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ORIGINAL ARTICLE

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Territory establishment in lekking marine iguanas, *Amblyrhynchus cristatus*: support for the hotshot mechanism

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Abstract The territory establishment of male marine iguanas and their subsequent mating success were analysed to identify spatial spillover (hotshot) and temporal spillover effects on lek formation. Males started to establish small display territories 2 months ahead of the mating season. Males did not establish territories in temporal synchrony and did not settle at sites where the probability of encountering females was highest. However, males arriving later preferentially established their territories in the neighbourhood of already established territories independently of the density of female-sized iguanas in these territories. Although settling in close proximity, there were no fights between those males. The number of fights between territorial males increased towards, and peaked during, the mating season. Fights did not result in the transfer of space, indicating that space per se was no resource. Instead, fights were directed towards central (hotshot) males. These central males had higher mating success than marginal males. Female density during the time of territory establishment did not predict the mating success of males, because females changed their spatial preferences between early establishment and mating periods. Similarly, the areas where males achieved the highest numbers of copulations changed during 4 years of our study. Thus, there was no evidence for temporal spillover between subsequent seasons. However, most male–male interactions served to distract successful males and may lead to spatial spillover of females into territories of unsuccessful males. In marine iguanas, territorial establishment appears largely governed by hotshot processes.

Keywords Hotshot · Iguana · Lek · Mating · Territory establishment

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Introduction

Leks are aggregations of males that defend small territories containing no resources besides the males themselves (Wiley 1991). One of the most interesting aspects of leks is the tight spatial clustering of males at specific sites. A number of not mutually exclusive hypotheses have been proposed to explain why males cluster their territories at specific places rather than occupy isolated non-resource based territories (Deutsch 1994; Höglund and Alatalo 1995). The hotspot model predicts that males congregate at areas of high female density (Bradbury and Gibson 1983; Bradbury et al. 1986; Westcott 1997). The clustering of males is thus determined by the clustering of females which, in turn, could be determined by the clustering of resources (Höglund and Alatalo 1995). That leks are sited on the points of greatest female density is indirectly supported in some species of birds. For example, in the ruff, *Philomachus pugnax*, leks are often situated near small ponds that females probably visit for feeding and drinking (Höglund et al. 1993). Similarly, hotspot models were supported for sage grouse, *Centrocercus urophasianus* (Bradbury et al. 1989; Gibson 1996) and for ochre-bellied flycatcher, *Mionectes oleaginus* (Westcott 1997) by analysing quantitatively the relationship between female movement patterns and male display locations. However hotspots may only account for spatial clustering of males on a broad scale. Other processes may explain the tight local clustering of lek territories at specific sites. The hotshot or spatial spillover mechanism suggests that unattractive males join hotshot males to take advantage of their attractiveness to females (Arak 1983; Beehler and Foster 1988; Höglund and Robertson 1990; Rintamäki et al. 1995). In black grouse, *Tetrao tetrix*, for example, females choose the most vigorous males that are dominant in male–male interactions. Ornaments and behavioural activity have some additional effect on female choice. Mating success of males was higher if they were neighbours to successful males. Attractive males end up in the centre of the lek presumably because less attractive males occupy territories close to attractive ones (Alatalo et al. 1991; Rintamäki et al 1995).

The second hypothesis that explains tight local clustering, the temporal spillover hypothesis, suggests that females copulate at previously popular mating sites or territories (Wiley 1974; Warner 1987; McDonald 1989; Gibson 1992). Studies on the sage grouse indicate that temporal spillover can influence the locations and clustering of male territories, since territories vacated by the most successful males became foci for clusters of territories in the following year (Gibson 1992).

To determine how important each of the two mechanisms is for the tight clustering of males, we need to precisely understand the processes during the formation of territorial aggregations. Marine iguanas offer an ideal system to investigate the establishment of territories, which lasts more than 2 months in this lekking reptile (Wikelski et al. 1996). Individual males can be captured and observed long before they become territorial, and their space use and interactions between males are easy to track. Territory establishment proceeds much slower in these ectotherms compared to territory establishment in, for example, birds. Furthermore, there is no predation to disturb establishment pattern.

A few mechanisms that potentially explain the clustering of territorial males in other species are excluded in marine iguanas. First, display territories contain no significant resources required by females except the males themselves (Wikelski et al. 1996). Second, there is no predation pressure on territorial males (Trillmich and Trillmich 1984). Third, sexual harassment of females – a prominent explanation for territorial clusters in some ungulates (Stillman et al. 1993, 1996) – does not explain the clustering of marine iguanas territories. Wikelski et al. (1996) showed that in spatially isolated single territories the intensity of sexual harassment was the same as in leks. Likewise, habitat limitation was not responsible for clustering of male marine iguanas. However, there are indications that female choice influences the mating pattern in marine iguanas (Wikelski et al. 2001) and may significantly contribute to the evolution of lekking in marine iguanas.

