Variation in Lek Attendance and Copulation Success of Independent and Satellite Male Ruffs Calidris pugnax

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Variation in lek attendance and copulation success of Independent and Satellite male Ruffs *Calidris pugnax*

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In lekking male Ruffs, three genetically distinct morphs compete for copulations with the visiting females. Faeder males are female mimics, whereas Independents and Satellites show marked sexual dimorphism, including an elaborate ornamental plumage. Independent males holding a territory on a lek (Residents) have higher mating success than Independents that do not (Marginals), whereas heterogeneity among Satellites is less well understood. Therefore, we compare variation in lek attendance and copulation success between Independent and Satellite males on five leks in northern Norway, over one mating season. Among Independents, Residents were more likely to return to the same lek between years, had longer tenure, higher visitation rate, longer visit duration, fewer arrivals and departures from the lek together with females, and higher daily and seasonal lek attendance than Marginals. We observed qualitatively similar between-individual variation in behaviour among Satellites. Thus, we define two types of individuals: Central Satellites with high lek attachment and Peripheral Satellites with low lek attachment. A notable difference between the morphs was that some Central Satellites (but no Resident Independents) were highly attached to more than one lek on the same day. Lek attendance correlated with copulation success, both on a daily basis and considering the entire season, and this relationship did not differ significantly between the morphs. Given that the mere presence of a male on the lek when a female visited to copulate predicted his copulation success, the unequal distribution of copulations on a lek can be largely explained by unequal lek attendance. After correction for variation in presence, one male on each lek obtained more than his expected share of copulations. Our observations suggest that endurance rivalry, whereby energetic limitations determine the lek attendance of competing males, could be an important determinant of copulation success on Ruff leks.

Key words: Ruff, *Calidris pugnax*, *Philomachus pugnax*, lek, attendance, tenure, alternative mating tactic, sexual selection, endurance rivalry

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Lekking is a rare, but interesting polygynous mating system with intense male-male competition. Leks constitute aggregations of displaying males visited by females only for mating; males do not defend resources and do not provide parental care, whereas females appear to be free to choose a male (Bradbury 1981). These four characteristics distinguish leks from other mating systems, but even between lekking species a wide variety in degree of aggregation, social organization of the males, and female visitation and choosing behaviour exists.

A meta-analysis on lekking species across a wide variety of taxa showed that male mating success depends on three male traits: lek attendance, display activity and aggression rate (Fiske *et al.* 1998). Although increased lek attendance may simply result in presence at more mating opportunities, lekking may also be a behaviour reflecting endurance. Lek attendance is probably costly, because (1) displays and aggressive interactions on the lek can be energetically costly in particular when they elevate the animal's metabolic rate for a relatively long period and (2) lekking is incompatible with foraging, thus having an impact on the intake side of the daily energy budget (Widemo *et al.* 1994, Clark 2012).

In most lekking species males are larger and/or more ornamented than females (Höglund 1989, Trail 1990). A particularly interesting lekking species is the Ruff *Calidris pugnax*, where male competition for access to females has led to the evolution of extensive variation in both morphology and behaviour (mating tactic). First, male Ruffs come in three genetically distinct morphs: Independent, Satellite and Faeder (Lank *et al.* 1995, Küpper *et al.* 2016, Lamichhaney *et al.* 2016). Faeder males are female mimics, which account for c. 1% of males (Jukema & Piersma 2006, Verkuil *et al.* 2008), and whose behaviour in the wild is largely unknown. Independent and Satellite males show marked sexual dimorphism, developing an elaborate ornamental (supplemental) plumage each spring (Hogan-Warburg 1966, Jukema & Piersma 2000). The ornamental plumage is morph-specific in most individuals (Hogan-Warburg 1966, present study). Independent and Satellite males also have distinct behaviour on leks: most importantly, Independents display aggressive behaviour directed at ornamental males, whereas Satellites do not (Hogan-Warburg 1966, van Rhijn 1973). Earlier studies proposed that Independent and Satellite are alternative strategies, having equal fitness payoffs (Hugie & Lank 1997, Widemo 1998a).

Second, Independent males have been classified into Residents and Marginals, based on territoriality, attachment to the lek and ethological differences (Hogan-Warburg 1966). Residents stay on and defend a small territory on the lek, the ‘residence’. Compared to Residents, Marginals visit leks irregularly and usually stay at the margin, frequently driven away by the Residents (Hogan-Warburg 1966). These two categories are not fixed: Marginals can raise their status to Resident within the same lekking season or between seasons, and a Resident can lose his residence and become a Marginal (Hogan-Warburg 1966). On average, Residents returning to the same lek in subsequent years establish themselves earlier in the season and have higher copulation success (Widemo 1997). Resident and Marginal were proposed to be conditional tactics (Widemo 1998a).

Finally, Hogan-Warburg (1966) distinguished between Central and Peripheral Satellites based on attachment to the lek and ethological differences. In comparison to Peripheral Satellites, Central Satellites visit the lek more frequently and for longer periods, are more tolerated by Resident males – especially on smaller leks – and can have strong attachment to one particular lek. However, subsequent studies no longer considered this heterogeneity among Satellites (van Rhijn 1983, Höglund *et al.* 1993, Widemo 1998a).

More than half of the females (so-called ‘Reeves’) are behaviourally and genetically polyandrous, the highest rate known for a lekking bird species (Lank *et al.* 2002). Individual Reeves visit leks during a 10-day period, about one week before laying their first egg (Lank *et al.* 2002). Females only copulate in 10% of their lek visits, typically one to four days before the start of laying, and do not visit leks during incubation (Lank *et al.* 2002). The frequency of female lek visits is not uniformly distributed over the lekking season (Lank & Smith 1987), and the seasonal mating peak varies between years (own unpubl. obs.). The number of females visiting varies between leks and may be related to local patch quality (Höglund *et al.* 1998) and lek size (Lank & Smith 1992, Höglund *et al.* 1993).

Here, we report on variation in lek attachment and copulation success of Independent and Satellite male Ruffs, based on observations on five leks in northern Norway across an entire mating season. The first goal of the study was to quantitatively describe variation in measures of lek attachment (between-year return to the same lek, lek tenure, lek attendance, lek visitation rate, visit duration, arrival and departure on the lek together with females) among Satellite males and to compare this with variation among Independents. We analysed attendance separately for periods when females were present on the lek or absent. Whereas extended periods without foraging can be costly (Widemo *et al.* 1994), males may benefit from attending leks when females are absent: Independents through territory acquisition and defence, and both morphs because a higher number of waiting males may attract more females to the lek (Lank & Smith 1992). Based on previous work (van Rhijn 1983, Lank & Smith 1987, Widemo 1998a, Höglund *et al.* 1993) we predicted that Satellites would have low lek attachment, visit multiple leks, arrive at and leave from leks predominantly together with females and attend leks less when females are absent. However, based on Hogan-Warburg (1966) and our own preliminary observations during three preceding seasons, we also expected to find substantial individual variation among Satellites, similar to that observed among Independents.

Our second aim was to investigate whether lek attendance is an important correlate of copulation success for both morphs on Ruff leks. Previous work showed that lek attendance is significantly related to mating success among Independent Ruffs (Hill 1991). It is interesting to assess whether this is also the case for Satellites, because display behaviour differs substantially between morphs. Because Independents are the more aggressive morph (Hogan-Warburg 1966) and aggressiveness generally correlates with mating success on leks (Fiske *et al.* 1998), we expected lower mating success for Satellites. On the other hand, because Satellites do not have to invest in holding a territory and appear free to follow females between leks, their copulation success was expected to be higher.

Our final aim was to investigate how unequal lek attendance contributed to the unequal distribution of lek copulations in male Ruffs. Unequal distribution of mating success (skew) is observed in many lekking species (Kokko *et al.* 1999), including Independent Ruffs (Hill 1991, Widemo & Owens 1995). In view of the apparently choosy behaviour of Reeves on the lek (Hogan-Warburg 1966, Lank *et al.* 2002, own unpubl. obs.), we expected that some (preferred) males would be more successful than expected simply based on attendance, whereas others might be less successful (non-preferred). Hence, we tested for non-random allocation of copulations among males present on the lek during visits of females that ended up copulating.

METHODS

Study species and area

The Ruff is a Palaearctic migratory wader. The vast majority of the population winters in the Sahel and Southern Africa, and breeds in the subarctic zone in northern Eurasia (reviewed in Cramp & Simmons 1983, Scheufler & Stiefel 1985, Zwarts *et al.* 2009).

We studied Ruff leks in myres along an 80 km stretch of the northern coast of the Varanger Fjord, Finnmark, Norway (between 70.07869°N and 70.45059°N), in the transition zone between subarctic forest and Arctic tundra. The data presented here were collected on five leks (A–E) in 2016. Additional data collected on six leks (A–F) in 2014 and 2015 were included as specified in the Results section. All six leks are ‘true leks’ as defined by Lank & Smith (1987). Leks A, B and F were located on dry peat mounds, while C and D were on moraine ridges. Thus, on these leks no food or water resources were available to male or female Ruffs. Lek E, located on grass tussocks on the shore of a small lake, is exceptional in the sense that some females visited the lek to forage and bathe at its margins. However, the majority of visiting females did not use these resources. In contrast to ‘Interception leks’ (Lank & Smith 1987), all six leks, including lek E were established before females visited the area, and males rarely foraged on the lek. The distances between neighbouring leks varied between 0.8–27 km (Figure S1). Despite close proximity of leks C and D, they are located in visually separated myres, such that all activity on the neighbouring lek, including wing flutter displays and arrivals and departures of conspecifics, are invisible from the other lek.

Systematic observation of other traditional, temporary or solitary display sites in the study area fell beyond the scope of the present study. Extensive searches in suitable habitat in 2013–2017 revealed traditional lekking at a minimum of six other sites along the same coast (Figure S1). Each season, usually starting at the beginning of June, lekking also occurred at less than ten non-traditional sites (Figure S1). Non-traditional leks and solitary display sites were unstable over time and space, and were usually associated with female foraging.

Data collection

In our study area, the first males arrived on a lek by mid-May and leks were populated until mid-June (own unpubl. obs.). In 2016, observations started before the first male settled on any of the leks; leks were observed between 11 May and 16 June for a total of 243 h (for schedule see Table S1). Depending on natural cover, the observer (RV) sat at a distance of 50–100 m from the lek. In all cases, birds on the lek – including short-term male or female visitors – showed no sign of disturbance. Observations were made daily during two periods: a morning session between 3:02 and 11:55 with a mean duration of 324 min (range: 143–390 min, excluding observations of empty leks in the beginning of the season) and an afternoon session between 14:25 and 21:06 with a mean duration of 190 min (range: 60–254 min, excluding observations of empty leks in the beginning of the season). The start and end of an observation period was independent of activity on the lek. Data collection was continuous for all individual males on the lek during the observation period. Observations were conducted with binoculars or with a 20–60× telescope. Depending on activity, the lek was photographed or filmed using a digital reflex camera with 400-, 600- or 800-mm lens, and data were collected in writing or by voice recording. Time of events was recorded to the completed minute.

Behavioural classification of Independent and Satellite males

We classified males as Independent or Satellite based on behaviour following Hogan-Warburg (1966). Independents can show forward postures, can attack

Independent or Satellite males and can fight with other Independents. In the forward postures the bill is pointed forward and directed at the opponent, the body axis is held horizontally or slightly pointing down, the ruff is fully expanded and bent forward as a shield, and the tufts are also bent forward (Hogan-Warburg 1966). Independents adopt a characteristic posture in the so-called 'twosome', the tight association of a Satellite with an Independent whereby the Satellite is in a squatting posture and the Independent (the 'host') is in 'half-squat', resting his bill on the head of the Satellite (the 'guest'), or in 'spread-tail forward' and frequently pecking at the head of the Satellite (Hogan-Warburg 1966). The twosome was also called the 'dyad' (Höglund *et al.* 1993), 'coupling' (Widemo 1998a) or 'mutual squat' (Hugie & Lank 1997). Host-guest interactions mostly occur on the residence, can be initiated by the Satellite (Hogan-Warburg 1966) and can also involve Marginals.

Satellite males do not show forward postures, never attack Independents or other Satellite males and can visit the residence of an Independent male (Hogan-Warburg 1966). A Satellite was seen fighting only once in 2016. We frequently observed an oblique (open-wing) posture (Figure S2) in Satellites but not in Independents, that did not clearly match postures described earlier (Hogan-Warburg 1966).

Faeders can often be recognized in the field (D. Lank pers. comm. and own unpubl. obs.; see also so-called 'Naked-Nape' males in Hogan-Warburg 1966). However, because individual recognition of Faeders is difficult, we did not obtain sufficient data to justify their inclusion here.

Classification of males based on plumage

By comparing pictures, we identified a total of 252 individual males based on the colour patterns of the ruff, the tufts, the scapulars, the wing coverts and the tertials and on the colour of the bill, wattles and legs. Images of seven males did not show enough detail and these males were excluded from all analyses. Data from captive birds suggested that plumage of the same individual remains constant over successive years (p. 483 in van Rhijn 1983, Lank *et al.* 1995). Thus, we used plumage to identify individuals present in multiple years (2014–2016).

Based on Hogan-Warburg (1966) and on 117 males with known behaviour (59% Independents, 41% Satellites), we scored males with more than 40% black tuft feathers, or more than 40% black ruff feathers, or less than 10 white feathers in tufts and ruff, or a barred pattern on the ruff as Independent. With this definition, four of the 117 males (3%) had a conflicting plumage:

On average, a lek in the study area counted one Central Satellite (here the male with white tufts and ruff), and four Residents (here the three males with coloured tuft and ruff). Residents defend a territory which typically includes a small trampled area (see male on the right), whereas the Central Satellite moves between territories (Norway, May 2016).

one male with a satellite-type ruff behaved as an Independent and three males with an independent-type ruff behaved as a Satellite (Figure S3). Note that Hogan-Warburg (1966) also concluded that males could not be classified unambiguously based on plumage alone, but the percentage of males with 'anomalous' plumage was not specified. Using the plumage definition of Independents, 135 males for which we lacked sufficient behavioural information (54% of all males) could be classified as Independents (94%, n = 127) or as Satellites (6%, n = 8).

Classification of Resident and Marginal Independents

Following Hogan-Warburg (1966), we classified Independents into Residents and Marginals. Residents occupy a small territory on the lek, the 'residence' (Hogan-Warburg 1966). Residents often walked back and forth over several meters between favoured areas on the lek, in line with an alternative name for the territory (the 'run'; Bancke & Meesenburg 1952), and some Residents commuted between two residences. All other Independents were classified as Marginals. This included (1) Independents that were accepted on the lek during long periods of low activity (no females present), but that were attacked at other times and then retreated, and (2) Independents that tried to occupy and defend a residence, but were easily chased away by other Residents.

Classification of Central and Peripheral Satellites

Hogan-Warburg (1966) distinguished between Central and Peripheral Satellites as follows. A Central Satellite typically shows a high attachment to a lek and adopts the 'oblique' posture when interacting with a Resident in the absence of visiting females or other Satellites. In contrast, a Peripheral Satellite shows low attachment to a lek and typically stays on the periphery of the lek. When on a residence it is never observed in the oblique posture, but instead immediately adopts the 'squat'.

In line with Hogan-Warburg (1966), we observed substantial variation in lek attendance among Satellites (see Results). However, postures characteristic for high-attendance Central Satellites (Hogan-Warburg 1966) were also displayed by 24 out of 47 low-attendance Satellites, and could therefore not be used to assign lek attachment status (see Table 1). As for Independents, measures of lek attendance varied gradually between high and low-attendance Satellites (see Results), also precluding objective categorization. We classified Satellites based on seasonal lek attendance fractional rank (Sæther *et al.* 2005), as follows. For each lek, Independents were ranked by decreasing seasonal lek attendance, and the fractional rank of the Resident with lowest attendance on the lek (i.e. the highest fractional rank) was determined (Figure S4). Subsequently, Satellites were also ranked by seasonal lek attendance. Individuals observed at least 60 min on the lek and with a fractional rank smaller than the highest fractional rank of Residents on the same lek were considered high attendance Satellites (referred to as Central Satellite here), whereas all others were low attendance Satellites (referred to as Peripheral Satellite here). Albeit somewhat arbitrary, this categorization based on seasonal lek attendance is helpful for heuristic reasons (to compare the morphs) and correlates with variation in other measures of lek attachment (returning between years, lek tenure, lek visitation rate and visit duration; see Results).

Classification by lek attachment as R- and M-males

We refer to individuals with high lek attachment as R-males, independent of morph, i.e. grouping Residents and Central Satellites as defined above. In contrast, we refer to individuals with low lek attachment status as M-males, grouping Marginals and Peripheral Satellites as defined above. We consider the R or M classification of a male as his 'status'.

Lek size

We define daily lek size as the number of different R-males (Residents and Central Satellites) observed on a given day. Weekly lek size is the average of the daily lek sizes during that week, and seasonal lek size is the average of the weekly lek sizes (Table S2).

Number of individuals visiting leks corrected for observation effort

Because leks were not observed continuously, the true number of individuals of each status visiting an average lek over an entire season was estimated as follows. First, we calculated linear regressions relating the number of different individuals observed on a lek within the same 24 h (y; combining observations when the same lek was observed twice within the same 24 h) with length of the observation periods within the same 24 h (d) for each male category (Residents: $y = 0.00 \times d + 4.02$, Marginals: $y = 4.54 \times \ln(d) - 20.86$, Central Satellites: $y = 0.00 \times d + 1.00$, Peripheral Satellites: $y = 1.11 \times \ln(d) - 4.93$). We then used these functions to estimate the number of individuals visiting a lek over a 24-h period for each category (Y): 4.0, 11.3, 1.0, 3.2, respectively. Finally, over a season of 35 days, and correcting for mean lek tenure (tenure of Independents switching status calculated separately for each class: Residents 13.76 d, Marginals 2.25 d, Central Satellites: 17.91 d, Peripheral Satellites 1.90 d) on average 10 different individual Residents, 176 Marginals, 2 Central Satellites and 59 Peripheral Satellites visited a lek (calculated as $Y \times 35$/mean lek tenure).

Male age score

Hogan-Warburg (1966) showed that males in their second calendar year were more likely to be Marginals. Hence, we aged males based on leg colour (Pearson 1972): birds with grey, grey-yellow or grey-pink legs were considered yearlings (second calendar year), whereas birds with pink or orange legs were scored as adults. The proportion of yearlings should be considered a minimum estimate, because leg colour typically changes during the second calendar year (Pearson 1972).

