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Female choice selects for lifetime lekking performance in black grouse males

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'Good genes' models assume that females can use a signal such as mating effort to assess a male's lifetime fitness. Inferring long-term performance from short-term behavioural observations can be unreliable, and repeated sampling may be needed for more accurate assessment of males. Additionally, if sexual advertisement is viewed as a life-history trait subject to trade-offs, reliable comparison of mates should yield information on all life-history components rather than on one trait value in one season. We show that in the lekking black grouse (*Tetrao tetrix*), a male's success is best explained by assuming that females are informed of the past history of males up to the beginning of the study (eight years). Much of this extremely lasting 'memory' can be attributed to females observing long-term outcomes of male–male competition: current territory position is the only momentarily observable variable that has high power in predicting female choice, and it correlates to a male's past lekking effort on a cumulative lifetime scale. We conclude that females can use territory position as a signal that conveys information of a male's lifetime performance that combines lekking effort and longevity. Females may thus overcome the problem of male allocations varying in time, without the need to pay costs associated with repeated sampling.

Keywords: honest signalling; female choice; male–male competition; long-term benefits

1. INTRODUCTION

To be reliable, female choice should rely on honest cues of male qualities. Honesty, in the form of 'strategic handicaps', requires that the optimum balance of costs and benefits ranks males according to their qualities (Nur & Hasson 1984; Grafen 1990). However, the theory of honest signalling (Grafen 1990; Bradbury & Vehrencamp 1998) guarantees stronger signals for better males only in cases of fixed effort for each quality. Females may thus encounter several problems when assessing male advertisement. Error-prone assessment may render honesty to hold 'on average' only (Johnstone & Grafen 1992, 1993). Reliability also becomes more problematic if females can only observe the momentary effort of males, which males may adjust according to life-history trade-offs (Lotem 1993; Kokko 1997) and current mating opportunities (Wiley 1991). Traits whose appearance can be changed according to short-term benefits are especially prone to be unreliable if time available for assessing them is short; this suggests greater reliability of fixed morphological as compared with behavioural characters (Sullivan 1994*a*; Møller *et al.* 1998).

If behaviour is to be used as a cue, repeated sampling, where the final score of a male consists of a cumulative 'memory' of his past performance, should improve the discriminatory abilities of females (Sullivan 1990; Hutchinson *et al.* 1993; Luttbeg 1996). Such sampling should not impose too high costs on females, lest the costs of choice exceed its benefits (which are supposed to be meagre if they are restricted to genetic benefits; Andersson 1994; Kirkpatrick & Barton 1997). Even then, it must be recognized that behavioural traits should be viewed in the context of the whole life history of a male (Höglund & Sheldon 1998; Svensson & Sheldon 1998), and it is then not guaranteed that observing one component of a male's life history, e.g. mating effort in one spring, will reflect his overall fitness (Kokko 1997; Promislow *et al.* 1998).

Yet, a meta-analysis of mating success in lekking species (Fiske *et al.* 1998), where direct benefits are scarcely documented, suggests a somewhat greater role for behavioural variables, especially attendance on the lek, than for morphological traits. The black grouse *Tetrao tetrix* is a lekking species where females spend less than an hour on the lek before mating (Rintamäki *et al.* 1995), and behavioural and spatial characters of males seem more important in explaining male mating success than morphological characters (Höglund & Alatalo 1995; Hovi *et al.* 1995; Höglund *et al.* 1997). In this paper we provide evidence that black grouse females can partially overcome the difficulty of gaining long-term information of the life histories of males by setting up a competitive environment that consistently favours males with the most persistent lekking effort over long time-scales. Thus, the reliability of behaviour as an indicator of male quality can be upheld, as it is effectively measured continuously over the whole

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lifetime of the male, and successful males combine high effort with longevity.

