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Relationships between Blood Parasites, Mating Success and Phenotypic Cues in Male Sage Grouse *Centrocercus urophasianus*

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Abstract

In lek breeding Sage Grouse *Centrocercus urophasianus* in eastern California, male mating success is strongly correlated with individual differences in lek attendance, and in the rate and acoustic quality of courtship display, suggesting that these provide cues by which females choose mates. Increased lek attendance and high display rates are also associated with elevated metabolic expenditure. This paper examines the hypothesis that the ability to commit energy to display is related to the incidence of blood parasites. A single hematozoan genus, *Haemoproteus*, was found in 37.5% of 184 Sage Grouse sampled over a five-year period. Parasitism varied across years and increased through the breeding season. However, no measure of display performance or mating success was significantly correlated with decreased parasite load among adult males. Several additional lines of evidence, including numerically low infection intensities, the absence of detectable effects of parasites on hematocrit and erythrocyte production, and the seasonal distribution of parasite incidence all suggested that infections were unlikely to impact male courtship display. Alternative factors maintaining individual variation in male display performance in this population are also evaluated.

Introduction

Lek-breeding birds are of particular relevance to the proposed role of parasites in the evolution of mating preferences and sexually selected traits (Hamilton and Zuk, 1982). Strongly polygynous mating is characteristic of lek-breeding species and most observers of avian leks have been impressed that male mating success often appears strongly affected by female choice (Wiley, 1973; Lill, 1974; Hartzler and Jenni, 1987; though see also Beehler and Foster, 1988). Yet, because lek males provide neither resources nor parental care to

their mates, mate choice may be less likely to provide direct benefits in lek-breeding species than in those with alternative mating systems. This perception suggests that indirect benefits may be the main evolutionary force favoring mate choice. Lek breeding thus offers an opportunity to study the assumptions of indirect selection hypotheses, such as the Hamilton-Zuk model, in a system to which they may be particularly relevant.

Models of sexual selection via indirect selection of mating preferences have been the source of much recent debate (Bradbury and Andersson, 1987; Kirkpatrick, 1987). Two alternative types of model, Fisherian and viability-indicator (or "good genes") models have been proposed and a variety of approaches for discriminating their past and contemporary effects suggested (Heisler et al., 1987). The most fundamental distinction between these model classes, the assumption of a positive genetic correlation between expression of preferred male traits and total offspring fitness in the viability-indicator models, may be particularly difficult to test directly. However, several of the viability-indicator models also make specific predictions about the nature of preferred male traits that can be examined more readily using phenotypic data. For example, the Hamilton-Zuk hypothesis argues that the expression of such traits in males should be negatively correlated with parasite load. Failure to confirm this prediction should be sufficient to reject the model as a contemporary process. Confirmation can provide necessary support for the hypothesis but does not exclude alternatives. With this proviso in mind, this paper presents a phenotypic test of the Hamilton-Zuk prediction using data from a classical lek breeding bird, the Sage Grouse *Centrocercus urophasianus.*

Mating in Sage Grouse takes place at traditional locations where groups of from 10 to > 100 males assemble for a few hours at dawn each day over a 2- to 3-month display season. During the mating peak, which typically lasts 10–15 days, leks may also be intermittently active at dusk and on moonlit nights (Patterson, 1952). At typical stable leks (Gibson and Bradbury, 1987), males compete for small mating territories and, when females are present, repetitively perform a stereotyped vocal "strut" display (Wiley, 1973). Females usually visit leks for 1 to 3 days each before mating and often move widely through the lek, apparently "sampling" males, before soliciting copulation (Lumsden, 1968; Gibson and Bradbury, 1986; Bradbury et al., l989b). The occurrence of such behavior strongly suggests that females carefully assess potential mates. When coupled with the observation that mating success is highly skewed, it also argues that different females are relatively unanimous in their evaluation of preferred males.