In this study we investigate the degree to which the two, not mutually exclusive, spillover mechanisms (temporal and spatial) may explain male territory settlement and mating success on marine iguana leks. For this, we examine the details of male territory establishment. We observed spatial settlement order of territorial males, female density, and the interactions between males throughout the establishment and mating period. Additionally we connected male mating success with territory position, female density and male–male interactions. We hypothesised that the hotshot or spatial spillover model applies if less attractive males establish territories around more attractive (more successful) males (Beehler and Foster 1988; Gibson et al. 1991; Gibson 1992). In addition, the areas with the highest number of copulations should differ between years if females choose attractive males and do not prefer specific sites for copulations. Therefore copulation sites should be randomly distributed between years. The temporal spillover model could contribute to the mating pattern of marine iguanas if copulations take place on the same site or in the same territories over subsequent years independent of the territorial male (Wiley 1974 ; Warner 1987; McDonald 1989).

Methods

Background natural history

Marine iguanas live in large aggregations on the coastline of the Galápagos Islands (Darwin 1883; Eibl-Eibesfeldt 1955; Carpenter 1966; Trillmich and Trillmich 1984) and feed exclusively on macrophytic marine algae in the inter-tidal zone during low tide (Trillmich and Trillmich 1984; Wikelski et al. 1993; Wikelski and Trillmich 1994; Wikelski and Hau 1995). These long-lived iguanas use rocks with interspersed crevices or bushes as resting sites. Males defend small clustered mating territories over more than two months and male mating success is not dependent on territory size (Wikelski et al. 1996) and on the timing of territory establishment (Trillmich and Trillmich 1984). Receptive females normally copulate only once during a bi-weekly mating season and leave these areas shortly thereafter to lay eggs (Trillmich 1983; Trillmich and Trillmich 1984). Egg laying sites are usually hundreds of metres away from territorial clusters.

Study side

Marine iguanas were studied from October 1995 to mid January 1996 at the study site ‘Miedo’ (0°50′S, 90°02′W) on Santa Fé island in the Galápagos archipelago. Iguanas at this study site have been investigated every year since 1981 and approximately 800 individuals were permanently marked by small brandings on the flanks (Laurie 1989). The study site consists of lava rocks stretching out to the sea on the southwest of the island (see Laurie and Brown 1990). Our observations took place on a small peninsula covering an area of 440 m² which marine iguanas crossed en route to feeding sites in the intertidal zone. Laurie (1989) mapped this area into 64 zones, whose boundaries were determined by well visible topographic characters like lava grooves and hills.

Animals

A total of 52 males and 38 females was captured prior to territorial activities at the end of September; 22 of the males later established territories on our study site. One of these territorial males was expelled by another male before the onset of the mating season. Therefore the total number of territorial males was 23. We usually determined the sex of individuals by external morphology, but if necessary we identified sex by cloacal probing (Dellinger and von Hegel 1990). Marine iguanas were painted with numbers of their flanks (using a non-permanent paint) to ease observations. We conducted observations from a prominent area, using binoculars if necessary. The colour numbers did not affect the behaviour of the animals, nor the reaction of other animals towards the painted iguanas (Wikelski and Audet, unpublished data). At the end of the mating period (4 January 1996) all territorial males were recaptured and weighed again.

Observations

Four observers were trained during two observation days to achieve inter-observer reliability. Intense observations were conducted between 30 September 1995 and 3 January 1996. This interval covered the entire reproductive season from the start of territory establishment to the end of the mating period. Daily scan-samples at 0900 hours and 1500 hours were conducted by one observer to count the number of, and if possible identify, female-sized and male iguanas in every zone. We chose an inter-scan interval of 6 h (half a tidal cycle) to determine and correct for the influence of the tides on iguana distributions. Zones were always counted in the same order. We could not securely distinguish between unmarked females and female-sized juvenile males – a problem that territorial males also face. However, 95% of iguanas captured as females were found to be females (Wikelski et al. 1996). We refer to females only if the sex of individuals is known and call all other non-male individuals ‘female-sized iguanas’. In addition, there could be non-receptive females amongst the female-sized iguanas. Females are non-receptive during a given mating season because they skip reproduction during a given year (Laurie and Brown 1990). For the analysis we used the density of female-sized iguanas (numbers/m^2), a measure that corrected for the territory size of each territorial male.

