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To: Martini, Jay
Subject: Re: I need some of your past work!
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ahhh - here you go. autographs extra

On Wed, May 14, 2014 at 10:41 AM, Martini, Jay <jay_martini@fws.gov> wrote:

> Thanks Pat,
>
> Having tons of fun doing the BLM lit review stuff...
>
> On Wed, May 14, 2014 at 10:21 AM, Pat Deibert <pat_deibert@fws.gov> wrote:
>
> > Hmmm - can't believe I didn't make google scholar! Will see if I have electronically when I get back to the office. Basically girls don't like guys with bugs - duh.
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> > >
> > > Deibert, P.A. 1995. Effect of parasites on sage grouse (Centrocercus urophasianus) mate selection. PhD Thesis, Univ. of Wyoming, 127 pp.
> > >
> > >
> > > Thanks
> > > --
> > > Jay Martini
> > > U.S. Fish and Wildlife Service
> > > Utah Ecological Services Field Office
> > > 2369 W. Orton Circle
> > > West Valley City, Utah 84119
> > > ph: 801-975-3330, ext. 144
>
> --
> Jay Martini
> U.S. Fish and Wildlife Service
> Utah Ecological Services Field Office
> 2369 W. Orton Circle
> West Valley City, Utah 84119
> ph: 801-975-3330, ext. 144

--
Pat Deibert
National Sage-grouse Conservation Coordinator
U.S. Fish and Wildlife Service
5353 Yellowstone Road, Suite 308A
Cheyenne, WY 82009
307-772-2374, ext. 226

got leks?

EFFECT OF PARASITES ON SAGE GROUSE (*Centrocercus urophasianus*) MATE SELECTION

by

Patricia A. Deibert

A thesis submitted to the Department of Zoology and Physiology and The Graduate School of The University of Wyoming in partial fulfillment of the requirements for the degree of

DOCTORATE OF PHILOSOPHY
in
ZOOLOGY AND PHYSIOLOGY

Laramie, Wyoming
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Deibert, Patricia A. Effects of parasites on Sage Grouse (Centrocercus urophasianus) mate selection, PhD., Department of Zoology and Physiology, December 1995.

Research was conducted in southeastern Wyoming to clarify the role of the Hamilton and Zuk hypothesis in evolution and maintenance of lekking in sage grouse (*Centrocercus urophasianus*). Three parasites, avian malaria (*Plasmodium pediocetii*) and two species of lice (*Lagopoecus gibsoni, Goniodes centrocerci*, Order Phthiraptera) influence male sage grouse mating success.

Breeding male sage grouse had lower hematocrits than non-breeders. No other morphological comparison was significantly different between these groups. But, breeders attend the lek and display more frequently than non-breeders. Avian malaria negatively influenced male mating success by reducing lek attendance. Infected breeders secured copulations late in the season, when females are likely to be yearlings or adults in poor condition. The presence of lice was associated with increased body mass, longer body lengths, shorter bills, longer tarsi, and higher condition indices. We were unable to demonstrate that any of these features were related to female mate choice. "Lousy" breeders secured fewer copulations than uninfected breeders, and bred late in the season. Prevalence of both parasites varied among years, which may provide

evidence of a constantly changing host-parasite interaction. Females were less likely to bear either parasite than males.

A reduction of parasite prevalence in yearling birds was related to intensity of female choice for un-parasitized males and relative fitness of un-parasitized males indicates sage grouse may have a heritable resistance to malaria, but not lice. Therefore, malaria data support the Hamilton and Zuk hypothesis for sage grouse. The lice data are more consistent with a parasite avoidance model.

Electrophoretic analysis of blood enzymes revealed sage grouse have genetic variability comparable to other birds even though expected effective population sizes for lekking species are small. Inter-lek migration may help maintain variability in this species. Significant allelic frequency differences were found between birds with and without malaria and adult males and females. Also, yearling males were less heterozygous than adult males. These results suggest malaria, intersexual differences in selection pressures, and heterosis may also maintain genetic variability in sage grouse.

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Effect of Avian Malaria and Lice on Mate Selection in Sage Grouse (*Centrocercus urophasianus*).

Introduction

In lekking species, near unanimity of female choice for a small proportion of available males results in an asymmetrical distribution of male reproductive success (Bradbury et al. 1985; Hartzler and Jenni 1988). Males provide no nest defense or parental care to females or their offspring. The only apparent advantage to females from such strong selection is the male's genetic "quality" (Bradbury and Andersson 1987). However, intense selection for preferred traits erodes their heritability, and eventually all males should be genetically similar. Therefore, it is difficult to understand why females show such strong preference for certain mates. In species that gain clear economic benefits by being selective, mate choice mechanisms do not seem as highly developed. This is the lek paradox (Borgia 1979; Taylor and Williams 1982).

In 1982, Hamilton and Zuk offered their bright bird hypothesis as a possible "good genes" mate choice alternative. They proposed that condition and degree of development of secondary sexual characteristics may reflect resistance of a potential mate to parasites or pathogens. Their hypothesis assumes parasite resistance is heritable and, therefore, females may select mates which confer that resistance to their offspring. Dynamic interactions between parasite and host may maintain genetic variability for resistance and, thereby, preferred traits. The Hamilton and Zuk

Kirkpatrick (1986) concluded host-parasite systems possess the interactive dynamics necessary to influence evolution, as long as required initial gene frequencies for preferred characteristics exist. But most parasite/sexual selection studies fail to examine the relationship between mate choice and heritable resistance, even though results may support two or three predictions of the Hamilton and Zuk hypothesis. Only Hillgarth (1990) and Moller (1990b) have provided evidence linking mate choice and heritable parasite resistance. Their studies, however, offer no evidence of the parasite and host dynamics necessary to prevent genetic fixation of preferred traits (Clayton 1991a).

Lekking species, such as sage grouse (*Centrocercus urophasianus*), provide an excellent opportunity to examine the potential role of the Hamilton and Zuk hypothesis in mate selection because males often possess elaborate secondary sexual characteristics. Female evaluation of these characters may provide information regarding a potential mate's parasite status. Since males provide only sperm, complications due to male contribution to parental care are avoided (Hoglund et al. 1992). The Hamilton and Zuk hypothesis may also offer an intriguing solution to the lek paradox (Taylor and Williams 1982) by explaining genetic variation for traits under intense sexual selection (Boyce 1990; Kirkpatrick and Ryan 1991) (but see also Mackenzie et al. 1995).