Identification of male traits that provide the cues for female choice has been the objective of a number of recent studies. Although initial analyses came to conflicting conclusions concerning the importance of male phenotypic traits versus territorial characteristics (Wiley, 1973; Hartzler, 1972; Hartzler and Jenni, 1987), a recent study of a population in eastern California has provided evidence that male mating success is related to several individually variable components of lek display (Gibson and Bradbury, 1985, 1986; Gibson et al., unpublished). The most consistent predictors of mating success identified are lek attendance, the repetition rate of the strut display, and its acoustic "quality." The last includes specific temporal and frequency characteristics of vocal display components. By contrast such potential cues as territory location, body size, and age (above one year) appear less important. The combination of regular lek attendance and high display rates,

typical of successful males, is also associated with substantially elevated energetic expenditure (Vehrencamp et al., 1989) but without apparent longer-term mortality costs (unpublished data). This suggests that females are choosing males that are able to maintain high levels of energetically expensive display. This possibility is of particular interest for viability-indicator hypotheses, including the Hamilton-Zuk model, since the ability to meet increased energetic costs without elevated mortality could be associated with superior health and phenotypic vigor.

This paper extends the analysis of cues to examine whether individual variation in reproductively important components of male courtship display is related to the incidence of blood parasites. Studies of several other populations have demonstrated the existence of a variety of hematozoa in this species (Stabler et al., 1977; Boyce, 1990). Here I describe the pattern of occurrence of hematozoa sampled from a population in eastern California over a 5-year period and analyze its relationship to components of male display and breeding success. The analysis shows that hematozoa occur commonly in this population, but that levels of infection are low and are not related to display performance or mating success of adult males in ways predicted by the Hamilton-Zuk hypothesis. The discussion considers why these results differ from those obtained in another population (Boyce, 1990) and what alternative factors may account for differences in display performance in this population.

Study Area and Methods

Data were collected from a resident population of Sage Grouse in the Long Valley (Crowley Lake) area, Mono County, California, between January and May, 1984–1988. In each year, approximately 250 males displayed at 8 to 9 leks throughout the area. Movements of marked birds showed that leks were not associated with different subpopulations. Further details of the study area and population dispersion are given in Bradbury et al. (1989a, b). Birds were captured for marking and blood sampling by spot-lighting winter flocks during January and February, and in the vicinity of 3 different leks during the display season (early March to May). A few individuals were captured at leks using rocket nets. Birds were sexed based on size and plum age, and aged as adults (> 1 year) or yearlings using wing molt (Eng, 1955). In subsequent years banded birds were assigned minimum ages based on age at capture and elapsed time. All birds were marked with unique combinations of colored leg bands to facilitate individual recognition. For most individuals blood was collected from a clipped hallux nail to provide a thin film smear (for parasite screening) and a single 75 μl microcapillary tube for hematocrit estimation.

Data on mating success and display of parasite-sampled birds come from a single lek studied in each year from 1984 to 1987 and attended by an average of 20 to 30 males annually. The analysis of mate choice cues is based on a larger sample including two years' data from a second lek (Gibson et al., unpublished). Leks were observed by teams of 2 to 4 observers from a raised vantage point ca. 200 m from the lek. Observations of matings, and attendance and display rates of individual males were made from before dawn until the termination of the morning lek each morning between March 15 and the end of April. Using 15–40× telescopes it was possible to identify and monitor the activities of individual

males over the entire lek area. Sound recordings were made using Sennheiser MKH815 or 816TFU microphones and either high-quality reel-to-reel recorders (Nagra IV, Stellavox SP8) or a Canon VR40A videorecorder, from small blinds placed on the lek. Further details are given in Gibson and Bradbury (1985).

These samples yielded measures of the following variables:

Parasite infection: Blood smears were fixed with methanol, stained with Giemsa, and examined under oil immersion at ca. 1,000× magnification for presence or absence and infection levels of particular parasite genera. Five fields (approx. 1,000–1,500 red blood cells) were examined per slide. Parasite prevalence was scored as the presence/absence of detectable infection and infection intensity as the fraction of erythrocytes infected.