Lek tenure

We defined lek tenure as the number of days between the first and the last observation of an individual on a specific lek in the study area. Note that this may be an underestimate of true lek tenure, because leks were not observed daily (Table S1).

Lek visitation rate

Individuals do not only differ in tenure at a particular lek over the season, but also in how much time they spend on the lek (Hill 1991). In contrast to leks at more southern latitudes (The Netherlands; Hogan-Warburg 1966), where males left the lek at night and returned at dawn, Resident Independents and Central Satellites in Northern Norway also attend the lek during the night, presumably because of continuous daylight.

During each observation period the number of arrivals and departures of each individual was tallied. Arrivals or departures were scored as ‘together with females’ if at least one female arrived or departed within the same minute. Thus, we included males arriving or leaving in the same flock as the females, but also males returning to or leaving the lek in flocks without females if this happened clearly in response to female movements – e.g. males feeding in view of the lek. Daily and seasonal visitation rates were calculated for each individual by dividing the number of visits by the observation time.

Lek attendance

For each male, we recorded the time of arrival on and departure from the lek to the completed minute and determined the duration of each visit. We then calculated daily or seasonal lek attendance for each individual as the sum of all visit durations divided by the total (daily or seasonal) observation time. When a lek was visited in the morning and in the afternoon on the same day, the data were not pooled, but two daily values were calculated. When a male visited more than one lek, attendance was calculated for each lek separately. Thus, our measure of ‘lek attendance’ reflects the attendance of an individual to a specific lek, not the total time an individual spent on any lek.

For each male, we also calculated daily (morning/afternoon) and seasonal attendance separately for periods when at least one female was present on the lek and during periods of female absence.

Female lek attendance and visitation rate

As measures of daily variation in female lek visitation, we used female lek attendance and visitation rate as follows. We recorded each arrival and departure of a female (walking or flying in or out) to the completed minute. Female lek attendance was then defined as the percentage of the observation period during which at least one female was present on the lek. Female visitation rate was the number of female arrivals divided by the observation time.

Observed and expected copulation success

Following Widemo (1997), we scored a copulation when a male mounted a crouching female and cloacal contact seemed likely. Following Höglund *et al.* (1993) we used the term ‘copulation’ both to describe a single copulation or a copulation bout, i.e. a series of copulations in rapid succession involving the same pair. Over the season, we observed 168 copulations in 127 bouts with females. In contrast to previous publications, we excluded copulations (7%, $n = 12$) with females suspected to be Faeders (based on their size and behaviour). Because on lek A only two copulations were observed, we excluded this lek from analysis of seasonal variation in the individual proportion of copulations as indicated in the Results. We calculated individual copulation rate as the number of copulations observed divided by the individual’s total attendance during female visits.

For each copulation visit of a Reeve, we tallied all the individual males present on the lek and assigned each male the same probability to obtain the copulation (e.g. if four males were present, and the female copulated with one male each male would receive a score of 0.25). We then calculated the expected total number of copulations for each male over the season under the assumption of random mating as the sum of his scores obtained at all female copulation visits. Obtaining a copulation requires being present, being chosen by the visiting female, and not being disturbed by male interference. For each male, we then compared the number of copulations actually obtained with the random expectation, using a two-tailed exact test of goodness-of-fit (binom.test function in R, with 'successes' = the actual number of copulations obtained, 'total' = the number of copulations observed on the lek over the season, 'numerator' = the expected number of copulations under random copulation, 'denominator' = the total number of copulations observed on the lek). For males with a small numerator, the goodness-of-fit test has low power, therefore the relationship between expected and observed copulations including all males present at least once at a copulation visit was also analysed with a generalized linear mixed model (GLMM) assuming a negative binomial distribution.

Data analysis

Male Ruffs can visit more than one lek during one season, even on the same day. Therefore, individual data collected on a single lek can only be used to analyse individual performance when normalized for individual attendance on that lek, not for observation time (see also Widemo 1998a). For males observed on two leks, we considered data collected on each lek separately in all analyses. Independent males could change status on a lek during one season (Resident and Marginal), whereas we assumed that Satellites kept their status on the lek. Therefore, when comparing seasonal patterns of Residents and Central Satellites, we pooled the data of Independents that changed status. However, for the daily analyses, we used the specific status on a given day for Independents.

All analyses were conducted using the statistical software R v. 3.4.2 (R Development Core Team 2008). We calculated linear mixed-effect models (LMM) and GLMM with the package 'lme4' v. 1.1.14 (Bates *et al.* 2015). We determined the significance of an effect for LMM with a likelihood ratio test comparing a full model including fixed and random effects, with a null model without the effect of interest.

For the analysis of daily variation, we used mixed models (LMM and GLMM) to control for repeated sampling by including date, male identity, lek identity and period (AM or PM) as random factors. Models for analysis of tenure and seasonal variation included male and lek identity as random factors. All model descriptions are given in the Supplementary Data.

We analysed the seasonal distribution of copulations for each lek separately using the 'fitdist' and 'gofstat' functions of the package 'fitdistrplus' v. 1.0.11 (Delignette-Muller & Dutang 2015, Table S6). Indices of skew were calculated with Skew Calculator 2003 (Nonacs 2003), setting the number of simulations at 1000, and calculation of confidence intervals for *B* at 'accurate' (Table S7).

Parameter estimates are shown ±1 SD.

Ethical note

We did not capture birds and took care to minimize disturbance as specified under 'Data collection', in the interest of the birds and to ensure observation of natural behaviour. We avoided using hides to minimize the impact on the view the birds had of their surroundings and to reduce visibility to the public. No permits were required to access the lek surroundings and to observe leks without disturbing the birds.

Table 1. Classification of male Ruffs. Independents (n = 196) were classified as Resident or Marginal based on territoriality. Satellites (n = 56) were classified as Central or Peripheral based on seasonal lek attendance fractional rank (attendance) or on their posture while interacting with Independents (behaviour).

		Independent (Territoriality)			Satellite (Attendance)		
		Resident	Resident & Marginal	Marginal	Central	Central & Peripheral	Peripheral
	n	25	20	151	8	1	47
	One lek	25	15	148	6	0	44
	Two leks	0	5[a]	3	2	1	3
	Peripheral				0	0	15
Behaviour	Central				8	1	24
	Unknown				0	0	8

[a] one male Resident and Marginal on both leks

RESULTS

Frequency of male morphs and lek attachment status

Based on behaviour and plumage characteristics combined, we identified 196 (78%) Independent and 56 (22%) Satellite males on leks (see Methods for details; Table 1).

Of the 196 Independents, 45 (23%) were defending a territory at least on one day. Of those, 25 (56%) were only seen as a Resident on one lek, 15 (33%) changed their status, i.e. visited the same lek as a Marginal either earlier or later in the season, four were seen as a Marginal on a neighbouring lek, and one male was seen on two neighbouring leks where he behaved both as a Resident and as a Marginal within the same season. The remaining 151 Independents (77%) never held a residence and were therefore classified as Marginals. Of these, 148 (98%) were seen on one lek only, while three (2%) visited two neighbouring leks. The Independent with conflicting plumage (see Methods) behaved as a Marginal. The mean number of Residents over 5 leks and 5 weeks was 4.0 ± 1.6 per lek per observation period (Table S2). The mean number of different Residents observed per lek per season was 9.2 ± 2.9.

Of the 56 Satellites, nine had high lek attendance, of which two were on two neighbouring leks, and were thus classified as Central Satellite (see Methods). The remaining 47 Satellites had low lek attendance, and were classified as Peripheral Satellite (see Methods). The mean number of individual Central Satellites over 5 leks and 5 weeks was 1.0 ± 0.7 per lek per observation period (Table S2). The mean number of different Central Satellites observed per lek per season was 2.2 ± 0.4.

In 2016 the proportion of yearling males was low (4.6%), and did not differ significantly between Residents and Marginals or between Central and Peripheral Satellites (Table S3). Combining observations from three seasons, we found a significantly higher proportion of yearling males among Marginals (relative to Residents), but not among Peripheral Satellites (relative to Central Satellites).

Of the males that were Resident in 2016, 25 (56%) had been observed in one or both of the previous years (2014–2015). In contrast, only five Marginals (3%) had already been observed on the study area in 2014–2015. Similarly, among the Satellites from 2016, six Central (67%) and three Peripheral (6%) individuals were already observed in the previous years. R-males were significantly more likely to return between years ($z = 3.5$, $P < 0.001$), but there was no difference between the morphs ($z = 0.3$, $P = 0.8$).

Lek tenure

Most Independents were seen only on one day in the study area and those were almost always Marginals (Figure 1B). This was not simply a consequence of the fact that leks were not observed daily. When the

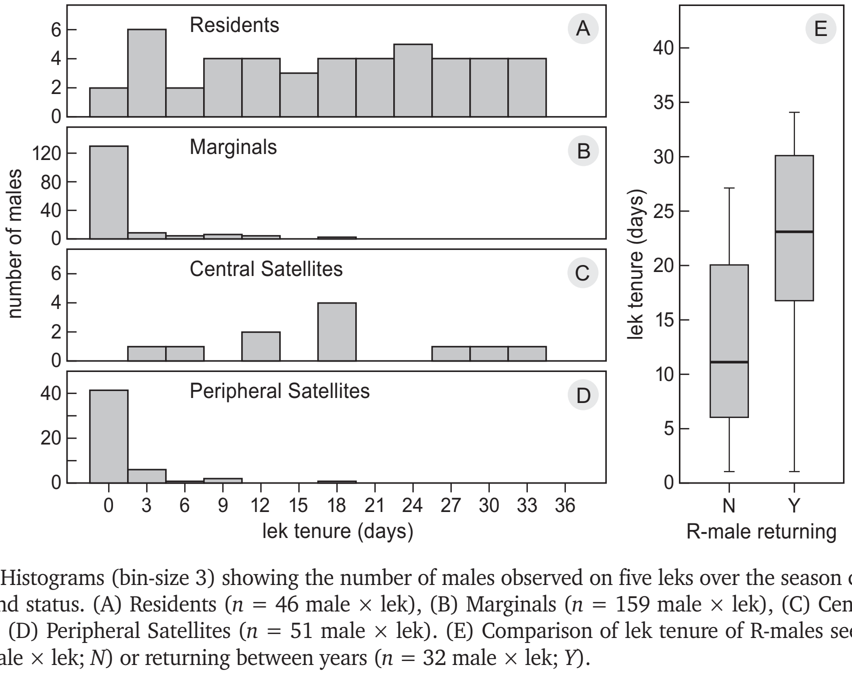

Figure 1. (A–D) Histograms (bin-size 3) showing the number of males observed on five leks over the season classified by lek tenure and by morph and status. (A) Residents (n = 46 male × lek), (B) Marginals (n = 159 male × lek), (C) Central Satellites (n = 11 male × lek) and (D) Peripheral Satellites (n = 51 male × lek). (E) Comparison of lek tenure of R-males seen for the first time in 2016 (n = 25 male × lek; *N*) or returning between years (n = 32 male × lek; *Y*).

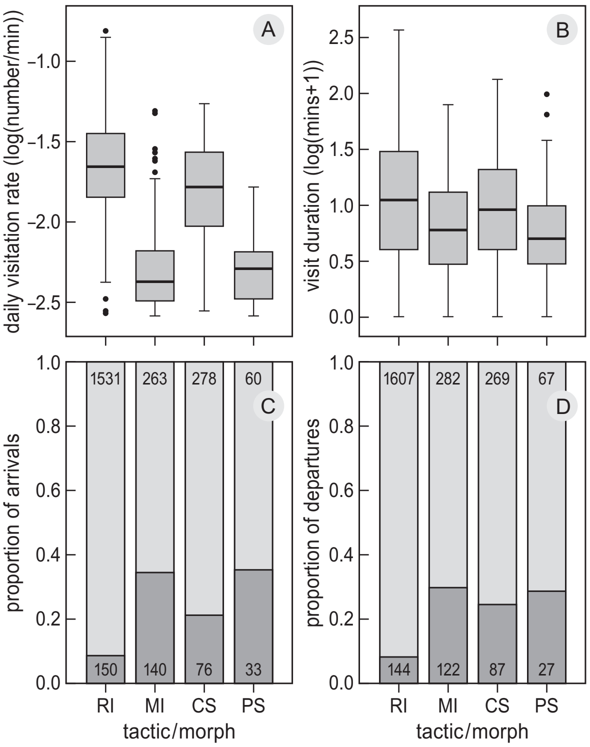

Figure 2. (A) Daily lek visitation rate of Residents ($n = 280$ male × days; RI), Marginals ($n = 235$ male × days; MI), Central Satellites ($n = 74$ male × days; CS), and Peripheral Satellites ($n = 64$ male × days; PS). The daily rate of female lek visitation over 5 leks was 0.037 ± 0.036. (B) Duration of all visits to the lek by Residents ($n = 1927$), Marginals ($n = 400$), Central Satellites ($n = 377$) and Peripheral Satellites ($n = 94$). (C) Males arrived on a lek together with females (dark grey) or not (light grey). The number in the bar refers to the sample size. Residents arrived together with females on 9%, Central Satellites on 21%, Marginals and Peripheral Satellites on 35% of their arrivals, (D) Residents left the lek in the company of females on 8% of their departures, which was lower than Central Satellites (24%), Peripheral Satellites (29%) and Marginals (30%). Boxplots show the median (line), the 25th and 75th percentile (hinges), the interquartile range (IQR, box size), 1.5 × IQR (whiskers) and outliers (individual points).

analysis was restricted to nineteen pairs of observation periods of the same lek on consecutive days, only eight out of 134 Marginals (6%) were seen on both observation days. Data from the two most frequently visited leks, lek F in 2015 and lek D in 2016 (Table S1), showed that 60% and 67% of Independents had a tenure ≤ 2 days, respectively (Figure S5). Thus, the distribution of tenure is unlikely to be a consequence of low sampling frequency, but reflects heterogeneity between individuals.

Among Satellites, 35 (60%) were seen only on one day and those were all Peripheral Satellites (74% of Peripheral Satellites; Figure 1D). When the analysis was restricted to nineteen pairs of observation periods of the same lek on consecutive days, only five out of 36 Peripheral Satellites (14%) were seen on both days.

Lek tenure was significantly higher for R-males than for M-males ($\chi^2_1 = 145$, $P < 0.0001$), and higher for males that returned between years than for those that did not (Figure 1E; $\chi^2_1 = 35$, $P < 0.001$). Lek tenure did not differ between the morphs ($\chi^2_1 = 0.06$, $P = 0.8$).

Daily lek visitation rate and visit duration

Daily visitation rate of Satellites was lower than that of Independents (Figure 2A; $\chi^2_1 = 7$, $P < 0.01$), whereas R-males visited leks more frequently than M-males (Figure 2A; $\chi^2_1 = 176$, $P < 0.0001$). Lek visitation rate decreased significantly with increasing female attendance ($\beta = -0.00031 \pm 0.00006$, $\chi^2_1 = 19$, $P < 0.0001$) and female visitation rate ($\beta = -0.066 \pm 0.023$, $\chi^2_1 = 8$, $P < 0.01$). Daily visitation rate did not differ between R-males that returned between years and those that did not (Table 2; $\chi^2_1 = 1$, $P = 0.3$).

Satellites had shorter visit durations than Independents (Figure 2B; $\chi^2_1 = 14$, $P < 0.001$), and M-males visited leks more briefly than R-males (Figure 2B; $\chi^2_1 = 90$, $P < 0.0001$). Male visit duration increased with increasing female lek attendance ($\beta = 0.42 \pm 0.08$, $\chi^2_1 = 25$, $P < 0.0001$) and female visitation rate ($\beta = 108 \pm 28$, $\chi^2_1 = 14$, $P < 0.001$). There was no difference in lek visit duration for R-males that had returned between years and those that did not (Table 2; $\chi^2_1 = 0.03$, $P = 0.9$).

Arrival and departure with females

R-males arrived on leks and departed from leks together with females less often than M-males (Figure 2C, D; arrivals: $z = -12$, $P < 0.0001$; departures: $z = -8.6$, $P < 0.0001$; see also Table S4). Overall, there was no difference between morphs in their propensity to arrive ($z = 0.27$, $P = 0.8$) or depart ($z = -0.97$, $P = 0.3$) together with females. However, Central Satellites arrived ($z = 3.3$, $P = 0.001$) and departed ($z = 3.6$, $P < 0.001$) more often together with females than Residents (Figure 2C, D).

Lek attendance

CORRELATES OF DAILY VARIATION IN MALE LEK ATTENDANCE

Daily lek attendance of Satellites was lower than that of Independents (Figure 3; $\chi^2_2 = 15$, $P < 0.001$). Central Satellites had lower lek attendance than Residents (Figure 3; $\chi^2_2 = 33$, $P < 0.0001$), equally when females were present or absent from the lek (Figure 3; $\chi^2_1 = 0.20$, $P > 0.05$). R-males had a much higher daily attendance than M-males (Figure 3; $\chi^2_2 = 659$, $P < 0.0001$), especially when females were present on the lek (interaction of status with female presence: $\chi^2_1 = 42$, $P < 0.0001$). Lek attendance increased when females were present ($\chi^2_5 = 239$, $P < 0.0001$) and decreased slightly with daily lek size ($\chi^2_2 = 11$, $P < 0.01$). Among Residents and Central Satellites, there was no difference in daily lek attendance between males seen for the first time in 2016 and returning males ($\chi^2_2 = 1.8$ $P > 0.05$). Tenure did not explain variation in daily attendance ($\chi^2_2 = 4.9$ $P > 0.05$).

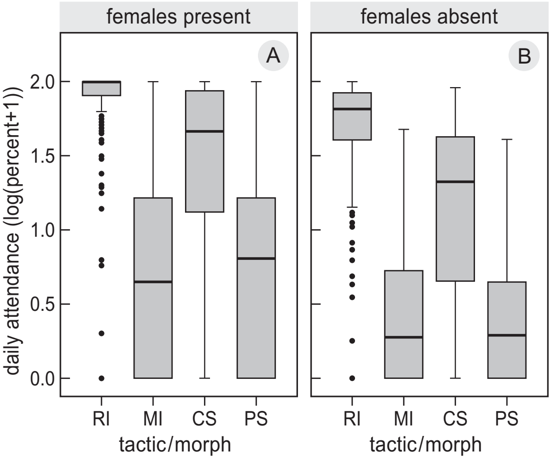

Figure 3. Daily lek attendance of Residents (RI), Marginals (MI), Central Satellites (CS), and Peripheral Satellites (PS), (A) when females were present on the lek, or (B) when females were absent. Logarithms were used for representation of the data only. Sample sizes (male × days) were as in Figure 2A. Daily, at least one female was present on the lek (5 leks) 11.2 ± 18.1% of observation time. For details on boxplots see Figure 2.