During the entire reproductive season (between 30 September 1995 and 3 January 1996) a second observer continuously surveyed the peninsula during daylight hours and recorded all fights, chases, copulations and new territorial establishments. Observers changed every 2 h. No recordings were done on 8, 11, 13, 15, 21 or 29 October, on 4, 5, 12, 19 or 26 November or on 3 or 10 December. During the mating season we did not carry out scan-sampling on 14, 17, 24 or 25 December.

Territorial and mating behaviour

We observed territorial behaviour and quantified number of head-bobs, posturing toward adjacent territorial males, chases and fights (see Trillmich 1983; Wikelski et al. 1996). Males were classified as territorial if they consistently occupied one area for more than 5 days and head-bobbed against other males. For each male we retrospectively used the first day of its territoriality as the day of territory establishment. Fights were defined as encounters that resulted in the physical contact of two animals for longer than 10 s. A fight ended when one male actively left the fighting area and did not attack again for 10 min. This time period was chosen because males sometimes interspersed fights with short breaks. We used the absolute values (number of fights per day) instead of rates (number of fights per male minute) because males were constantly on their territory during the entire observation period. With the day-light observations during the entire reproduction season we were able to observe nearly all fights that occurred on the peninsula. Unfortunately we often could not determine the initiator of fights. Thus, it was not possible to analyse the fight initiation.

Territory boundaries in marine iguanas appear largely determined by geographical features of their habits, e.g. crevices or small lava boulders. Thus there are practically no differences in territorial maps between years, although there is substantial male turnover, for example because most males skip reproduction every second year. However, this does not imply that males do not negotiate territories. Some males may expel their neighbours from their territory and take over the entire space, or new males may take over territories of such expelled ones. Territorial boundaries were determined by observing conflicts with neighbouring males. For males without direct neighbours, territorial boundaries were delineated where the territory owner chased other marine iguanas or fought with other males. The projected surface area (in m^2) of each territory was determined by weighing cut-out paper-sheets of the territorial map against standards (16-m^2 paper-sheets). The territory boundaries corresponded well with the boundaries of zones. The mean size of territories (n=22) was 13.2±7.4 m^2. Territorial males were considered to be neighbours if their territories were not separated by topographical conditions (like deep crevices) and if they could see each other.

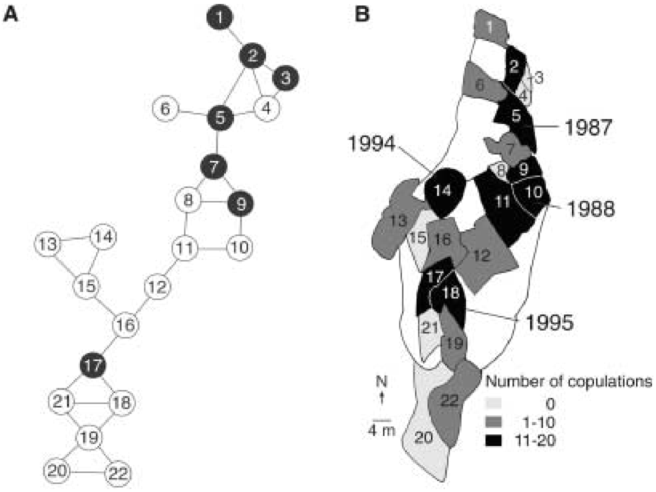

Fig. 1 **A** Idealised pattern of the spatial distribution of territories at our study site on the island Santa Fé during 1995–1996. The pattern resembles the natural distribution of territories (see *map* on the right hand with *lines* indicating territory boundaries). *Circles* represent territories. Neighbouring territories are connected with a *line*. The numbers of territories are randomly chosen from top to bottom. *Filled circles* depict the first seven males that established territories. **B** Total number of copulations pooled for the years 1987, 1988, 1994 and 1995 (n=140) on our study site. The *lines* depict the territory boundaries. Territories connected with a year indicate this territory with the highest copulation number in the respective year. *Shading* indicates the number of copulations. *White fields* on the peninsula without numbers depict no territories

Copulation attempts by territorial males consisted of a head-bob sequence accompanied by a slow side walk approach (Trillmich 1980). Only for the analyses of the interactions (fights) between territorial males we divided territorial males into two mating success categories: Males with none or only one copulation were defined as ‘unsuccessful’ males. We assigned males achieving one copulation as unsuccessful because even non-territorial sneaker males may gain one copulation per season (Wikelski et al. 1996). Thus only males gaining two or more copulations were considered to be consistently ‘successful’ males. In all other analyses we used the mating success (number of copulations) as a continuous variable. To estimate the central location we used the number of resident neighbours of each male as an approximation for the centrality of territories.

To better describe the sequence of events, we divided the study period (30 September 1995–3 January 1996) into seven time intervals: (1): 30 September–14 October 1995; (2): 16–29 October 1995; (3): 30 October–13 November 1995; (4): 14–28 November 1995; (5): 29 November–13 December 1995; (6): 14–28 December 1995; (7): 29 December 1995–3 January 1996. The mating period was defined as the time period between the first and the last copulation (14–28 December 1995; interval 6).