Hematocrit (fractional packed red cell volume): This was measured after centrifuging blood samples for 10 min at ca. 2,000 rpm as the length of the packed red cell column divided by total fluid column length.

Polychromatophilic cell %: The percentage of immature (polychromatophilic) erythrocytes was made from a count of 200 cells per slide using criteria given by Dein (1984). This measure should be higher in birds with elevated erythrocyte production and, in conjunction with hematocrit, serves to separate regenerative from nonregenerative anemia.

Lek attendance: The number of days between March 15 and April 30 that a male was present at the lek, expressed as a fraction of days on which the lek was surveyed. To eliminate spurious variation in attendance due to failure to recognize individuals early in the season, attendance data were computed only for males that were banded before or early in the current season.

Display rate: Display rates were computed from several (5 to > 30) samples in which the times of 21 consecutive strut displays were logged on a portable TRS80-100 computer and display rate computed as the mean of the reciprocal inter-strut interval lengths. All samples were taken when females were present at the lek. Raw display rate was simply the mean display rate across samples. This was available for a larger sample of birds but is subject to a contextual bias because males tended to elevate display rates when females were nearby. Moreover, males vary in their propensity to elevate display rates in response to female proximity. To control for context, display rates were regressed on female proximity (square root-transformed) separately for each male with ≥ 10 samples (n = 35) and the slope and intercept of the relationship used to characterize that individual's display "strategy." Both slope and intercept independently predicted mating status (whether a male obtained any matings) in a discriminant analysis (Gibson et al., unpublished). Because the discriminant score appropriately weights slope and intercept in terms of their reproductive significance, I used individual discriminant function scores as a single, contextually corrected measure of display rate. Despite the sampling bias inherent in raw display rate, the two measures were highly correlated (r = 0.802, n = 35, P < 0.0001).

Acoustic display quality: An extensive analysis of acoustic variability in the strut display (Gibson et al., unpublished) identified several measures of sounds emitted during the ter-

minal section of the display (two popping sounds 180–200 msec apart separated by a frequency-modulated whistle) as both individually variable and significantly correlated with mating success. Of these measures, some were related to mating success only in particular years. As a measure of acoustic quality, this analysis uses inter-pop interval, the interval between the amplitude envelope peaks of the two popping sounds, which was the most consistent acoustic correlate of mating success at lek 4. Seasonal mean inter-pop intervals were based on at least 10 displays per male per year, measured using Soundwave software on a Macintosh computer. Inter-pop interval was highly repeatable within individuals, both within and between seasons.

Mating success: This was the total number of females with which a male mated during each morning display session summed over the season. Because we were present each morning and could monitor the entire lek continuously, it is unlikely that we missed matings during the morning lek. Unobserved matings may also have occurred at low levels in the evenings and on moonlit nights, although males do not attend leks regularly at these times. Mating success serves as an integrated measure of male attractiveness to females, combining the effects of identified male traits plus any unidentified components. Although fighting between males could also be influential at unstable, nonterritorial leks (Gibson and Bradbury, 1986, 1987), it was probably unimportant in this sample because few matings occurred away from male territories.

Statistical analysis

With the exception of parasite prevalence, which was analyzed as a binary variable using logistic regression, parametric statistical methods were used throughout. Variables were transformed where necessary to meet assumptions of normality. Individuals for which both parasite and display measures were obtained formed only a subset of the total birds for which either variable was sampled, resulting in small sample sizes in each year. Therefore data for these contrasts were pooled across years. Since individuals were seldom resampled for parasites in different years, this does seriously affect independence. However, annual shifts in mean values of either traits or parasites could have biased results. To guard against this, mating success was standardized across years by dividing by its annual mean value (to yield relative mating success). No display measure varied significantly across years. Annual shifts in mean parasite incidence were statistically controlled by including mean annual parasite intensity as a covariate in the partial correlation analyses (cf., Heisler and Damuth, 1987).