Blood parasites and avian mate choice

In their original parasite/sexual selection paper, Hamilton and Zuk (1982) found a positive relationship between extravagance in plumage brightness and song and the incidence of blood parasite infections (Moller 1990c). Although re-analysis of the data suggests phylogeny is more influential than parasites in determining passerine song complexity (Moller 1990b), other avian studies provide clear evidence of a negative blood parasite influence on mate choice. Blood parasite infections are negatively correlated with male showiness across ten species of birds-of-paradise (Pruett-Jones et al. 1990), a characteristic influential in female mate choice. Black grouse (*Tetrao tetrix*) males with *Leucocytozoan* infections are less successful in securing mates than uninfected males (Hoglund et al. 1992). Infected male grouse also had shorter tails and lower body mass, both important cues in female mate selection. Other studies have also demonstrated a negative relationship between blood parasite infections and some measure of reproductive success (Boyce 1990; Moller 1990a; Moller et al. 1990; Zuk 1990).

Ectoparasites and Avian Mate Choice

Many studies have identified ectoparasites as an important influence on avian mate choice. One of the most thorough demonstrated the negative influence of a common hematophagous mite, *Ornithonyssus bursa*, on barn swallows (*Hirundo rustica*). Male barn swallows with longer tails had fewer mites, arrived earlier in the breeding season (Moller 1990a), and were preferred as mates (Moller 1988). Further

studies illustrated that male swallows with long tail ornaments had offspring with smaller mite loads, implying heritability of parasite resistance (Moller 1990b). Females also preferred males with symmetrical tails, suggesting symmetry may provide a reliable indication of male quality (Moller 1992, Thornhill 1992). These results support the Hamilton and Zuk hypothesis.

Presence of chewing lice also decreases reproductive success for captive rock doves (*Columba livia*) because of less frequent courtship display (Clayton 1990). An inverse correlation between female mate preferences and level of male parasitic infestation was also found for satin bowerbirds (*Ptilonorhynchus violaceus*) and their common ectoparasite, *Myrsidea ptilonorhynchi* (Borgia and Collis 1989). Results of both studies were consistent with some predictions of the Hamilton and Zuk hypothesis. However, female preference for uninfested mates of both bird species was also consistent with other parasite avoidance hypotheses. Females may avoid males with ectoparasites because presence of a parasitic infestation indicates low overall male resistance to disease (correlated infection hypothesis) (Borgia and Collis 1990), or because avoidance decreases the probability a female will become infested (parasite avoidance hypothesis) (Borgia and Collis 1990).

Parasites and Sage Grouse Mate Choice

Avian malaria (*Plasmodium pediocetii*) appears to negatively influence sage grouse mate choice (Boyce 1990; Johnson and Boyce 1991). Parasitized males are usually avoided (Johnson and Boyce 1991; Spurrier et al. 1994), and male lek

attendance has been correlated with a lack of infection (Johnson and Boyce 1991). Female sage grouse are very selective. As few as 5% of the males on a lek may account for 90% of the copulations (Wiley 1978, 1991; Johnson and Boyce 1991). These results are consistent with the Hamilton and Zuk hypothesis. But little information is available on morphological cues that assist female sage grouse in selecting mates and discerning malarial males. Gibson (1990) was unable to identify any morphological feature that appeared to influence mate choice in sage grouse. He also did not find any correlation between a hematozoan infection and sage grouse mating success.

Chewing lice also appear to influence mate selection in sage grouse. These parasites are more common on non-breeding males, and uninfested breeders secure more copulations than infested breeders (Johnson and Boyce 1991). Presence of hematomas on male gular sacs is positively correlated with a louse infestation, suggesting the parasites cause these marks as a result of feeding on dermal material. Females appear to use this cue to select louse-free mates (Johnson and Boyce 1991). Application of artificial hematomas on gular sacs, simulating a louse infestation, decreased the attractiveness of males to females (Spurrier et al. 1991).

While initial results of the interactions between sage grouse and malaria, and sage grouse and lice are intriguing, the only conclusions that can be drawn is that these parasites affect mate choice in sage grouse. I designed a field study to identify physical and behavioral cues female sage grouse use to select mates, and how females distinguish between males with and without a malarial or louse infection. By examining

a wide range of both behavioral and morphological parameters, I assessed the influence, if any, of malaria or lice on preferred characteristics. Heritability (h^2) may be estimated by measuring a response to selection, as described by $h^2 = R/S$, where R is response to selection, and S is selection differential (Falconer 1989). If sage grouse are resistant to malaria and/or lice, and the resistance is heritable, prevalence should decline over time in response to selection for uninfected mates. Similarly, if un-parasitized males are more fit, and resistance to the parasite is heritable, parasite prevalence may decline over time. I attempted to determine if sage grouse have resistance to malaria or lice by measuring parasite loads in subsequent generations based on mate selection for un-parasitized males.

Methods

Measurement of sage grouse physical characteristics

My research was conducted on eight leks in southeastern Wyoming, 25 to 100 km north of Laramie (Fig. 1), from 1987 through 1990. Sage grouse were captured on or near leks by spotlighting and rocket netting during the breeding season (Giesen et al. 1982). A series of morphological measurements were taken for each bird captured: body mass, tail, keel, tarsus, toe, comb, and total body length; and bill length and depth. Tail feathers were counted and a tail was categorized as asymmetrical if it contained an uneven number of feathers. A condition index was calculated as weight/(keel length)^3 (Johnson and Boyce 1991). Color of gular sacs and combs were determined by direct comparison to a philatelic color strip.

One to 3 ml of blood were taken from the brachial vein. Two blood films were made for each bird and preserved in methyl alcohol. Slides were later stained with Giemsa and examined under oil immersion (1000x) for the presence of *Plasmodium* spp. Ten fields (a total of approximately 2000 - 3000 red blood cells) were examined per slide (Gibson 1990). A hematocrit was determined by centrifuging two 75 ul capillary tubes of blood for 5 min at 2000 rpm (Gibson 1990). The average of two samples per bird was used as the hematocrit estimate for each individual.

Birds were examined for presence of lice in areas difficult to preen, such as back of the head, combs, and gular sacs (Ash 1960). Samples of ectoparasites were collected for identification.

Each bird was marked with a unique color combination of numbered patagial tags for subsequent identification during behavioral observations. Feathers were clipped from the patagium to make the tags more visible. Collected feathers were later examined for evidence of louse damage. The marked bird was then released on the same lek of capture.

For every bird recaptured during the lekking season body mass was re-measured. Another blood sample was taken to examine any change in blood parasite status and each bird was again examined for the presence of ectoparasites. An entire series of morphological and blood measurements were taken for each bird recaptured in subsequent years.