2. MATERIAL AND METHODS

A black grouse lek was observed annually from 1990 to 1997 near Petäjävesi, central Finland, during the peak mating season in late April and early May (see Rintamäki *et al.* (1995) for more details on sampling and study site). Detailed behavioural observations were made during a total of 160 h on 84 days. The attendance and behaviour of colour-ringed males was recorded at frequent intervals (median 5 min, range 1–66 min), and classified into activity levels 0 (present but activity unrecorded; less than 5% of the observations), 1 (being passive: preening etc.), 2 (advertisement, such as rookooing), and 3 (fighting). Classes 2 and 3 together are analysed as being active. The unrecorded class 0 was used in counts of males' attendance and territory position but excluded from analyses of other behavioural variables.

Since the observation procedure was not primarily developed for equal-length-scheduling, the recording intervals could not be forced to be equal in length. However, 80% of the intervals were shorter than 10 min, and 93% less than 20 min. Male positions were recorded to the accuracy of 1 m with the aid of a 10 m × 10 m grid system marked with sticks, and the current lek centre was defined as the median of x- and y-coordinates of currently attending males. The definition of the current lek centre was hence constantly updated; this is to make the definition correspond to a momentary assessment that a newly arrived female could tell about the relative positions of males.

To investigate the determinants of momentary success, we calculated the number of copulations per hour for each male, corrected for the attendance time of that particular male, and related this to the overall attendance and activity of the male. To disentangle cause and effect between copulatory success and activity, we also related the success of each copulating male to a cumulative sum of his past behaviour relative to that of other males that were present at the time of the copulation, optionally also giving more weight to recent behaviour (which leads to assuming that the 'memory' of the lekking system as a determinant of male mating success decays with time). If several females copulated with a male during the same recording, these were counted as one copulation, to provide conservative estimates in the possible presence of female copying (Höglund *et al.* 1990, 1995).

Six behavioural variables were measured: attendance time, time spent active, time spent fighting, proportions of attendance time spent active and fighting, and distance to the current lek centre, during the previous T h (T ranging from 0.01 h to 10^5 h) immediately preceding the copulation. In the analyses, each result was confirmed in two ways: either each observation was weighted by the interval length it represents, or each time-point was counted as a single observation, thus unweighted in any way. As an example, if a male was recorded active once during a 4 min recording interval and passive once during a 3 min interval, its activity proportion would equal $4/(4+3) = 0.57$ of the total observation time in the weighted alternative, and $1/2 = 0.5$ in the unweighted one. We present weighted results here; conclusions drawn from the unweighted alternative do not show any qualitative differences.

Additionally, if memory decay was used, each behavioural action was weighted by $\exp(-dt)$, where t is the time elapsed (in hours) between the action and the time of the copulation, and the parameter d scales the memory decay rate. Using the above example, the activity proportion $4/(4+3) = 0.57$ reduces to $4 \times \exp(-0.01 \times 48)/(4 \times \exp(-0.01 \times 48)+3) = 0.45$ if memory decay $d = 0.01\,\mathrm{h}^{-1}$ is assumed, and the active fraction of the behaviour occurred 48 h ago while the passive observation was made immediately before the copulation. Setting $d = 0$ indicates no decay, where all past male actions are assumed equally important as predictors of current female choice.

