

Non-defendable resources affect peafowl lek organization: A male removal experiment

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Abstract

A lekking mating system is typically thought to be non-resource based with male providing nothing to females but genes. However, males are thought to clump their display sites on areas where they are more likely to encounter females, which may depend on non-defendable resource location. We tested this hypothesis on a feral population of peacocks. In agreement, we found that, within the lek, display site proximity to food resources had an effect on female visitation rate and male mating success. The attractiveness of display sites to male intruders was explained by the distance to the feeding place and by the female visitation rate.

We randomly removed 29 territorial males from their display sites. Display sites that were more attractive to male intruders before removal remained highly attractive after removal and display sites closer to the feeding area attracted the attention of intruders significantly more after removal. Similarly, display sites that were more visited by females before removal remained more visited after removal, suggesting again that the likelihood of encountering females is determined by the display site location. Overall, these results are in agreement with non-defendable resources affecting lek spatial organization in the peafowl.

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1. Introduction

A lek is an aggregated male display area that females attend primarily for the purpose of fertilization (Höglund and Alatalo, 1995). Males clustering in “classical” leks defend specific display sites, which encompass few or no resources attractive to females beside the males themselves. Therefore, males provide females with nothing but their genes (Bradbury, 1981; Wiley, 1991). The distribution of matings is highly skewed among males (Davies, 1978; Payne, 1984). Studies of lek spatial organization have shown that central positions are often occupied by dominant males that achieve a disproportionate share of female copulations (e.g., Bradbury and Gibson, 1983). Several not mutually exclusive hypotheses have been put forward to

explain the lek aggregation of males during the breeding season. Each hypothesis has received great attention and has been at least partly supported by models, computer simulation, or field work (e.g., Lank and Smith, 1992; Droney, 1994; Höglund et al., 1995; Jones and Quinell, 2002). However, determinants of the spatial organization within the lek and the influence of this spatial organization on mate preferences remains poorly understood among many lekking species.

Females may prefer mating at leks because of an arbitrary Fisherian preference for larger groups of males or because clustered males reduce female costs in terms of time spent searching for mates and this facilitates comparison of potential mates (Queller, 1987; Gibson et al., 1990; Jones and Quinell, 2002). An extension of this idea, the position hypothesis, suggests that females use the position of males within the lek to choose a mate because it indicates male quality, males competing for preferred positions (Höglund and Robertson, 1990). In the initial model, preferred positions were supposed to be central positions but they also may be predator safe places (Gosling, 1986; Gosling and Petrie, 1990; Balmford and Turyaho, 1992; Deutsch and Weeks, 1992), or places where females can avoid

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sexual harassment (Stillman et al., 1993; Clutton-Brock et al., 1992).

Males may cluster their display sites on particular and limited “hotspots” sites associated with extremely high female encounter rates (Bradbury and Gibson, 1983; Bradbury et al., 1986; McNaughton, 1988; Gosling, 1986). The “hotspot” hypothesis predicts that leks should be located at sites of maximum female density or at traffic routes used by females when travelling between areas (Westcott, 1997a). However, female density and/or movements are usually determined by external factors such as predator risks or location of resources (Alexander, 1975; Bradbury et al., 1986; McNaughton, 1988).

Attractive males occupying the centre of the lek may also be a consequence of low quality males displaying close to particularly attractive “hotshot” males in the attempt to increase their own reproductive success by intercepting females (hotshot or spatial spillover effect: Beehler and Foster, 1988) or in the attempt to inherit a display site or a social status (temporal spillover effect: Gibson et al., 1991; McDonald and Potts, 1994) through “queuing” (Kokko et al., 1998).