Sage grouse behavior

Leks were observed from 1/2 hr before sunrise until 1 hr after sunrise. Total number of males and females present, lek attendance by marked individuals, breeding status, and number of copulations were recorded. The number of struts per 5 min interval (strutting frequency) were counted for each marked bird. Since proximity of females and time of day influence strutting frequency (Hartzler and Jenni 1988), data were corrected for these effects using the regression procedure described by Gibson and Bradbury (1986).

Effects of malaria and lice on sage grouse morphology

To determine female preference for any male morphological characteristic, measured differences between breeders and non-breeders were examined. A breeder was defined as any male which secured at least 1 copulation during the lekking season. Juvenile (yearling) males were rarely selected as mates, and exclusion of this cohort from statistical analyses reduced the confounding effect of age on morphological development (Hoglund et al. 1990). Effect of malaria or lice on morphology was estimated by comparing infected and uninfected adult males. Color was analyzed by determining numerical values of the three Munsell color components (hue, chroma, and color; Endler 1990) for each gular sac and comb color. Potential differences of gular sac and comb colors were compared between breeders and non-breeders, and infected and uninfected birds.

I compared tail symmetry between breeders and non-breeders, and males with and without malaria or lice. The potential effect of tag color and tag "symmetry" (the same color of tags on both wings) on mate selection was determined by comparing the number of breeders and non-breeders with each color. Influence of tags on mate selection was also determined by comparing the number of unmarked breeding and non-breeding males observed on each lek with the number of marked breeders and non-breeders attending the lek.

With the exception of gular sac and comb color, all morphological comparisons were analyzed with a t-test for means. Differences in gular sac and comb colors were tested via a multiple linear regression, with the components (hue, chroma, and color), and their interaction as variables. Symmetry and tag comparisons were analyzed with a chi square test. A possible sampling bias due to date of observation was also examined via a chi square analysis. Power analyses were conducted on all non-significant results to determine probability of a type II error (false acceptance of a null hypothesis) (Cohen 1988; Peterman 1990).

Parasite prevalence

Both malaria and lice prevalence in sage grouse were measured for each lek and year to determine if there were significant temporal variations as predicted by the Hamilton and Zuk hypothesis (Boyce 1990). To determine if malaria prevalence changed during the breeding season, a regression was made of the number of males positive for malaria against their initial date of capture. Data were pooled across leks,

but years were examined independently. Prevalence of both parasites was determined for each lek and compared with the number of copulations secured on each lek to determine if females may select against leks with a high prevalence of either parasite.

Female choice, male fitness, and heritable resistance

If females prefer un-parasitized males, those males should secure more copulations than birds with parasites. Intensity of female choice, *I*, was calculated as [number copulations by parasite free males/ number copulations of all males] - [1-(total number copulations observed x prevalence of parasite)/number of copulations of all males]. If mate choice is independent of male parasitic condition *I* should equal 0. Intensity of female choice values were calculated for each year.

Because some parasitized males do breed (Johnson and Boyce 1991), I also calculated a measure of relative fitness for uninfected breeders. Determination of this value used number of copulations and proportion of adult and yearling hen attendance relative to date. Females attending the lek late in the season tend to be in poor condition or are yearlings or re-nesting females (Johnson and Boyce 1991). Yearling female sage grouse do breed, but they ovulate fewer follicles, lay smaller clutches and are less successful at raising a brood (Wallestad and Pyrah 1974; Moller 1990a). Re-nesters also lay a smaller clutch. Therefore, it is presumably advantageous for males to breed as early in the season as possible to enhance their reproductive success.

Fitness for parasite-free male breeders was estimated to be:

$$W_f = C_{fc}[(p_{ac}*6.92)+(p_{jc}*3.07)] + C_{fl}[(p_{al}*6.92)+(p_{jl}*3.07)]$$

where:

C_{fe} = number of copulations/male by un-parasitized males early,

C_{fl} = number of copulations/male by un-parasitized males late,

p_{ae} = proportion of adult females attending early,

p_{je} = proportion of yearling females attending early,

p_{al} = proportion of adult females attending late,

p_{jl} = proportion of yearling females attending late,

6.92 = average clutch size of adult females, and

3.07 = average clutch size of yearling females (Wallestad 1975).

"Early" or "late" was determined by the peak of hen attendance each year, defined here to be April 19. Females attending prior to or at the peak of hen attendance were included in the "early" group. Females attending after that date were included in the "late" group.

Likewise, fitness for parasitized male breeders was calculated as:

$$W_p = C_{pe}[(p_{ae}*6.92)+(p_{je}*3.07)] + C_{pl}[(p_{al}*6.92)+(p_{jl}*3.07)]$$

where:

C_{pe} = number of copulations/male by parasitized males early, and

C_{pl} = number of copulations/male by parasitized males late in the season.

With the assumption of equal survivorship between males with and without parasites, relative fitness for un-parasitized breeders was then defined to be:

$$W_r = (W_f - W_p)/\overline{W};$$

A positive W_r suggests a higher fitness for un-parasitized breeders, while a negative W_r implies higher fitness for breeders with parasites. The W_r values were calculated for each lek and year.

Possible heritability of resistance to either parasite was estimated by regressing the change in prevalence in all birds (Y_a) from year t to year t+1 against both I and W_r. This analysis was repeated for change in prevalence in male birds only from year t to year t+1 (Y_m). I also calculated the differences in parasite prevalence between yearling and adult birds from year t to year t+1 (Y_{aj}). Parasite prevalence differences between yearling birds only at year t and year t+1 were also calculated (Y_{jj}). All prevalence differences were calculated for each lek and year. The differences were individually regressed against both I and W_r. I repeated these calculations using male data only. Changes in parasite prevalence between years t and t+1 were also calculated between adult and yearling males only (Y_{am}), and between yearling males only (Y_{jm}). These values were then independently regressed against both I and W_r. All abbreviations are summarized in Table 1.

Scale of female choice

Females may move between leks during the breeding season before selecting a mate (Patterson 1952; Dunn and Braun 1985). If females prefer males without either malaria or lice, they may avoid leks with a high prevalence of these parasites. Therefore, data were also analyzed excluding any lek on which fewer than five copulations were observed. This reduces the potential errors in data interpretation if

females are selecting against leks with high prevalence of either parasite. Similarly, individual leks are unlikely to be individual populations. Regressions were also run on two groups of leks which were defined as distinct populations based on presence of approximately 30 km of grassland, unsuitable habitat for sage grouse, between the groups (Fig. 1). Mixing of birds between these areas is possible, but unlikely given typical dispersal distances (Dunn and Braun 1985; Connelly et al. 1988). The southern "population" consisted of four leks (Mud Springs, Long Lake, Sybille Springs, and Viewpoint), while the northern "population" consisted of two (North and Cordingly). Power analyses were conducted on all non-significant results.

