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The Costs of Female Choice in a Lekking Bird

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Abstract

We investigated the costs of active female choice in sage grouse, *Centrocercus urophasianus*, a lekking species in which females make repeated, lengthy visits to leks to assess males before mating. Several potential costs were measured by monitoring changes in hens' ranging behavior, time budgets, and encounter rates with predators when they visited leks. Two costs were identified: hens moved farther per day and encountered golden eagles, *Aquila chrysaetos*, more frequently when visiting leks. However, extra travel due to visiting leks increased predicted daily energetic expenditure by only about 1%, and the risk of predation by golden eagles over a typical series of lek visits (compared to a single short visit for mating) was estimated to reduce annual survival by < 0.1%. Two other potential costs were not supported: visiting leks did not depress foraging time or conflict with nest defense. These results indicate that any costs of mate choice are slight and imply that even very small benefits could be sufficient to maintain female choice. We present calculations which suggest that increased offspring viability due to choosing fitter males could balance predation costs even if the heritability of fitness is low and if females identify fitter males with only moderate accuracy. Despite recent emphasis on the direct benefits of mate choice, we conclude that either indirect or direct benefits could provide a plausible solution to the lek paradox.

The prevalence of active mate choice in species with nonresource-based systems, such as leks, is often regarded as an evolutionary paradox. Active sampling of prospective mates appears to be a costly process. Mate choice is therefore unlikely to be maintained by selection unless it provides compensating benefits. One view is that these benefits are obtained indirectly through increased sexual attractiveness of sons, the Fisher process, or increased viability of offspring of both sexes, the good genes hypothesis (Maynard Smith, 1991). These hypotheses have the merit of generality, but they face the difficulty that indirect genetic benefits are likely to be small. Therefore, such mechanisms could maintain choice only if sampling costs were correspondingly slight. Another view, emphasized in some recent reviews (Kirkpatrick and Ryan, 1991; Reynolds and Gross, 1990), is that mate choice

provides direct benefits deriving, for example, from reduced social interference (Trail, 1985), disease transmission (Borgia and Collis, 1990), or increased fertility (Avery, 1984). Such benefits might be large and thus maintain choice in the face of substantial sampling costs. However, the existence of these direct benefits is an open question.

Measurements of the cost of mate choice offer a possible resolution of this issue. Because indirect genetic benefits are likely to be small, a demonstration that females who choose males incur large costs would favor the direct selection hypothesis, whereas sufficiently small costs would be consistent with either indirect or direct benefits. It has also been suggested that even small costs would prevent the maintenance of choice by the Fisher process (Kirkpatrick, 1987; Lande, 1981; Pomiankowski, 1988). However, more recent work has shown that the Fisher process is compatible with costly choice provided that there is a mutational bias on the attractive male trait (Pomiankowski et al., 1991). To date there have been few empirical studies of the costs of mate choice (Alatalo et al., 1988; Engelhard et al., 1988; Slagsvold et al., 1988) and, to our knowledge, none in lekking species. In this paper, we attempt to fill this gap by analyzing the costs of female choice in a lekking bird, the sage grouse, *Centrocercus urophasianus*.

Two observations suggest that female choice could be costly in lekking species. First, females often visit leks repeatedly and spend time with several different males before mating (Gibson and Bradbury, 1986; Pruett-Jones and Pruett-Jones, 1990; Trail and Adams, 1989). Such behavior would be costly if movement to leks increases energetic expenditure on travel, exposes females to increased predation risks, or takes time from other activities beyond that necessary for mating. Second, in some species females adopt secondary tactics of mate assessment, such as fidelity to former mating sites (Gibson et al., 1991; Lill, 1974) or copying the choices of others (Gibson et al., 1991; Höglund et al., 1990), which could reduce the time spent on mate assessment and thus reduce any associated costs. However, these observations alone do not justify the conclusion that choice is costly, because it is possible that visiting leks has little effect on risk of predation or on daily time and energy budgets. It is also possible that secondary tactics of mate assessment are driven by benefits other than cost reduction. Direct measurements of costs are needed to resolve these issues.

Most female sage grouse visit leks on 2 or 3 mornings each spring and mate once on the last visit, obtaining enough sperm to fertilize a clutch of 6–10 eggs. Each visit lasts from a few minutes to more than 2 h and typically includes visits to the territories of several males. Because mating can be completed in a single brief visit, both repeated visits to leks and the time invested in sampling per visit are clearly in excess of what is needed to mate. There are at least three ways in which this additional sampling might be costly. First, visits to a lek could increase energetic expenditure on travel above typical daily levels. Large excess expenditure might represent an important cost for hens whose energetic requirements are already elevated by the need to accumulate reserves for laying and incubation. Second, time at leks might expose hens to higher risks of predation, particularly from golden eagles (*Aquila chrysaetos*), which regularly attack leks (Bradbury et al., 1989a; Hartzler, 1972; Lumsden, 1968; Scott, 1942; Wiley, 1973). Finally, time spent at leks might reduce opportunities to forage or defend nesting territories (Gibson et al., 1991).

