ungulate leks. *Behav. Ecol.* **4**, 1–6.
- Trail, P. W. & Adams, E. S. 1989: Active mate choice at cock-of-the-rock leks, tactics of sampling and comparison. *Behav. Ecol. Sociobiol.* **25**, 283–292.
- Trillmich, K. G. K. 1980: *Amblyrhynchus cristatus* Iguanidae. Paarungsverhalten. Inst. Wiss. Film, Göttingen.
- Trillmich, K. G. K. 1983: The mating system of the marine iguana *Amblyrhynchus cristatus*. *Z. Tierpsychol.* **63**, 141–172.
- Trillmich, F. & Trillmich, K. G. K. 1984: The mating system of pinnipeds and marine iguanas: Convergent evolution of polygyny. *Biol. J. Linn. Soc.* **21**, 209–216.
- Von Dellinger, T. & Hegel, G. 1990: Sex identification through cloacal probing in juvenile marine iguanas *Amblyrhynchus cristatus*. *J. Herpetol.* **24**, 424–426.
- Watkins, G. G. 1997: Inter-sexual signaling and the functions of female coloration in the tropidurid lizard *Microlophus occipitalis*. *Anim. Behav.* **53**, 843–852.

- Watson, P. J., Arnqvist, G. & Stallmann, R. R. 1998: Sexual conflict and the energetic costs of mating and mate choice in water striders. *Am. Nat.* **151**, 46–58.
- White, F. N. 1973: Temperature and the Galapagos marine iguana – insights into reptilian thermoregulation. *Comp. Biochem. Physiol.* **45A**, 503–513.
- Wikelski, M. & Trillmich, F. 1994: Foraging strategies of the Galapagos marine iguana *Amblyrhynchus cristatus*: Adapting behavioural rules to ontogenetic size change. *Behaviour* **128**, 255–279.
- Wikelski, M. & Hau, M. 1995: Is there an endogenous tidal foraging rhythm in marine iguanas? *J. Biol. Rhythms* **10**, 345–360.
- Wikelski, M. & Baurle, S. 1996: Pre-copulatory ejaculation solves time constraint during copulations in marine iguanas. *Proc. Roy. Soc. Lond. B. Biol. Ser.* **263**, 439–444.
- Wikelski, M. & Trillmich, F. 1997: Natural and sexual selection on body size fluctuates between marine iguana island populations. *Evolution* **51**, 922–936.
- Wikelski, M. & Wrege, P. H. 2000: Niche expansion, body size & survival in Galápagos marine iguanas. *Oecologia* **124**, 107–115.
- Wikelski, M., Gall, B. & Trillmich, F. 1993: Ontogenetic changes in food-intake and digestion rate of the herbivorous marine iguana *Amblyrhynchus cristatus*, Bell. *Oecologia* **94**, 373–379.
- Wikelski, M., Carbone, C. & Trillmich, F. 1996: Lekking in marine iguanas, female grouping and male reproductive strategies. *Anim. Behav.* **52**, 581–596.
- Wikelski, M., Carrillo, V. & Trillmich, F. 1997: Energy limits to body size in a grazing reptile, the Galápagos marine iguana. *Ecology* **78**, 2204–2217.
- Wiley, R. H. 1991: Lekking in birds and mammals, behavioural and evolutionary issues. *Adv. Study. Behav.* **20**, 201–291.
- Wiley, R. H. & Poston, J. 1996: Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution* **50**, 1371–1381.

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