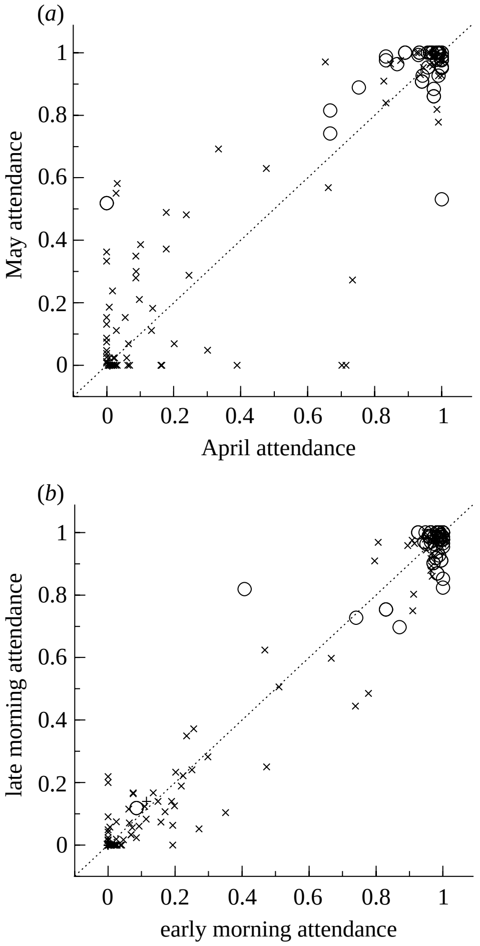

Figure 1. Average attendance of individual black grouse males within one mating season, divided into (*a*) early and late season, or (*b*) early and late morning. Late morning is defined to start 1 h before sunrise, which divides the data roughly into two halves. Crosses denote males that were unsuccessful in this season, open circles successful males. In the pooled data for all years, $r_s = 0.78$ and 0.91 for (*a*) and (*b*), respectively ($p < 0.001$ for both); see table 1 for correlations in individual years.

Predictive power was measured as the proportion of copulations of a male whose behaviour value exceeded (or in case of distance to lek centre, fell below) the median of males that were present on the lek at the time of the copulation. The expected power equals 0.5 if success is random with respect to that variable.

3. RESULTS

Within a mating season, males had very constant performance in time. Dividing the data into early and late halves, both within the mating season (April versus May) and within days (up to 1 h before sunrise versus thereafter), reveals the constancy of behaviour in high- and low-performing males regarding attendance, activity and fight scores (figure 1, table 1). The data show that

Table 1. *Spearman's rank correlations between male behavioural variables in different parts of the same mating season*
($^{*}p<0.05$, $^{**}p<0.01$.)

	1990	1991	1992	1993	1994	1995	1996	1997
April versus May (April data not available for 1996)								
attendance	0.84^{**}	0.89^{**}	0.82^{**}	0.84^{**}	0.74^{**}	0.73^{**}	—	0.73^{*}
fight time	0.83^{**}	0.88^{**}	0.90^{**}	0.61^{*}	0.49	0.28	—	0.65^{*}
activity time	0.77^{**}	0.87^{**}	0.74^{**}	0.13	0.52^{*}	0.13	—	0.86^{**}
fight proportion	0.59^{**}	0.89^{**}	0.85^{**}	0.56	0.33	0.48	—	−0.09
activity proportion	0.37	0.80^{**}	0.61^{*}	0.15	0.23	0.10	—	0.92^{**}
early morning versus late morning								
attendance	0.86^{**}	0.92^{**}	0.90^{**}	0.80^{**}	0.90^{**}	0.85^{**}	0.87^{**}	0.69^{*}
fight time	0.95^{**}	0.96^{**}	0.91^{**}	0.72^{*}	0.66^{**}	0.52	0.57	0.94^{**}
activity time	0.90^{**}	0.90^{**}	0.86^{**}	0.80^{**}	0.72^{**}	0.58^{*}	0.02	0.93^{**}
fight proportion	0.64^{**}	0.91^{**}	0.61^{**}	0.53^{*}	0.37	0.58^{*}	0.61	0.90^{**}
activity proportion	0.61^{**}	0.69^{**}	0.37	0.37	0.01	0.42	0.60	0.94^{**}

Table 2. *Spearman's correlation between number of copulations per hour within a season (i.e. success corrected for attendance time), and the arrival (start) and departure (stop) times of individual males*

($^{*}p<0.05$; $^{**}p<0.01$. Daily start and stop times are defined as average timing (hours + minutes/60) of the first and last observation of the male on each morning when it was present. Timings of first and last observations are recorded on a continuous time-scale within a season, i.e. a male whose first recording is late within a morning is recorded as being earlier than a male that appears early but on the next morning. Successful males tend to be more enduring, implied by a negative correlation between success and start time, and a positive correlation between success and stop time. However, the former effect appears far more consistent than the latter.)