CORRELATES OF SEASONAL LEK ATTENDANCE

Variation in seasonal lek attendance was explained by the same variables as daily lek attendance (Suppl. Data). Additionally, for R-males seasonal attendance increased with tenure (Figure 4A; $\chi^2_2 = 70$, $P < 0.0001$) and was higher for R-males that were observed in previous years compared to R-males seen for the first time in 2016 (Figure 4B; $\chi^2_2 = 24$, $P < 0.0001$).

Independents spent 871 h on leks (88% of total male hours; range per lek: 86–95%), and Satellites 114 h (12%, range: 5–14%). This is similar to the proportions reported in previous studies (Table 3).

Copulations

CORRELATES OF DAILY COPULATION SUCCESS

On days on which at least one copulation was observed on the lek, the probability that a male obtained a copulation increased with his daily lek attendance ($z = 6.8$, $P < 0.0001$). No significant difference was detected between morphs ($z = -0.02$, $P > 0.05$). M-Males were

Table 2. Descriptive statistics of lek attachment of male Ruffs. For each variable mean ± SD (first row) and range (second row) are shown. Lek tenure: days. Daily visitation rate: number of visits/minute observation time. Visit duration: minutes between arriving and departing from the lek. Daily attendance: time present as % of daily observation time. Daily attendance at female presence: time present together with at least one female as % of daily observation time that at least one female was present. Daily attendance at female absence: time present when females were absent as % of daily observation time that no females were present. Seasonal attendance: time present as % of seasonal observation time.

	Independent		**Satellite**		**R-male returning**	
Variable	Resident	Marginal	Central	Peripheral	No	Yes
Lek tenure	17.2 ± 10.3 1–34	1.8 ± 2.5 1–17	17.9 ± 9.5 2–32	1.9 ± 2.9 1–18	12.4 ± 8.5 1–27	21.2 ± 9.5 1–34
Daily visitation rate	0.029 ± 0.022 0.003–0.158	0.006 ± 0.006 0.003–0.050	0.019 ± 0.012 0.003–0.056	0.006 ± 0.003 0.003–0.017	0.025 ± 0.020 0.003–0.123	0.027 ± 0.021 0.003–0.158
Visit duration	25.1 ± 40.3 0–365	9.2 ± 11.8 0–79	15.4 ± 20.4 0–131	8.2 ± 13.3 0–97	24.5 ± 40.1 0–353	23.3 ± 37.3 0–365
Daily attendance	66.8 ± 24.5 3.8–100.0	5.5 ± 7.4 0.3–43.3	31.4 ± 25.9 0.3–91.3	4.5 ± 6.2 0.0–35.6	58.4 ± 29.6 0.7–100.0	59.8 ± 28.3 0.3–100.0
Daily attendance during female presence	83.8 ± 26.3 0.0–100.0	12.5 ± 20.0 0.0–100.0	50.4 ± 36.8 0.0–100.0	13.1 ± 22.4 0.0–100.0	72.3 ± 32.9 0.0–100.0	78.4 ± 31.4 0.0–100.0
Daily attendance during female absence	60.7 ± 27.6 0.0–100.0	3.7 ± 6.7 0.0–46.4	25.6 ± 24.6 0.0–88.6	3.6 ± 6.8 0.0–39.6	51.2 ± 33.2 0.0–100.0	54.1 ± 29.5 0.0–100.0
Seasonal attendance	33.2 ± 21.9 4.4–72.9	0.7 ± 1.0 0.0–5.0	16.2 ± 12.9 3.6–50.0	0.5 ± 0.6 0.0–3.1	20.1 ± 16.1 4.4–63.8	37.7 ± 22.2 3.6–72.9

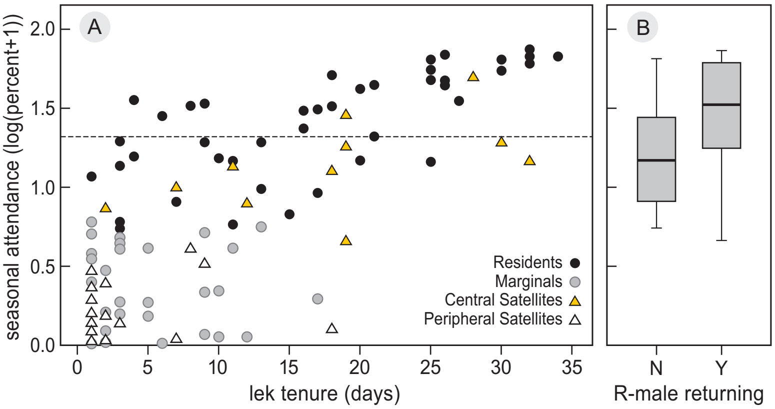

Figure 4. Seasonal lek attendance and (A) lek tenure of Residents Marginals, Central Satellites and Peripheral Satellites. The dotted line represents the average time that at least one female was present on the lek ($n = 5$) over the season (19.9 ± 5.5% of the observation time). (B) R-males seen on the lek in previous years (*Y*) had higher seasonal lek attendance than R-males seen for the first time in 2016 (*N*). Sample sizes were as in Figure 1.

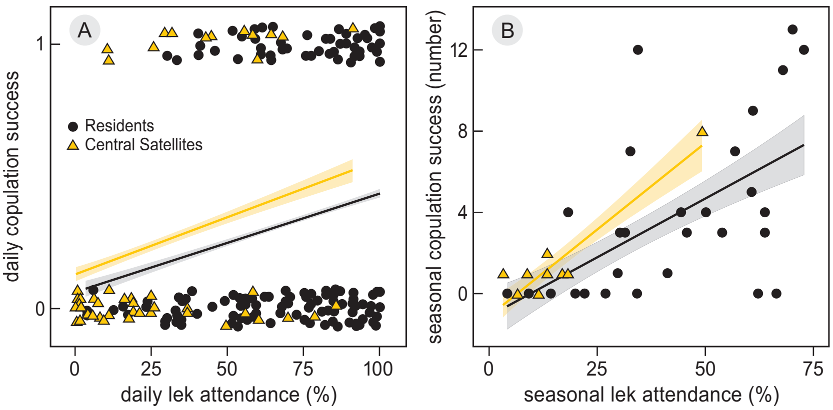

Figure 5. Copulation success of R-males and lek attendance (% observation time). (A) Daily copulation success scored as not copulating (0) or obtaining at least one copulation (1), of Residents ($n = 157$ male × days) and Central Satellites ($n = 50$ male × days), on days that at least one female copulated on the lek. Data-points were staggered vertically to improve clarity. Lines represent copulation success predicted by a logistic GLMM. (B) The number of copulations obtained by R-males (40 Independents, 9 Satellites) was correlated with their seasonal lek attendance (Spearman rank correlation $\rho = 0.68$, $n = 49$, $P < 0.0001$). Lines represent copulation success predicted by a GLMM assuming a negative binomial distribution.

never observed to copulate. Among R-males, daily copulation success increased with lek attendance (Figure 5A; $z = 2.9$, $P < 0.01$), and males that returned between years had a higher probability to obtain a copulation, but this effect was not significant ($z = 1.9$, $P > 0.05$).

CORRELATES OF SEASONAL COPULATION SUCCESS

The distribution of copulations over the entire season by R-males on each lek (four leks) did fit a negative binomial distribution better than a Poisson distribution or normal distribution (Table S6). The same was true for single copulations by Residents, also using published data (Table S6; Hill 1991, van Rhijn 1991).

Table 3. Comparison between morphs of percentages of total male hours observed on leks and of number of individuals on leks.

	Male hours (%)		**Individuals** (%)	
Reference	Independent	Satellite	Independent	Satellite
van Rhijn 1983	87	13	-	-
Höglund *et al.* 1993[a]	88	12	77	23
Widemo 1998a	88	11	81	19
This study	88	12	78	22

[a] Based on the mean number of Independents and Satellites during 5 min scans (Table 1 in Höglund *et al.* 1993)

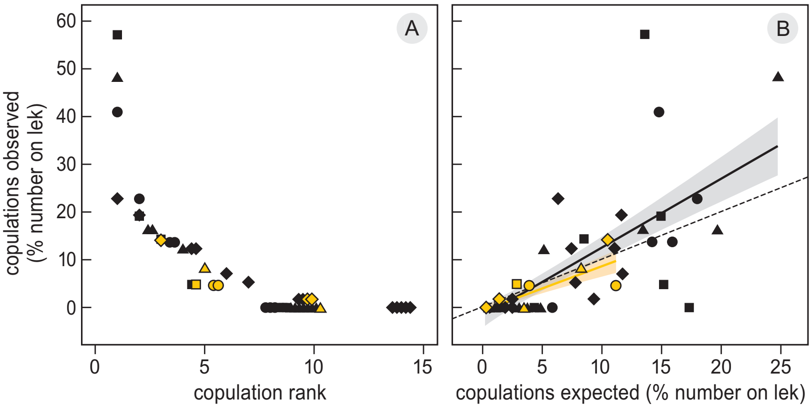

Figure 6. (A) The percentage of all copulations obtained on a lek by males of different rank. Residents (n = 40; black) and Central Satellites (n = 9; yellow) were ranked within lek B (circle), C (square), D (diamond) and E (triangle) according to their proportion of copulations obtained. When males shared the same rank on a given lek, data-points were staggered horizontally for clarity. (B) Relationship between the proportion of copulations observed per individual across the season in relation to the proportion expected based on presence on the lek during visits of copulating females (Spearman rank correlation for all males ρ = 0.74, n = 84, P < 0.0001, for R-males only: ρ = 0.75, n = 43, P < 0.0001). All Independents (n = 68; black) and Satellites (n = 16; yellow) present on the lek (symbols as in panel a) at least once when a female copulated were included in this analysis. Lines for each morph (Independent: black; Satellite: yellow) were based on values predicted by a GLMM assuming a binomial distribution. The dotted line represents equality.

The seasonal number of copulations obtained by individual R-males increased with their lek attendance (Figure 5B; z = 4.7, P < 0.0001). There was no significant difference between morphs (z = 1.2, P > 0.05). The seasonal total number of copulations obtained did not differ between R-males that returned between years and those that did not (z = 0.77, P > 0.05).

Among the R-males, Residents obtained 91% of all copulations (range on four leks with > 20 copulations: 82–95%; Figure 6). Although all Independents combined obtained a much larger share of the total number of copulations than all Satellites combined, the morphs had similar copulation success corrected for lek attendance: 0.13 copulations/h for Independents versus 0.14 copulations/h for Satellites (data from five leks combined). This was also true when attendance during female visits was considered instead of total attendance (Independents: 0.39 copulations/h, Satellites: 0.36 copulations/h). Furthermore, individual Residents (including their days as Marginal) and Central Satellites had similar seasonal copulation rates (defined as the total number of copulations/attendances during female visits on a lek; Welch's two sample t-test: $t_{32.3}$ = –0.04, P = 0.97).

Of all males, 159 (63%) were never observed on a lek when a female copulated. To verify whether the mere presence of a male on the lek determined the number of copulations he obtained, we compared the observed number of copulations with that expected, taking into account male presence during visits of copulating females and the number of other males present (see Methods). An exact goodness-of-fit test for each male separately (n = 207, four leks) showed that on each lek one Resident obtained more copulations than expected (P < 0.05), and on one lek one Resident obtained less copulations than expected (P < 0.05). A negative binomial GLMM including males present on the lek at least once when a female copulated (n = 93, five leks) confirmed that the number of copulations observed was correlated with the number expected (Figure 6B; z = 6.8, P < 0.0001), whereas there was no difference between morphs (Figure 6B; z = 0.9, P > 0.05).

The skew index B (Nonacs 2003; Table S7) indicated unequal sharing of copulations among R-males: for each lek, the minimum possible value of B (expected through equal sharing) and 0 were outside the 95% confidence interval, and the observed B-values were unlikely under random chance (P < 0.01). However, the skew index B corrected for presence at female copulation visits revealed that equal sharing could not be excluded in three of four leks, and the observed B-values were not different from expectation under random sharing of benefits on lek B (P > 0.05), and only marginally different on lek E (P < 0.05).

Although the number of observed leks is small, our data confirm the predicted relationship between mean lek size and mating skew (Widemo & Owens 1995): inequality was lowest on the largest lek (Figure 6, lek D, Figure S6).

DISCUSSION

Lek attachment of Independent and Satellite male Ruff

On Ruff leks, two classes of Independent males differing in territoriality, behaviour and lek attachment have long been recognized (Hogan-Warburg 1966, van Rhijn 1983, Höglund *et al.* 1993, Widemo 1998a). Here, we compared lek attachment of Residents and Marginals quantitatively, and found significant differences for all measures. Among Independents, holding a territory (Residents) or not (Marginals) explained much of this variation, in line with and extending previous studies (Hogan-Warburg 1966, van Rhijn 1983, Widemo 1998a).

Qualitatively, variation in seasonal lek attendance was remarkably similar between the morphs. This justifies the classification of Satellites based on seasonal lek attendance, mirroring that of Independents, as proposed by Hogan-Warburg (1966). For both morphs other measures of lek attachment correlated with variation in seasonal lek attendance: high attendance males were more likely to return to the same lek between years, had longer tenure, higher visitation rate, longer visit duration, less arrivals and departures from the lek together with females and higher daily lek attendance. This strongly suggests that there are also two lek attachment classes among Satellites, as described by Hogan-Warburg (1966): males with high and low lek attachment, which we refer to as Central and Peripheral Satellites. A notable qualitative difference between the morphs was that Central Satellites, but not Residents (Independents) could be attached to more than one lek.

Lek attachment differed quantitatively between morphs depending on status: Central Satellites had similar tenure but lower daily visitation rate, shorter visit durations, somewhat higher tendency to arrive and depart from a lek together with females, and lower daily and seasonal lek attendance than Residents, in line with van Rhijn (1983, 1991). Residents and Central Satellites returning between years had longer tenure and seasonal lek attendance than males seen for the first time, but their daily lek attendance was similar. In contrast, Peripheral Satellites did not differ from Marginals in these behaviours. Thus, we conclude that it is meaningful to distinguish between R-males (Residents and Central Satellites) and M-males (Marginals and Peripheral Satellites), independent of morph.

Of all males we observed on leks, 22.2% were Satellites. This proportion is similar to the 19.1% Satellites among all males visiting leks observed by Widemo (1998a). Interestingly, in the latter study the proportion of Satellites did not change (18.7%) when all males observed less than two hours on leks were excluded, indicating a similar morph ratio among males with high and low lek attachment (Widemo 1998a). Independents spent 88% and Satellites 12% of total male hours on leks, similar to the proportions reported in previous studies (Table 3). This suggests that the ratio between morphs regarding both the number of individuals per lek and individual lek attendance are consistent at different latitudes, in different habitats and in different decades.

Independent male tactics

Over a season, most Independents observed on a lek were Marginals (79%, 35.0 ± 14); their estimated number was even higher after correction for observation effort (95%, 176). Marginals did not obtain any copulations on the leks we observed, in line with van Rhijn (1983). However, our results also show that the low copulation success of Marginals did not differ from expectation if females randomly select a male on the lek and can be explained simply by their low lek attendance. Other studies have reported a small number of copulations by Marginals: one individual (<1%; Hogan-Warburg 1966), and 2% of copulations by 'floaters' (Widemo 1997). Visits of short tenure to the breeding site associated with low copulation or reproductive success have been observed in several other polygynous species. Leks of the Great Snipe *Gallinago media* are visited by non-territorial males having short tenure and low attendance (Lemnell 1978). These subordinate males amount to 40–52% of the males visiting leks, do not attract females (Höglund & Robertson 1990), and do not obtain matings (Lemnell 1978). Similarly, in the Pectoral Sandpiper *Calidris melanotos*, most males have short tenures and few of these males sire offspring locally (Kempenaers & Valcu 2017). On leks of the Buff-breasted Sandpiper *Calidris subruficollis* however, a minimum of 57% of males stay a day or less at stable leks (Lanctot & Weatherhead 1997), but these males can own a territory, attract females and obtain matings (Lanctot *et al.* 1998).

Within both the Independent and Satellite strategies, males can switch between three conditional spacing tactics to display to females (Lank & Smith 1987): Following when moving together with females (van Rhijn 1983), Intercepting when waiting for females at sites where food or water are present, and True Lekking when waiting for females on the lek, i.e. at a location without resources. Males pursuing each tactic spent a similar proportion of their time displaying to females, but because the average lek ratio, defined as the proportion of the local male population that is actually present on leks, was only 12%, 90% of displays occurred away from leks (Lank & Smith 1987). Although classifying Marginals under a common denominator is justified from an ethological point of view (Hogan-Warburg 1966), Marginals may be a mixture of males attempting to settle on a lek (Lekking, Intercepting and True Lekking combined), males that visit together with females (Following), males that sample many potential breeding areas (Sampling) and individuals passing through without local mating intent (Migrating). We discuss our results in this context in the following paragraphs.

Of all Marginals observed on five leks, only five (3%, $n = 171$ individuals) were known Residents on another lek, all on a nearby lek (< 1 km). Even though the home range of males is currently unknown, it seems unlikely that many more were Resident on another lek in the study area, because none was found on the known leks not included in the study and the area was searched extensively for leks. Previous work also suggests that visits of Residents to other leks are "exceptional" (Hogan-Warburg 1966). Sixteen Marginals (9%) did acquire a residence on the lek later or earlier in the season, in agreement with descriptions by Hogan-Warburg (1996). It is unknown how many of the remaining Marginals tried to settle on the lek, but failed to do so.

Marginals having short tenure, low lek attendance and short visit durations, might have been inexperienced or in poor condition. Yearling males are more likely to be Marginals (Hogan-Warburg 1966), but the majority of Marginals observed here were adults (at least two years old). The non-territorial status of most Marginal males visiting leks is probably not a consequence of poor condition, because Bachman & Widemo (1999) found that they were on average heavier and fatter than both Residents and Satellites.