In this paper we assess the likelihood and magnitude of each of these hypothesized costs by measuring how visiting leks affects female ranging behavior, encounter rates with

golden eagles, time budgets, and proximity to nests. We then consider whether measured costs would be sufficient to override indirect sexual selection on female choice.

Methods

We studied a population of sage grouse resident in Long Valley, Mono County, California, USA, between 16 February and 30 May, 1991. Background data on body mass and annual mortality were collected during earlier studies dating back to 1984. The study area comprises approximately 300 km² of sagebrush-dominated plant communities on the floor of the valley and surrounding mountains and hosted 10 active leks in 1991.

We measured the movements, time budgets, and off-lek encounter rates of hens with golden eagles from observations of 12 radio-tagged hens. Seven birds were captured by spotlighting and the remaining five by cannon-netting at a lek. We fitted each bird with a poncho-mounted, two-stage radio transmitter weighing 20–25 g and gave each bird a unique combination of three colored plastic leg bands and one aluminum leg band for visual recognition. We also aged birds by wing molt and weighed each on a spring balance. Each hen was located by triangulation at 1–3-day intervals (occasionally longer for birds that dispersed into remote areas) using a five-element yagi antenna, mounted in a pickup truck, and a CE-12 receiver. We also followed individual hens continuously from before dawn until after dusk on 2–7 days each between 26 February and 3 May (a total of 39 bird days and 546 observation h). Each all-day follow was undertaken by a team of at least three observers each working in shifts of 4–6 h. Seven different observers collected data. To minimize possible bias, observers rotated shifts between days. We continued to locate hens until the end of May to monitor nesting.

We sampled lek attendance by tagged hens, visit durations, and encounter rates of hens with golden eagles at leks at five different leks on 39 days between 29 March and 3 May (a total of 78 lek days and 155 observation hours). The five leks were sampled on 2, 7, 16, 25, and 31 days each. Lek sizes varied from 9.0 ± 3.5 to 81.8 ± 13.7 males per day (mean \pm SD). Leks were inactive for most of March due to unusually heavy snowfalls, mating peaked in mid-April, and female attendance had declined to zero by the beginning of May. Observers (1–3 per lek) arrived at least 1 h before sunrise, when males typically began to display, and made observations from a range of 200 m with binoculars and zoom telescopes until the last birds departed 1–3 h later. At 10-min intervals observers counted numbers of birds of each sex present and scanned radio frequencies for tagged hens. On 32 lek mornings, arrival and departure times were recorded for some or all of the hens attending the lek. Complete records of arrivals were obtained on 17 days (78 hen days) and of visit durations on 13 days (48 hen days) at three leks. All sightings of raptors were also noted. We maintained careful records of mating at one lek on 11 days during the mating peak.

We estimated overnight metabolic expenditure on thermoregulation using measures of operative temperature (T_e : Bakken, 1980) and wind speed. Operative temperature was measured using a female skin mounted on a hollow copper body and placed on the ground in sagebrush habitat at the University of California's Sierra Nevada Aquatic Research Laboratory on the eastern edge of Long Valley. The summed output of three thermocouples in the mount was fed into a Bailey-BAT digital thermometer and recorded at 15-min intervals

by a TRS80-100 computer connected through a Remote Measurement Systems ADC. Mean hourly wind speed, based on samples taken at 1-min intervals, was measured by an automatic weather station at the same site. Operative temperature values were rarely below lower critical temperature (6°C ; Vehrencamp et al., 1989) during daylight but typically fell well below this at night. Thermoregulatory expenditure overnight should increase with both the deviation of T_e below lower critical temperature and by wind speed (which elevates thermal conductance by disturbing the boundary layer around the bird). For each hour of the night (1800–0600 h), we estimated thermoregulatory expenditure from mean hourly T_e and wind speed using the method of Goldstein (1983) and then summed these values over the entire 12-h period. Our analyses use measures extracted from these data as described below.

Ranging

We measured the effect of lek visits on ranging at two temporal scales. First, distances moved between successive days were calculated for all pairs of days from 22 days before to 20 days after each hen's last lek visit. Hens were still in winter ranges 3 weeks before mating, mated on the last lek visit, and began incubation as early as 20 days later. We determined the date of the last lek visit for nine birds. Locations were triangulated at a mean distance of 796 ± 677 m ($n = 239$ bird days). We made these observations after the morning lek and before movement to the evening roost, a period that rarely included major relocations. Second, we computed distances moved between successive hours of the day throughout each all-day follow during the period 29 March–3 May. Focal hens were triangulated at least every hour during all-day follows at an average distance of 536 ± 424 m ($n = 647$ samples). For each hen, we divided days into those with a lek visit versus those without, and computed mean displacements for each hour of the day for each category.