A lek being an area where males and females encounter potential mates, both are expected to settle to favour reproduction. Empirically disentangling the role of male and female behaviours in lek formation and lek spatial organization remains a challenging issue because both processes potentially operate simultaneously and interact with each other (Sæther et al., 2005). For example, in both the position hypothesis and the hotspot hypothesis, the spatial organization of the lek is shaped by both intra-sexual agonistic behaviour of males and female mate choice or female habitat use. Indeed, males jockey for a position where the probability to be visited by a female is high (hotspot hypothesis) or where the probability to mate is high (position hypothesis). Therefore, experimental studies leading to clear predictions might be more informative than observational ones. With this in mind, we took advantage of a species where the male–male competition for display sites is high and where floating males and sometimes territorial males display on the sites of territorial males that rapidly chase them (Loyau et al., 2005a). We studied a population of free-ranging common peafowl. We performed a male removal experiment to specifically test whether vacant display sites were attractive to the remaining males and to females. If males settle as a function of the probability to encounter a female, the attractiveness of a given site may be determined by its location. Therefore, removing the resident male should not influence the site attractiveness perceived by male intruders nor by females. Conversely, if the intrusion rate on a display site is shaped by the male quality, a display site that was attractive because there is an attractive male in close proximity should no longer be attractive to males as well as to females if this attractive male is removed.

The mating system of the peacock, *Pavo cristatus*, fulfils the criteria of a classical lek (Rands et al., 1984; Petrie et al., 1991). Males aggregate and defend display sites where females come to choose a mate (Petrie et al., 1991). A previous study showed that the likelihood of establishing and defending a display site was correlated with male tarsus and train length (Loyau et al., 2005a). Moreover, males with longer tarsi were in a more central

position within the lek and sites belonging to males with longest train and highest display activity seemed to be more attractive to floaters.

In this paper, we tested whether the display site location and the male phenotypic attractiveness shape the lek spatial organization in this population of peacocks. First, we identified males and sites that were attractive both to other males and to females, and investigated their site quality. Then, we performed a male removal experiment to test the predictions outlined above.

2. Material and methods

2.1. Study location and population studied

The study was conducted at the Parc zoologique de Clères, National Museum of Natural History, France. The park of 13 ha consists mainly of lawns, surrounded by bushes and woodland. We studied a population of free-ranging common peafowl marked with numbered and coloured metallic rings. The number of adults varied from 102 (61 males and 41 females) in 2001 to 88 (51 males and 37 females) in 2003. Their diet consists of natural forage (e.g., grass shoots, seeds, small fruits, insects) and of food supplementation provisioned twice daily. In 2001, 74% of males defended a display site, whereas 23% were floaters (Loyau et al., 2005a). Territorial males clustered at two areas separated by at least 200 m, we therefore assumed they were forming two leks. We focused on the largest one.

2.2. Behavioural observations

We observed male display sites during three consecutive years from 2001 to 2003 to assess the number of territorial males and floaters, and the male site fidelity within the lek. On average, 200 h of observations were performed per year. Using data collected in 2003, we calculated the distance between the male displaying site and the place where peafowl were fed twice a day.

During spring 2003, from April 14th to July 07th, sexual displays of 29 territorial peacocks were extensively monitored with a total of 300 h of focal observations. Observation sequences were performed between 09:00 and 17:30 h with a mean length of about 2 h per sequence.

We gathered preliminary information between April 14th and May 04th 2003. We recorded the number of male intrusions (i.e., a male displaying on a display site he does not own) and the number of male–male interactions won by a territorial male. An intrusion usually incites an attack from the resident male that chases the intruder. Moreover, we recorded parameters involved in mate choice such as the number of eyespots and the display rate (Loyau et al., 2005a). The number of eyespots in the train was counted from digital photographs of males with the train fully displayed. We also recorded the female visitation rate and the male mating success. A female visit was defined as a female interacting with a displaying male to assess a potential mate. The sequences of events have been described by Petrie et al. (1992). The female approaches a display site and stops in front of the male that is turning away. If the female follows the male’s movement, the male attempts to mate with the female.

2.3. Male removal

When this preliminary information was gathered we randomly captured each of these 29 peacocks. We measured tarsus length and train length from the base of the tail to the tip of the longest feather. Before release, each territorial male was kept for 17 days alone in an aviary (3 m × 5 m) where food and water were provided ad libitum. Maximally 12 peacocks were removed at the same time. Vacant display sites were observed and the behaviour of any male on the display site was recorded as described before.