	1990	1991	1992	1993	1994	1995	1996	1997
average daily start	-0.78^{**}	-0.48^{*}	−0.22	-0.73^{**}	-0.53^{**}	−0.42	−0.55	−0.49
average daily stop	0.62^{**}	0.54^{**}	0.41^{*}	−0.02	0.21	0.27	0.00	0.38
time of first observation	-0.79^{**}	-0.55^{**}	-0.85^{**}	−0.45	−0.24	-0.49^{*}	−0.42	−0.40
time of last observation	0.26	−0.01	−0.36	0.34	0.00	0.27	0.13	0.13

early arrival on the lek, both within days and on the time-scale of the whole mating season, is strongly associated with success, while the association of success and late departure is somewhat less clear (table 2).

Males that were active whenever they were present on the lek, but did not score high in terms of attendance, had no success even when correcting for their attendance time (figure 2). Hence, momentary behaviour does not suffice to explain momentary mating success. However, variation in attendance alone does not explain success either: males with below-average activity were not successful, regardless of their attendance. Successful males thus combined above-average attendance with high average activity levels when present (figure 2).

The pattern in figure 2 could be generated if high success is a cause for subsequent high effort (Bartoš & Losos 1997; Dyson *et al.* 1998), and not vice versa. However, the analysis of past effort up to the time-point of each occurring copulation confirms the causality: accumulated past effort predicts current success in the black grouse (figure 3). We sought for the best predictive power of mate choice through behavioural variables, among assumptions that females know the last T h of male behaviour (range $T=0.01$ to 10^5 h), and that the importance of past male interactions decays with a rate d (range $d=0.0001\,\text{h}^{-1}$ to $10^0\,\text{h}^{-1}$ in addition to $d=0$). The actions of a male immediately preceding the

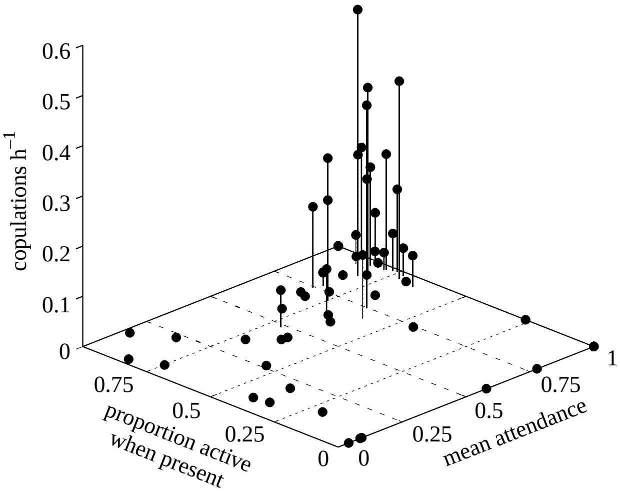

Figure 2. Average success per unit time spent on lek for all males that were seen at least twice on the lek, plotted against mean attendance (attendance time/total observation time between the first and last sighting of the male) and the proportion of time that the male was active during behavioural observations made when the male was present. Attendance and activity are positively correlated ($r_s=0.31$, two-tailed $p=0.0138$), and successful males have larger values for both variables than unsuccessful males (Wilcoxon ranked-sum test, $p<0.001$ in both cases).