Results

Morphological, hematocrit, and tag differences between breeders and non-breeders

No morphological differences were statistically significant between breeders and non-breeders (Table 2). But, breeding males had lower hematocrit values than non-breeding males (t=2.55, 135 d.f., P=0.019, N=328) (Table 3). Presence of patagial tags appeared to influence mate choice; breeders were more likely to have tags than non-breeders (X^2=62.09, 1 d.f., P<0.001, N=328) (Table 4). However, breeding status was apparently not influenced by tag color (X^2=4.1, 6 d.f., P=0.65, N=328, power=0.31) or tag symmetry (X^2=0.10, 1 d.f., P=0.89, N=328, power=0.03) (Table 4).

Malaria, morphology, and hematocrits

Only one morphological difference was statistically significant between adult male sage grouse without malaria and adult males with malaria. Males without malaria had longer tails (t=2.12, 325 d.f., P=0.037, N=328) (Table 5). No differences in gular, air sac colors or hematocrits were detected (Table 6).

Lice, morphology, and hematocrits

Lice removed from captured sage grouse were identified as *Lagopoecus gibsoni* and *Goniodes centrocerci*, of the suborder Ischnocera. Species of this suborder are obligate parasites that feed on feather and dermal debris. They usually complete their entire life cycle on one host, but will transfer between hosts during direct contact (Clayton et al. 1992).

Several morphological characteristics differed significantly between male sage grouse with and without lice when data from all years were combined (Table 7). Males without lice weighed less (t=2.16, 324 d.f., P=0.034, N=328), had shorter total body lengths (t=2.95, 326 d.f., P=0.005, N=328), and longer bills (t=4.52, 326 d.f., P<0.001, N=328) than infested males. Tarsi were longer in males carrying a louse infestation (t = 2.12, 326 d.f., P=0.037, N=328), and "lousy" birds had a higher condition index (t=2.29, 326 d.f., P<0.001, N=316). I found no apparent effect of lice on tail symmetry (X^2=0.115, 1 d.f., P=0.84, N=219, power=0.07). No difference in gular sac colors, comb colors, or hematocrits were found between males without lice and males with lice (Table 8).

In 1987 and 1988, bill lengths of uninfested adult males were significantly longer than those of infested males (t=2.44, 103 d.f., P=0.016, N=105, and t=2.00, 86 d.f., P=0.05, N=88). This difference was not observed in 1989 and 1990 although bill length was significantly shorter in males with lice when all years are combined (see above). To determine if bill length varied in response to changing lice prevalence, change in mean bill length from time t to time t+1 was regressed against prevalence of lice within a lek at time t. I found no significant correlation between these variables, but statistical power of the analyses is low (power = 0.07).

No feather damage as the result of lice was observed on feathers collected from the patagium. However, this may not accurately indicate that either species of lice significantly damages feathers in sage grouse, as these parasites are not commonly found on the patagium (Ash 1960).

Breeding status and behavior

Number of struts per 5 min interval (corrected for distance to hens and time from sunrise, Gibson and Bradbury 1986) was significantly higher for breeding males than non-breeders (t=5.11, 1 d.f., P<0.001, N=1078) (Table 9). Analysis on all years of data revealed consistent lek attendance by adult males prior to the peak of hen attendance (usually on or near April 19) was also a reliable predictor of breeding success (logistic regression, X^2=29.32, 6 d.f., P<0.001).

Effect of malaria on sage grouse behavior

No difference in strutting frequency was observed between sage grouse with and without malaria (t=1.45, P=0.39, N=917, power=0.68). In 1987 and 1988, male sage grouse with malaria attended leks less frequently than non-infected birds (t=3.01, 1 d.f., P=0.005, N=206). However, in 1989 and 1990, lek attendance was significantly higher for males with malaria (t=2.55, 1 d.f., P=0.019, N=243). This may be a result of observer bias, as behavioral observations in 1989 and 1990 were more frequent after the peak of hen attendance than they were in 1987 and 1988 (X^2=6.35, 2 d.f., P=0.04, N=388) (Fig. 2). There was no difference in number of copulations secured by breeders with and without malaria (X^2=0.303, 1 d.f., P=0.76, N=127, power=0.20) (Table 9), but breeders with malaria (N=9) copulated significantly later than uninfected breeders (N=29) (X^2=11.60, 2 d.f., P=0.004) (Table 9; Fig. 3).

Effect of lice on sage grouse behavior

Adult male sage grouse with lice strutted as frequently as uninfested males (struts per 5 min interval) (t=0.84, 189 d.f., P=0.40, N=192, power=0.26). The presence of lice had no apparent effect on male sage grouse lek attendance (t=0.967, 269 d.f., P=0.34, N=196, power = 0.03). Breeders with lice (N=11) secured significantly fewer copulations than louse-free males (9 and 76 copulations, respectively) (X^2=10.40, 1 d.f., P=0.002), indicating a female preference for uninfested birds (Table 9). Additionally, infested breeders bred later in the lekking season than breeders without lice (X^2=3.87, 1 d.f., P=0.049, N=134).

Prevalence of malaria and lice

Malarial prevalence was not significantly different between breeding (23.7%) and non-breeding males (27.8%) (X^2=0.29, 1 d.f., P=0.75, N=328, power=0.33) (Table 10). But malaria was significantly more frequent in adult males captured late in the season (t=2.40, 327 d.f., P=0.017, N=267), a trend not observed among all birds, or breeding males only. No difference in prevalence of infection was observed between yearling (26.1%, N=88) and adult males (26.5 %, N=339) (X^2=0.0061, 1 d.f., P=0.93, power=0.02), but female sage grouse were less likely than males to carry a malarial infection (X^2=37.74, 1 d.f., P<0.001, N=144) (Table 10).

Male malarial prevalence rates for all leks combined were significantly different among all years (X^2=7.95, 3 d.f., P=0.048, N=392) (Table 11). There was no change in the malarial status of any male recaptured within the same breeding season. Prevalence averages also varied significantly between northern and southern groups of leks (X^2=16.64, 1 d.f., P<0.001) (Table 11). Malaria prevalence on northern leks ranged from 17% (1987) to 32% (1990), with a four year average of 19%. Prevalence on southern leks ranged from 18% (1989) to 37% (1987), with an average of 26% for all four years. Average prevalence for leks with more than five observed copulations was less than leks for which fewer than five copulations were observed (0.18 and 0.21, respectively), although this difference was not statistically significant. This suggests females may be selecting against leks on which males have a high prevalence of malaria.