Spatial pattern of territory establishment

For the analysis of spatial pattern of establishment, all territories (n=22) were drawn on a map as circles (Fig. 1). The spatial repre-

Table 1 Estimates of the probability $Pr(N_{22}) \leq N_k \times (22\text{-}k)!/22!$, where $k=1,...,n$ (number established territories), such that $Z(x_i) \leq Z(d_i)$; N_k is the number of settlement possibilities for $k=1,...,n$; α is the significance level, at which H_0 could be rejected

k	N_k	$N_k \times (22\text{-}k)!/22!$	Significance level
2	58	0.126	≥α= 0.05
3	178	0.019	≤α= 0.05
4	594	0.0034	≤α= 0.01
5	2,098	0.0006	≤α= 0.01
6	7,992	0.00015	≤α= 0.01
7	127,872	0.00015	≤α= 0.01
8	1,918,080	0.00015	≤α= 0.01

sentation of territories on the map corresponded to the natural one. Neighbouring territories were connected by a line. Territories were randomly numbered in ascending order (Fig. 1). We tested whether occupation of territories on the peninsula was random (null hypothesis H_0) or whether males preferred to colonise territories that were close to already established territories (hypothesis H_1). To explain a possible spatial pattern in the colonisation of the 22 territories the order of territory establishment was collected in a 22 dimensional vector $D=[D_{(i)}]_{i=1,...;22}$ ($D_{(i)}$ is the number of the territory that was the i-th to be occupied). The null hypothesis (H_0) was that males selected each of the non-occupied territories with probability $1/n\text{-}k$, where n equals the number of territories (22) and k equals the number of already inhabited territories ($k=0,..., n\text{-}1$). Under this null hypothesis each of the 22 possible series of colonisations is equally likely. If X represents one of the 22 possible series of colonisations, then the probability of X is $P(X)=1/22!$. For a given X we can compute the probability C^X. The question of interest is now, what is the probability to observe a colonisation order such that $C_i^X \leq C_i^D$ for all $i=1,...,22$. To compute this probability, we defined N_k=number of partial vectors $X_k=(x_1,...,x_k)$ for $k=1,...,n$ (number of established territories) such that $C_i^X \leq C_i^D$ for $i=1,...,k$. The probability follows from $Pr[\{C^X \mid C_i^X \leq C_i^D, i=1,...,22\}]=N_{22}/n!$. Because N_{22} is large, we estimate the probability as follows: It is obvious that $N_{22} \leq N_k \times (22\text{-}k)!$. Therefore $Pr(N_{22}) \leq N_k \times (22\text{-}k)!/22!$. Which leads us to conclude $Pr(Z(X) \leq Z(D)) \leq N_k \times (22\text{-}k)!/22!$.

If $N_k \times (22\text{-}k)!/22!$ is smaller than a prescribed significance $\alpha=0.05$, then the result is for D unlikely under H_0, thus we reject H_0 and assume that hypothesis H_1 is true. Table 1 gives the estimates of $Pr(N_{22})$ for increasing k. Due to the enormous computation time required estimates were only computed until the k-value of 8. However, the probability did not change very much above the k-value 6.

Comparison between years

To test whether females consistently preferred certain territories of the peninsula for mating in successive years, we used the method by Rintamäki et al. (1995). We correlated the number of copulations in each territory for the consecutive years 1987–1988 and 1994–1995 (the present study). Dellinger (1991) provided data from the years 1987 (41 copulations) and 1988 (20 copulations). Wikelski et al. (1996) supplied data of copulations for 1994 (48 copulations). During this study (1995) we observed 32 copulations. Each data set contained the number and identity of territorial males. For the comparison of copulations between consecutive years we analysed only territories where copulations were counted at least in one year of the two analysed years (see Fig. 1). This is a conservative approach because we thereby excluded non-informative data that would otherwise influence correlation coefficients.

Statistical analysis

Data were processed with SPSS (1991) for Windows. Two-tailed test statistics were used. Data are given as means ± SD or as means ± SE if not otherwise indicated. The distribution of data was inspected for normality by Kolmogorov-Smirnov one-sample tests. To check for a relationship between variables we used Spearman's rank order correlations (r_s).

Results

Territory establishment

Temporal pattern

Two of 22 males were already territorial at the start of our observations (74 days before the first copulation occurred). The median of territory establishment was 59 days ahead of the first copulation (first quartile= 68 days; third quartile=44 days).