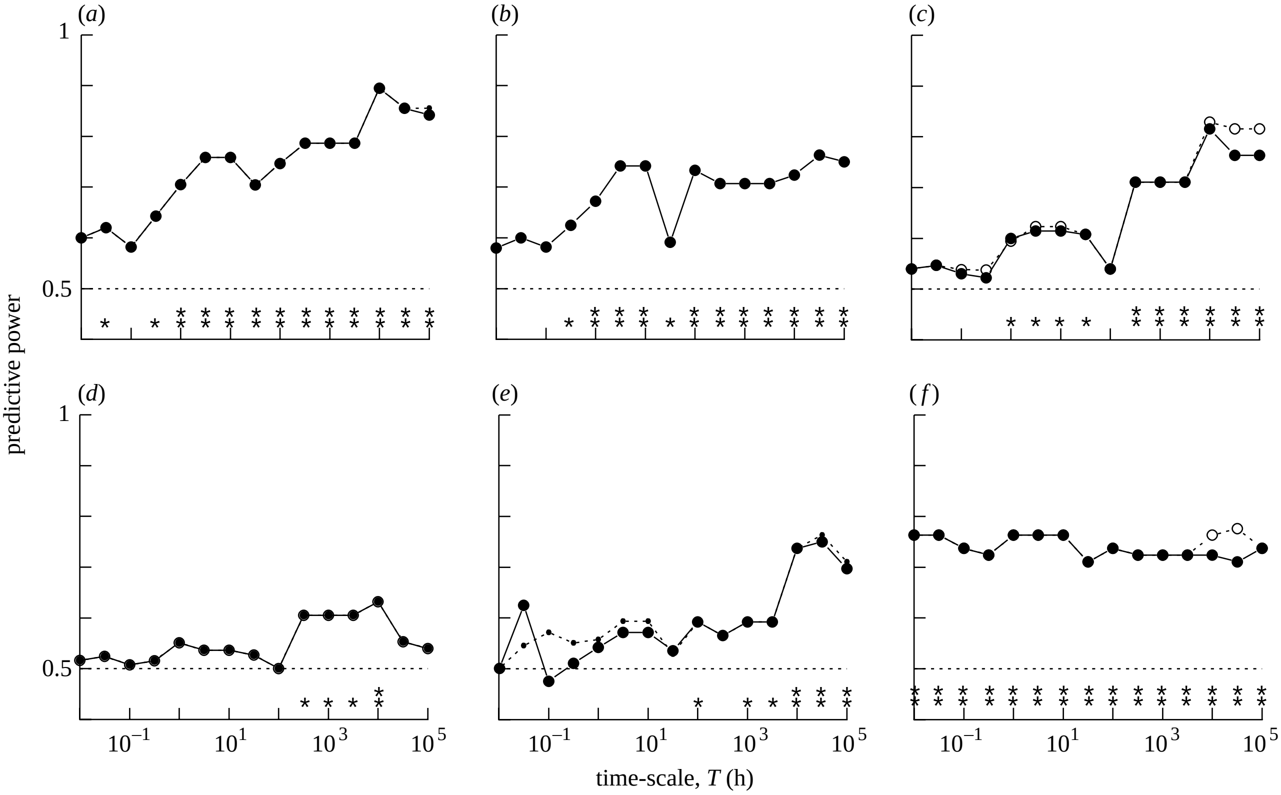

Figure 3. Power (see §2 for definition) of six cumulative variables of past behaviour in predicting female choice, calculated with the assumption that females know past behaviour of the male from $T = 0.01$h up to the past 10^5 h preceding the copulation. (*a*) Fight time, (*b*) fight proportion, (*c*) activity time, (*d*) activity proportion, (*e*) attendance, and (*f*) distance to lek centre. Data exclude time-points where there is no variation among attending males regarding the explanatory variable. Solid dots give predictive power with no memory decay ($d=0$), and the best alternative with $d>0$ is given as small dots ($d=0.0001$) or open dots ($d=0.001$) in cases where $d>0$ improved the prediction. Significance is indicated for each T ($^*p<0.05$, $^{**}p<0.01$); these do not differ between $d=0$, and $d>0$, where $d>0$ is included. Explaining current success requires considering long time-spans (large T) for all variables except territory proximity to lek centre (*f*).

copulation ($T<1$ h) turn out to be relatively unimportant and explain current mating success only weakly (figure 3). Instead, predicting each copulation becomes most reliable by assuming that male success depends on extremely long time-spans of past male behaviour ($T=10^4$ to 10^5 h, where 10^4 h covers the whole current and the previous mating season, and 10^5 h the whole study length of eight years, exceeding the typical male lifespan), and that memory decay of the system is very weak ($d=0.0001$ to $0.001\,\mathrm{h}^{-1}$) or does not exist ($d=0\,\mathrm{h}^{-1}$). With $d=0$, any previous action is remembered infinitely long and contributes to a male's current success equally strongly as his current behaviour. With $d=0.0001\,\mathrm{h}^{-1}$ (or $0.001\,\mathrm{h}^{-1}$), actions performed in the previous mating season still count $\exp(-d\times24\times365)=92\%$ (or 41%) as important as an action performed immediately preceding the copulation, and actions two years ago have still retained 84% (or 17%) of their importance.