Marginals often adopt the Following tactic: they frequently follow groups of females flying between leks and feeding grounds (van Rhijn 1983, Lank & Smith 1987, Widemo 1998b). Marginals arrived and departed from the lek together with females more often than Residents (van Rhijn 1983, present study). Visits by large mixed-sex flocks can destabilize the lek and contribute to the fitness of the Following tactic: all copulations by 'floaters' observed by Widemo (1997) occurred when the lek "boiled over". Nevertheless, over 40% of Marginals we observed were on the lek without females present, and the majority of Marginals arrived (65%) and departed (70%) without females. Furthermore M-males had lower lek attendance than R-males especially when females were present.

Finally, Marginals could be males that sample potential breeding areas over a larger geographical scale and quickly assess the lek for mating opportunities. Large-scale breeding site sampling has been described in a polygynous shorebird, the Pectoral Sandpiper, which shows a similar distribution of local tenure (Kempenaers & Valcu 2017 and Figure 1). It remains unknown whether Independents adopt a Following and/or Sampling tactic as their exclusive seasonal or life-time mating tactic, or whether all Marginals eventually attempt to acquire a territory on a lek. The spatial range used by Followers or Samplers is currently unknown, but given that most Marginals had short lek tenure and were rarely seen again, it probably exceeds the size of our study area.

Satellite male tactics

Hogan-Warburg's (1966) description of the behaviour characteristic for low-attendance Peripheral Satellites is not entirely consistent with our observations (see Methods; Table 1): half of the low-attendance Satellites adopted an oblique posture when interacting with a Resident in the absence of visiting females or other Satellites rather than remaining in a half-squat posture. A possible explanation for this difference is the smaller size of leks in our study area, because Hogan-Warburg (1966) reported that the behaviour typical for Central and Peripheral Satellites varies with lek size. Therefore, we used the fractional rank of Resident seasonal lek attendance to classify Satellites into two groups (see Methods; Figure S4).

Central Satellites had similar lek tenure than Residents, but somewhat lower lek visitation rates and shorter visit durations and hence shorter daily and seasonal lek attendance (Figure 2A, B, 4A). Central Satellites arrived at and departed from the lek more often together with females compared to Residents, which may compensate somewhat for their overall lower lek attendance. Nevertheless, most of their visits were still independent of female arrivals and departures, and their lek attendance was lower both when females were present and when females were absent. We conclude that Central Satellites, similar to Residents, attend leks and adopt the Lekking rather than the Following tactic.

Three Central Satellites attended two nearby leks (C and D, < 1 km apart, other studied leks were > 10 km apart; see Figure S1). One showed strong attachment to one lek only, whereas the two others behaved as Central Satellites on both leks. This is a notable difference with Residents, who can hold a territory on only one lek at a time. Studies of more leks with different spatial distributions are needed to investigate variation in lek attachment among Central Satellites. Attending more than one lek may compensate for lower lek attendance of Central Satellites at a given lek. Interestingly, after correcting for size, Satellites visiting leks were lighter and less fat than Residents (Bachman & Widemo 1999), suggesting that Satellites may maintain reduced energy reserves to minimize flight costs, while the larger fat stores of Independent males are consistent with the benefits of endurance as a territory holder (Bachman & Widemo 1999).

Lek attachment of Peripheral Satellites was similar to that of Marginals. Peripheral Satellites, like Marginals, may be a mixture of males attempting to settle on a lek (Lekking), Followers, Samplers and Migrants. Peripheral Satellites were not more likely to be yearling males than Central Satellites, but we cannot exclude that they were less experienced or in lower condition. Like Marginals, Peripheral Satellites were never seen copulating. Fifteen of 47 (32%) Peripheral Satellites were never observed visiting a residence and engaging in a hosting interaction, suggesting that they did not attempt to settle on the lek. Most Peripheral Satellites (33 of 47, 70%, own unpubl. obs.) were never attacked by a Resident. This suggests that they did not fail to settle and become a Central Satellite because of agonistic interactions. Seventeen (36%) Peripheral Satellites visited a lek when there were no females present, indicating that they did not use the Following tactic. Peripheral Satellites arrived and departed together with females as often as Marginals, but the majority of their arrivals and departures occurred independently of female movements (65 and 71%, respectively).

The relationship between lek attendance and copulation success

Previous studies showed strong and significant relationships between lek attendance and lek copulation success of Residents (Hill 1991, van Rhijn 1991, Widemo *et al.* 1994). However, neither study included data on Satellite mating success. In Ruffs, the display behaviour of Satellites and Independents on leks is fundamentally different: most importantly, Satellites do not show aggressive behaviour towards other ornamental males, and do not own a residence on the lek (Hogan-Warburg 1966). Whereas Residents mate on their own territory, Satellites obtain at least part of their copulations on the territory of a Resident (Hogan-Warburg 1966, van Rhijn 1973).

Our study confirms that copulation success of R-males increased with increasing lek attendance, both on a daily and a seasonal basis ($\rho = 0.68$; Figure 5B), and with increasing presence during female copulation visits ($\rho = 0.75$; Figure 6B). The effect size is comparable to those found in the studies mentioned above (range of published β or r-values: 0.54–0.72). However, we also show that this relationship did not differ between the two morphs (Figure 5B, 6B). M-males did not acquire copulations, in line with earlier reports for Marginals. There was no significant difference between copulation success of R-males returning between years and R-males seen for the first time. On each lek, individual Residents and Central Satellites had, on average, similar copulation rates. Note that individual seasonal success could be higher for R-males attending more than one lek (sequentially for all R-males, or simultaneously for Central Satellites).

If seasonal lek attendance was a major determinant of copulation success, in particular in partitioning copulations between the morphs, the proportion of total male hours spent on leks by Satellites is expected to be constant in the population, and should correspond to the proportion of Satellites in the population (Hugie & Lank 1997). However, the proportion of time Satellites spent on leks is clearly lower than the proportion of Satellites observed on leks (Table 3). Satellites may still have equal reproductive success (1) if the probability that a copulation leads to a fertilization is higher in Satellites (e.g. because they produce more sperm or more competitive sperm), (2) if Satellites obtain more copulations off-lek, or (3) if Satellites have a longer reproductive period within a season or over their life-time (Widemo 1998a).

Here, and in previous studies of Ruff leks, many males obtained no or few copulations (most M-males). The number of copulations accumulated over the season by individual R-males did not follow a Poisson distribution, but a negative binomial distribution (Table S6). Unequal distribution of matings among males is frequently observed in lekking species (Kokko *et al.* 1999), including the Ruff. Indices of inequality suggested that the propensity of R-males or Residents to obtain a copulation is different from random (Table S7A, B). However, after correcting for presence of successful males, skew index B indicated that equal propensity could no longer be excluded on two to three leks (Suppl. Data 7C). Finally, using two approaches including successful as well as unsuccessful males, we found evidence that on each lek only the α-male obtained more copulations than expected based on his presence during female copulation visits and accounting for the number of other males present at each of these visits (Table S5, Figure 6B). Published data support this distinction between the α-male and lower-ranking males on Ruff leks (Figure 6; Hill 1991, Widemo & Owens 1995).

Relationship between tenure and lek attendance

The frequency of female lek visits is not uniformly distributed over the lekking season (Lank & Smith 1987) and the seasonal peak of mating opportunities varies between years (own unpubl. obs.). Thus, to increase annual mating success, males have to maximize their tenure at the lek, unless they are able to track and follow females during the breeding season. In our study, males with the longest tenure also had the highest seasonal lek attendance (Figure 5A), especially when considering attendance when females were present on the lek. This is simply because males with long tenures are more likely to be present on the lek during the female mating peak.

Among R-males with short tenure, some missed the mating peak, whereas others were no longer present after the mating peak. Most likely these males left the study area (no evidence for predation), possibly sampling other areas where breeding occurred later. Because attendance was higher when females were present on the lek, differences in timing of the tenure could explain the seasonal correlation of lek attendance and copulation success. However, in the analysis of daily copulation success only males present on days when females copulated were compared, and lek attendance was still a significant predictor of success.

Lek attendance and sexual selection in Ruffs

The seasonal and daily pattern of lek attendance and its variability between individuals differs widely among lekking species. This may explain why lek attendance contributes differently to mating success in different species. In some species, most males attend the lek almost continuously during the daily lek activity period across their entire tenure period (e.g. Lawes's Parotia *Parotia lawesii*, Pruett-Jones & Pruett-Jones 1990; Great Snipe, Lemnell 1978, R. Ekblom pers. comm.). In these species, tenure is the major determinant of lek attendance, but there is either no (Pruett-Jones & Pruett-Jones 1990), or no consistent relationship with mating success (Fiske *et al.* 1994). Especially when the daily lek activity period is short, males have ample opportunity to feed throughout the mating season. In a second group of species, males also attend continuously during the daily activity period, but not every day of their tenure. In those species, the number of days present on the lek typically correlates strongly with mating success. Tenure can be interrupted frequently, as in many anurans (e.g. Friedl & Klump 2005 and references therein), or it can be short compared with the length of the entire breeding season, as in Fallow Deer *Dama dama* (Apollonio *et al.* 1992). The Ruff represents a third group because males leave the lek frequently during the daily activity period (Hill 1991, Höglund *et al.* 1993, present study), and overall attendance is determined by tenure and daily time present. For species of the second group, the energetic cost of attending leks is considered high. This may also apply to the Ruff (Widemo *et al.* 1994), because males cannot eat or drink while on the lek, leks are occupied during long daily periods (around the clock in our study area), and successful males have long tenures. Support for the energetic cost of lekking comes from the finding that Residents caught twice during the lekking season did lose body weight and fat (Bachman & Widemo 1999).

Thus, in Ruffs, sexual selection might first act through male-male competition to acquire the R-status and subsequently through endurance attending the lek while waiting for mating opportunities. If endurance rivalry (Andersson 1994, Murphy 1998) was the main selection mechanism among Independents on ancestral leks, it may have facilitated the spread of the Satellite inversion allele 500,000 years ago (Lamichhaney *et al.* 2016), as a non-aggressive, non-territorial alternative strategy. It is interesting to note that low rates of aggressive behaviour were significantly associated with higher mating success of Residents (Hill 1991).

Our observation that most males do not obtain more copulations than expected under random mating suggests a limited role for female choice in this species, which seems to contradict the apparently choosy behaviour of Reeves visiting leks (Hogan-Warburg 1966, Lank *et al.* 2002, own obs.). It cannot be excluded that lekking Ruffs acquire copulations through a non-random process with an outcome close to random. For example, it is possible that (1) females visit leks repeatedly to keep an attendance record (Hill 1991), (2) females attempt to identify the α-male, (3) male ranking gradually changes over the season, and (4) females have strong individual preferences. If females would actively keep an attendance record, our results suggest that they would score Independents and Satellites equally.

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SAMENVATTING

Op baltsplaatsen (‘leks’) van Kemphanen *Calidris pugnax* concurreren drie genetisch verschillende typen haantjes (Onafhankelijken, Satellieten en Faren) om copulaties met de hennetjes die de lek bezoeken. Faren lijken op hennetjes, terwijl Onafhankelijken en Satellieten een sterk seksueel dimorfisme vertonen: ze zijn aanzienlijk groter dan hennetjes en in het broedseizoen dragen ze een opvallend baltskleed. Onafhankelijke haantjes die een territorium verdedigen op een lek (Honkmannetjes) hebben een groter copulatiesucces dan Onafhankelijke haantjes zonder territorium (Randmannetjes). Hoe dat bij Satellieten zit is minder goed bekend. Daarom hebben we in het noorden van Noorwegen gedurende één broedseizoen op vijf leks de variatie in tijd doorgebracht op de lek en het copulatiesucces bij Onafhankelijken en Satellieten vergeleken. Bij de Onafhankelijke haantjes bleken Honkmannetjes in een later jaar vaker naar dezelfde lek terug te keren dan Randmannetjes, een langere periode van het seizoen op de lek te komen, vaker en langer op de lek aanwezig te zijn (per bezoek, dagelijks en over het gehele seizoen genomen), en minder vaak samen met een hennetje naar de lek toe te komen of die te verlaten. Bij Satellietmannetjes vonden we een kwalitatief gelijke interindividuele variatie in gedrag. Bijgevolg definiëren we twee typen Satellieten: Centrale Satellieten met een sterke binding aan de lek en Perifere Satellieten met een zwakke binding aan de lek. Een belangrijk verschil met Honkmannetjes is dat sommige Centrale Satellieten sterk gebonden waren aan meer dan één lek op dezelfde dag. De mate van aanwezigheid op de lek was gecorreleerd met het copulatiesucces, zowel per dag als over het gehele seizoen genomen, en het verband verschilt niet tussen Onafhankelijken en Satellieten. Het aanwezig zijn van een haantje op de lek tijdens het bezoek van een hennetje dat wil copuleren, voorspelde het copulatiesucces van de haantjes. De ongelijke verdeling van copulaties op een lek wordt dus in hoge mate verklaard door een ongelijke mate van aanwezigheid van de mannetjes op de lek. Na correctie voor variatie in aanwezigheid had één haantje per lek meer copulaties dan verwacht. Onze waarnemingen suggereren dat ‘endurance rivalry’, waarbij energiereserves de aanwezigheid van concurrerende haantjes op de lek begrenzen, zou kunnen bijdragen aan het copulatiesucces van mannetjes op de lek.

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SUPPLEMENTARY MATERIAL

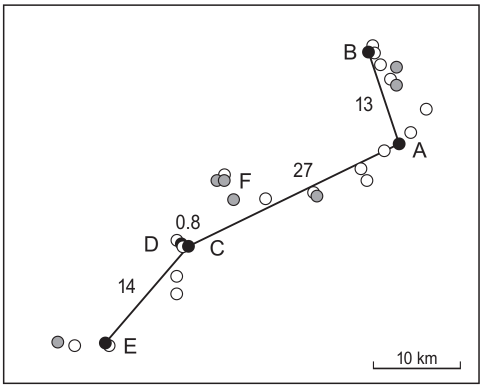

Figure S1. Map of the study area, showing the location of leks studied in 2014–2016 (A-E, black) and 2014–2015 (F). Leks used between years (black and grey circles) and display sites used irregularly between years, usually in June (white circles) are indicated. Numbers show the distance in km between nearest neighbouring leks (lines) studied in 2016.

Figure S2. Open wing posture. Satellites frequently adopt an oblique posture with partially opened wings. This posture did not clearly match a posture described in Hogan-Warburg (1966).

Figure S3. Males with conflicting plumage. Based on Hogan-Warburg (1966) and on 117 males with known behaviour (59% Independents, 41% Satellites), we scored males with more than 40% black tuft feathers, or more than 40% black ruff feathers, or less than 10 white feathers in tufts and ruff, or a barred pattern on the ruff as Independent. With this definition, four of the 117 males (3%) had a conflicting plumage: one male with a satellite-type ruff behaved as an Independent (A) and three males with an independent-type ruff behaved as a Satellite (B–D).

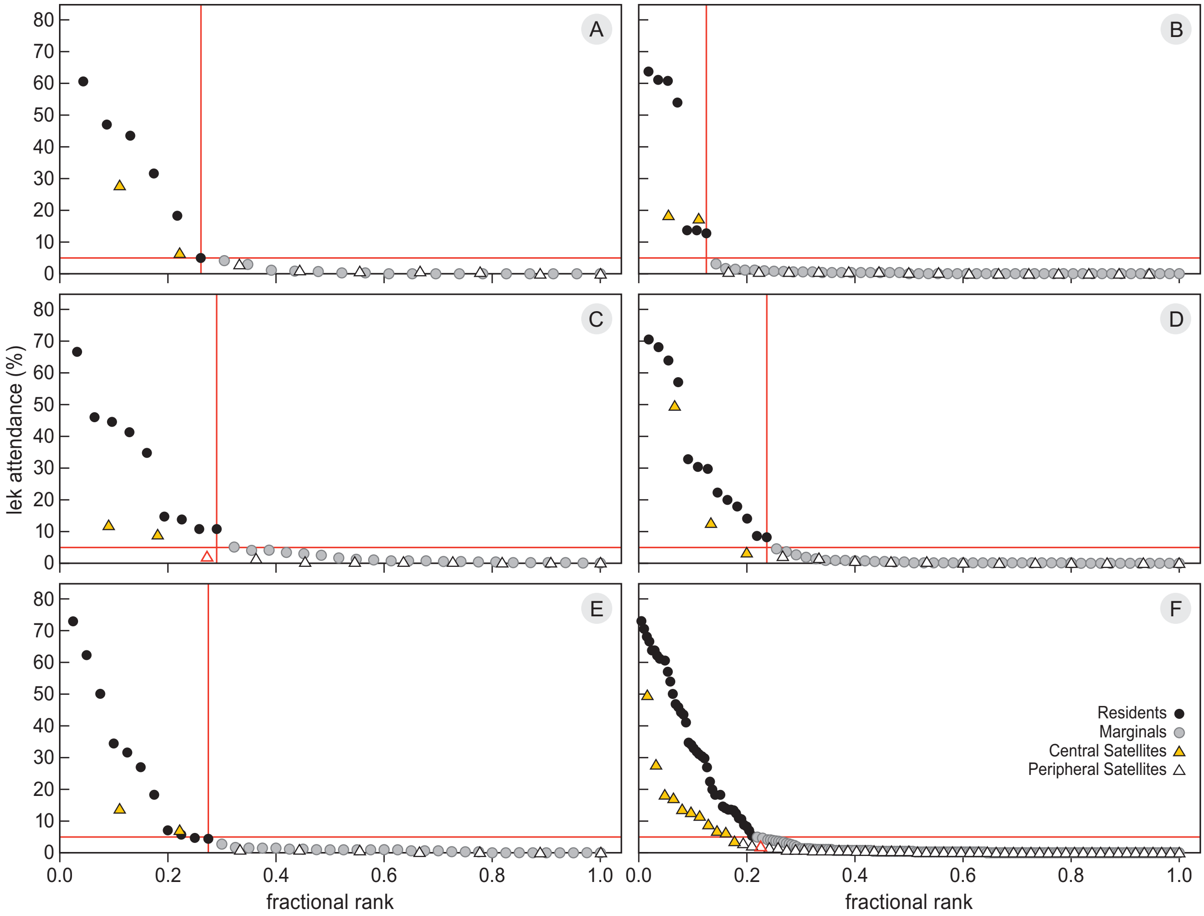

Figure S4. Independents (Residents (black) and Marginals (grey) combined), were ranked by decreasing seasonal lek attendance (% seasonal observation time), and for each male the fractional rank was calculated as the rank divided by the total number of Independents observed on the lek. Subsequently, Satellites were also ranked by decreasing seasonal lek attendance, and the fractional rank calculated. Satellites with fractional rank equal or smaller than the Resident ranked highest (vertical red line), were classified as Central Satellites (yellow). All other Satellites were Peripheral Satellites (white). One Satellite observed less than 60 minutes on lek C was classified as Peripheral Satellite (red circle). (A) lek A, (B) lek B, (C) lek C, (D) lek D, (E) lek E, (F) five leks combined.