Spatial pattern

The following settlement order was observed. Territory: 2, 5, 1, 3, 7, 9, 17, 11, 16, 12, 10, 15, 18, 19, 21, 8, 13, 4, 14, 6, 20, 22 (Fig. 1). Figure 1 displays the partial colonisation for the first seven animals. Note that the first six territories form a connected component of the graph. The seventh male occupied territory 17 which is isolated from the rest of the already established territories. The vector $C^D=(c_1^D;...;c_{22}^D)$ describes the number of connected components at each stage of the colonisation. We obtain $C^D=(1; 1; 1; 1; 1; 1; 2; 3; 3; 2; 1; 1; 1; 1; 1; 1; 1; 1; 1; 1; 1; 1)$. The first six components of $C(D)$ equal 1 indicating that during the first six colonisation steps only territories were occupied that were neighbours of an already occupied territory. In contrast the seventh occupied territory ($D_7=17$) was isolated, therefore the vector is $c_7^D=2$. Newly colonised territories are almost always directly adjacent to already established territories. The data support the hypothesis H_1 that territorial males preferred to establish territories in close proximity to already established territories. The probability to get the observed settlement sequence by chance can be derived from Table 1. The likelihood that marine iguanas settled randomly was less than 1.5×10^{-4}.

Fights

A total of 87 fights was recorded. At the start of the territory establishment (interval 1), when most males settled into their territories, fights occurred rarely (0.08/day). The closer the mating period approached, the more fights occurred (Fig. 2). The number of fights reached a maximum of 2.21±0.42 SE fights/day during the mating period (interval 6). After the mating period (interval 7) the number of fights decreased to 0.67±0.42 SE fights/day. We observed a total of 28 contests during which non-territorial males tried to gain territories. Only two contests (7.1%) were successful in winning space or gaining territories. 21 (95,5%) of 22 males maintained their territorial status during the entire

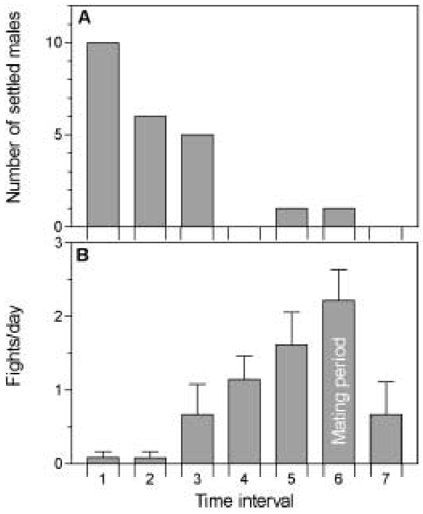

Fig. 2 **A** Number of newly established territorial males per time interval over the entire observational period (7 intervals) during the 1995–1996 mating season on Santa Fé island. **B** Mean (±SE) number of fights per day during each interval. Interval 6 corresponds to the mating period

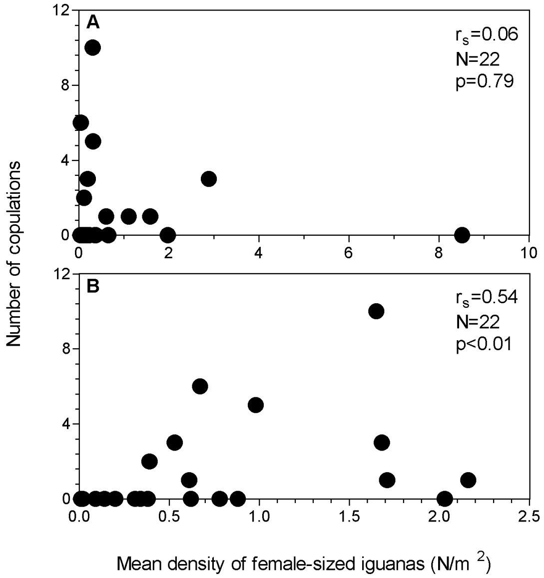

Fig. 3 **A** Male mating success on each territory in relation to the density of female-sized iguanas (n/m^2) during the beginning of territory establishment and **B** during the mating period

observation period. During the mating period, fights occurred more often in territories with a higher mean density of female-sized iguanas (r_s=0.43, n=22, P<0.05; n is the number of territories where fights occurred).