The superior predictive ability of the assumption of long-lasting memory holds for five of the six variables studied: the male's cumulative time spent fighting, proportion of attendance time spent fighting, cumulative time spent active (advertising or fighting), proportion of attendance time spent active, and cumulative attendance time on the lek. The sixth variable, distance of the male to the current lek centre, deviates from this pattern as it succeeds in predicting male success already when observed only momentarily, and assuming that past territory positions play a role does not improve the prediction (figure 3*f*).

Thus, females behave as if they used long-term memory for mate assessment. Since females do not, however, spend sufficient time on the lek to have complete direct records of long-term male behaviour (Rintamäki *et al.* 1995) but can observe current territory location with ease, we investigated if the distance of the male relative to the current lek centre can serve as a cue summing up a male's past behaviour. Current centrality is related to current activity, but much more strongly to past long-term activity. For all variables except the proportional time spent active, the correlation between the males' long-term accumulated behaviour and current distance to lek centre has a significantly more negative distribution than the momentary correlation between the males' current behaviour and distance to centre (figure 4). A long history of attendance improves a male's current position (figure 4*e*), especially if the cumulative fight time has been long (figure 4*a*), but proportional fight time also contributes to current position (figure 4*b*).

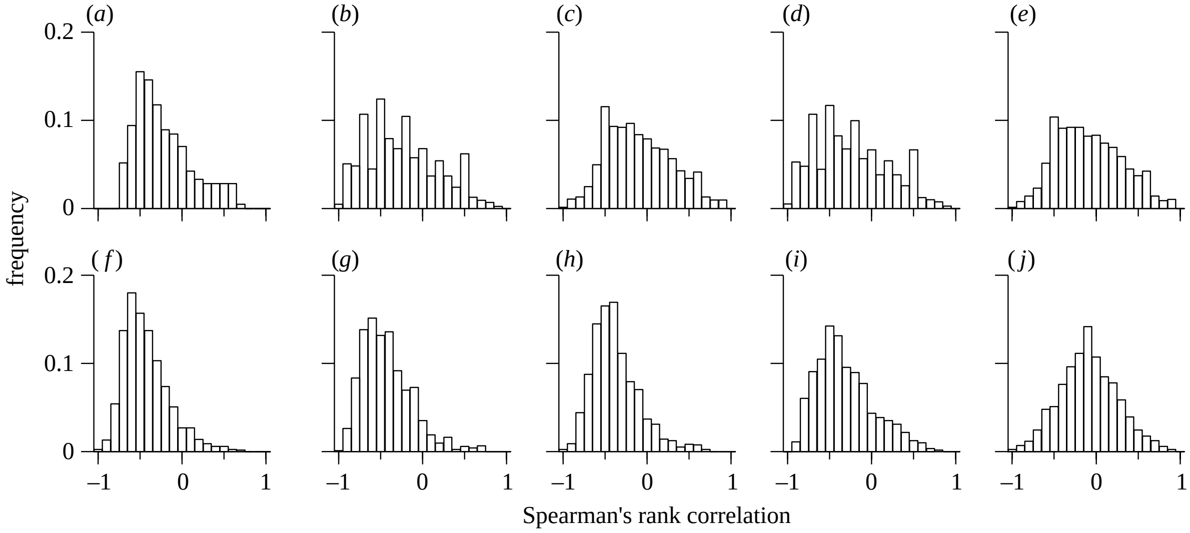

Figure 4. Correlation of past behavioural variables in generating current territory position. (*a*, *f*) Attendance, (*b*, *g*) fight time, (*c*, *h*) activity time, (*d*, *i*) fight proportion, and (*e*, *j*) activity proportion. The frequency plots give values of Spearman's rank correlations between cumulative variables and the current distance, calculated for all *n* time-points where territory locations were observed and the behavioural variable had non-zero variance. (*a*–*e*) The relationship between current position and past behaviour for the smallest time-scale for which any variation was observed: $T_{\text{short}} = 3 \times 10^{-2}$ h for attendance, $T_{\text{short}} = 0.01$ h for other variables. (*f*–*j*) The same relationship for the maximally long time-period $T_{\text{long}} = 10^5$ h. *n* ranges from 213 for short-term attendance up to 1224 for long-term attendance, fight and activity. In cases (*a*–*d* and *f*–*i*), long-term correlations are significantly more negative than those of the short-term distribution (Wilcoxon ranked-sum test, $p < 0.001$ for all cases), whereas case (*e*, *j*) shows no significant difference (Wilcoxon ranked-sum test, $p = 0.64$).