To assess the energetic costs of travel to leks, we computed the cost of additional flight and then expressed this as a fraction of predicted field metabolic rate (FMR). We computed flight costs by dividing the mean additional distance traveled by flight speed (174 m min^{-1} , from five hens videotaped flying over a 20 m distance) and multiplying by 14 times basal metabolic rate (BMR), a reasonable estimate of the rate of energy expenditure of flapping flight (Nagy KA, personal communication). BMR and FMR were estimated from the non-passerine allometric equations of Lasiewski and Dawson (1967) and Nagy (1987), respectively, using a mass of 1312 g, the mean of 27 hens captured during 29 March–3 May from 1984 to 1991.

Predation by golden eagles

Mortality risk per lek visit was computed as eak/n , where e is the probability that an eagle appears during a lek visit, a is the proportion of sightings in which golden eagles attacked a grouse, k is the probability of a kill per attack, and n is the number of other birds present during the visit (representing risk dilution). We estimated each component of risk separately for on- and off-lek situations and, for hens at leks, for both a typical series of lek visits and a hypothetical single "no-choice" lek visit of 14 min (the shortest mating visit recorded). Mortality risk for a series of visits was computed assuming that the risk was constant across visits and that 54.5% of hens made two lek visits and the remainder made

three per season (Gibson RM and Bachman GC, unpublished data). Estimation of components of risk is explained below.

Encounter rates with eagles were estimated from observations of eagle arrival times at leks and of hens' arrival and departure times for a sample of 35 lek visits. For each hen's visit we computed the probability that at least one eagle came between her arrival and her departure, using the survival function shown in Figure 1, and then took the average of these values across all visits. Encounter rates for a 14-min visit were obtained in the same way after truncating each of the 35 visits at 14 min after arrival. We constructed an equivalent off-lek survival curve for eagle arrival using observations of eagles during 33 all-day follows off leks and used this with the visit durations to compute an eagle encounter rate for hens spending the same period of time away from a lek.

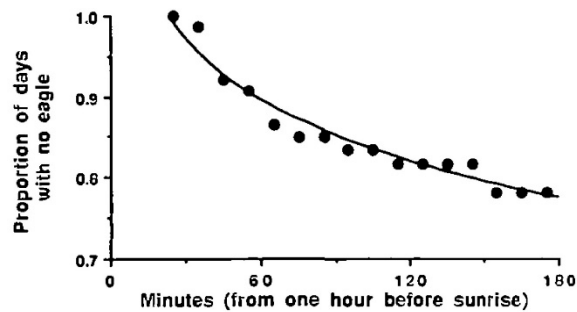


Figure 1. Survivorship plot for arrival times of golden eagles at leks. We divided observations from 78 lek days into 10-min blocks starting 1 h before sunrise and computed a survival curve for time to the first eagle using the actuarial method (Dixon et al., 1988). The fitted curve [$P = 1.438 + 0.254 \log(\text{min})$] explains 95.7% of the variance in survival probability ($p < .0001$). The probability that a hen encountered an eagle during a lek visit was computed as the difference between the values of this function at her arrival and departure times.

Because ad libitum visual observations of lek visits might have been biased toward late arrivals, we restricted our sample of lek visits to cases taken either from radio-tagged hens or from days on which all arrivals and departures were recorded visually. Also, to ensure that visit durations represented the risk hens were willing to accept, we excluded visits terminated by eagle arrival (and thus whose voluntary durations were unknown). To test the reliability of this method, we compared our estimate of eagles per lek visit with a more direct measure, the ratio of hens present at leks when an eagle arrived to the total number of female lek visits recorded ($n = 705$). The values were similar (0.066 and 0.081).

An eagle was considered to have attacked if it stooped on or closely pursued a grouse in flight. The probability of attacks per eagle sighting at leks was computed from 17 sightings in 1991 and 13 collected from 1984 to 1990. The proportion of attacks per sighting was similar in both samples. Off-lek attack probability was based on 31 golden eagle sightings off leks during 39 all-day follows during this study. No kills were observed in 1991 (although one hen was grasped by an eagle but struggled free). Consequently, we based our

estimate of kills per attack on observations of 54 attacks seen at leks in an earlier study (Bradbury et al., 1989b). Finally, risk dilution at leks was incorporated by dividing the probability of eagle arrival during each lek visit by the number of birds of both sexes present. This assumes that eagles are equally likely to take males and females. This seems reasonable, although at present we do not have sufficient data for a robust test. It is more difficult to assess risk dilution for hens off leks because focal hens and their groups were rarely seen (see below). For comparisons with lek group sizes, we report mean group sizes for 14 hen groups observed away from leks during the early morning when leks are active (see Table 2). The latter data were obtained during all-day follows.

For each mortality risk estimate, an approximate 95% confidence interval was obtained by repeating the calculation using the lower or upper confidence limit for each component. We used the variance among the 35 visits to estimate confidence intervals for encounter rates (e and e/n) and binomial proportions (Rohlf and Sokal, 1981) for attack and kill probabilities.