2.4. Analyses

The R 3.0 “Autocorrelation” program was used to investigate spatial autocorrelations (Legendre and Vaudor, 1991). We drew correlograms and used Moran’s spatial autocorrelation coefficients (Moran’s I) (1950) to measure spatial autocorrelation in display rate, and intrusion rate. We mapped male display sites and the feeding area with ArcView GIS 3.1.

We examined correlates of the distance from the display site to the peafowl feeding place using a Generalized Linear Model (proc GLM, SAS Institute, Cary, USA, 1999).

We also investigated whether female visits, female mate choice, and male displaying intrusions were explained by male phenotypic attractiveness or by site location using Generalized Linear Models with Poisson distribution of errors and log link function (proc GENMOD, SAS Institute, Cary, USA, 1999). The date of capture was included in the models. Distance to the feeding place and male phenotypic attractiveness were correlated. Independent variables were obtained by regressing distance to the feeding place on number of eyespots, and regressing number of eyespots, display rate and female visitation rate on distance to the feeding place. We then used the residuals as independent variables in the models.

We compared lek organization before and after male removal using Spearman correlations. Sequential Bonferroni correction for multiple tests (Rice, 1989) was used to assess the significance of the correlograms and correlations.

3. Results

3.1. Male site fidelity

Display sites occurred at specific locations which were used year after year, and at which territorial males were highly faithful. Ninety four percent (32/34) of territorial males in 2001 that were alive in 2002 occupied the same display site within the lek, and 91% (31/34) in 2003. Moreover, the males who changed their territory seemed to prefer pre-existing display sites on specific locations within the lek.

3.2. Lek organization before male removal

The correlograms showed evidence for spatial autocorrelation in male displaying activity (Fig. 1a) and in attracting

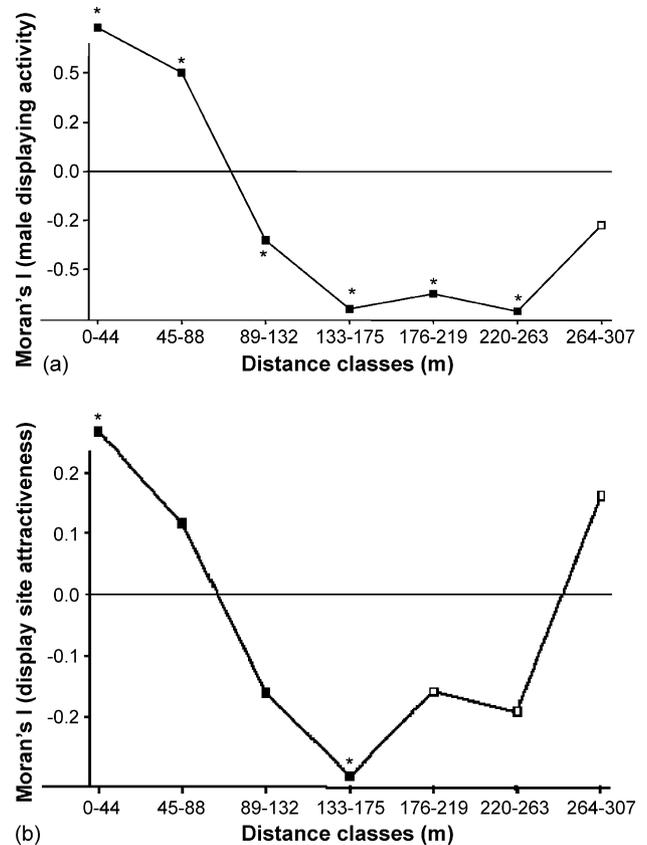


Fig. 1. Spatial autocorrelation in: (a) male displaying activity and (b) in display site attractiveness to intruders. Moran's spatial autocorrelation coefficients (Moran's I) were plotted against the distance classes between pairs of display sites. Black symbols represent significant values at the 0.05 level whereas white symbols represent non-significant values. Starred black symbols represent significant values at the corrected Bonferroni level ($\alpha' = 0.05/7 = 0.007$).

intruders (Fig. 1b). Males were clumped as a function of their displaying activity (Fig. 2) and their display site attractiveness to male intruders. To investigate display site intrinsic attractiveness to other males, we calculated the distance between male display site and the place where peafowl were fed twice a day. Establishing a display site close to the feeding site was not explained by the tarsus length, the train length nor the number of eyespots ($F_{1,25} = 3.21$, $p = 0.086$; $F_{1,25} = 0.40$, $p = 0.535$; $F_{1,25} = 0.40$, $p = 0.532$; respectively).