4. DISCUSSION

Black grouse females prefer males that hold central territories on the lek (Höglund & Alatalo 1995; Hovi *et al.* 1994). Previous work indicates that male black grouse begin as peripheral and then become more central as they become older (Kruijt & de Vos 1988; Kokko *et al.* 1998). This suggests that it may pay for young males to lek even if their current success is low, and that females, conversely, may use centrality as a long-term indicator of male lekking behaviour. Our result confirms the importance of previous attendance, but also shows that strongly fighting males become central more quickly per unit time spent on the lek. Successful males therefore combine high lek attendance with high activity levels while on the lek, and, with very long time-spans, with longevity as well: simple cumulative variables in figure 3 explain male success better than proportional measures, which correct for total time spent on the lek and hence exclude effects of longevity.

Territoriality alone is not, however, a sufficient predictor of male success, since assuming that the current territory location only counts does not yield as high predictive power as assuming that the cumulative fight time over the last 10^4 to 10^5 h plays a role (figure 3). We cannot exclude direct repeated assessment of females as a means to gain this additional knowledge, and there are possible forms of assessment that do not incur high costs on females. Females are known to divide their total time on the lek into samples on several mornings (Rintamäki *et al.* 1995), to spend time in the same winter flocks as the males (Klaus *et al.* 1990), to favour old males over yearlings (Höglund & Alatalo 1995), and to be faithful to previously encountered males (Rintamäki *et al.* 1995). These factors suggest that at least older females may actively use memory to evaluate currently displaying males; such ability has been demonstrated experimentally in zebra finches, albeit over shorter time-periods (Sullivan 1994*b*). Together with the possibility of young females copying older ones (Höglund *et al.* 1990, 1995), these mechanisms may give females extra performance in picking out males that have the strongest and longest histories of lekking effort.

When female choice is based on characters that convey long-term information on male performance, a short-term dominance peak during the mating season, as observed in some lekking ungulates (Clutton-Brock *et al.* 1993), ceases to be an optimal male strategy. Instead, a simple model of optimal lekking effort throughout the season reveals the importance of early effort if some fraction of each day's effort is 'remembered' in the future. If competition on any day is of equal importance to the future benefit (as it is with no memory decay, $d = 0$), advertisement effort will simply follow a negative relationship to its current costs, independent of timing as such (figure 5*a*). Thus, lekking can be expected to be vigorous also in the autumn, even though followed by a drop in activity in midwinter, especially in regions where seasonality is pronounced. By contrast, in a system with short memory, autumn effort should be much diminished or lacking (figure 5*b*). In both cases, males should retain their relative ranking order throughout the season.

Data on black grouse male behaviour agree with the predictions of the long-term memory model, as relative measures of male behaviour remained remarkably constant both within days and within the mating season. Long memory, indicated by very weak decay, predicts that males should start their advertisement far earlier