The analysis of success of lekking males is often restricted to a subset of males, namely those with higher attendance, with an arbitrary cut-off such as presence during at least five nights (Fiske *et al.* 1994), presence during at least two hours (Widemo 1998a), territoriality during at least three hours (Apollonio *et al.* 1992), one day (Isvaran & Jhala 2000) or five days (Gibson & Bradbury 1985). In our study, four R-males had seasonal lek attendance lower than 5% (4.99–3.59%), whereas all M-males had seasonal lek attendance under 5% (4.96–0.00 %). Thus, using 5% seasonal attendance as a cut-off to define R- and M-males (horizontal red line), as opposed to fractional rank, changes the status of only four males (1.6%).

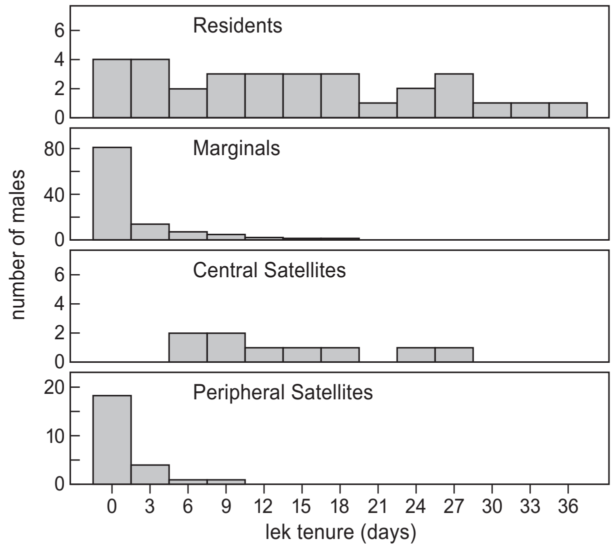

Figure S5. Histograms (bin-size 3) showing the number of males observed on two frequently observed leks (lek F in 2015, lek D in 2016) over the season classified by lek tenure, and by morph and status as Resident (n = 31), Marginal (n = 109), Central Satellite (n = 9) and Peripheral Satellite (n = 24). Status of Independents was determined based on territoriality in both years, but in 2015 lek attendance was not measured and status of Satellites was assigned based on tenure, behaviour, and subjective assessment of lek attendance.

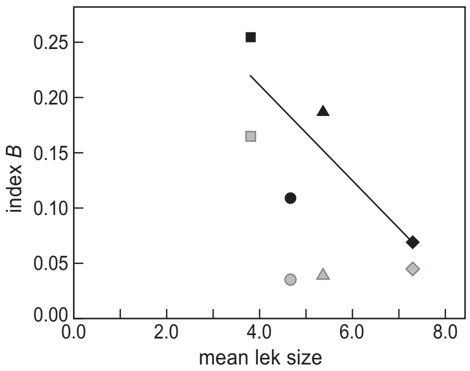

Figure S6. Relationship between lek size (seasonal mean, Table S2) and index B (black; Table S7B), and index B corrected for presence (grey; Table S7C) for lek B (circle), C (square), D (diamond), and E (triangle).

Table S1. Observation periods.

Lek	Date	Start	End	Observation period (min)
A	12/05/2016	14:46	15:46	60
A	16/05/2016	14:01	18:02	241
A	23/05/2016	05:30	10:30	300
A	27/05/2016	15:52	20:06	254
A	28/05/2016	04:44	10:15	270
A	02/06/2016	16:42	19:42	180
A	03/06/2016	18:00	20:00	120
A	04/06/2016	05:12	10:12	300
A	12/06/2016	18:25	20:25	120
A	16/06/2016	08:25	09:25	60
B	12/05/2013	10:55	11:55	60
B	17/05/2016	05:19	11:34	353
B	22/05/2016	05:30	11:30	360
B	22/05/2016	15:07	19:07	240
B	26/05/2016	16:39	19:39	180
B	27/05/2016	04:50	09:51	301
B	03/06/2016	04:28	11:00	388
B	04/06/2016	16:38	20:03	205
B	05/06/2016	05:30	10:38	308
B	13/06/2016	04:49	11:02	373
B	15/06/2016	04:55	09:55	300
B	15/06/2016	16:23	20:23	240
C	11/05/2016	06:26	08:49	143
C	12/05/2016	17:02	21:06	184
C	13/05/2016	04:52	10:52	360
C	13/05/2016	13:58	14:58	60
C	15/05/2016	05:06	11:06	360
C	18/05/2016	05:05	10:12	307
C	21/05/2016	04:45	09:46	301
C	25/05/2016	04:38	09:45	307
C	01/06/2016	04:50	09:57	297
C	06/06/2016	16:30	19:30	180
C	13/06/2016	19:50	20:50	60
D	13/05/2016	16:47	18:01	74
D	14/05/2016	05:03	11:08	365
D	15/05/2016	14:25	17:25	180
D	17/05/2016	15:50	19:50	240
D	18/05/2016	14:25	18:25	240
D	19/05/2016	03:29	10:19	360
D	20/05/2016	05:11	11:41	390
D	20/05/2016	15:47	20:55	210
D	21/05/2016	16:08	20:08	235
D	23/05/2016	15:21	19:21	240
D	24/05/2016	16:01	20:05	244
D	26/05/2016	04:47	09:47	300
D	29/05/2016	17:44	20:44	180
D	30/05/2016	04:52	09:44	292
D	01/06/2016	16:15	20:23	248
D	02/06/2016	04:23	10:23	360
D	06/06/2016	03:02	09:00	358
D	07/06/2016	17:26	20:26	180
D	13/06/2016	16:28	19:28	180
E	10/05/2016	18:29	18:59	30
E	14/05/2016	14:45	17:00	135
E	16/05/2016	04:43	10:43	360
E	19/05/2016	16:56	18:56	120
E	24/05/2016	05:06	10:06	300
E	25/05/2016	17:25	19:25	120
E	29/05/2016	03:42	09:00	318
E	31/05/2016	17:37	20:37	180
E	07/06/2016	04:13	10:13	360
E	14/06/2016	05:20	10:20	300
F	12/05/2015	18:01	21:30	107
F	13/05/2015	04:50	06:45	115
F	13/05/2015	08:00	16:50	530
F	13/05/2015	17:38	19:24	106
F	14/05/2015	05:00	08:48	228
F	16/05/2015	14:41	20:59	366
F	17/05/2015	04:00	09:56	315
F	17/05/2015	13:15	18:15	300
F	18/05/2015	04:45	08:45	240
F	18/05/2015	09:34	20:59	685
F	19/05/2015	04:16	09:45	299
F	19/05/2015	10:20	20:20	600
F	20/05/2015	04:09	11:45	456
F	20/05/2015	12:50	20:53	483
F	21/05/2015	04:34	05:10	36
F	21/05/2015	05:52	07:20	88
F	22/05/2015	23:24	05:08	344
F	24/05/2015	23:42	04:29	287
F	25/05/2015	16:41	18:48	127
F	25/05/2015	20:49	22:08	79
F	26/05/2015	04:09	10:51	376
F	26/05/2015	14:52	20:36	270
F	26/05/2015	23:14	00:00	46
F	27/05/2015	00:00	04:42	282
F	29/05/2015	21:13	23:45	152

Table S2. Lek size. The number of different males (RI: Resident, MI: Marginal, CS: Central Satellite, PS: Peripheral Satellite) observed daily, and weekly and seasonal averages.

					Day				Week				Season			
Lek	**Week**	**Date**	**Start Observ.**	**Duration**	RI	MI	CS	PS	RI	MI	CS	PS	RI	MI	CS	PS
D	1	13/05/2016	16:47	01:14	4	1	0	0	5.6	3.2	1.4	0.6	5.7	3.7	1.6	0.8
		14/05/2016	05:03	06:05	4	5	1	1								
		15/05/2016	14:25	03:00	6	4	1	2								
		17/05/2016	15:50	04:00	7	2	2	0								
		18/05/2016	14:25	04:00	7	4	3	0								
	2	19/05/2016	03:29	06:00	6	5	3	0	6.4	5.2	2.6	1.0				
		20/05/2016	05:11	10:00	7	9	3	1								
		21/05/2016	16:08	03:55	7	7	2	2								
		23/05/2016	15:21	04:00	5	4	3	0								
		24/05/2016	16:01	04:04	7	1	2	2								
	3	26/05/2016	04:47	05:00	7	3	1	2	7.3	4.3	1.5	1.5				
		29/05/2016	17:44	03:00	7	6	1	2								
		30/05/2016	04:52	04:52	8	4	2	1								
		1/06/2016	16:15	04:08	7	4	2	1								
	4	2/06/2016	04:23	06:00	7	9	2	1	5.3	4.7	1.3	1.0				
		6/06/2016	03:02	05:58	6	3	1	2								
		7/06/2016	17:26	03:00	3	2	1	0								
	5	13/06/2016	16:28	03:00	4	1	1	0	4.0	1.0	1.0	0.0				
A	1	12/05/2016	14:46	01:00	0	0	0	0	1.0	1.5	0.5	1.0	3.2	2.2	0.8	0.5
		16/05/2016	14:01	04:01	2	3	1	2								
	2	23/05/2016	05:30	05:00	3	0	1	2	3.0	0.0	1.0	0.0				
	3	27/05/2016	15:52	04:14	5	4	1	1	5.0	3.0	1.0	1.0				
		28/05/2016	04:44	04:30	5	2	1	1								
	4	2/06/2016	16:42	03:00	5	7	2	0	4.0	4.3	1.3	0.7				
		3/06/2016	18:00	02:00	4	0	2	1								
		4/06/2016	05:12	05:00	3	6	0	1								
	5	12/06/2016	18:25	02:00	3	2	0	0	3.0	2.0	0.0	0.0				
	6	16/06/2016	08:25	01:00	3	0	0	0								
C	1	12/05/2016	17:02	03:04	5	0	0	0	5.0	5.0	1.0	1.0	3.2	1.8	0.6	1.2
		13/05/2016	04:52	07:00	6	7	0	0								
		15/05/2016	05:06	06:00	5	11	2	2								
		18/05/2016	05:05	05:07	4	2	2	2								
	2	21/05/2016	04:45	05:01	4	1	2	0	4.0	2.0	1.0	0.0				
		25/05/2016	04:38	05:07	4	3	0	0								
	3	1/06/2016	04:50	04:57	4	7	1	4	4.0	1.0	1.0	4.0				
	4	6/06/2016	16:30	03:00	2	1	0	1	2.0	1.0	0.0	1.0				
	5	13/06/2016	19:50	01:00	1	0	0	0	1.0	0.0	0.0	0.0				
B	1	12/05/2013	10:55	01:00	0	0	0	0	1.0	1.5	0.5	1.0	3.5	5.1	1.1	2.2
		17/05/2016	05:19	05:53	2	3	1	2								
	2	22/05/2016	05:30	10:00	4	2	1	2	4.0	2.0	1.0	2.0				
	3	26/05/2016	16:39	03:00	4	3	1	2	4.0	4.5	1.0	1.5				
		27/05/2016	04:50	05:01	4	6	1	1								

Table S2. Continued.

Lek	Week	Date	Start Observ.	Duration	Day				Week				Season			
					RI	MI	CS	PS	RI	MI	CS	PS	RI	MI	CS	PS
B	4	3/06/2016	04:28	06:28	6	20	2	6	4.7	9.0	1.7	4.3				
		4/06/2016	16:38	03:25	4	1	1	4								
		5/06/2016	05:30	05:08	4	6	2	3								
	5	13/06/2016	04:49	06:13	4	9	2	3	4.0	8.5	1.5	2.0				
		15/06/2016	04:55	09:00	4	8	1	1								
E	1	14/05/2016	14:45	02:15	4	3	2	0	4.0	4.5	2.0	0.0	4.4	3.8	0.9	0.9
		16/05/2016	04:43	06:00	4	6	2	0								
	2	19/05/2016	16:56	02:00	4	3	1	0	4.7	4.3	1.7	0.3				
		24/05/2016	05:06	05:00	5	10	2	1								
		25/05/2016	17:25	02:00	5	0	2	0								
	3	29/05/2016	03:42	05:18	6	4	0	1	6.5	2.0	0.0	2.0				
		31/05/2016	17:37	03:00	7	0	0	3								
	4	7/06/2016	04:13	06:00	3	3	0	1	3.0	3.0	0.0	1.0				
	5	14/06/2016	05:20	05:00	4	5	1	1	4.0	5.0	1.0	1.0				

Table S3. Leg colour. We aged males based on leg colour (Pearson 1972): birds with grey, grey-yellow or grey-pink legs were considered yearlings (2 CY), whereas birds with pink or orange legs were scored as adults (> 2CY). The proportion of yearlings should be considered a minimum estimate, because leg colour typically changes during the second calendar year (Pearson 1972). Status of Independents was determined based on territoriality in all three years, but in 2014–2015 lek attendance was not measured and status of Satellites was assigned based on tenure, behaviour, and subjective assessment of lek attendance.

Year	Morph	Tactic	2 CY Legs	>2CY Legs	*P*[a]
2016	Independent	Resident	1	45	0.3
		Marginal	12	149	
	Satellite	Central	0	11	1
		Peripheral	0	51	
2015	Independent	Resident	4	70	0.03
		Marginal	20	107	
	Satellite	Central	0	16	1
		Peripheral	2	32	
2014	Independent	Resident	16	86	0.002
		Marginal	57	115	
	Satellite	Central	0	9	0.3
		Peripheral	8	36	
Combined	Independent	Resident			0.001[b]
		Marginal			
	Satellite	Central			0.9[c]
		Peripheral			

[a] Fisher's exact test

[b] combined *P* with sum of logs method calculated with 'metap' package: $\chi^2_6 = 21.8$

[c] combined *P* with sum of logs method calculated with 'metap' package: $\chi^2_6 = 2.4$

Table S4. Arrival and departure from the lek together with females (♀). RI: Resident, CS: Central Satellite, MI: Marginal, PS: Peripheral Satellite.

		Arrival				**Departure**			
Lek	**Class**	With ♀	%	Without ♀	Total	With ♀	%	Without ♀	Total
A	MI	11	34.38	21	32	9	28.13	23	32
A	PS	4	28.57	10	14	2	14.29	12	14
A	RI	29	15.26	161	190	18	9.14	179	197
A	CS	7	22.58	24	31	6	18.18	27	33
B	MI	38	36.19	67	105	34	33.33	68	102
B	PS	11	32.35	23	34	10	30.30	23	33
B	RI	33	9.94	299	332	35	10.48	299	334
B	CS	20	21.05	75	95	17	18.48	75	92
C	MI	20	26.32	56	76	23	29.87	56	79
C	PS	6	50.00	6	12	3	23.08	10	13
C	RI	22	8.12	249	271	16	5.86	255	271
C	CS	8	15.69	43	51	12	23.08	40	52
D	MI	43	32.33	92	135	32	24.06	103	135
D	PS	10	43.48	13	23	7	30.43	16	23
D	RI	47	7.21	605	652	59	8.81	611	670
D	CS	34	22.08	118	152	44	28.03	111	155
E	MI	28	50.91	27	55	24	42.59	32	56
E	PS	2	20.00	8	10	5	45.45	6	11
E	RI	19	8.05	217	236	16	5.73	263	279
E	CS	7	28.00	18	25	8	33.33	16	24
A-E	MI	140	34.74	263	403	122	30.20	282	404
A-E	PS	33	35.48	60	93	27	28.72	67	94
A-E	RI	150	8.92	1531	1681	144	8.22	1607	1751
A-E	CS	76	21.47	278	354	87	24.44	269	356

Table S5. For each copulation visit of a Reeve, we tallied all the individual males present on the lek (leks B-E), and assigned each male the same probability to obtain the copulation. We then calculated the expected total number of copulations for each male over the season under the assumption of random mating as the sum of his scores obtained at all female copulation visits. For each male, we then compared the number of copulations actually obtained with the random expectation, using a two-tailed exact test of goodness-of-fit ('binom.test' function in R, with 'successes' = the actual number of copulations obtained, 'total' = the number of copulations observed on the lek over the season, 'numerator' = the expected number of copulations under random copulation, 'denominator' = the total number of copulations observed on the lek). On each lek one male obtained more copulations than expected ($P < 0.05$; shaded), and on one lek one male received less copulations than expected ($P < 0.05$; **bold**). RI: Resident, CS: Central Satellite, MI: Marginal, PS: Peripheral Satellite.

Class	Lek	Successes	Total	Numerator	Denominator	*P*
RI	B	3	22	3.12	22	1.00000
RI	B	9	22	3.25	22	0.00266
RI	B	3	22	3.50	22	1.00000
RI	B	5	22	3.97	22	0.57792
RI	B	0	22	0.45	22	1.00000
RI	B	0	22	0.45	22	1.00000
RI	B	0	22	1.28	22	0.63649
RI	C	0	21	0.45	21	1.00000
RI	**C**	**0**	**21**	**3.64**	**21**	**0.03788**
RI	C	12	21	2.85	21	0.00000
RI	C	4	21	3.14	21	0.54268
RI	C	0	21	0.90	21	1.00000
RI	C	3	21	1.78	21	0.41684
RI	C	1	21	3.19	21	0.35446
RI	C	0	21	0.25	21	1.00000
RI	C	0	21	0.25	21	1.00000
RI	D	13	57	7.19	57	0.02747
RI	D	7	57	6.29	57	0.67477
RI	D	0	57	1.04	57	0.62915
RI	D	11	57	6.62	57	0.09317
RI	D	7	57	4.22	57	0.19611
RI	D	4	57	6.66	57	0.40627
RI	D	3	57	4.42	57	0.62535
RI	D	0	57	0.00	57	1.00000
RI	D	1	57	5.30	57	0.06235
RI	D	0	57	1.39	57	0.65119
RI	D	1	57	1.43	57	1.00000
RI	D	0	57	0.27	57	1.00000
RI	D	0	57	0.00	57	1.00000
RI	E	12	25	6.20	25	0.01748
RI	E	4	25	4.92	25	0.80414
RI	E	0	25	0.83	25	1.00000
RI	E	4	25	3.36	25	0.76671
RI	E	0	25	1.20	25	0.63147
RI	E	0	25	0.00	25	1.00000
RI	E	3	25	1.28	25	0.13387
RI	E	0	25	0.00	25	1.00000
RI	E	0	25	0.94	25	1.00000
RI	E	0	25	0.00	25	1.00000
RI	E	0	25	0.00	25	1.00000
CS	B	1	22	2.45	22	0.50418
CS	B	1	22	0.85	22	0.57973
CS	C	1	21	0.59	21	0.45034
CS	C	0	21	0.33	21	1.00000
CS	D	8	57	5.96	57	0.38257
CS	D	1	57	1.86	57	1.00000
CS	D	1	57	0.76	57	0.53472
CS	E	2	25	2.06	25	1.00000
CS	E	0	25	0.86	25	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.10	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.67	22	1.00000
PS	B	0	22	0.11	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.40	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	B	0	22	0.00	22	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.14	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.14	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	C	0	21	0.00	21	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.13	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	D	0	57	0.00	57	1.00000
PS	E	0	25	0.00	25	1.00000
PS	E	0	25	0.00	25	1.00000

Table S5. Continued.