Breeding males were as likely to carry lice (X^2=2.10, 1 d.f., P=0.21, N=328, power = 0.33) as non-breeders (N=290) (Table 12). Female sage grouse (N=173) were less likely than males to carry a louse infestation (X^2=32.03, 1 d.f., P<0.001) (Table 12). There was no change in the louse status of any male recaptured within the same breeding season. Louse infestations varied significantly among all years (X^2=18.82, 3 d.f., P< 0.001) (Table 13). There was also a significant variation in louse prevalence between northern and southern leks (X^2=26.58, 3 d.f., P<0.001) (Table 13). Prevalence of lice on sage grouse on northern leks ranged from 8% (1989) to 51% (1987), with an average of 34% for all four years. Prevalence on southern leks ranged from 13% (1988) to 36% (1987), with a four year average of 25%. Average prevalence for leks with less than five observed copulations was higher than leks on which more than five copulations were observed (0.33 and 0.27, respectively), but this difference was not statistically significant. These results may suggest females select against leks with many infested males.

Power Analysis

Power analyses of non-significant morphological, hematocrit, and behavioral comparisons between breeders and non-breeders, males with and without malaria, and males with and without lice, suggest a high probability of a Type II error (Tables 14, 15, 16). However, in these comparisons low statistical power was actually the result of small effect sizes (differences between groups) (Peterman 1990). For each morphological characteristic a range of alternative effect sizes was analyzed by keeping

my original sample size constant, until a power of 0.95 or statistical significance was obtained. In all cases, effect sizes of morphological characteristics necessary to obtain a high statistical power were small enough to be well within the range of observed values between groups (Tables 14, 15, 16). However, manipulation of effect sizes for tag color, symmetry, and non-significant prevalence results (differences between breeders and non-breeders and adult and yearling males), indicated that sample sizes were insufficient, and the probability of a Type II error for these analyses is high (Tables 17 and 18).

Female choice, male fitness, and heritable resistance

A positive value of I indicates that males without parasites are selected more frequently as mates than parasitized males. A negative value illustrates a preference for males with parasites, and 0 indicates that females are selecting mates regardless of the males' parasitic status. The W_r value ranged from -2 (all breeders carried parasites) to +2 (no breeder had parasites). A value of 0 indicates fitness between parasitized and un-parasitized breeders is equal. In general, most female choice intensity (I) values reflected a preference for un-parasitized mates. Similarly, this preference resulted in higher relative fitness (W_r) for preferred males (Table 18). These trends were also observed when parasite prevalence data for males only were used (Table 19). All change in prevalence values for both parasites are found in Appendix 1.

Malaria

Data from leks with five or more observed copulations yielded a significant, positive correlation between change in prevalence from year t to year t+1 for all birds (Y_a) and relative fitness of un-parasitized breeders (W_r) (r=0.77, t=2.92, N=8, P=0.019) (Fig. 4). These results suggest malarial prevalence increases as relative fitness of un-parasitized breeders increases. Using male malaria prevalence only, for all leks, I found a significant, positive relationship between change in prevalence from year t to year t+1 (Y_m) and both intensity of female choice (I) and relative fitness of breeders without malaria (W_r) (Y_m and I: r=0.79, t=3.71, N=10, P=0.007) (Fig. 5) and (Y_m and W_r: r=0.80, t=3.83, N=10, P=0.006) (Fig. 4, Table 20). Both correlations persisted when using data from leks with samples of five or more observed copulations. Change in malaria prevalence in all males from year t to year t+1 was significantly and positively correlated with intensity of female choice at year t (r=0.82, t=3.46, N=8, P=0.019) (Fig. 5), and relative fitness of breeders without malaria at year t (r=0.82, t=3.46, N=8, P=0.019) (Fig. 4, Table 20). These data do not support a heritable resistance to malaria in sage grouse.

When leks are grouped into northern and southern populations, a significant, negative correlation was found between change in yearling prevalence from year t to year t+1 (Y_{ij}) and intensity of female choice (r=-0.94, t=5.39, N=6, P=0.005, (Fig. 6). Change in yearling prevalence relative to prevalence of malaria in all birds (Y_{aj}) was also negatively correlated with intensity of female choice (r=-0.94, t=5.62, N=6, P=0.006) (Fig. 6, Table 20) and relative fitness of uninfected breeders (r=-0.78, t=2.45, N=6,

P=0.05) (Fig. 7, Table 20). These results indicate that female choice may influence malarial prevalence in subsequent generations through heritability of malarial resistance. No significant correlations were found when grouping leks into northern and southern populations using male data only (Table 20). All non-significant correlations suffered from a high probability of a type II error, as a result of small sample sizes.

Lice

Change in prevalence over time was not significantly correlated with either intensity of female choice or relative fitness of un-parasitized males, regardless if data from all birds or males only were used. Although my results do not suggest sage grouse have a heritable resistance for lice, I was unable to infer any definite conclusions due to low statistical power of these analyses (Cohen 1988; Peterman 1990).

Discussion

Breeding status, morphology, hematocrits, and tags

Variation in male morphology can influence avian sexual selection (Goransson et al. 1990; Hoglund et al. 1990; Moller 1990a; Hill 1991; Moller 1991a, 1991b; Petrie 1994; Mateos and Carranza 1995), but I was unable to detect any morphological influence on sage grouse mate choice. Only differences in hematocrits were statistically significant between breeders and non-breeders. Lower hematocrit values in breeding males have been observed in another sage grouse population (Vehrencamp et al. 1989). "Less active" sage grouse had higher packed red blood cell volumes as a result of

insufficient foraging and consequent dehydration. "Actively displaying" sage grouse (those more likely to be breeders) foraged further from the lek than less active birds, acquiring food resources of higher quality and water content (Vehrencamp et al. 1989). I did not measure foraging in this population of sage grouse, but it may be possible that the disparity in hematocrit values is due to foraging differences between breeders and non-breeders. Alternatively, low hematocrits may result from enormous energetic demands associated with courtship. Kidney fat indices in sable antelope (*Hippotragus niger*) are positively correlated with hematocrits (Wilson and Hirst 1977). Although I am unaware of similar correlations in birds, endogenous fat reserves of displaying male sage grouse decline significantly during courtship (Hupp and Braun 1989). Female preference for high strut rates (Gibson and Bradbury 1985; Hartzler and Jenni 1988; Johnson and Boyce 1991; this paper) may therefore result in low hematocrit values among breeders.