Results

Incidence of blood parasites

A single haemosporidian parasite genus, *Haemoproteus*, was found in 37.5% of 184 birds examined between January 1 and May 30. The sample included 148 males (124 adults, 22 yearlings, 2 not aged) and 36 females (16 adults, 19 yearlings, 1 not aged). Among infected individuals up to 6% of erythrocytes were infected but intensities were typically lower (mean = 0.557%, SD = 1.06, n = 69). No other blood parasites were detected.

The proportion of birds infected with *Haemoproteus* varied significantly between years and through the season (Table 1). *Haemoproteus* prevalence increased through the breeding season in each year. Simple bivariate analyses suggested that infections were also more frequent in males than females and in adults than in yearlings. However, after controlling for year and capture date, the partial effects of age and sex became nonsignificant (Table 1). There was also no evidence that parasite incidence varied across leks. Among 127 males trapped during the display season the proportions of infected individuals did not differ significantly between three leks separated by 3–5 km from each other (simple $\chi^2 = 2.53$, df = 2, $P = 0.282$; partial effect of lek, controlling for year and date: $\chi^2 = 0.06$, df = 2, $P = 0.972$).

Table 1. Effects of year, date, age, and sex on the prevalence of *Haemoproteus* infections in Sage Grouse at Long Valley, 1984–1988*

	Simple regressions			Partial regression		
Variable	χ^2	df	*P*	χ^2	df	*P*
Year	17.59	4	0.0015	10.0	4	0.0403
Date	32.41	1	<0.0001	18.86	1	< 0.0001
Sex	7.91	1	0.0049	2.15	1	0.1425
Age	5.33	1	0.021	1.74	1	0.1874
Multiple logistic regression model				47.27	7	< 0.0001

* Logistic regressions: $n = 179$

Hematological correlates of parasitism

Severe hematozoan infections might be expected to lower hematocrit, or to stimulate increased erythrocyte production, or to have both effects. To evaluate the severity of the observed infections, I examined relationships between *Haemoproteus* infection intensity (% cells infected) and both hematocrit and the proportion of polychromatophilic cells, a measure of erythrocyte production (see Methods). Hematocrits were available for a subsample of birds screened for parasites. Polychromatophilic cell counts were made only for males whose hematocrit and parasite levels had both been sampled.

Hematocrit values were high (mean = 0.584, *sd* = 0.048, $n = 89$; all sex and age classes pooled) relative to published values for other avian species (Sturkie, 1986) and showed no significant negative correlations with *Haemoproteus* infection level whether computed for the entire sample ($r = 0.027$, $n = 89$, $P = 0.802$), or for particular age and sex classes. The only significant relationship was a positive correlation, counter to the predicted direction, among yearling males ($r = 0.71$, $n = 10$, $P = 0.0215$). Hematocrit varied slightly between age and sex classes, being elevated 3–4% in yearling over adult males and depressed by a similar amount in yearling compared to adult females (age vs. sex interaction: $F_{1,85} = 5.731$, $P = 0.019$). It was also positively correlated with body weight among adult males ($r = 0.276$, $n = 57$, $P = 0.038$) and declined through the breeding season among females ($r = 0.552$, $n = 21$, $P = 0.001$). The latter effect was particularly marked among females that were known to have nested, and may be an effect of egg production, which is known to lower hematocrit in other avian species (Sturkie, 1986). Although either of these additional factors might

have confounded simple correlations between *Haemoproteus* levels and hematocrit, no parasite-related depression of hematocrit was detected even removing the effects of body weight (for males) or date (for females) using partial regression.

The proportion of immature (polychromatophilic) erythrocytes was low (≤ 11%) in all birds examined ($n = 50$ males). Values in excess of 10% are considered to be associated with elevated erythrocyte production (Dein, 1984). Within the observed range of variation there was also no evidence that *Haemoproteus* infection raised erythrocyte production: in fact correlations were negative, rather than positive, for both adult ($r = –0.221$, $n = 41$, $P = 0.162$) and yearling males ($r = –0.835$, $n = 9$, $P = 0.005$).

Overall, these data suggest that the observed levels of *Haemoproteus* infection neither depressed hematocrit nor increased erythrocyte production.