Spatial distributions of female-sized iguanas

At the beginning of territory establishment (interval 1) only 10 of 22 territories were frequented by at least one female-sized iguana. The maximum density per territory was 8.5 m^{-2} and the median was 0.095 m^{-2} (first quartile=0.02; third quartile=0.25). During the mating season (interval 6), one or more female-sized iguanas distributed themselves over 18 territories with the highest density of 2.2 m^{-2} per territory and the median density of 0.59 m^{-2} (first quartile=0.17; third quartile=0.98). The total mean number of female-sized iguanas on the peninsula was 171.2 during interval 1 and 168.9 during interval 6. In other words, total numbers of females were similar, but locations with high density changed between these two periods on the peninsula. Female-sized iguanas were distributed over more territories during the mating period (interval 6). The initial density of female-sized iguanas within each territory was not related to the subsequent number of copulations achieved by the respective territorial male (r_s=0.06, n=22, P=0.79, Fig. 3). However, the density of female-sized iguanas during the mating season was a predictor of the number of copulations for each male (r_s=0.54, n=22, P<0.01, Fig. 3).

Evidence for the hotshot model (spatial spillover)

We analysed whether individual males settled in those areas that contained the highest density of female-sized iguanas at the respective time of territory establishment. For each male, we ranked (in %) all unoccupied territories on the day of its territory establishment according to the density of female-sized iguanas. If males chose territories according to the density of female-sized iguanas then they should occupy high ranked territories. Only 7 of 22 males chose the territories with the highest available density of female-sized iguanas. There was no significant difference if we compared our observed rank values with the median rank of all territories as the expected value (Wilcoxon signed-ranks test: Z=–0.8048, n=19, P=0.42). We conclude that the observed establishment pattern does not provide evidence for territorial establishment around females as a potential resource.

If there was a hotshot effect, we expected unsuccessful territorial males to disturb their successful neighbours so that females leave their resting places on the territories of successful males and possibly copulate on neighbouring territories. Because territorial males with more neighbours are expected to have more territorial interactions, we corrected the total number of fights per male for the number of its neighbours. There were significantly more fights between unsuccessful males and their successful neighbours than between neighbouring unsuccessful males (Wilcoxon signed-ranks test: Z=-2.3664, n=7, P<0.02, Fig. 4). If the reason of fights toward successful males is to move females from central territories and/or increase a male's attractiveness to females, one could expect these fights to occur when more females were present on the neighbour's territory. During fights between unsuccessful males and their successful neighbours a higher mean number of female-sized iguanas rested in the territories of successful males than in the territories of neighbouring unsuccessful males fighting

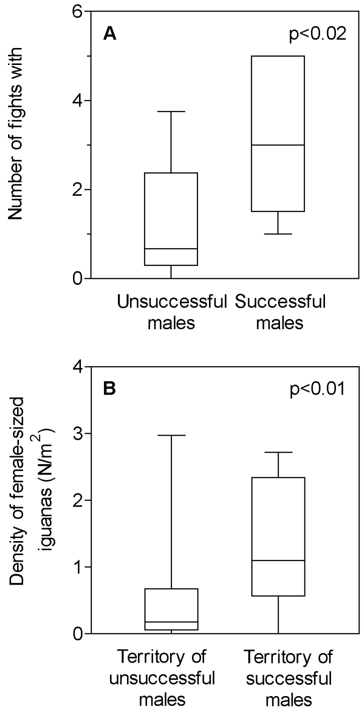

Fig. 4 **A** Number of fights from 7 unsuccessful territorial males (gained none or only one copulation) with other neighbouring unsuccessful or neighbouring successful territorial males. **B** Density of female-sized iguanas (*n*/m^2) in territories of unsuccessful males and neighbouring successful males during their fights (*n*=13)

with the successful males (Wilcoxon signed-ranks test: Z=–2,97, n=13, P<0.01, Fig. 4). Sixteen of 17 fights between unsuccessful males and their successful neighbours occurred in the territory of the successful male indicating that neighbours of successful males caused these fights (Chi-square test: n=17; P<0.01). Another prediction of the hotshot model is that central males are more attractive males and thus should have a significantly higher copulation success. Our data confirmed this prediction: males with a higher number of neighbours generally had a higher copulation success (r_s=0.49, n=22, P<0.05, Fig. 5).

Evidence against the temporal spillover model between seasons

To standardise for unequal number of copulations in each year, we used the proportion of copulations on each territory. There was no spatial relationship between the proportion of copulations among consecutive years (r_s=0.08, n=40, P=0.61; Fig. 6). Thus, females were neither faithful to the same territories in consecutive years, nor was there any general effect of location on the number of copulations. We conclude that there was no temporal spillover of matings between two consecutive years. The lack of site preferences for copulations is illustrated by the change in the position of the most preferred territory for copulation over the 4 study years. During every year, the position of territories with the highest number of copulations varied. The most successful male gained 7 of 41 copulations in 1987, 3 of 20 copulations in 1988, 12 of 48 copulations in 1994 and 10 of 32 copulations in 1995 (Fig. 1).