Female visitation rate was negatively explained by the distance to the feeding place and not by the number of eyespots in the train, the display rate nor the date of capture ($F_{1,24} = 12.03$, $p < 0.001$; $F_{1,24} = 2.48$, $p = 0.115$; $F_{1,24} = 0.28$, $p = 0.594$; $F_{1,24} = 0.52$, $p = 0.469$; respectively). Male mating success was negatively explained by the distance to the feeding place only ($F_{1,24} = 4.60$, $p = 0.032$; $F_{1,25} = 0.40$, $p = 0.526$; $F_{1,24} = 0.36$, $p = 0.550$; $F_{1,24} = 0.21$, $p = 0.649$; respectively; Fig. 3a). The distance to the feeding place ($F_{1,24} = 11.30$, $p < 0.001$; Fig. 3b) and the female visitation rate ($F_{1,24} = 5.00$, $p = 0.025$) and not the male phenotypic attractiveness (number of eyespots: $F_{1,24} = 1.80$, $p = 0.180$) nor the date of capture ($F_{1,24} = 3.70$, $p = 0.054$) explained intrusions of males on a territory they did not own.

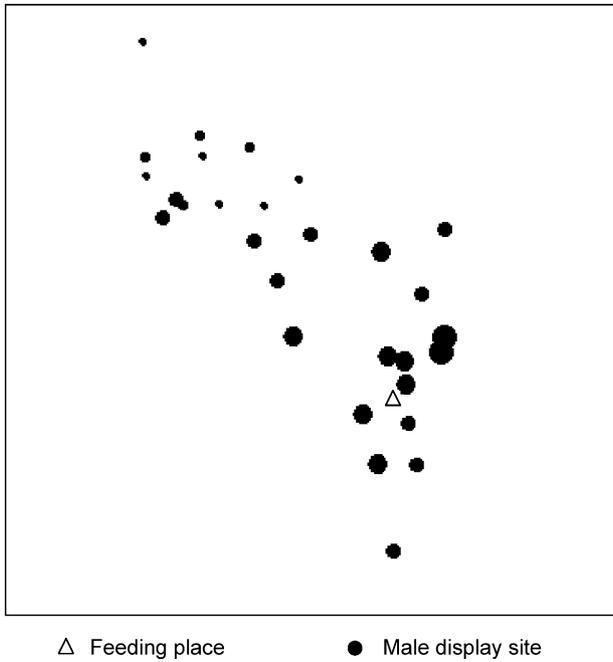
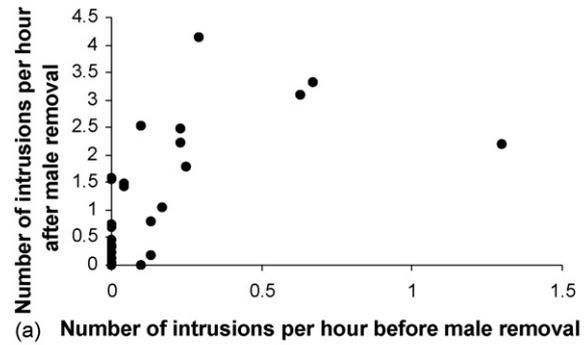
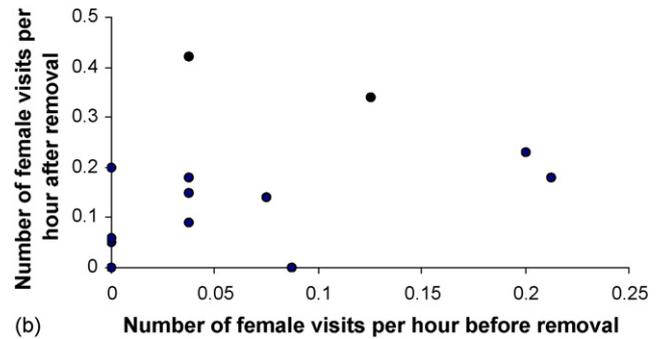


Fig. 2. Male display sites and the feeding place. Dots of different size refer to different values of displaying activity (0–3 displays per hour).