Class	Lek	Successes	Total	Numerator	Denominator	*P*
PS	E	0	25	0.00	25	1.00000
PS	E	0	25	0.00	25	1.00000
PS	E	0	25	0.00	25	1.00000
PS	E	0	25	0.00	25	1.00000
PS	E	0	25	0.00	25	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.10	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.10	22	1.00000
MI	B	0	22	0.35	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.33	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.20	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.11	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.13	22	1.00000
MI	B	0	22	0.11	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	B	0	22	0.00	22	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.53	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.50	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.42	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.14	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.00	21	1.00000
MI	C	0	21	0.25	21	1.00000
MI	C	0	21	0.75	21	1.00000
MI	C	0	21	0.50	21	1.00000
MI	C	0	21	0.25	21	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	1.09	57	0.63030
MI	D	0	57	0.37	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.48	57	1.00000
MI	D	0	57	0.10	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.14	57	1.00000
MI	D	0	57	0.60	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.09	57	1.00000

Table S5. Continued.

Class	Lek	Successes	Total	Numerator	Denominator	*P*
MI	D	0	57	0.16	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.14	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.17	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.11	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	D	0	57	0.00	57	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.14	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.75	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.92	25	1.00000
MI	E	0	25	0.92	25	1.00000
MI	E	0	25	0.25	25	1.00000
MI	E	0	25	0.00	25	1.00000
MI	E	0	25	0.25	25	1.00000
MI	E	0	25	0.11	25	1.00000

Table S6. Distribution of copulations by individual R-males and Residents. We analysed the seasonal distribution of copulations for each lek separately using the 'fitdist' and 'gofstat' functions of the package 'fitdistrplus' v. 1.0.11 (Delignette-Muller & Dutang 2015). The distribution of copulations over the entire season by R-males on each lek (4 leks) did fit a negative binomial distribution better (grey) than a Poisson distribution or normal distribution. The same was true for single copulations by Residents, also using published data (Hill 1991, van Rhijn 1991).

Distribution			**Lek**								
			Present study				Hill (1991)				
		Parameter	B	C	D	E	1985 St. Ören	1987 St. Ören	1985 Stenåsa	1987 Stenåsa	van Rhijn (1991)
Copulations (bouts) R-Males	Negative binomial	Mean	2.44	1.91	3.56	1.92	NA	NA	NA	NA	NA
		Est SD	3.00	3.62	4.30	3.43	NA	NA	NA	NA	NA
		Skewness	1.47	2.57	1.08	2.41	NA	NA	NA	NA	NA
		Kurtosis	5.02	10.03	2.96	9.53	NA	NA	NA	NA	NA
		Size	0.82	0.30	0.60	0.24	NA	NA	NA	NA	NA
		mu	2.44	1.91	3.56	1.92	NA	NA	NA	NA	NA
		Loglikelihood	–18.64	–18.90	–37.80	–21.95	NA	NA	NA	NA	NA
		AIC	41.28	41.80	79.61	47.89	NA	NA	NA	NA	NA
		BIC	41.67	42.59	81.15	49.02	NA	NA	NA	NA	NA
		χ^2 statistic	0.06	0.16	1.60	0.04	NA	NA	NA	NA	NA
		χ^2 *P*-value	0.80	NA	0.21	NA	NA	NA	NA	NA	NA
	Poisson	lambda	2.44	1.91	3.56	1.92	NA	NA	NA	NA	NA
		Loglikelihood	–23.51	–32.38	–57.26	–37.48	NA	NA	NA	NA	NA
		AIC	49.02	66.76	116.53	76.96	NA	NA	NA	NA	NA
		BIC	49.21	67.15	117.30	77.53	NA	NA	NA	NA	NA
		χ^2 statistic	7.49	13.80	69.41	22.94	NA	NA	NA	NA	NA
		χ^2 *P*-value	0.02	0.00	0.00	NA	NA	NA	NA	NA	NA
	Normal (discrete)	norm mean	2.44	1.91	3.56	1.92	NA	NA	NA	NA	NA
		norm sd	2.83	3.45	4.17	3.29	NA	NA	NA	NA	NA
		Loglikelihood	–22.14	–29.23	–45.54	–33.94	NA	NA	NA	NA	NA
		AIC	48.28	62.46	95.08	71.87	NA	NA	NA	NA	NA
		BIC	48.68	63.26	96.63	73.00	NA	NA	NA	NA	NA
		χ^2 statistic	2.84	5.07	10.31	7.28	NA	NA	NA	NA	NA
		χ^2 *P*-value	0.09	NA	0.00	NA	NA	NA	NA	NA	NA
Copulations (single) Residents	Negative binomial	Size	0.45	0.20	0.49	0.15	0.18	0.23	0.21	0.79	0.27
		mu	4.43	3.89	4.61	3.82	1.83	3.00	2.60	3.50	4.05
		Loglikelihood	–17.58	–18.49	–33.24	–21.06	–9.33	–13.69	–9.17	–9.50	–45.67
		AIC	39.15	40.98	70.47	46.13	22.65	31.39	22.34	23.01	95.35
		BIC	39.04	41.38	71.60	46.92	22.24	31.28	21.56	21.78	97.44
		χ^2 statistic	0.39	0.01	0.96	0.02	0.01	0.02	0.01	0.19	3.06
		χ^2 *P*-value	NA	NA	NA	NA	NA	NA	NA	NA	0.08
	Poisson	lambda	4.43	3.89	4.62	3.82	1.83	3.00	2.60	3.50	4.05
		Loglikelihood	–27.93	–52.01	–54.78	–65.86	–17.83	–29.70	–18.77	–13.36	–141.24
		AIC	57.85	106.02	111.56	133.72	37.65	61.40	39.55	28.71	284.48
		BIC	57.80	106.21	112.12	134.12	37.45	61.35	39.16	28.10	285.53
		χ^2 statistic	103.58	128.69	186.59	193.43	11.47	40.26	20.10	7.80	219.74
		χ^2 *P*-value	0.00	0.00	0.00	0.00	NA	NA	NA	0.01	0.00
	Normal (discrete)	norm mean	4.43	3.89	4.62	3.82	1.83	3.00	2.60	3.50	4.05
		norm sd	4.59	7.40	5.00	7.73	3.29	5.10	4.27	3.91	9.77
		Loglikelihood	–20.61	–30.78	–39.37	–38.11	–15.65	–21.34	–14.35	–11.12	–77.67
		AIC	45.21	65.57	82.74	80.21	35.31	46.67	32.71	26.25	159.33
		BIC	45.10	65.96	83.87	81.01	34.89	46.56	31.93	25.02	161.42
		χ^2 statistic	3.44	3.32	3.84	5.91	4.18	3.00	2.73	1.99	27.18
		χ^2 *P*-value	NA	NA	NA	NA	NA	NA	NA	NA	0.00

Table S7A. Indices of skew were calculated with Skew Calculator 2003: S (Reeve & Ratnieks 1993), Sc (Keller & Krieger 1996), S3 (Pamilo & Crozier 1996) ; Q (monopolization index; Ruzzante *et al.* 1996); lambda (Kokko & Lindström 1997), Idelta (Morisita index; Tsuji & Tsuji 1998), Ip (standardized Morisita index; Tsuji & Tsuji 1998). The mean for each study (present study: B-E; Hill 1991: 1985–87), and three studies combined (9 leks) is also calculated.

				Index						
Study details	**Lek**	**Sample**	**Successful**	S	Sc	S3	Q	lambda	Idelta	Ip
Present study, copulation bouts, R-males	B	9	6	0.41	0.34	0.64	0.13	0.41	2.03	0.54
	C	11	5	0.65	0.58	0.84	0.29	0.56	3.93	0.63
	D	16	11	0.36	0.33	0.62	0.08	0.25	2.13	0.53
	E	13	5	0.66	0.60	0.81	0.21	0.46	3.55	0.59
	B-E	12.3	6.8	0.52	0.46	0.73	0.18	0.42	2.91	0.57
Present study, single copulations, Residents	B	7	4	0.46	0.44	0.60	0.15	0.45	1.91	0.56
	C	9	4	0.71	0.70	0.88	0.44	0.68	4.49	0.71
	D	13	8	0.41	0.40	0.59	0.08	0.28	1.99	0.53
	E	11	4	0.74	0.73	0.88	0.40	0.63	4.96	0.69
	B-E	10	5	0.58	0.57	0.74	0.27	0.51	3.34	0.62
Hill (1991), single copulations, Residents	1985 Stora Ören	6	2	0.80	0.76	0.92	0.61	0.83	4.04	0.77
	1987 Stora Ören	7	3	0.71	0.69	0.87	0.46	0.71	3.73	0.71
	1985 Stenåsa	5	2	0.79	0.77	0.91	0.65	0.85	3.59	0.79
	1987 Stenåsa	4	3	0.51	0.47	0.74	0.37	0.71	2.11	0.62
	1985–87	5.5	2.5	0.70	0.67	0.86	0.52	0.78	3.37	0.72
Van Rhijn (1991), single copulations, Residents	1968 Roderwolde	21	12	0.58	0.57	0.90	0.28	0.49	6.66	0.64
Three studies, single copulations, Residents	9 leks	9.2	4.7	0.64	0.61	0.81	0.38	0.63	3.72	0.67

Table S7B. The skew index *B* (*B* observed) calculated with Skew Calculator 2003 (Nonacs 2003). '*P*-level (random)': a one-tailed probability level that the observed *B* value is due to random chance, calculated by simulation (set at 1000 simulations). The program also simulates a random distribution across all leks to determine the probability level of the observed mean *B*-value (present study: B-E; Hill 1991: 1985-87; all three studies: 9 leks). For the observed *B*-index, a two-tailed confidence interval is calculated (0.95% C.I.; 'significance' set at 0.05 and 'calculation' set at accurate). '*B* under equality': the minimum possible *B* value through equal sharing of the group benefits. '*B* under monopoly': the maximum possible *B* value if all the benefits are monopolized by the individual with the highest gain rate. On all leks the lower C.I. excludes '*B* under equality', thus an equal distribution of observed benefits can be excluded. The upper C.I. does not include 'B under monopoly', thus total monopoly by one individual can be excluded. The C.I. does not include 0, and '*P*-level random' is smaller than 0.05, thus random sharing can also be excluded.

Study details	Lek	Sample	Successful	*B* observed	*P*-level (random)	95% C.I.	*B* under equality	*B* under monopoly
Present study, copulation bouts, R-males	B	9	6	0.11	0.002	0.03–0.25	–0.04	0.85
	C	11	5	0.25	0	0.12–0.44	–0.04	0.87
	D	16	11	0.07	0	0.04–0.12	–0.02	0.92
	E	13	5	0.19	0	0.09–0.33	–0.04	0.89
	B-E	12.3	6.8	0.16	0			
Present study, single copulations, Residents	B	7	4	0.13	0	0.05–0.25	–0.03	0.83
	C	9	4	0.38	0	0.23–0.54	–0.03	0.86
	D	13	8	0.07	0	0.04–0.13	–0.02	0.91
	E	11	4	0.35	0	0.23–0.50	–0.02	0.89
	B-E	10	5	0.23	0			
Hill (1991), single copulations, Residents	1985 Stora Ören	6	2	0.46	0	0.18–0.72	–0.08	0.76
	1987 Stora Ören	7	3	0.37	0	0.19–0.59	–0.04	0.82
	1985 Stenåsa	5	2	0.48	0	0.21–0.71	–0.06	0.74
	1987 Stenåsa	4	3	0.26	0	0.07–0.53	–0.05	0.70
	1985-87	5.5	2.5	0.39	0			
Van Rhijn (1991), single copulations, Residents	1968 Roderwolde	21	12	0.27	0	0.20–0.39	–0.01	0.94
Three studies, single copulations, Residents	9 leks	9.2	4.7	0.31	0			

Table S7C. The skew index *B* (Nonacs 2003) corrected for presence at female copulation visits. A restriction of the method is that all unsuccessful individuals are given the same presence; the average presence of unsuccessful males on the lek was used here. With this partial correction, the lower C.I. includes '*B* under equality' on three leks, thus an equal distribution of benefits can no longer be excluded. The upper C.I. does not include '*B* under monopoly', thus total monopoly by one individual can still be excluded. The value of the *B*-index is closer to 0 (random sharing) after correction for presence, and the C.I. includes 0 on three leks, and '*P*-level (random)' is larger than or close to 0.05 on two–three leks, thus random sharing cannot be excluded.

Study details	**Lek**	**Sample**	**Successful**	***B* observed**	***P*-level (random)**	**95% C.I.**	***B* under equality**	***B* under monopoly**
Present study, copulation bouts, R-males	B	9	6	0.03	0.09	–0.04–0.14	–0.04	0.76
	C	11	5	0.16	0	0.07–0.31	–0.04	0.76
	D	16	11	0.04	0	–0.02–0.80	–0.02	1.07
	E	13	5	0.04	0.04	–0.03–0.17	–0.03	1.00
	B-E	12.3	6.8	0.07	0			
Present study, single copulations, Residents	B	7	4	0.05	0.01	0.01–0.16	–0.03	0.74
	C	9	4	0.30	0	0.18–0.44	–0.02	0.75
	D	13	8	0.01	0.08	–0.01–0.06	–0.01	1.08
	E	11	4	0.12	0	–0.02–0.21	–0.02	0.58
	B-E	10	5	0.12	0			

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SUPPLEMENTARY DATA

Model descriptions

Abbreviations (suffix '.S' added to the scaled variable name)

B01	Copulation success (N/Y)
B02	Copulation success (0/1)
BN	Copulations (number)
BNO	BN observed
BNE	BN expected
DVR	Daily visitation rate
DS	Day of season
F01	With female (N/Y)
FA, FV	Female attendance
FVR	Female visitation rate
ID	Male ID
Lek	Lek
M	AM or PM
Mo, Mo2	Morph
PA	Attendance (%)
PAFV	PA (%) females present
PAFA	PA (%) females absent
PBE	Copulations expected (%)
PBO	Copulations observed (%)
PFA	Female attendance (%)
RM	Number of R-males
T01	Returning (N/Y)
T2	Lek tenure
Ta1, Ta	Daily status
Ta2	Seasonal status
VD	Visit duration

Grey background: models using scaled variables

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Tables: Variable, Chi-square test statistic and *p*-value. Summarize the output of anova comparing two models: the full model, and a model omitting the variable
Grey fill: random effects
→: variable tested in a separate model, replacing the variable on the previous line

Frequency of male morphs and lek attachment status

Returning between years: effect of morph and status (all males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: T01 ~ Mo2+Ta2+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid
   128.1    146.1    -59.1    118.1      262

Scaled residuals:
      Min        1Q    Median        3Q       Max
-0.032978 -0.000048 -0.000030 -0.000030  0.121393

Random effects:
 Groups Name        Variance  Std.Dev.
 ID     (Intercept) 1.726e+03 4.154e+01
 Lek    (Intercept) 1.683e-10 1.297e-05
Number of obs: 267, groups:  ID, 252; Lek, 5

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -20.8422     4.5417  -4.589 4.45e-06 ***
Mo2S          0.9656     3.5743   0.270 0.787037
Ta2R         11.5652     3.3213   3.482 0.000497 ***

Correlation of Fixed Effects:
     (Intr) Mo2S
Mo2S -0.014
Ta2R -0.935 -0.051
```

Lek Tenure

Lek tenure: effect of returning between years, morph and status (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: T2 ~ Mo2+Ta2+T01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid
  1604.0   1629.1   -795.0   1590.0      260

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.9943 -0.1341 -0.0985 -0.0985  3.4274

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept)  0.1996  0.4467
 Lek      (Intercept)  0.0000  0.0000
 Residual             22.3832  4.7311
Number of obs: 267, groups:  ID, 252; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)   1.4701     0.3710   3.963
Mo2S          0.1701     0.6901   0.247
```

```
Ta2R         12.6006     0.8715  14.459
T01Y          5.9710     0.9802   6.091

Correlation of Fixed Effects:
     (Intr) Mo2S   Ta2R
Mo2S -0.450
Ta2R -0.281  0.047
T01Y -0.120 -0.012 -0.579
```

Variable	Chisq	p
Mo2	0.061	0.8053
Ta2	145.460	< 2.2e-16
T01	34.561	4.132e-09

Daily lek visitation rate

Daily lek visitation rate: effect of morph, tactic, and female attendance (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: DVR ~ Mo+Ta1+FA+(1|ID)+(1|DS)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 -3649.9  -3609.5   1833.9  -3667.9      644

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.4236 -0.4555 -0.0769  0.3041  7.9641

Random effects:
 Groups   Name        Variance  Std.Dev.
 ID       (Intercept) 1.341e-05 0.003662
 DS       (Intercept) 2.789e-05 0.005281
 Lek      (Intercept) 3.749e-05 0.006123
 M        (Intercept) 2.226e-06 0.001492
 Residual             1.841e-04 0.013570
Number of obs: 653, groups:  ID, 253; DS, 33; Lek, 5; M, 2

Fixed effects:
              Estimate Std. Error t value
(Intercept)  1.379e-02  3.395e-03   4.063
MoS         -4.166e-03  1.551e-03  -2.686
Ta1R         1.906e-02  1.254e-03  15.200
FA          -3.139e-04  6.106e-05  -5.141