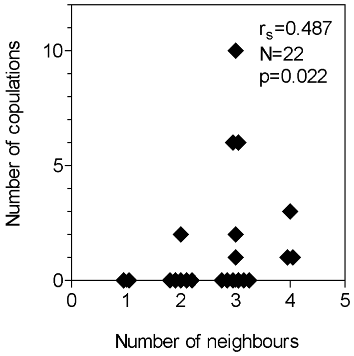

Fig. 5 Mating success and number of neighbours of individual territorial males

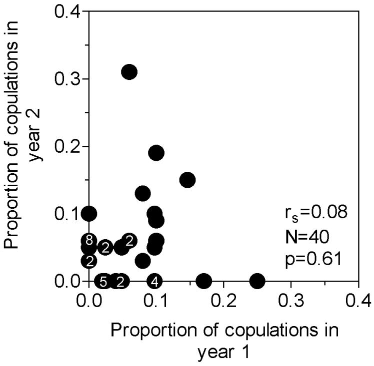

Fig. 6 Proportion of copulations on each territory of the peninsula compared between two consecutive years. *N* is the number of territories where copulations were counted at least in one year of the two analysed years

Discussion

Male marine iguanas established their small display territories 2 months ahead of the mating season without major fights. Female density in territories at the time of territory establishment did not influence the settlement order and did not predict the mating success of males. There was no evidence for a mating site preference of females between years, which contradicts the temporal spillover hypothesis. However, males preferentially settled in close vicinity of already established males. During the mating season, central males had more females on their territories and were challenged by surrounding males, but nevertheless had the highest mating success. These territorial and mating pattern are best explained by hotshot processes (Beehler and Foster 1988).

Territory establishment

45% of all territorial males established their territories approximately 8 weeks ahead of the mating period (Fig. 2). Thereafter, the number of newly established males decreased exponentially. A similar sequence of territory establishment was observed on Caamaño islet by Trillmich (1983). Why do males establish territories so early? The interannual variance in the time of the first copulation is usually 3–5 days (Wikelski, personal observation), thus early settlement does not function as an insurance against seasonal timing errors. Furthermore, early settlers did not gain more copulations than later settlers. This was shown by Trillmich (1983) on Caamaño islet, where huge males from a nearby island invaded a few days before the mating season started and expelled local territorial males from central territories. The invaders gained an overproportional number of copulations, either due to the centrality of their territories or due to their large body size. In the present study, however, the body sizes of territorial males were very similar and we did not find any relationship between body size and mating success (Partecke, unpublished data). It is possible that early establishment is advantageous due to a bourgeois effect. Stamps and Krishnan (1994, 1995) showed that the costs of expelling a settler from an area increase as a function of the amount of time it has already spent in that area. The territorial establishment in marine iguanas appears to follow similar rules (Wikelski, unpublished data).

The fact that territorial newcomers settled in close spatial proximity to conspecifics indicates that new males were attracted by already territorial iguanas. This pattern led to spatial clusters. The mechanism for such spatial aggregations of display territories closely resembles the mechanisms known for resource based clusters. For example, new settlers are attracted by the songs of conspecifics, supposedly because this indicates territories of good quality, e.g. in terms of food, nesting possibilities or mates (whinchat, *Saxicola rubetra*, Schmidt and Hantge 1954; pied flycatcher, *Ficedula hypoleuca*, Alatalo et al. 1982; chaffinch, *Fringilla coelebs*, and brambling, *F. montfringilla*, Mikkonen 1985). Similarly, in a study of juvenile lizards, *Anolis aeneus*, Stamps (1988) showed that newly-arriving juveniles were attracted to territorial residents. In all these cases new settlers used the resident conspecifics as indicators for habitat or resource quality (Alatalo et al. 1982; Stamps 1987, 1988; Shields et al. 1988). Because territories of lekking animals contain no significant resources except females, the reason for clustering may be to take advantage of the attractiveness of other males (Bradbury 1981; Bradbury and Gibson 1983). Thus, males would do best to assess the attractiveness of other males and try to settle next to males that are preferred by females. This is corroborated by the fact that mating success was best predicted by the number of territorial neighbours in our study.

Interactions

Two observations on territorial interactions shed particularly clear light on the mechanisms of clustering. First, there were hardly any fights during the first days of territory establishment. This implies that space per se was not an important resource. Furthermore, it confirms that territories do not offer any specific material benefit. Else, males should try to occupy such particularly resourceful areas first and fight for access to them.

Second, males did not acquire space or territories as a result of winning contests, which in turn is often the case in resource-based systems (Maynard Smith and Parker 1976; Krebs 1982; Maynard Smith 1982; Enquist and Leimar 1983; Grafen 1987; Stamps 1994). Only once did a non-territorial male expel a territorial male during an escalated fight in our study. In all other cases, territory boundaries remained unchanged during non-escalated head-push or head-bob interactions. Such a situation is similar to Stamps and Krishnan’s (1997) concept of fighting to ‘make neighbours’. The increase in fighting frequency during the reproductive season is likely linked to a new ‘resource’, receptive females.