To scale mortality risk, we estimated annual survival using unpublished records from 50 hens radio tagged between 1984 and 1991 and followed for up to 2 years. We divided time between capture and 240 days later into 15-day blocks and used survival analysis (Dixon et al., 1988) to compute a survivorship curve. Beyond 240 days, sample sizes were too small to be reliable (due to battery failure). An annual survival rate was obtained by fitting a negative exponential function to the survival curve up to this point (probability of survival = $1.0475 \times 10^{-0.001 [\text{days since capture}]}$; $r^2 = .958$, $p < .0001$) and extrapolating to 1 year. If radio transmitters increase mortality, the resulting estimate would be low, but this possible bias is conservative relative to our conclusions.

Foraging time

Foraging time was measured from records of activity during all-day follows. Due to their cryptic behavior, it was rarely possible to observe hens for extended periods, so we inferred activity from fluctuations in the amplitude between successive pulses of the radio signal (Kenward, 1987). At the start of each 5-min period, an observer scored signal amplitude as constant or variable in each of three successive periods of 21 radio pulses. The sample as a whole was classified as variable if any of the three periods was variable. This method proved satisfactory for all except one hen whose transmitter's amplitude fluctuations were too small to be scored consistently.

Table 1 illustrates the correlation between amplitude variability in the signal and behavior for one hen that was observed continuously for 2.5 h. Movements of the transmitter's antenna caused by foraging and other activities produced deep fluctuations in signal strength between pulses, which disappeared when the bird was inactive. Most fluctuating signals in this sample were produced by foraging, which supports the use of the proportion of time signals that were variable as a relative measure of foraging activity. In all samples, periods of activity fell into several long bouts, which were unlikely to have been generated by alternative activities such as preening.

Table 1. The correlation of radio signal amplitude fluctuation with activity

Behavior	Radio signal amplitude	
	Constant	Variable
Inactive	24	0
Active		
Foraging	1	8
Walking, preening	1	3

Counts are the numbers of 1-min samples, taken at 2–5-min intervals over a 2.5-h observation period for one hen on 2 March 1991. One observer watched the bird and scored its activity, while a second recorded amplitude variation in the radio signal. Signal variability is significantly associated with all activity ($\chi^2 = 28.899$, $df = 1$, $p < .0001$) and with foraging ($\chi^2 = 19.924$, $df = 1$, $p < .0001$).

For each day on which a hen visited a lek, we estimated the time available for foraging as the interval from lek departure to roost and estimated actual foraging time as the number of hours during this period that the radio signal was variable. Hens rarely foraged at leks, which were all located in areas with little or no sagebrush, the primary food source in early spring. For comparison, we also computed the following measures:

1. The time that would have been available for foraging in the absence of the lek visit. This was the time from first activity in the morning to last activity at dusk. For cases in which a hen was tracked from arrival at the lek rather than roost departure, time available was estimated from the regression of roost-to-roost time on date for dawn-to-dusk follows ($Y = 9.547 + 0.045 \times \text{Julian day}$; $r^2 = .935$, $p < .0001$).

2. The time that the same hen would have spent foraging over the entire day if she had not visited the lek. For 10 hens each sampled on at least 2 days without a lek visit ($n = 28$ days), total time active increased through the season and varied among individuals (ANCOVA: both effects $p < .0005$; there was no significant interaction). Residual activity was not significantly correlated with our estimate of overnight metabolic expenditure, or with mean operative temperature, wind speed, or total precipitation during the day. We used the ANCOVA model including date and identity to predict foraging time for particular individuals on the days that they attended leks.

3. The time that the same hen would have spent foraging between the times of lek departure and going to roost if she had not attended the lek. This was calculated in an identical manner to measure (2), except that before computing the ANCOVA, we truncated observed off-lek activity up to the observed time of lek departure (scaled relative to sunrise). This necessitated a separate analysis for each lek visit.

Nest defense

We measured the opportunity for nest defense by the proximity of hens to their nests, using the distance between daily locations and nest location for each day from 15 days before the last lek visit until the onset of incubation. As a more sensitive measure, we used the

time that hens spent in relatively close proximity to their nests (100 m) for each of 14 all-day follows during the same period. These data were from six hens that nested; two others were killed by raptors before nesting, and four did not nest.

Statistical analysis

We used one-tailed tests wherever hypotheses made directional predictions and, to maximize power, parametric rather than nonparametric tests except where measures could not be normalized by transformations. Descriptive statistics are given as mean \pm SD.

Results

Ranging

Lek visits increased the distances that females ranged both within and between days (Figure 2). Figure 2A compares hourly movements of five hens on days when they visited leks with nine hens on days without lek visits. Hens that had visited leks moved farther between 0600 and 0700 h, when moving from leks to foraging areas, and again when going to roost in the evening (paired t tests: one-tailed $p = .027$ and $.014$, $n = 6$ and 4 , respectively). The mean extra distance, summed across both periods, is 0.867 km.