Correlation of Fixed Effects:
     (Intr) MoS    Ta1R
MoS  -0.105
Ta1R -0.197  0.014
FA   -0.302  0.017  0.060
```

Daily visitation rate: effect of morph, tactic, and female visitation rate (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: DVR ~ Mo+Ta1+FVR+(1|ID)+(1|DS)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 -3636.3  -3596.0   1827.2  -3654.3      644

Scaled residuals:
    Min      1Q  Median      3Q     Max
-2.1169 -0.4761 -0.0625  0.2935  8.1057
```

```
Random effects:
 Groups   Name        Variance  Std.Dev.
 ID       (Intercept) 1.431e-05 0.003783
 DS       (Intercept) 4.019e-05 0.006339
 Lek      (Intercept) 5.077e-06 0.002253
 M        (Intercept) 3.070e-06 0.001752
 Residual             1.873e-04 0.013685
Number of obs: 653, groups:  ID, 253; DS, 33; Lek, 5; M, 2

Fixed effects:
             Estimate Std. Error t value
(Intercept)  0.011473   0.002433   4.715
MoS         -0.004147   0.001574  -2.635
Ta1R         0.019129   0.001270  15.061
FVR         -0.066366   0.023185  -2.862

Correlation of Fixed Effects:
     (Intr) MoS    Ta1R
MoS  -0.161
Ta1R -0.277  0.018
FVR  -0.431  0.046  0.058
```

Variable	Chisq	p
Mo	6.8092	0.009069
Ta1	175.8	< 2.2e-16
FA	21.411	3.706e-06
→ FVR	7.8651	0.00504
ID	15.127	0.0001005
DS	29.183	6.584e-08
Lek	22.333	2.292e-06
M	1.7122	0.1907

Daily lek visitation rate: effect of returning between years (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: DVR ~ Mo+T01+FVR+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 -1764.1  -1729.5    891.1  -1782.1      339

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.8580 -0.6080 -0.0661  0.4598  6.0848

Random effects:
 Groups   Name        Variance  Std.Dev.
 ID       (Intercept) 3.282e-05 0.005729
 DS       (Intercept) 8.846e-05 0.009406
 Lek      (Intercept) 1.621e-05 0.004026
 M        (Intercept) 5.448e-06 0.002334
 Residual             2.795e-04 0.016718
Number of obs: 348, groups:  ID, 51; DS, 33; Lek, 5; M, 2

Fixed effects:
             Estimate Std. Error t value
(Intercept)  0.030367   0.004096   7.414
MoS         -0.008570   0.003226  -2.657
T01Y         0.003057   0.002829   1.080
```

```
FVR         -0.087397   0.036244  -2.411

Correlation of Fixed Effects:
     (Intr) MoS    T01Y
MoS  -0.143
T01Y -0.467 -0.006
FVR  -0.340 -0.016 -0.035
```

Variable	Chisq	p
Mo	6.6223	0.01007
T01	1.1376	0.2862
FVR	5.5574	0.0184
→ FA	14.418	0.0001464
DS	38.556	5.319e-10
ID	12.152	0.0004903
Lek	3.2434	0.07171
M	1.846	0.1742

Lek visit duration

Lek visit duration: effect of morph, status and female attendance (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: VD ~ Mo+Ta1+FA+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 27664.7  27718.1 -13823.4  27646.7     2789

Scaled residuals:
   Min     1Q Median     3Q    Max
-1.386 -0.515 -0.231  0.142  9.461

Random effects:
 Groups   Name        Variance  Std.Dev.
 ID       (Intercept) 2.416e+01  4.9154
 DS       (Intercept) 6.232e+01  7.8944
 Lek      (Intercept) 3.421e+01  5.8491
 M        (Intercept) 9.629e-02  0.3103
 Residual             1.104e+03 33.2273
Number of obs: 2798, groups:  ID, 253; DS, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error t value
(Intercept)   1.9152     3.6778   0.521
MoS          -9.5310     2.3287  -4.093
Ta1R         18.7065     1.9015   9.838
FA            0.4157     0.0817   5.088

Correlation of Fixed Effects:
     (Intr) MoS    Ta1R
MoS  -0.116
Ta1R -0.389  0.020
FA   -0.355 -0.014  0.065
```

Lek visit duration: effect of morph, status and female visitation rate (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: VD ~ Mo+Ta1+FVR+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 27675.5  27729.0 -13828.8  27657.5     2789
```

```
Scaled residuals:
    Min      1Q  Median      3Q     Max 
-1.3746 -0.5132 -0.2337  0.1420  9.3676 

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept)   24.35   4.934  
 DS       (Intercept)   78.05   8.834  
 Lek      (Intercept)   18.39   4.288  
 M        (Intercept)    0.00   0.000  
 Residual             1107.09  33.273  
Number of obs: 2798, groups:  ID, 253; DS, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error t value
(Intercept)    4.039      3.250   1.243
MoS           -9.485      2.334  -4.064
Ta1R          18.522      1.904   9.729
FVR          107.761     28.452   3.788

Correlation of Fixed Effects:
     (Intr) MoS    Ta1R  
MoS  -0.136              
Ta1R -0.434  0.021       
FVR  -0.372 -0.003  0.051
```

Variable	Chisq	p
Mo	14.356	0.0001513
Ta1	89.632	< 2.2e-16
FA	25.055	5.572e-07
→ FVR	14.236	0.0001612
DS	67.060	2.634e-16
ID	24.511	7.388e-07
Lek	17.793	2.463e-05
M	0.003	0.9566

Lek visit duration: effect of returning between years (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: VD ~ Mo+FA+T01+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid 
 23131.1  23182.7 -11556.5  23113.1     2293 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-1.4213 -0.5123 -0.2429  0.1345  8.5812 

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept)   41.797  6.465  
 DS       (Intercept)   98.192  9.909  
 Lek      (Intercept)   48.538  6.967  
 M        (Intercept)    1.554  1.247  
 Residual             1284.376 35.838  
Number of obs: 2302, groups:  ID, 54; DS, 33; Lek, 5; M, 2

Fixed effects:
```

```
            Estimate Std. Error t value
(Intercept)  20.9390     4.6347   4.518
MoS         -14.2632     3.4094  -4.183
FA            0.4900     0.1002   4.891
T01Y         -0.4543     2.8153  -0.161

Correlation of Fixed Effects:
     (Intr) MoS    FA
MoS  -0.088
FA   -0.315 -0.021
T01Y -0.408 -0.072  0.012
```

Variable	Chisq	p
Mo	14.219	0.0001628
T01	0.026	0.872
FA	23.207	1.455e-06
DS	71.439	< 2.2e-16
ID	26.053	3.321e-07
Lek	12.294	0.0004543
M	0.261	0.6094

Arrival together with females

Arrival together with females: effect of morph*status (all males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: F01 ~ Mo1*Ta1+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
  1946.3   1993.0   -965.1   1930.3     2545

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.1292 -0.4140 -0.2720 -0.2006  5.3760

Random effects:
 Groups Name        Variance Std.Dev.
 ID     (Intercept) 0.007752 0.08805
 DS     (Intercept) 0.633049 0.79564
 Lek    (Intercept) 0.077131 0.27772
 M      (Intercept) 0.039656 0.19914
Number of obs: 2553, groups:  ID, 256; DS, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -0.6503     0.2680  -2.427  0.01523*
Mo1S          0.0698     0.2615   0.267  0.78952
Ta1R         -1.8099     0.1481 -12.223  < 2e-16 ***
Mo1S:Ta1R     1.0114     0.3090   3.273  0.00106 **

Correlation of Fixed Effects:
          (Intr) Mo1S   Ta1R
Mo1S      -0.199
Ta1R      -0.340  0.321
Mo1S:Ta1R  0.176 -0.836 -0.463
```

Departures together with females

Departure together with females: effect of morph*status (all males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: F01 ~ Mo1*Ta1+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
  1913.8   1960.6   -948.9   1897.8     2578

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.2308 -0.4218 -0.2739 -0.1831  7.0163

Random effects:
 Groups Name        Variance  Std.Dev.
 ID     (Intercept) 2.422e-01 4.921e-01
 DS     (Intercept) 6.079e-01 7.797e-01
 Lek    (Intercept) 1.816e-09 4.261e-05
 M      (Intercept) 1.442e-10 1.201e-05
Number of obs: 2586, groups:  ID, 264; DS, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept)  -0.9876     0.1951  -5.063 4.14e-07 ***
Mo1S         -0.2847     0.2946  -0.966 0.333892
Ta1R         -1.5178     0.1774  -8.556  < 2e-16 ***
Mo1S:Ta1R     1.3960     0.3872   3.605 0.000312 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
          (Intr) Mo1S   Ta1R
Mo1S      -0.285
Ta1R      -0.473  0.298
Mo1S:Ta1R  0.219 -0.742 -0.448
```

Lek attendance: correlates of daily variation in male lek attendance

Daily lek attendance, females present or absent on the lek (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo*F01+Ta*F01+RM*F01+FV*F01+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 11556.1  11633.4  -5763.1  11526.1     1261

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.9638 -0.4837 -0.0287  0.5414  3.4982

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept)  89.720   9.472
 DS       (Intercept)  72.713   8.527
```

```
 Lek      (Intercept)   0.000   0.000
 M        (Intercept)   2.802   1.674
 Residual             414.675  20.364
Number of obs: 1276, groups:  ID, 253; DS, 33; Lek, 5; M, 2

Fixed effects:
             Estimate Std. Error t value
(Intercept)  11.31754    4.53382   2.496
MoS         -10.07758    2.64218  -3.814
F01Y         15.62439    4.62861   3.376
TaR          50.02654    2.09359  23.895
RM           -1.02644    0.57007  -1.801
FV           -0.05853    0.06261  -0.935
MoS:F01Y      1.60727    2.79992   0.574
F01Y:TaR     15.12887    2.30061   6.576
F01Y:RM      -1.12848    0.60112  -1.877
F01Y:FV       0.03644    0.06530   0.558

Correlation of Fixed Effects:
         (Intr) MoS    F01Y   TaR    RM     FV     MS:F01 F01Y:T F01Y:R
MoS      -0.170
F01Y     -0.461  0.065
TaR      -0.187  0.024  0.142
RM       -0.813  0.041  0.421 -0.012
FV       -0.328  0.033  0.214  0.046  0.151
MoS:F01Y  0.062 -0.515 -0.122 -0.002  0.005 -0.008
F01Y:TaR  0.138 -0.005 -0.255 -0.535  0.007 -0.050  0.005
F01Y:RM   0.414  0.004 -0.902  0.011 -0.475 -0.132 -0.010 -0.028
F01Y:FV   0.202 -0.007 -0.453 -0.045 -0.124 -0.504  0.010  0.074  0.294
```

Variable	Chisq	p
Mo	15.173	0.0005073
Ta	658.94	< 2.2e-16
F01	239.34	< 2.2e-16
RM	10.862	0.004379
FV	0.8653	0.6488
→ FVR	1.048	0.5921
F01 : Mo	0.3295	0.566
F01 : RM	3.5135	0.06087
F01 : Ta	42.391	7.472e-11
F01: FV	0.3113	0.5769
→ F01 : FVR	0.7964	0.3722
DS	69.629	< 2.2e-16
ID	131.69	< 2.2e-16
Lek	0	1
M	2.3166	0.128

Daily lek attendance, females present or absent on the lek (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo*F01+Ta*F01+RM.S*F01+FV.S*F01+(1|DS.S)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
 11556.1  11633.4  -5763.1  11526.1     1261

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.9638 -0.4837 -0.0287  0.5414  3.4982

Random effects:
 Groups   Name        Variance  Std.Dev.
 ID       (Intercept) 8.972e+01 9.472e+00
```

```
 DS.S      (Intercept) 7.271e+01 8.527e+00
 Lek       (Intercept) 1.067e-13 3.266e-07
 M         (Intercept) 2.802e+00 1.674e+00
 Residual              4.147e+02 2.036e+01
Number of obs: 1276, groups:  ID, 253; DS.S, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error t value
(Intercept)   3.8660     2.4761   1.561
MoS         -10.0776     2.6422  -3.814
F01Y          8.6787     1.7811   4.873
TaR          50.0265     2.0936  23.895
RM.S         -2.0628     1.1457  -1.801
FV.S         -1.0688     1.1433  -0.935
MoS:F01Y      1.6073     2.7999   0.574
F01Y:TaR     15.1289     2.3006   6.576
F01Y:RM.S    -2.2679     1.2081  -1.877
F01Y:FV.S     0.6655     1.1925   0.558

Correlation of Fixed Effects:
          (Intr) MoS    F01Y   TaR    RM.S   FV.S   MS:F01 F01Y:T F01Y:R
MoS       -0.239
F01Y      -0.357  0.176
TaR       -0.346  0.024  0.374
RM.S       0.067  0.041 -0.012 -0.012
FV.S      -0.059  0.033  0.034  0.046  0.151
MoS:F01Y   0.118 -0.515 -0.334 -0.002  0.005 -0.008
F01Y:TaR   0.247 -0.005 -0.691 -0.535  0.007 -0.050  0.005
F01Y:RM.S  0.000  0.004  0.000  0.011 -0.475 -0.132 -0.010 -0.028
F01Y:FV.S  0.025 -0.007 -0.074 -0.045 -0.124 -0.504  0.010  0.074  0.294
```

Daily lek attendance, females present or absent on the lek (R-males)

T2 and T01 tested in separate models. FVR and FV tested in separate models.

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo*F01+RM*F01+T01*F01+FV*F01+(1|DS)+(1|ID)+(1|Lek)
              +(1|M)

     AIC      BIC   logLik deviance df.resid
  6357.6   6425.5  -3163.8   6327.6      668

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.5055 -0.5318  0.1047  0.6732  2.3132

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 120.677  10.985
 DS       (Intercept) 175.456  13.246
 Lek      (Intercept)  24.944   4.994
 M        (Intercept)   3.428   1.851
 Residual             508.035  22.540
Number of obs: 683, groups:  ID, 54; DS, 33; Lek, 5; M, 2

Fixed effects:
             Estimate Std. Error t value
(Intercept)  65.99203    7.63692   8.641
MoS         -35.09988    5.19303  -6.759
F01Y         30.41413    6.54002   4.650
RM           -2.02771    1.05978  -1.913
T01Y          2.30109    4.34927   0.529
```

```
FV             0.07042    0.10150   0.694
MoS:F01Y       1.89922    4.27455   0.444
F01Y:RM       -2.02549    0.88211  -2.296
F01Y:T01Y      3.55459    3.94628   0.901
F01Y:FV        0.17180    0.09766   1.759

Correlation of Fixed Effects:
          (Intr) MoS    F01Y   RM     T01Y   FV     MS:F01 F01Y:R F01Y:T
MoS       -0.090
F01Y      -0.370  0.021
RM        -0.692 -0.028  0.270
T01Y      -0.359 -0.043  0.169 -0.012
FV         0.004  0.006  0.042 -0.397  0.009
MoS:F01Y   0.018 -0.389 -0.045  0.042 -0.008  0.010
F01Y:RM    0.285  0.036 -0.762 -0.367  0.034  0.124 -0.088
F01Y:T01Y  0.167 -0.010 -0.388  0.019 -0.431 -0.012  0.009 -0.082
F01Y:FV    0.036  0.012 -0.158  0.116 -0.017 -0.429 -0.042 -0.253  0.041
```

Variable	Chisq	p
Mo	32.615	8.273e-08
F01	171.48	< 2.2e-16
RM	13.663	0.001079
T01	1.8394	0.3986
T2	4.858	0.08812
FV	5.4772	0.06466
→ FVR	1.9274	0.3815
F01 : Mo	0.1973	0.6569
F01 : RM	5.2411	0.02206
F01 : T01	0.8104	0.368
F01 : T2	3.429	0.06406
F01 : FV	3.0786	0.07933
→ F01 : FVR	0.6479	0.4209
DS	79.05	< 2.2e-16
ID	58.928	1.636e-14
Lek	1.0298	0.3102
M	0.728	0.3935

Daily lek attendance, females present or absent on the lek (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo*F01+RM.S*F01+T01*F01+FV.S*F01+(1|DS.S)+(1|ID)
              +(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
  6357.6   6425.5  -3163.8   6327.6      668

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.5055 -0.5318  0.1047  0.6732  2.3132

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 120.677  10.985
 DS.S     (Intercept) 175.456  13.246
 Lek      (Intercept)  24.944   4.994
 M        (Intercept)   3.428   1.851
 Residual             508.035  22.540
Number of obs: 683, groups:  ID, 54; DS.S, 33; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error t value
```

```
(Intercept)   54.224      5.093  10.647
MoS          -35.100      5.193  -6.759
F01Y          21.074      3.516   5.994
RM.S          -4.192      2.191  -1.913
T01Y           2.301      4.349   0.529
FV.S           1.327      1.913   0.694
MoS:F01Y       1.899      4.275   0.444
F01Y:RM.S     -4.187      1.823  -2.296
F01Y:T01Y      3.555      3.946   0.901
F01Y:FV.S      3.237      1.840   1.759

Correlation of Fixed Effects:
          (Intr) MoS    F01Y   RM.S   T01Y   FV.S   MS:F01 F01Y:R F01Y:T
MoS       -0.170
F01Y      -0.329  0.107
RM.S       0.153 -0.028 -0.032
T01Y      -0.551 -0.043  0.359 -0.012
FV.S      -0.067  0.006  0.001 -0.397  0.009
MoS:F01Y   0.090 -0.389 -0.258  0.042 -0.008  0.010
F01Y:RM.S -0.020  0.036  0.078 -0.367  0.034  0.124 -0.088
F01Y:T01Y  0.270 -0.010 -0.831  0.019 -0.431 -0.012  0.009 -0.082
F01Y:FV.S  0.010  0.012 -0.055  0.116 -0.017 -0.429 -0.042 -0.253  0.041
```

Lek attendance: correlates of seasonal lek attendance

Seasonal lek attendance in the presence or absence of females (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo2*F01+Ta2*F01+RM*F01+PFA*F01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid
  3896.6   3952.0  -1935.3   3870.6      511

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.1937 -0.1786  0.0002  0.1416  4.8632