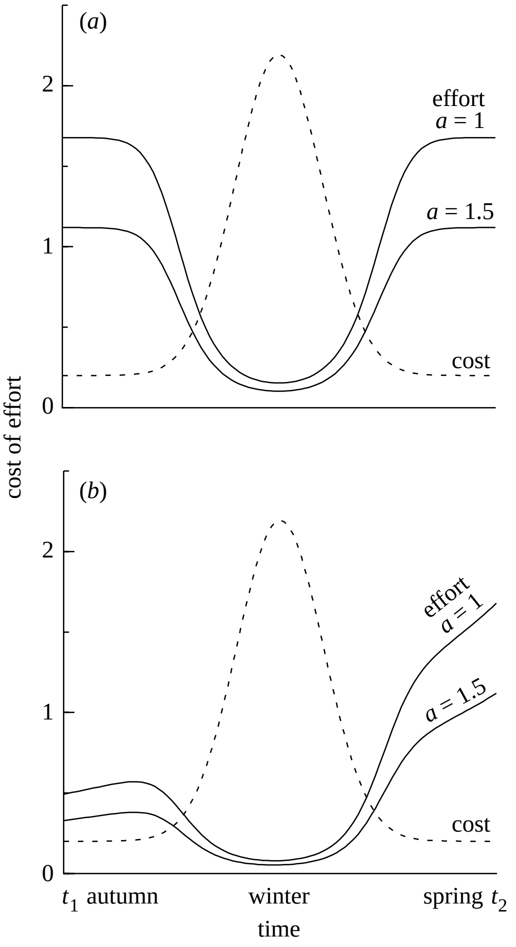

Figure 5. A two-player model for the effect of seasonal costs on advertisement level. We assume that effort that male i puts into competition at time t contributes to his rank by the pay-off $R_i(t) = A_i(t)/(A_i(t)+A_j(t))$, where $A_j(t)$ is the effort of his competitor. Matings start at t_2 and give a fitness pay-off relative to (a) the accumulated ranking pay-offs $\int_{t=t_1}^{t_2} R_i(t)\mathrm{d}t$, or ($b$) the accumulated pay-offs weighted with strongly decaying memory ($d = 1$), $\int_{t=t_1}^{t_2} R_i(t)\mathrm{e}^{-1}\mathrm{d}t$. Effort on each day imposes a cost $C_i(t) = \exp(a_i c(t) A_i(t))$, which assumes increasing marginal cost of daily effort. $c(t)$ describes the seasonal harshness of the environment (dashed line), with an increase in midwinter, and $a_i \geqslant 1$ is a cost factor that makes advertisement more costly for inferior individuals. Solid lines give the optimal effort of the two males at each time-point, and it is obtained by solving the equations (a) $\partial(R_1(t) - C_1(t))/\partial A_1 = 0$, $\partial(R_2(t) - C_2(t))/\partial A_2 = 0$, (or ($b$) $\partial(R_1(t)\mathrm{e}^{-t} - C_1(t))/\partial A_1 = 0$, $\partial(R_2(t)\mathrm{e}^{-t} - C_2(t))/\partial A_2 = 0$. In both cases, the relative effort of the males remains constant throughout time.

than females mate. Also, the timing pattern of lekking fits the long-term requirement of lekking: black grouse males fight vigorously on leks in the autumn as well as in the spring, although no copulations occur in the autumn (Rintamäki *et al.* 1999). Our results show that successful males tend to arrive at the lek earlier also at shorter time-scales. Further qualitative support for an inverse relationship between current cost and lekking effort under long-term benefit accumulation (figure 5) is seen in winter lekking: in Finnish and Swedish populations, lekking activity dramatically decreases during midwinter (Koivisto 1965; Rintamäki *et al.* 1999), but in milder Scottish climates males are seen to visit leks throughout the winter (Baines 1996).

A choosy female's problem is whether observing only one component of a male's life-history allocation (momentary mating effort) can guarantee male quality. In the black grouse, successfully fighting males also have higher survival (Alatalo *et al.* 1991), which suggests that fighting can be used as an honest signal of quality. Females may thus be selected to observe the outcome of male–male competition (Cox & Le Boeuf 1977; Hovi *et al.* 1995; Wiley & Poston 1996; Candolin 1999; but see also Sæther *et al.* 1999), and given the extremely long-term effort required from black grouse males to obtain a central position on a lek, centrality will guarantee good performance in all relevant components of their life history. Such a cumulative trait is indicative of high fitness much more reliably than observing one fitness component in one year (Kokko 1997, 1998). Lekking in the black grouse thus gives an empirical description of a system where the continuous testing of 'armaments' applies (Berglund *et al.* 1996), and this continuity can extend to a lifetime requirement through extremely long memory induced by spatial arrangements on traditional lekking sites.

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