Hens also moved farther between successive days during the period when they visited leks most frequently. Mean day-to-day displacement for all hens increased up to the last lek visit and decreased afterward (Figure 2B). Most lek visits by these hens (83% of 18) occurred during the 4 days up to the last lek visit. Daily displacement during this period was higher than for the periods before and afterward (paired t tests: one-tailed $p = .0382$ and $.0471$, $n = 6$ and 8 hens, respectively), mainly as result of movements between nesting areas and leks. The mean increase in individual displacement from pre-lek to lek visiting periods was 2.335 km per day.

The energetic costs of this additional movement appeared to be small. We estimated the extra expenditure on a lek visit day to be 4.6 kJ, or 0.4% of daily FMR, and the increment due to additional day-to-day movement as 12.4 kJ, or 1.2% of FMR. Details of these calculations are explained in Methods. Thus, although hens undertook additional ranging associated with movement to and from leks, the resulting energetic costs were probably little more than 1% of daily energy expenditure. A hen making a typical series of lek visits would incur this cost on only 1 or 2 more days annually than an individual that attended a lek once to mate.

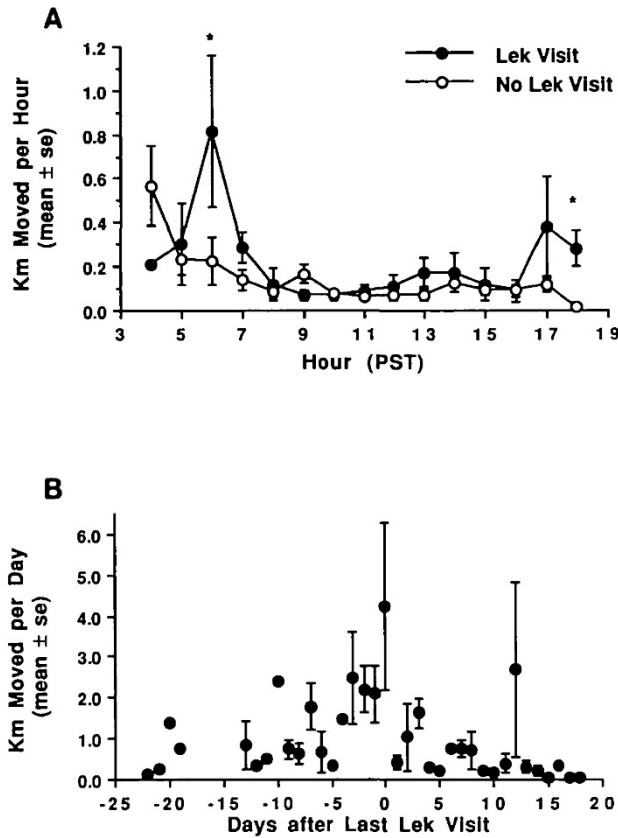


Figure 2. The effects of lek visits on female ranging. (A) Mean distance moved per hour plotted against time of day for days when hens visited leks (filled circles) versus days when there was no lek visit (open circles). Each point is the mean of 1–5 (lek visit) or 7–9 individuals (no lek visit), each sampled on 1–3 days. Asterisks indicate significant differences between means (paired *t* tests). (B) Mean distances moved by hens from one day to the next plotted against days after the last lek visit (mating). Each point is the mean across 1–6 hens (mean = 2.1). Daily displacement increased up to the day of mating (days -22 to -1: $r_1 = .576$, $n = 17$ days, $p < .02$) and then declined (days 0 to 20: $r_1 = .486$, $n = 20$ days, $p < .05$).

Attempted predation by golden eagles

Hens appeared to experience an elevated predation risk from golden eagles when visiting leks. We saw at least one eagle on 15 of 78 lek mornings, but only one during the corresponding period in 33 mornings spent with focal hens away from leks ($\chi^2 = 4.933$, $df = 1$, $p = .0263$). We sighted another common raptor, the northern harrier (*Circus cyaneus*), which does not prey on adult sage grouse, at similar rates on and off leks during the lek period (6 of 76 days at leks versus 3 of 33 off leks: $\chi^2 = 0.061$, $df = 1$, $p = .805$), which suggests that the higher rate of golden eagle sightings at the lek was not a consequence of any differences in observation methods. Golden eagles sighted at leks were also more likely to attack. Of 30 eagles sighted at leks from 1984 to 1991, 8 (26.7%) attacked a grouse, whereas none of 31 sighted near radio-tagged hens off leks in 1991 did so ($\chi^2 = 9.514$, $df = 1$, $p = .002$). The

proportion of attacks at leks would probably have been higher, except that eagles only occasionally surprised grouse at leks. In 60% of the 30 lek sightings the grouse flushed off the lek well ahead of the eagle's arrival, preempting an attack.