Presence of patagial tags appeared to influence mate selection, as males selected for mates were more likely to wear tags than un-preferred males (Table 4). But I believe preference for marked males is the result of sampling error, and not an actual female preference. To increase sample sizes I targeted breeding males in my capture efforts, and trapping activity was concentrated on and near leks. Breeding males are more consistent in lek attendance than non-breeding birds (Johnson and Boyce 1991; this paper), thereby resulting in a increased probability of capture. Marked males often "appeared" in the center of hen clusters immediately after capture. I also could not distinguish one unmarked breeder from another, and the number of unmarked breeders

per lek used for statistical analysis was the maximum number observed on the day when the most unmarked breeders copulated. This assumption may have underestimated the number of unmarked breeders. I therefore do not believe that presence of patagial tags significantly influenced mate choice, despite my results. However, I cannot eliminate that possibility.

Malaria, host morphology, and hematocrits

Tail lengths among males with malaria were significantly shorter than in uninfected males. Long tails in other avian species positively influence mate selection (Andersson 1989; Moller 1989; Hoglund et al. 1992; Mateos and Carranza 1995), with the preference possibly resulting from indications of a male's quality (Kirkpatrick and Ryan 1991; Jones and Montgomerie 1992; Mateos and Carranza 1995). But I was unable to detect a female preference for long tails among male sage grouse.

Malaria may influence tail length through a negative effect on growth (Springer 1984). But it seems odd that a negative influence would only be observed in one measure of growth, and not others, such as tarsus length or body size. If grouse are infected with malaria after reaching adult size, any negative morphological effects of this parasite on growth would not be present. However features that change once a bird reaches maturity, such as annual feather replacement, may be negatively influenced by the parasite thus resulting in "shortened" tail feathers. Presence of microfilaria in black grouse (*Tetrao tetrix*) negatively influences tail length, but the mechanism is unknown (Hoglund et al. 1992). Although tail lengths may provide information about

a male's parasitic status frequent tail damage due to male-male interactions during courtship and predator avoidance may limit this characteristic's value to provide mate selection information to females (Dawkins and Guilford 1991; Hoglund et al. 1992; Mateos and Carranza 1995).

I was unable to detect any effect of malaria on hematocrit values, despite the parasite's typical erythrocytic destruction during merozoite eruption. Although avian malaria can result in severe anemia (Springer 1984), some species, such as penguins, have too little erythrocytic involvement to lead to significant erythrocyte destruction (Redig et al. 1993). Perhaps the pathology of malaria in sage grouse is similar to penguins, or the infection was detected too early in a recrudescence for hematocrit differences to be present.

Lice, host morphology, and hematocrits

Lice species of the suborder Ischnocera feed exclusively on feather and dermal material and rarely penetrate their host's skin (Ash 1960; Clayton et al. 1992). When present in large numbers they have the potential to reduce host fitness (Clayton 1991b) because feather damage can result in loss of host thermoregulatory abilities, and subsequently poor winter survival (Clayton et al. 1992). Also, host metabolic energy can be reduced due to constant skin irritation (Moreng and Avens 1985). Ischnocerans are not demonstrated vectors for avian endoparasites or pathogens (Clayton 1990).

Despite the negative influence chewing lice may have on avian growth rates (Moreng and Avens 1985), morphological comparisons suggest infested sage grouse

are larger than uninfested birds. Sage grouse with lice weighed more, had a longer total body length, longer tarsi, and were in better condition. While these differences may not be independent (i.e., larger birds weigh more), my results may suggest that *Lagopoecus gibsoni* and *Goniodes centrocerci* have little negative influence on sage grouse. Prevalence of lice may also increase as a bird ages. Therefore, fewer lice would be expected on smaller adult males if they are younger (2-3 years of age) than the larger adult males (4-5 years of age). Alternatively, observed differences may not be the result of louse parasitism, but rather larger birds may host more lice (Dobson 1988), making presence of an infestation more obvious.

Infested sage grouse had shorter bills than uninfested birds despite infested males having a larger body size. While the average difference in bill length between groups is small (0.9 mm, 2% of average bill length), it may be sufficient to reduce preening effectiveness (Ash 1960; Brown 1974; Moller et al. 1990), allowing for greater individual louse loads. Rock doves fitted with bits creating a one to three millimeter mandibular gap experienced a significant increase in prevalence of lice relative to un-bitted, wild birds (Clayton 1991b). Zuk et al. (1990) concluded parasites may have a disproportionate effect on secondary sexual characteristics versus non-sexually selected characters. But selection against "lousy" male sage grouse may result in an indirect selection against bill size, a non-sexually selected characteristic, if males with larger bills are more effective at controlling lice. Presence of lice had no effect on host hematocrit. Since the lice found on this population of sage grouse do not feed on blood, this result is not surprising.

With the exception of bill length, my data suggest female sage grouse do not use the measured morphological differences between males to select a mate without lice. Bill length is probably not a primary cue to male parasitic condition, but rather a characteristic that influence parasite status on its host. However, females may use multiple cues, cues in sequence (e.g. strutting frequency may attract a female to a male's territory, and then she uses other features to assess male quality) (Balmford 1991), or features to assess male louse status I did not examine. Presence of lice on sage grouse is positively correlated with hematomas on air sacs (Johnson and Boyce 1991) and simulation of a louse infestation by placing artificial hematomas on air sacs of uninfested, captive sage grouse decreased attractiveness of these birds to females (Spurrier et al. 1991). Feather damage or physical results of consequent poor thermoregulatory ability may also provide critical information in selecting a louse-free mate (Clayton 1991b). These features may provide sufficient information to females about a male's louse status, with other observed differences in morphology unnecessary for selection of an un-parasitized male.

Breeding status and behavior

Behavior appears to provide the most influential cues for sage grouse mate selection. Preferred males have a higher strut frequency and lek attendance (Gibson and Bradbury 1985; Johnson and Boyce 1991), which is consistent with observations on other lekking species, such as Jackson's widowbirds (*Euplectes jacksoni*) (Andersson 1989, 1994). Also lek attendance among breeding males is more frequent

than attendance by non-breeding males prior to and at the peak of hen attendance. This temporal period was when most copulations were observed. Assuming no difference between strutting display and frequency, these results suggest a reproductive advantage for males attending the lek early in the breeding season. These males are also more like to encounter adult females which are more successful at rearing a brood. Due to the enormous energetic expense associated with strutting, early breeders expend their fat reserves (Hupp and Braun 1989), and no longer regularly attend the lek after the peak of hen attendance.