Parasitism, courtship display, and mating success of adult males

Increased parasite loads might reduce male attractiveness to females by lowering any of lek attendance, display rate, or acoustic display quality. These, plus any additional effects on unidentified components of male attractiveness, should cumulatively depress male mating success.

Table 2 shows correlations between *Haemoproteus* levels and measures of each component of male courtship display for lek 4 males from 1984–1987. Without controlling for the date on which parasites were sampled, most of the correlations between display traits and *Haemoproteus* level are positive (and nonsignificant) rather than negative. However, these contrasts are only appropriate if, as seems unlikely, individuals maintain the same parasite levels throughout the season. With seasonal changes in *Haemoproteus* level held constant by partial correlation, some of the relationships became negative but none was significant (Table 2). This assumes that males retain the same relative parasite level through the season. Finally, since parasite levels increase rapidly in late April and might be uncorrelated with those earlier in the season when female attendance and matings peak, the analysis was repeated using only parasite data collected before mid-April; again there were no significant negative relationships. Similar results were obtained from a logistical regression analysis that examined the prevalence of *Haemoproteus* (proportion of birds infected) rather than infection intensities. Individual variation in courtship display and mating success were thus unrelated to *Haemoproteus* infection.

Table 2. Correlations between *Haemoproteus* infection intensity and components of courtship display and breeding success among adult male Sage Grouse at lek 4, 1984–1987

	Comparison*		
	I	II	III
Courtship trait	*r*(n)	*r*(n)	*r*(n)
Attendance	0.126 (27)	–0.050 (27)	–0.291 (18)
Display rate (raw)	0.050 (31)	0.057 (31)	0.028 (15)
Display rate (corrected)	0.140 (21)	0.125 (21)	–0.104 (9)
Inter-pop interval	0.068 (22)	–0.162 (22)	–0.484 (8)
Relative mating success	–0.042 (42)	–0.211 (42)	0.342 (18)

*I: Partial correlations, controlling for annual changes in parasite level using the annual mean. II: Partial correlations controlling for both year (as for I) and season using both date and date-squared. III: Simple correlations, using only early season parasite data (no annual or seasonal bias was detectable in this subsample). Rationales for each contrast are discussed in the text. None of the correlations is significant at the 5% level.

Although *Haemoproteus* appears unimportant, it is feasible that other parasites, not necessarily located in the circulatory system affected display. Because any parasite that consumes blood might be detectable through lowered hematocrits and/or elevated erythrocyte production (Dein, 1984), I also examined the relationships of the same set of display traits to hematocrit and polychromatophilic cell index to determine whether there might be undetected parasites that could be playing a role suggested by the Hamilton-Zuk hypothesis. If so, display traits should be related positively to hematocrit and negatively to the proportion of polychromatophilic (immature) erythrocytes. However, there were no significant positive correlations between hematocrit and any of the display traits or mating success (n varied from 10 to 24 across traits). High negative correlations were found between the polychromatophilic cell index and three measures: corrected display rate ($r = –0.651$, $n = 8$, $P = 0.080$), inter-pop interval ($r = –0.699$, $n = 13$, $P = 0.008$), and relative mating success ($r = –0.598$, $n = 20$, $P = 0.005$). These are in the predicted direction, but the low proportion of polychromatophilic cells (see above) argues that erythrocyte production was not elevated above normal levels in any of these individuals. The data thus do not strongly support the idea that differences in courtship display and breeding success were affected by undetected parasites.

Discussion

The data provided evidence that hematozoa occur commonly in this population of Sage Grouse, that levels increase through the breeding season and also vary annually. A similar seasonal increase in hematozoa was reported by Stabler et al. (1977) in Colorado. The seasonal pattern might represent either a relapse among chronically infected individuals, perhaps as a result of reproductive stress, or an increase in infection rates, or both. If the former were true the effect should be particularly marked among adult males, the population segment most heavily involved in lek display, but there was little supporting evidence. The latter possibility is consistent with the evident build-up of potential insect vector populations during April (personal observations).