Despite the spectacular nature of eagle attacks on leks and their relatively high frequency, the mortality risk to hens appeared to be slight. Table 2 compares components of risk for an average lek visit versus the same period of time spent away from a lek. Details of the computations are explained in Methods. Although risk off the lek appears to be zero, the risk at the lek is also small. If we assume the off-lek risk during the early morning to be zero, then the mortality cost of mate choice can be estimated as the difference between mortality risk at the lek over a typical series of lek visits (0.0050) and the risk during a single short "no-choice" visit (0.00086), i.e., 0.00041. When normalized to an annual survival rate of 0.485 (from 50 radio-tagged hens over 8 years; see Methods), this value represents a decrease in annual survival of 0.084%, with a 95% confidence interval from 0.0043 to 0.253%.

Table 2. Components of mortality risk to hens due to predation from golden eagles during a typical lek visit versus spending the same period of time spent away from a lek

	On lek	Off lek
Encounters/visit	0.066	0.007
Attacks/encounter	0.267	0
Kills/attack	0.167	—
Group size (mean \pm SD)	17.3 \pm 7.8	2.7 \pm 2.9
Mortality risk	0.00020	0

Note that the off-lek probability of encountering an eagle refers only to the period of a lek visit; the value over the whole day would be considerably higher (0.482). Derivation of each component is described in Methods.

Golden eagles also disturbed mating and may have amplified other costs by forcing return visits. At one lek where matings were recorded on 11 days in mid-April, a smaller proportion of hens mated on 6 days when the lek was disturbed by golden eagles (7.2% of 27 hens) than on 5 other mornings (42% of 33; Mann-Whitney test: $p = .05$). Hens occasionally returned to the lek to mate on the same morning, and the only radio-tagged hen disturbed by an eagle returned the next day. Assuming that eagle disturbance forces an extra lek visit only for hens that would otherwise mate during their interrupted visit, the probability of disturbance increases from 0.02 for a single short visit to 0.064 for a visit of typical duration. Thus, the probability that travel costs will be amplified as a result of eagle-delayed mating is only 0.044.

Foraging

Visiting leks reduced the time available for foraging. For six dawn-to-dusk follows that included a lek visit, the time available for foraging was reduced by an average of 60 ± 48 min, or 7% of the roost-to-roost interval (paired $t = 3.083$, $df = 5$, one-tailed $p = .0137$). Time

spent at leks also appeared to conflict directly with normal foraging activity. Hens tracked off leks became active on average 49 ± 17.9 min before sunrise (not significantly different from the times of 88 lek arrivals: Kolmogorov-Smirnov test, $n = 18$ and 88 , $p = .205$) and were active on $78.8 \pm 15.1\%$ of observations throughout the next 2 h, a period that included almost all lek visits.

Despite this reduction in foraging opportunity, lek visits did not appreciably depress foraging over the entire day. We obtained complete time budgets following lek visits for 5 days. These were from four hens and followed lek visits ranging in length from 15 min to more than 2 h. Hens were active for 9.51 ± 1.88 h after visiting a lek, which is only slightly less than predicted for the entire day without a lek visit (9.86 ± 2.02 h; see Methods). The difference is not statistically significant (paired t test), suggesting that lost foraging time was made up after leaving the lek. Consistent with this idea, post-lek activity tended to be higher than that predicted for the equivalent period of the day without a lek visit (8.76 ± 2.36 h). Only one observation suggested that lek visits might have reduced foraging activity: across the five visits there was a strong negative relationship between visit duration and subsequent activity ($r = -.883$, one-tailed $p = .0236$). While this suggests that longer visits could have curtailed foraging, an alternative explanation is that an unidentified factor affected both foraging time and visit duration.

In summary, although a lek visit takes an average of 7% of the time available for foraging, foraging was not appreciably depressed by time spent at leks. This may be because hens undertake compensatory foraging activity after leaving the lek.

Nest defense

Although some hens visited their nesting areas within the 2 weeks preceding mating, they were rarely close to their eventual nest location during this period (Figure 3). In contrast, almost all birds had moved to within 500 m of their nests by the fourth day after mating and then remained in close proximity until incubation started. Individuals showed no significant change in mean distance from their nests between the pre-lek and lek-visiting periods ($t = 0.836$, $df = 3$, $p = .4647$), but were significantly closer to their nests after mating ($t = 2.883$, $df = 5$, two-tailed $p = .0345$).

This impression was supported by more detailed observations made during all-day follows. In eight full-day follows (on four hens) taken from 15 days before the last lek visit until 1 day after, no hen came within 200 m of her eventual nest and only one spent any part of the day within 500 m. In contrast, for six follows (on four hens) taken 6–15 days after the last lek visit, all hens were within 500 m of their nests throughout the day and spent an average $26.8 \pm 21.9\%$ of the day within 100 m of the nest, a significant increase over the earlier period (Mann-Whitney test: $p < .001$). This finding suggests that if hens defend nesting territories, they are unlikely to do so until they begin laying 2–3 days after mating. Thus, despite the fact that hens were often far from their nests when mating, it is doubtful that time spent at leks conflicts with nest defense.