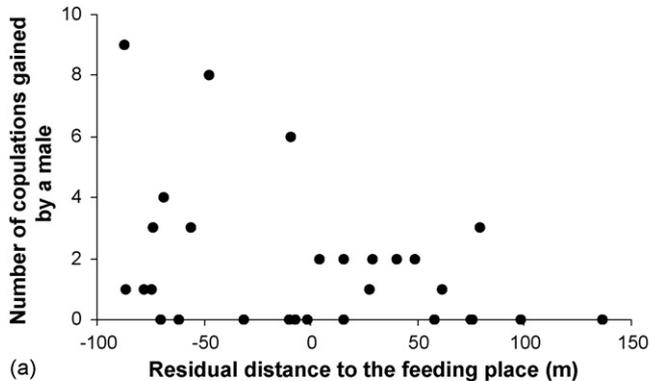


(a) Number of intrusions per hour before male removal

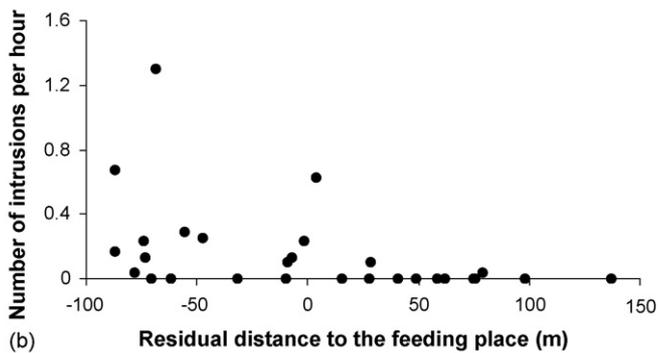


(b) Number of female visits per hour before removal

Fig. 4. (a) Positive correlation between intrusions rate after male removal and intrusion rate before male removal; (b) positive correlation between female visitation rate after male removal and female visitation rate before male removal.



(a) Residual distance to the feeding place (m)



(b) Residual distance to the feeding place (m)

Fig. 3. (a) Negative correlation between the male mating success (number of copulations accepted by a female) and the residual distance from display site to the peafowl feeding place (m); (b) negative correlation between intrusion rate (number of intrusions of displaying male per hour) and residual distance from display site to the peafowl feeding place (m). Residual distance to the feeding place was obtained by regressing the distance to the feeding place on the number of eyespots in the train.

3.3. Lek organization after male removal

To test whether males aggregate on particular display sites because of owner attractiveness to other males or because of display site attractiveness, we performed a male removal experiment and observed if the vacant display sites were thereafter occupied or not. Our results show that, during removal of the owner, the display rate of the intruders was explained by the distance to the feeding place and not by the number of eyespots of the owner nor the date of capture ($F_{1,25} = 9.39$, $p = 0.002$; $F_{1,25} = 2.16$, $p = 0.142$; $F_{1,25} = 0.00$, $p = 0.971$; respectively) suggesting that display site location rather than the owner himself determines the intrusion rate by other males. The female visitation rate was explained by the display rate of the intruders alone (display rate: $F_{1,25} = 23.11$, $p < 0.001$; distance to the feeding place: $F_{1,25} = 0.10$, $p = 0.749$; date of capture: $F_{1,25} = 1.80$, $p = 0.180$). The higher intrusion rates on vacant display sites were found on display sites that underwent more intrusions before male removal (Spearman's $r = 0.704$, $n = 29$, $p < 0.0001$; Fig. 4a). Display sites that were more visited by females before removal remained more visited after removal (Spearman's $r = 0.603$, $n = 29$, $p = 0.0005$; Fig. 4b). We computed the removal-induced change in male intrusion frequency (intrusion rate after male removal minus the intrusion rate before) and correlated these values with the distance of the display site to the peafowl feeding place. Display sites closer to the feeding place increased more their intrusion rate (Spearman's $r = -0.476$, $n = 29$, $p = 0.0090$; Fig. 5).