There was little evidence, however, that individual variation in male courtship display and mating success are linked to variation in hematozoan infections. The absence of significant negative relationships between parasite load and components of display is not compelling on its own, since detection of weak effects might require larger sample sizes. However, several other observations combine to suggest that hematozoan infections were not severe enough to impact courtship display. These include the numerically low infection intensities, absence of detectable effects on hematocrit and erythrocyte production, and the fact that infections were particularly light during the period when most females visited leks and mated.

If hematozoa were not involved, what other factors can explain individual variation in display and mating success? One possibility is that other undetected parasites or pathogens were involved. This cannot be excluded because the samples could not have detected parasites located in other tissues or any that exerted long lasting effects following transient infections. Nevertheless, the former alternative is somewhat weakened by the failure of the hematological measures to provide evidence of regenerative anemia that could have implicated other parasites. A second hypothesis that has often been suggested, is that females choose males on the basis of traits that reveal age and that older birds, through natural selection and/or greater experience, are more effective in accruing resources for reproduction. However, age explained little of the variation in mating success or any correlated display traits (Gibson et al., unpublished).

An alternative hypothesis is suggested by the results of a recent study of energy metabolism in displaying males in this population (Vehrencamp et al., 1989). The study found that higher levels of lek attendance and display rate were associated with increased metabolic expenditure. Increased metabolic activity was apparently not supported by greater reliance on endogenous reserves. Although all males lost some weight during the breeding season, higher levels of display and metabolic rates were associated with reduced rather than increased weight loss. Instead the data suggest that increased courtship activity could be fueled by increased quantity or quality of food intake, since more actively displaying males utilized foraging ranges located further from the lek. While it remains to be seen whether foraging ranges are causally linked to display effort and, if so, what factors maintain differential range utilization, current data do suggest a basis for individual differences in display that is an alternative to the unsupported parasite hypothesis.

These results present an interesting contrast to those from a population in Wyoming (Boyce, 1990 and personal communication). Lek mating behavior was broadly similar in the two populations, but there were clear differences in both the diversity of hematozoa present and in their relationship to male mating success. Whereas *Haemoproteus* was present in both populations, several other forms also occurred in the Wyoming birds and one of these (*Plasmodium*) occurred less frequently among reproductively successful males. Thus blood parasite incidence can, but need not, be related to differential mating success at leks in this species. If females choose males based on differences in courtship display performance, as our earlier studies suggest, then this may not be surprising. The ability to sustain high levels of energetically costly courtship display on a daily basis over several weeks is liable to depend on a variety of factors, of which parasites are only one. Behavioral performance cues are likely to integrate the effects of many different factors, whose relative

contribution to individual variation in display may vary between populations and over time. Parasites may be expected to play a role in populations where particularly virulent forms are prevalent, or where infection intensities are particularly high. Neither appeared to be the case for hematozoan parasites in the Long Valley population.

The implication of performance cues that can but need not be related to hematozoan infection in Sage Grouse is compatible with a number of different views of the Hamilton-Zuk parasite hypothesis. One is that parasites provide the main selective force maintaining mate choice, but that there are periods when the process does not act. A second interpretation is that Hamilton-Zuk effects are only one of several mutually interchangeable processes maintaining mate choice. Finally it is possible that other forces have resulted in the evolution of these particular mate choice cues and the parasite effects in particular populations are incidental. Among the alternative models of indirect selection on mating preferences, the existence of performance cues is most obviously predicted by condition-dependent handicap models, but it could also be accommodated by Fisherian models (Heisler et al., 1987; Kirkpatrick, 1987). It is evident that phenotypic vigor could also be an indicator of fertility or an ability to deter competitors from interrupting mating activity, either of which might provide a direct selective advantage for mate choice (Clutton-Brock et al., 1988). Other kinds of evidence, including tests of the feasibility of alternative processes and theoretical study of the conditions under which the parasite hypothesis is effective, will be needed to evaluate these alternatives.

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