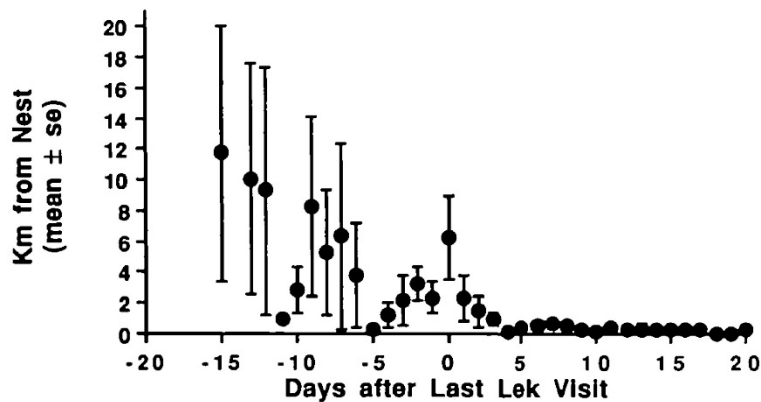


Figure 3. Mean distances of six hens from their nests plotted against days after the last lek visit (mating). Each value is based on 1–5 bird days (mean = 2.8).

Discussion

The results suggest two conclusions. First, as a result of making repeated and lengthy visits to leks, sage grouse hens incur costs through both increased travel and increased exposure to attack by golden eagles while at the lek, whereas time at leks does not appreciably affect foraging time or opportunities for defense of nesting territories. Second, the magnitude of these costs is slight. Relative to a hen making a single short visit to a lek for mating, the typical pattern of mate choice would be likely to produce a 1% elevation in metabolic expenditure on only 1 or 2 days each year and a decrease in annual survival of less than 0.1%.

The conclusion that costs are small would be misleading if we either underestimated the magnitude of identified cost components or failed to identify other cost components altogether. It is unlikely that travel cost estimates are low because the distances that hens moved between leks and nests were similar to those reported in previous studies (summarized in Bradbury et al., 1989b). Golden eagle predation is likely to vary among years or locations due to changes in the population density of this raptor and the availability of alternative preferred prey (Steenhof and Kochert, 1988). However, rates at which hens encountered eagles at leks were not unusually low. The proportion of days on which eagles were seen at leks (0.192) was higher than in three of four previous studies, all of which spanned several years (0.056–0.098 eagles per day: Bradbury et al., 1989a; Hartzler, 1972; Wiley, 1973). A fourth, 2-week study of one lek yielded a value of 0.357 (Lumsden, 1968), which is similar to the highest frequency of sightings for a single lek in this study (0.36, $n = 25$ days). To minimize the chance of missing cost components, we attempted to examine an exhaustive set of possible costs. Among these costs, a reduction in foraging is the most likely to have gone undetected as a result of small sample sizes. However, the small difference between predicted and observed foraging times when hens visited leks suggests that any undetected effect must be slight.

Small costs imply that equivalently small benefits would be sufficient to maintain choice. Are these costs sufficiently small to make indirect selection on preferences a plausible solution to the lek paradox? To answer this question, we considered the specific case in which the primary cost of choice is predation by golden eagles, and males vary in fitness as a result of carrying variable numbers of deleterious mutations. This example was chosen because of the direct relationship between predation and fitness (whereas the effect on fitness of small changes in energy expenditure is uncertain) and the availability of data on the additive genetic variation in fitness maintained by mutation (Charlesworth, 1987; see Appendix).

The benefits of choice in this situation are determined by two factors: how accurately females select fitter males and the heritability of fitness. Table 3 illustrates threshold values of the heritability of fitness for three different choice accuracies and three values of predation cost. As expected, threshold heritability values increase with increasing costs and with decreasing accuracy of choice. In all cases threshold heritability values are small. Even in the worst case, with predation risk at its upper confidence limit and females rejecting only the bottom 25% of males, a heritability of only 3% would be sufficient to ensure a net benefit for choice. This value drops by an order of magnitude if females reject all but the top 25% of males. This suggests that unrealistically high values for the heritability of fitness may not be necessary to maintain mate choice, although estimates of the heritability of fitness for comparison are scarce (Gustafsson, 1986).

Table 3. Minimal heritabilities of fitness necessary for the benefit of mate choice to balance mortality risks due to golden eagle predation

Mortality risk	Proportion of males above fitness threshold		
	0.75	0.5	0.25
0.00004	0.000008	0.000002	0.000001
0.00084	0.002949	0.000837	0.000328
0.00253	0.026754	0.007590	0.002973

It is assumed that additive genetic variance in fitness is maintained by mutation. Heritabilities are given for three values of predation cost (the estimated value and its lower and upper confidence intervals) and for three levels of choice accuracy, defined by the proportion of males above the fitness threshold for acceptance. The calculations are described in the Appendix.