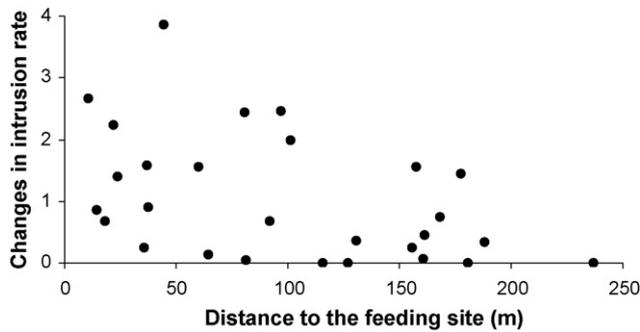


Fig. 5. Negative correlation between removal-induced change in intrusion rate (intrusion rate after male removal minus the intrusion rate before) and distance from display site to the peafowl feeding place (m).

4. Discussion

Overall, we found that non-defendable resources affect lek spatial organization in the peafowl. Females preferentially visited and mated with males displaying close to the resources. Consequently, males competed to settle on those particular display sites where the probability to encounter females was higher.

Studying lek organization in peafowl during three consecutive years, we found stable use of lek sites over time combined with extreme site fidelity between years. Widemo (1997) proposes that the traditional use of lek sites has evolved to minimize the costs of site establishment and defence. Remaining among neighbours whose competitive abilities have already been assessed may reduce the risk of male injury. Indeed, during site establishment, male–male competition is intense within the lek and direct mortality of males due to site disputes, though rare in peacocks, has been observed (Loyau, pers. obs.). After site establishment, costs of site defence are expected to be high, especially for top-quality males that suffer the highest male intrusion rates. The long and costly process of site establishment may explain why all territorial males did not takeover a better display site when they had the opportunity to. This hypothesis could easily be tested by removing males of various statuses before site establishment and observing how the remaining males deal with the vacant sites.

The high costs of top-quality males are compensated by a high mating success. It is less obvious why intermediate-quality males defend lekking sites while their probability to gain copulations is low. Intermediate-quality males may benefit from temporal spillover effect (Gibson et al., 1991; McDonald and Potts, 1994) through “queuing” (Kokko et al., 1998), or may increase their inclusive fitness from kin selection (Höglund, 2003; Kokko and Lindström, 1996). The proportion of males that are non-territorial is surprising given that establishing and defending a display site is a major determinant of mating success (Loyau et al., 2005a), and that area apparently available for settlement remains unoccupied. Westcott (1997b) demonstrated that territorial males attempt to prevent the establishment of new sites adjacent to their own, determining both the size of the lek and the size of the floater population through despotism

(Bradbury et al., 1986). On the other hand, floaters may benefit from kleptoparasitism since they have been seen performing few copulations (Loyau et al., 2005a). Removing up to 12 territorial males at the same time, a rather unrealistic situation in the wild, may have increased the floaters’ likelihood to display on the lek by reducing despotism, explaining why the intrusion rates increased dramatically after male removals.

We investigated the determinants of the spatial organization within a peafowl lek and the influence of this spatial organization on mate preferences. Spatial autocorrelograms showed that males cluster according to their displaying activity, which has been shown to be an honest cue of male quality (Loyau et al., 2005b). These results are consistent with classical findings in lek species (e.g., Bradbury and Gibson, 1983). In agreement with the position hypothesis, female visitation rate and male mating success within the lek were affected by the display site position independently of the male phenotypic attractiveness. Females preferred to mate on display sites close to a non-defendable resource, the feeding station. We removed territorial males of different mating success. We observed that the display site attractiveness to females increased after removal (probably because of reaching the peak of the breeding season) and could be classified in the same relative order. These results confirm that the display site itself had an intrinsic quality linked to the probability of encountering females and that indirect mate choice (Sæther et al., 2005), through the preference about where to mate, can shape the lek spatial organization in the peafowl. However, it is unlikely that, in this species, the display site position alone drives female preferences. Indeed, previous studies emphasized the role played by male phenotypic quality in mate choice (eye-spot number in the train: Petrie et al., 1991; Petrie and Halliday, 1994; Loyau et al., 2005a; courtship display rate: Loyau et al., 2005a).