Malaria and behavior

Presence of a malarial infection did not appear to affect strutting frequency. But in many lekking species female mate choice is based on a series of successive criteria (Balmford 1991). Females may use male strutting frequency to select which male territories on a lek to visit, but mate selection may depend on a specific behavioral or morphological cue which indicates presence of a malaria infection. Therefore, malaria may not influence strut rate, but may negatively affect other aspects of the courtship display that my data did not detect.

Malaria does influence lek attendance, an important cue to females for mate selection (Johnson and Boyce 1991; this paper). In 1987 and 1988, sage grouse with malaria attended the lek less frequently than non-infected birds. Since females usually watch prospective mates for several mornings before soliciting a copulation, they may use lek attendance to assess male parasite condition (Johnson and Boyce 1991).

Decreased lek attendance of infected grouse may result from reluctance to move or eat during a malarial recrudescence (Hewitt 1940; Hibler 1982).

In 1989 and 1990, lek attendance was higher for males with malaria. This seemingly conflicting result may be due to sampling bias. Due to the energetic expense associated with strutting (Hupp and Braun 1989), breeding males usually do not attend the lek after the peak of hen attendance. Since many early breeders were not infected with malaria females are more likely to encounter infected males on the lek later in the season. Behavioral observations were concentrated during the latter half of the strutting season in both 1989 and 1990, and may be biased in favor of infected grouse.

Infected males that were selected as mates bred significantly later than those without malaria. Reproductive advantage is amplified for parasite-free males if their parasitic status ensures they secure the most viable females (Darwin-Fisher mechanism) (Price et al. 1988; Moller 1991a). For example, male barn swallows without ectoparasites attracted females of high quality (Moller 1991a), thereby increasing the male's reproductive advantage. Since female sage grouse attending the lek late in the season are less successful at bringing off a brood (Johnson and Boyce 1991; Moller 1991b) breeders with malaria probably have poor reproductive success (this paper). Apparently, the Darwin-Fisher mechanism also operates for polygynous mate selection in sage grouse.

Lice and behavior

Breeders with lice secure significantly fewer copulations than uninfested breeders, providing strong evidence that females avoid "lousy" males. As with malaria some males with lice were selected as mates. These birds bred significantly later than breeders without lice, again implying the Darwin-Fisher mechanism is operating in sage grouse. Most infested breeders copulated after the peak of hen attendance (on or around April 19). Late breeding adult females are usually re-nesters (Patterson 1952). When faced with the choice of a "lousy" mate, or a total loss of the annual reproductive effort, tolerance may be extended to the "lousy" male.

Lice had no apparent affect on strut rate. A few males with heavy louse infestations attended the lek, but did not strut. The extent of the their infestation may have impaired thermoregulatory ability (Clayton 1990, 1991b), or limited energy for strutting due to metabolic costs of an intense infestation (Moreng and Avens 1985). Although breeders attended the lek more frequently than non-breeders, the presence of a louse infestation does not appear to affect this behavioral cue.

Prevalence of Malaria

Significant temporal variations in malarial prevalence are consistent with the predictions of the Hamilton and Zuk hypothesis. This variation is necessary to prevent genetic fixation of the resistance genes (Hamilton and Zuk 1982; Boyce 1990; Johnson and Boyce 1991). Prevalence variations may also result from fluctuations in vector populations with consequent changes in host parasite prevalence. However, neither

explanation of temporal prevalence variation excludes the other. If sage grouse have a genetic resistance to malaria, prevalence changes may occur in non-resistant individuals as a result of changes in the vector population. Prevalence differences between groups of leks (northern and southern) may also reflect differences in the vector population between these areas, or differences in the current host resistance-parasite virulence interactions.

Malaria was more frequently detected in adult male sage grouse as the lekking season progressed suggesting either an increase in attendance of infected males, or possible an increase in number of males with a recrudescence. However, no increase in the number of breeders with malaria was observed during the lekking season (although male breeders with malaria bred later than uninfected males). These results suggest that females are able to discern and select males without malaria as mates before the infection reaches an erythrocytic stage.

Differences in parasite prevalence between male and female sage grouse may reflect behavioral differences that affect their exposure to parasite vectors (Weatherhead et al. 1991). Malaria may also cause differential mortality between sexes, or infected females may simply not attend the lek. Genetic resistance to malaria may also be a sex-linked characteristic in sage grouse. Alternatively, the disparity may be a result of an earlier recrudescence in males due to the immunosuppressive effects of elevated sex hormones or stress (Beaudoin et al. 1971; Gibson 1990; Folstad and Karter 1992; Norris et al. 1994). Males begin strutting activity and territorial defense on a lek up to one month prior to hen arrival (Patterson 1952). Therefore, differences

in infection frequency between sexes may be a sampling error based on date. But a earlier male recrudescence offers an intriguing possibility. Infected males may be more obvious to females at the exact time she has to select a mate.

If malarial recrudescence in males is related to immunosuppressive effects of elevated sex hormones (Beaudoin et al. 1971; Gibson 1990; Folstad and Karter 1992; Norris 1994), it offers a potential resolution to differences in effects of parasites on mate selection between sage grouse populations. No measure of display or mating success was correlated with blood parasites in a California population of sage grouse (Gibson 1990). But, Gibson determined parasite status while males were still in winter flocks (January and February). Although *Haemoproteus* was present, other blood parasites or an increase in the lesions of *Haemoproteus* may not be as obvious, because lek establishment and increasing levels of sex hormones (Beaudoin et al. 1971) had not yet begun. Alternatively, given the isolation of the California sage grouse population, and low-frequency oscillations of parasites predicted by the Hamilton and Zuk hypothesis, there is a probability that parasites and diseases which negatively influence sage grouse morphology may have become locally extinct (Boyce 1990). Vectors for parasite transmission may also be limited in the area in which the California sage grouse population is located.

Lice Prevalence

Rates of louse infestations varied significantly between northern and southern leks and among years. Spatial and temporal variation is common in louse populations.

Although the fluctuations are usually associated with breeding and nesting (Ash 1960), they are also consistent with the Hamilton and Zuk hypothesis.