It is also plausible that females could discriminate fitter males. Several mechanisms by which this could be achieved have been proposed. First, optimal individual allocations of effort to display may increase with male fitness because fitter males pay lower costs for a unit increment in display effort (a condition-dependent handicap; Grafen, 1990a,b; Zahavi, 1975). Vehrencamp et al. (1989) found that metabolic expenditure of male sage grouse increased with both their lek attendance and rate of courtship display and that the most active males were able to sustain their higher effort at the cost of a smaller reduction in body reserves than individuals that displayed less. Because mating success increases with both lek attendance and display rate (Gibson and Bradbury, 1985; Gibson et al., 1991), female sage grouse appear to be choosing males that can sustain elevated metabolism at a lower cost. Other possible examples of condition-dependent handicaps have been described in

resource-based mating systems (Hill, 1991; Møller, 1989). It has also been suggested that females could obtain fitter mates either by preferring older males or by basing choice on traits that reveal a male's health, with the underlying assumption that health is strongly affected by genetic variation in resistance to disease (Hamilton and Zuk, 1982). However, in previous studies we have found no evidence that females favor older males, beyond 1 year of age (Gibson et al., 1991), or that they select parasite-free mates (Gibson, 1990; but see Boyce, 1990).

These examples illustrate that indirect selection might be sufficient to maintain female choice, but they do not preclude the operation of direct benefits. As noted earlier, social interference in mating, disease transmission, and lowered fertility are all potential sources of direct selection on female choice in lekking species. Although social interference may constrain choice in some species (Trail, 1985), in sage grouse rates of effective disruption of copulations by other males are low and appear not to affect female choice (Gibson and Bradbury, 1986). The possibility that fertility and disease are also factors remains an open question.

The conclusion that sampling costs are slight also has implications for the interpretation of secondary mate-choice tactics, such as fidelity to former mating sites and copying the choices of others. In a recent paper (Gibson et al., 1991), we suggested that such tactics minimize sampling costs. However, an alternative hypothesis is that such tactics improve the accuracy with which hens discriminate fitter mates (Boyd and Richerson, 1985). In view of the present results, we now think that the latter interpretation merits further study.

In summary, sage hens appear to incur only small costs as a result of mate choice at leks. These may be small enough for indirect selection on preferences to maintain mate choice, which suggests that either indirect or direct selection on mating preferences provides a plausible solution to the lek paradox. In addition, small costs suggest that secondary tactics of choice, such as copying, may be driven by the benefits of more accurate assessment rather than by cost minimization. Estimates of the magnitude of costs of choice from a variety of other species will obviously be needed to test the generality of our conclusions.

Appendix

The benefit of choice due to mutational variance in fitness

Charlesworth (1987) has provided an expression relating the benefits of choice to both the heritability of fitness and the accuracy of female choice under the assumption that additive genetic variation in fitness is generated only by mutational load. We have used this result to estimate the heritability of fitness necessary to balance the mortality costs estimated in this study with varying assumptions about the accuracy of female choice.

In Charlesworth's model, mate choice is controlled by a single locus with two alleles. Allele C causes a female to mate with males of above-average fitness; allele c causes random mating. The selective advantage of choice is $a/2$, relative to a fitness of 1 for random mating, where a is the breeding value for fitness of chosen males relative to a mean population fitness of unity. If fitness is normally distributed with a phenotypic variance, V_p , and a heritability of h^2 , and C females choose a male from the top fraction, x , of the distribution,

then $a = h^2 \cdot \sqrt{V_p} \cdot z/x$, where z is the ordinate of the normal probability distribution at the acceptance threshold. To estimate the heritability of fitness necessary to balance measured costs of choice, this can be rearranged as $h^2 = (a \cdot x/z)^2/V_A$, where V_A is the additive genetic variance in fitness.

We used this expression to estimate values for the heritability of fitness necessary to generate benefits that would balance the mortality costs of choice estimated in this study, given different degrees of choice accuracy. We computed a as $2[r/(m+r)]$, where r is the added risk of predation per season due to mate choice and m is annual survival for choosy hens. This assumes that the relative mortality costs of mate choice measured over one season are representative of the relative costs over a female's lifetime. As shown in the Results, $r/(m+r) = 0.00084$, with lower and upper 95% confidence limits of 0.000043 and 0.00253. Each of these values was used to bracket a range of possible costs. We considered three levels of choice accuracy, with $x = 0.75, 0.5,$ and 0.25 , corresponding to poor, moderate, and good discrimination of the fittest males. Finally, the additive genetic variance in fitness maintained by mutation was assumed to be 0.0053, the estimated value for *Drosophila melanogaster* (Charlesworth, 1987). Table 2 gives the results, which are considered further in the Discussion.

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