The definition of a “classical” lek states that male display sites contain no significant resources required by females except the males themselves (Bradbury and Gibson, 1983). Females typically spend little time feeding in the lek, and manipulation of food availability on the lek has been shown to have no effect on distribution of females (Clutton-Brock et al., 1988). Peacocks establish classical leks (Rands et al., 1984; Petrie et al., 1991) where territorial males did not defend food resources. However, studies supporting the hotspot hypothesis demonstrate that classical leks are often established in proximity to female non-defendable resources (Théry, 1992; Höglund et al., 1993; Westcott, 1997a; Jiguet et al., 2002). Females may gather benefits from food and male resources proximity. They may minimize costs of visiting the leks and thereby the cost of choice because they can assess potential mates while moving to feed.

Female preference for mating on particular display sites is expected to enhance male–male competition for those sites. Male–male agonistic interactions and intrusions of males displaying on a territory they do not own are common in peafowl (Loyau et al., 2005a). We investigated whether males introduce on display sites because of the owner phenotypic attractiveness (hotshot hypothesis) or because of the location of the display site (hotspot and position hypotheses). We found that the site position and not the owner’s attractiveness explained male intrusions,

invalidating the hotshot hypothesis as a determinant of the lek spatial organization in this species. A more recent observation reveals that males may settle where the probability to encounter females is the highest rather than where the resources are found. For research purposes, females were caught and housed away from the lekking area. We observed males giving up the lekking area to display near the females. Further work is definitely needed to experimentally test this idea.

To our knowledge, the present study is the first male removal experiment that provides a validation of the implication of resources location in lek spatial organization. Rippin and Boag (1974) and Robel and Ballard (1974) removed central males in sharp-tailed grouse, *Tympanuchus phasianellus*, and greater prairie chickens, *Tympanuchus cupido pinnatus*, respectively. In both cases the remaining males readily took over the vacant central area. Nevertheless, they did not control for removing peripheral males. On the contrary, in the great snipe, *Gallinago media*, when dominant males were removed, the display sites were left unoccupied by neighbouring males, whereas when subdominant or subordinate males were removed these display sites were immediately occupied, supporting the hotshot hypothesis (Höglund and Robertson, 1990).

The present study provides new insight on the mechanisms involved in lek spatial organization in peafowl. However, the approach used does present some limitations. First, only one lek was observed. Studying simultaneously several leks would allow to investigate inter-lek variations, and to have a control. Further, performing the present study on leks of different sizes would allow testing the female preference for larger leks. Second, the experiment concerned simultaneously removing multiple males and the method employed did not account for eventual interactions, especially if there is queuing between males of relative qualities. Indeed, the hypothesis that queuing is an additional mechanism involved cannot be rejected. Third, one can argue that the results do not prove that the site attractiveness observed after removal was not related to the new holder's quality. However, establishing on a new site and defending it is a long and energy-demanding process. Male intruders on vacant display sites after male removal were mainly floaters. It is very unlikely that floaters displaying close to the food resources would be of better quality than the remaining territorial males displaying further away because previous studies in this population have demonstrated that only better quality males with longer tarsi and longer train settle on a display site (Loyau et al., 2005a). Finally, the population observed was a feral captive population whose density and sex-ratio biased towards males may be high in comparison to a wild population and the spatial organization of the peacock leks may vary according to these parameters. Wild peacock populations established in close proximity to villages are commonly fed by humans in fixed places (R. Vijayan, pers. com.). However, peacock lek spatial organization remains to be investigated in wild populations not fed in fixed places. Although the present study is in agreement with both female preference and male–male competition shaping lek spatial organization in peafowl, more work is clearly needed to better understand lek evolution in this species both in captivity and in the wild.

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