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 95.75    9.785
 Lek      (Intercept)  0.00    0.000
 Residual             41.00    6.403
Number of obs: 524, groups:  ID, 247; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)  1.84346    2.63352   0.700
Mo2S        -3.08049    1.76480  -1.746
F01Y         6.15220    2.40899   2.554
Ta2R        27.26893    1.60230  17.019
RM           0.18020    0.47892   0.376
PFA         -0.07940    0.08571  -0.926
Mo2S:F01Y   -0.24671    1.32040  -0.187
F01Y:Ta2R   16.57149    1.36399  12.149
F01Y:RM     -0.47681    0.46932  -1.016
F01Y:PFA    -0.11831    0.06696  -1.767
```

```
Correlation of Fixed Effects:
          (Intr) Mo2S   F01Y   Ta2R   RM     PFA    M2S:F0 F01Y:T F01Y:R
Mo2S      -0.203
F01Y      -0.457  0.066
Ta2R      -0.143  0.056  0.036
RM        -0.656  0.008  0.376  0.080
PFA       -0.339  0.047  0.083 -0.094 -0.413
Mo2S:F01Y  0.080 -0.374 -0.175 -0.021 -0.004 -0.019
F01Y:Ta2R  0.038 -0.018 -0.084 -0.426 -0.005  0.035  0.049
F01Y:RM    0.351 -0.003 -0.766 -0.005 -0.490  0.158  0.009  0.011
F01Y:PFA   0.097 -0.018 -0.213  0.038  0.198 -0.391  0.049 -0.090 -0.404
```

Variable	Chisq	p
Mo2	3.8351	0.147
Ta2	463.38	< 2.2e-16
F01	160.26	< 2.2e-16
RM	1.0494	0.5917
PFA	6.1695	0.04574
F01 : Mo2	0.0349	0.8518
F01 : Ta2	114.18	< 2.2e-16
F01 : RM	1.0303	0.3101
F01 : PFA	3.1045	0.07808
ID	198.02	< 2.2e-16
Lek	0	1

Seasonal lek attendance in the presence or absence of females (all males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo2*F01+Ta2*F01+RM.S*F01+PFA.S*F01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid
  3896.6   3952.0  -1935.3   3870.6      511

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.1937 -0.1786  0.0002  0.1416  4.8632

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 95.75    9.785
 Lek      (Intercept)  0.00    0.000
 Residual             41.00    6.403
Number of obs: 524, groups:  ID, 247; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)   0.9911     0.9149   1.083
Mo2S         -3.0805     1.7648  -1.746
F01Y          0.9904     0.7125   1.390
Ta2R         27.2689     1.6023  17.019
RM.S          0.2352     0.6251   0.376
PFA.S        -0.7303     0.7883  -0.926
Mo2S:F01Y    -0.2467     1.3204  -0.187
F01Y:Ta2R    16.5715     1.3640  12.149
F01Y:RM.S    -0.6224     0.6126  -1.016
F01Y:PFA.S   -1.0882     0.6159  -1.767

Correlation of Fixed Effects:
          (Intr) Mo2S   F01Y   Ta2R   RM.S   PFA.S  M2S:F0 F01Y:T F01Y:R
Mo2S      -0.462
F01Y      -0.389  0.172
Ta2R      -0.391  0.056  0.186
```

```
RM.S        -0.029  0.008  0.004  0.080
PFA.S        0.010  0.047 -0.006 -0.094 -0.413
Mo2S:F01Y    0.179 -0.374 -0.459 -0.021 -0.004 -0.019
F01Y:Ta2R    0.170 -0.018 -0.438 -0.426 -0.005  0.035  0.049
F01Y:RM.S    0.003 -0.003 -0.008 -0.005 -0.490  0.158  0.009  0.011
F01Y:PFA.S -0.006 -0.018  0.016  0.038  0.198 -0.391  0.049 -0.090 -0.404
```

Seasonal lek attendance in the presence or absence of females, effect of lek tenure and returning tested in separate models (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo2*F01+T2*F01+RM*F01+PFA*F01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid
   936.0    971.5   -455.0    910.0      101

Scaled residuals:
     Min       1Q   Median       3Q      Max
-2.08586 -0.51499 -0.03961  0.50223  2.19937

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 167.67   12.949
 Lek      (Intercept)   0.00    0.000
 Residual              75.74    8.703
Number of obs: 114, groups:  ID, 54; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)   7.6859     8.2749   0.929
Mo2S        -18.9477     5.6002  -3.383
F01Y         22.0534     7.4053   2.978
T2            1.4101     0.2132   6.613
RM            0.1793     1.3304   0.135
PFA          -0.1149     0.2420  -0.475
Mo2S:F01Y     0.3151     4.1413   0.076
F01Y:T2       0.7808     0.1673   4.667
F01Y:RM      -1.8100     1.3028  -1.389
F01Y:PFA     -0.3625     0.1919  -1.889

Correlation of Fixed Effects:
          (Intr) Mo2S   F01Y   T2     RM     PFA    M2S:F0 F01Y:T F01Y:R
Mo2S      -0.140
F01Y      -0.447  0.052
T2        -0.413 -0.049  0.136
RM        -0.485  0.013  0.307 -0.178
PFA       -0.451  0.047  0.136  0.170 -0.403
Mo2S:F01Y  0.063 -0.370 -0.141  0.008 -0.002 -0.023
F01Y:T2    0.156  0.007 -0.348 -0.392  0.079 -0.068 -0.020
F01Y:RM    0.281 -0.001 -0.627  0.063 -0.490  0.153  0.004 -0.160
F01Y:PFA   0.154 -0.022 -0.343 -0.067  0.189 -0.396  0.059  0.171 -0.385
```

Variable	Chisq	p
Mo2	11.66	0.002925
F01	74.199	1.367e-14
T2	69.676	7.415e-16
→ T01	24.275	5.355e-06
RM	2.2926	0.3178
PFA	5.2121	0.07382
F01 : Mo2	0.0058	0.9393

F01 : T2	18.604	1.609e-05
→ F01 : T01	12.227	0.000471
F01 : RM	1.8997	0.1681
F01 : PFA	3.4682	0.06256
ID	42.291	7.867e-11
Lek	0	1

Seasonal lek attendance in the presence or absence of females, effect of lek tenure (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo2*F01+T2.S*F01+RM.S*F01+PFA.S*F01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid 
   936.0    971.5   -455.0    910.0      101 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-2.08586 -0.51499 -0.03961  0.50223  2.19937 

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 167.67   12.949  
 Lek      (Intercept)   0.00    0.000  
 Residual              75.74    8.703  
Number of obs: 114, groups:  ID, 54; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)  30.3142     2.3211  13.061
Mo2S        -18.9477     5.6002  -3.383
F01Y         17.2190     1.8155   9.484
T2.S         14.0902     2.1307   6.613
RM.S          0.2456     1.8222   0.135
PFA.S        -1.0726     2.2594  -0.475
Mo2S:F01Y     0.3151     4.1413   0.076
F01Y:T2.S     7.8017     1.6715   4.667
F01Y:RM.S    -2.4790     1.7845  -1.389
F01Y:PFA.S   -3.3843     1.7912  -1.889

Correlation of Fixed Effects:
           (Intr) Mo2S   F01Y   T2.S   RM.S   PFA.S  M2S:F0 F01Y:T F01Y:R
Mo2S       -0.417                                                        
F01Y       -0.391  0.163                                                 
T2.S        0.013 -0.049 -0.003                                          
RM.S        0.003  0.013  0.001 -0.178                                   
PFA.S      -0.030  0.047  0.010  0.170 -0.403                            
Mo2S:F01Y   0.172 -0.370 -0.440  0.008 -0.002 -0.023                     
F01Y:T2.S  -0.003  0.007  0.009 -0.392  0.079 -0.068 -0.020              
F01Y:RM.S   0.001 -0.001 -0.002  0.063 -0.490  0.153  0.004 -0.160       
F01Y:PFA.S  0.010 -0.022 -0.026 -0.067  0.189 -0.396  0.059  0.171 -0.385
```

Seasonal lek attendance in the presence or absence of females, effect of returning (R-males)

```
Linear mixed model fit by maximum likelihood  ['lmerMod']
Formula: PA ~ Mo2*F01+T01*F01+RM.S*F01+PFA.S*F01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid 
   981.4   1016.9   -477.7    955.4      101 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
```

```
-2.10345 -0.50650  0.02605  0.45462  1.91737

Random effects:
 Groups   Name        Variance Std.Dev.
 ID       (Intercept) 363.32   19.061
 Lek      (Intercept)   0.00    0.000
 Residual              87.12    9.334
Number of obs: 114, groups:  ID, 54; Lek, 5

Fixed effects:
            Estimate Std. Error t value
(Intercept)   21.237      4.597   4.620
Mo2S         -18.186      7.692  -2.364
F01Y          10.187      2.792   3.649
T01Y          15.758      5.996   2.628
RM.S           1.683      2.159   0.780
PFA.S         -2.118      3.079  -0.688
Mo2S:F01Y     -0.365      4.451  -0.082
F01Y:T01Y     12.760      3.669   3.478
F01Y:RM.S     -2.803      1.948  -1.438
F01Y:PFA.S    -3.464      1.932  -1.793

Correlation of Fixed Effects:
           (Intr) Mo2S   F01Y   T01Y   RM.S   PFA.S  M2S:F0 F01Y:T F01Y:R
Mo2S       -0.228
F01Y       -0.304  0.074
T01Y       -0.726 -0.077  0.219
RM.S        0.149  0.016 -0.079 -0.198
PFA.S      -0.161  0.040  0.051  0.191 -0.426
Mo2S:F01Y   0.078 -0.289 -0.257  0.021 -0.008 -0.015
F01Y:T01Y   0.218  0.020 -0.717 -0.306  0.111 -0.063 -0.069
F01Y:RM.S  -0.053 -0.005  0.175  0.075 -0.451  0.125  0.017 -0.245
F01Y:PFA.S  0.049 -0.014 -0.163 -0.061  0.180 -0.314  0.048  0.201 -0.398
```

Copulations: correlates of daily copulation success

Daily copulation success, effect of attendance and lek size (all males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: B01 ~ PA.S+RM.S+(1|DS.S)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
   287.7    315.6   -136.9    273.7      387

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.1347 -0.3391 -0.1922 -0.1720  4.6370

Random effects:
 Groups Name        Variance Std.Dev.
 ID     (Intercept) 0.12144  0.3485
 DS.S   (Intercept) 0.05544  0.2355
 Lek    (Intercept) 0.00000  0.0000
 M      (Intercept) 0.02340  0.1530
Number of obs: 394, groups:  ID, 178; DS.S, 23; Lek, 5; M, 2
```

```
Fixed effects:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept) -2.26335    0.30298  -7.470 8.01e-14 ***
PA.S         1.29231    0.19027   6.792 1.11e-11 ***
RM.S         0.06482    0.17181   0.377    0.706    

Correlation of Fixed Effects:
     (Intr) PA.S  
PA.S -0.623       
RM.S -0.031 -0.013
```

Daily copulation success, effect of morph and lek size (all males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: B01 ~ Mo+RM.S+(1|DS.S)+(1|ID)+(1|Lek)+(1|M)
Control: glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 2e+05))

     AIC      BIC   logLik deviance df.resid 
   348.9    376.7   -167.4    334.9      387 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-0.8565 -0.3259 -0.2313 -0.2029  3.1999 

Random effects:
 Groups Name        Variance Std.Dev.
 ID     (Intercept) 2.38810  1.5453  
 DS.S   (Intercept) 0.04558  0.2135  
 Lek    (Intercept) 0.00000  0.0000  
 M      (Intercept) 0.00000  0.0000  
Number of obs: 394, groups:  ID, 178; DS.S, 23; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept) -2.76766    0.67707  -4.088 4.36e-05 ***
MoS         -0.01313    0.57155  -0.023    0.982    
RM.S         0.10195    0.20076   0.508    0.612    

Correlation of Fixed Effects:
     (Intr) MoS  
MoS  -0.296      
RM.S -0.013  0.026
```

Daily copulation success, effect of attendance, lek size and returning (R-males)

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: B01 ~ PA.S+RM.S+T01+(1|DS.S)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid 
   258.5    285.1   -121.2    242.5      199 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-1.0427 -0.7218 -0.5023  1.1127  2.2479 

Random effects:
 Groups Name        Variance  Std.Dev.
```

```
 ID     (Intercept) 0.000e+00 0.000e+00
 DS.S   (Intercept) 1.568e-10 1.252e-05
 Lek    (Intercept) 0.000e+00 0.000e+00
 M      (Intercept) 2.205e-02 1.485e-01
Number of obs: 207, groups:  ID, 48; DS.S, 23; Lek, 5; M, 2

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.44253    0.37980  -3.798 0.000146 ***
PA.S         0.51511    0.17716   2.908 0.003643 **
RM.S        -0.02073    0.16180  -0.128 0.898062
T01Y         0.75210    0.40253   1.868 0.061700 .

Correlation of Fixed Effects:
     (Intr) PA.S   RM.S
PA.S -0.176
RM.S  0.122  0.042
T01Y -0.862  0.082 -0.163
```

Daily copulation success, effect of attendance, morph, lek size and returning (R-males). Used to predict values for Fig. 5a.

```
Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: binomial  ( logit )
Formula: B02 ~ PA+Mo1+RM+T01+(1|DS)+(1|ID)+(1|Lek)+(1|M)

     AIC      BIC   logLik deviance df.resid
   259.2    289.2   -120.6    241.2      198

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.1149 -0.7188 -0.4798  1.1087  2.4103

Random effects:
 Groups Name        Variance  Std.Dev.
 ID     (Intercept) 4.814e-09 6.938e-05
 DS     (Intercept) 0.000e+00 0.000e+00
 Lek    (Intercept) 2.801e-10 1.674e-05
 M      (Intercept) 3.906e-02 1.976e-01
Number of obs: 207, groups:  ID, 48; DS, 23; Lek, 5; M, 2

Fixed effects:
             Estimate Std. Error z value Pr(>|z|)
(Intercept) -2.785684   0.917281  -3.037  0.00239 **
PA           0.021116   0.006992   3.020  0.00253 **
MoS          0.526900   0.465743   1.131  0.25792
RM          -0.012566   0.087131  -0.144  0.88533
T01Y         0.778837   0.404107   1.927  0.05394 .

Correlation of Fixed Effects:
     (Intr) PA     MoS    RM
PA   -0.632
MoS  -0.416  0.573
RM   -0.664  0.027 -0.015
T01Y -0.306  0.103  0.067 -0.155
```

Copulations: correlates of seasonal copulation success

Seasonal copulation success, effect of attendance, morph, returning and lek size (R-males)

```
> ss <- getME(RMAS1,c("theta","fixef"))
> RMAS2 <- update(RMAS1,start=ss)

Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: Negative Binomial(365.3706)  ( log )
Formula: BN ~ PA2.S*Mo2+RM.S+T01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid 
   185.0    202.0    -83.5    167.0       40 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-1.2978 -0.5041 -0.1090  0.2353  1.2671 

Random effects:
 Groups Name        Variance  Std.Dev. 
 ID     (Intercept) 7.417e-01 0.8612128
 Lek    (Intercept) 1.328e-08 0.0001152
Number of obs: 49, groups:  ID, 46; Lek, 4

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept)  -0.3249     0.3966  -0.819    0.413    
PA2.S         1.1623     0.2454   4.737 2.17e-06 ***
Mo2S          0.7023     0.5947   1.181    0.238    
RM.S          0.1440     0.1878   0.767    0.443    
T01Y          0.3447     0.4498   0.766    0.443    
PA2.S:Mo2S    0.0119     0.6816   0.017    0.986    

Correlation of Fixed Effects:
           (Intr) PA2.S  Mo2S   RM.S   T01Y  
PA2.S      -0.282                            
Mo2S       -0.212  0.331                     
RM.S        0.104  0.112 -0.048              
T01Y       -0.663 -0.293 -0.174 -0.270       
PA2.S:Mo2S  0.162 -0.334  0.264 -0.200  0.023
```

Seasonal copulation success, effect of attendance, morph, returning and lek size. Model without interaction term (R-males). Model used to predict values in Fig. 5b.

```
> ss <- getME(RMAC1,c("theta","fixef"))
> RMAC2 <- update(RMAC1,start=ss)

Generalized linear mixed model fit by maximum likelihood (Laplace
  Approximation) [glmerMod]
 Family: Negative Binomial(365.6801)  ( log )
Formula: BN ~ PA2+Mo2+RM+T01+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid 
   183.0    198.1    -83.5    167.0       41 

Scaled residuals: 
    Min      1Q  Median      3Q     Max 
-1.2975 -0.5033 -0.1087  0.2358  1.2676 

Random effects:
 Groups Name        Variance  Std.Dev. 
 ID     (Intercept) 7.425e-01 0.8616698
 Lek    (Intercept) 1.933e-10 0.0000139
```

```
Number of obs: 49, groups:  ID, 46; Lek, 4

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept) -2.49652    0.89726  -2.782   0.0054 ** 
PA2          0.05300    0.01054   5.029 4.93e-07 ***
Mo2S         0.69956    0.57362   1.220   0.2226    
RM           0.10586    0.13465   0.786   0.4318    
T01Y         0.34451    0.44984   0.766   0.4438    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
     (Intr) PA2    Mo2S   RM    
PA2  -0.499                     
Mo2S -0.283  0.461              
RM   -0.783  0.050  0.005       
T01Y  0.036 -0.303 -0.187 -0.271
```

Seasonal proportion of copulations observed, effect of number of copulations expected (all males at least once present at a female copulation visit). Model used to predict values Fig. 6b.

```
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: Negative Binomial(445.1277)  ( log )
Formula: PBO ~ PBE*Mo2+(1|ID)+(1|Lek)

     AIC      BIC   logLik deviance df.resid 
   278.5    295.6   -132.3    264.5       77 

Scaled residuals: 
     Min       1Q   Median       3Q      Max 
-1.01878 -0.25353 -0.18388 -0.03368  1.56473 

Random effects:
 Groups Name        Variance Std.Dev. 
 ID     (Intercept) 3.26e+00 1.805e+00
 Lek    (Intercept) 2.61e-10 1.616e-05
Number of obs: 84, groups:  ID, 80; Lek, 4

Fixed effects:
            Estimate Std. Error z value Pr(>|z|)    
(Intercept) -3.54433    0.75599  -4.688 2.75e-06 ***
PBE          0.40249    0.05911   6.810 9.79e-12 ***
Mo2S         0.97618    1.13344   0.861    0.389    
PBE:Mo2S     0.06325    0.16625   0.380    0.704    

Correlation of Fixed Effects:
         (Intr) PBE    Mo2S  
PBE      -0.865              
```