However, it is still unclear whether high female density caused fights, or whether fighting males were chosen by females. Fights between neighbours could attract females because fights enable the assessment of male quality. Indeed, Wikelski et al. (1996) found that females were more likely to mate in areas where behavioural stimulation rates were higher. Conflicts between males could also disturb a male’s display, resulting in the loss of receptive females to neighbours. This would explain the higher fight frequency between successful males and their unsuccessful neighbours than between other territorial males (Fig. 4). Shelly (1987) observed a similar phenomenon in lekking fruitflies, *Drosophila conformis*.

A proximate reason for the low frequency of fights during the settlement period might be individual recognition between former neighbours. 70% of territorial males can be territorial again in the consecutive year, and if so, mostly in the same area (Trillmich 1983; Dellinger 1991; Wikelski 1994). During our study, one male occupied the same territory where it was territorial 8 years ago. Therefore we cannot exclude the possibility that territorial males know each other from previous years and thus tolerate each other’s territory establishment. But it is so far unknown whether individual recognition between males and/or females exists and whether this could be the mechanism responsible for the low aggressiveness between territorial neighbours, maybe even between years. However, males usually skip every second or third breeding season (Dellinger 1991), thus it seems unlikely that individual recognition accounts for much of the observed social dynamics.

What factors explain the territorial clustering in marine iguanas?

An exact analysis of the territory establishment allows us to determine the possible contribution of the spatial (hotshot) and temporal spillover model towards the tight clustering of male territories.

Indications for the hotshot model were found by Wikelski et al. (1996) in marine iguanas on Genovesa island, where the number of copulations for small territorial males increased with lek size. In the present study, three indirect lines of evidence suggest the hotshot model further:

1. The majority of males (15 of 22) did not occupy territories at sites that had the highest female density. These males rather settled in the vicinity of already established territorial males. This could indicate that the neighbourhood to an attractive male has a beneficial effect on the mating success rather than number of females in one territory.
2. Less successful males appeared to initiate more fights against their successful- than against other unsuccessful neighbours. We interpret this as an attempt of less successful males to get an access to a higher number of females or to make females leave the territories of successful males and to copulate with unsuccessful territory owner (spatial spillover). The interpretation is also partly supported by Trillmich (1983), Rauch (1985) and Wikelski et al. (1996) who observed that females left territories in which fights occurred. In this study we could find that the density of resting female-sized iguanas was higher in territories of successful males than in neighbouring territories of unsuccessful males during fights between those two territory owners.
3. The hotshot model is also consistent with the fact that males with central territories gained more copulations. The hotshot model explains this correlation as a consequence of grouping of less successful males around attractive hotshots. It is conceivable that the quality of territorial males is increasing with cluster size. Widemo and Owens (1995) showed that a conflict between attractive and unattractive males may erupt over the composition of a mating cluster. However, whether a central location is a cause or a consequence of high mating success in marine iguanas cannot be decided so far (but see for discussion, e.g. Bradbury and Gibson 1983; Gibson and Bradbury 1985; Höglund and Lundberg 1987; Gosling and Petrie 1990; Höglund and Robertson 1990; Gibson 1992). Presently, we cannot exclude the possibility that centrality was used by female marine iguanas as one of the cues in their mate choice (Trillmich 1983; Rintamäki et al. 1995).

The second process that can explain male clustering, temporal spillover of copulations appears not to apply to marine iguanas. Females did not prefer previously popular mating sites. Despite a male fidelity to territories of 70% in consecutive years (Dellinger 1991), the choice for copulations, sites and mates is renewed in the following reproduction period. During one season, the frequency of replacement of territorial males is negligible (1 of 22). Therefore the temporal spillover within a given season is not significant in the clustering of marine iguanas. Also, it is justified to consider temporal spillover in marine iguanas largely in terms of ‘space’, because males stay at one territory for the entire breeding season, and also come back to exactly the same territory in subsequent years. Generally, the evidence for temporal spillover is equivocal: while it may be important in sage grouse (Gibson 1992) and ungulates (Gosling and Petrie 1990; Balmford et al. 1992; Deutsch and Weeks 1992), there was no temporal spillover in lekking black grouse (Rintamäki et al. 1995), great snipe, *Gallinago media*, (Höglund and Roberston 1990) and in the Guianan cock-of-the-rock, *Rupicula rupicula* (Trail and Adams 1989).

Thus overall it appears that temporal spillover processes do not sufficiently explain the clustering of territories in marine iguanas. On the other hand, processes during territory clustering are consistent with the hotshot or spatial spillover model.

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