Prevalence of lice in females was significantly lower than that of males. Behavioral differences between sexes may influence their exposure to the parasite (Weatherhead et al. 1991; Clayton et al. 1992). Phthirapteran lice are more common on males in several avian species examined in Britain, but no explanation for this difference was provided (Ash 1960). No host sexual differences were found in prevalence of phthirapteran populations of alcids (Eveleigh and Threlfall 1976). I attribute prevalence differences between sage grouse sexes to the difficulty of finding lice on females. Female grouse have poorly developed gular sacs and combs where I commonly found lice on males. My results also may be subject to error, as visual examinations of birds for ectoparasites can be less effective than fumigation techniques, since larval and immature stages are often overlooked (Pruett-Jones and Pruett-Jones 1991).

Scale of female choice and copying

I have limited evidence that females choose leks with low malaria and louse prevalences for mating. Variation in parasite prevalence across leks may provide a basis for female selection against leks with a high parasite prevalences. Selecting a lek of low parasite prevalence will increase a female chances of encountering uninfected males for mate selection. If females use parasite prevalence to select leks on which to mate, they may significantly influence future parasite prevalences on those leks. A

subsequent increase in parasite prevalence may result from attraction of infected birds to areas of high female density and mating success, or a change of virulence in malaria as predicted by Hamilton and Zuk (1982). Changes in malarial prevalence may also be related to changes in the vector population and host densities.

Female sage grouse may copy mate selection of other females to avoid costs of mate assessment (i.e. exposure to predators), obtain a better mate if more experienced females select first, or increase accuracy of mate discrimination if individual assessment is subject to error (Gibson and Hoglund 1992). Although Spurrier et al. (1994) found no evidence of copying in captive sage grouse, they were unable to conclusively eliminate copying as a possibility for wild birds. Results from studies on other wild sage grouse populations imply that copying among females does occur (Gibson et al. 1991), and copying has been identified in other lekking species (Gibson and Hoglund 1992; Kirkpatrick and Dugatkin 1994). But copying is not incompatible with active selection against infected males or leks with a high parasite prevalence if the first females to select a mate accurately assess the male's parasitic condition. Temporal spillover, the fidelity of both males and females to previous mating sites (Gibson 1992) may also influence a female's decision on which lek to mate. Females may select particular males based on previous mating success (Gibson et al. 1991; Gibson 1992), or acquaintance in winter flocks. However, given the high predation on strutting male sage grouse by golden eagles and other predators, the temporal spillover hypothesis may only temporally (1 or 2 years) influence female choice as preferred males die.

Female choice, male fitness, and heritable resistance: Malaria

Movement of both sage grouse sexes between leks, within and among breeding seasons, (Patterson 1952; Dunn and Braun 1985) indicates populations are larger than individual leks. Pre-nesting ranges of female sage grouse commonly include several leks (Bradbury et al. 1989). Therefore, grouping leks into larger populations based on habitat restrictions likely provides the most accurate estimation of genetic characteristics. When leks are grouped into northern and southern populations, and data from all birds are considered, malaria prevalence in yearlings declines as female choice and relative fitness of un-parasitized breeders increases. The decrease in prevalence among yearling birds over time suggests sage grouse have a heritable resistance to malaria.

When data for individual leks from adult birds were used, malarial prevalence increased in the next year as fitness for un-parasitized breeders increases, and females become more selective. If females select against malaria regionally by mating on leks with low prevalence, an increase in prevalence may not be unexpected. Historical presence of many receptive females may increase popularity of a lek among males, including infected birds. This may be enhanced by "temporal spillover" (Gibson 1992) if females return to preferred mating sites prior to assessing malaria prevalence on those leks. A high female density on these leks, even if temporary, may attract more males to the leks. Increasing virulence of malaria may also result in an increase in prevalence in subsequent generations as predicted by the Hamilton and Zuk hypothesis. Presumably, host changes in resistance would subsequently result in a decrease of

malaria. Changing prevalence among males attending a lek may also be influenced by changes in the vector population.

My data provide tentative support for malaria resistance in sage grouse. But Kirkpatrick and Ryan (1991) argue direct fitness consequences of avoiding parasites may direct avoidance of infected males. Even though malaria cannot be transmitted via direct contact the fact a potential mate is parasitized may influence female mate choice. Also preferred males may be uninfected not because they are genetically resistant, but because they are in better general condition which allows them to overcome an infection (handicap hypothesis) (Zahavi 1975; Borgia and Collis 1990). Male sage grouse that attend the lek frequently, and had active display rates, were in better general condition than their counterparts (Vehrencamp et al. 1989). But failure to detect a change in malarial prevalence among breeding males as the lekking season progressed suggests malarial status may be less dependent on physical condition than on a resistance to the parasite. Also, a decline in yearling malaria prevalence supports genetic resistance to malaria in sage grouse. A change in prevalence may not be expected using data for all birds as the time for a complete generation turnover exceeds the length of this study. "Carry over" of infected birds from previous generations may obscure data reflecting a heritable resistance to malaria. Therefore the parasite avoidance hypothesis does not provide a likely explanation for the influence of malaria on mate selection in sage grouse.

Female choice, male fitness, and heritable resistance: Lice

Female sage grouse avoided breeders with lice, which subsequently increased relative fitness for uninfested breeders. Females also appear to select against lice on a regional level by avoiding leks where louse prevalence is high among attending males (louse prevalence was less on leks for which >5 copulations were observed). However, I found no significant correlations between change of prevalence of a louse infestation, and intensity of female choice and relative fitness of breeders without lice, regardless of the prevalence data used for analysis. Low statistical power due to small sample sizes indicates possibility of a Type II error (Cohen 1988; Peterman 1990).

Moller (1990a) found strong selection against male barn swallows with mites, which apparently conferred genetic resistance to the next generation, thereby supporting Hamilton and Zuk (1982). However, barn swallow mites were hematophagous, and as such may generate a host immune response. Immune responses to lice which actively penetrate their host's bloodstream are common (Wikel 1982; Devaney and Augustine 1988), but have not been recorded for species which feed only on shed dermal scruff. Since neither species of lice found on this population of sage grouse penetrate the host's skin (Ash 1960; Clayton et al. 1992) a host immune response is not likely. Therefore sage grouse may have little basis to generate a genetic resistance to their ectoparasites.

My lice data are more consistent with Borgia and Collis's (1990) parasite avoidance hypothesis - females avoid males with lice which decreases her chances of acquiring the infestation. Immediately after copulation, female shake vigorously, and

preen for several minutes before leaving the lek. This also suggests an avoidance behavior against louse transmission (Boyce 1990).

Conclusion

The influence of malaria on sage grouse mate selection satisfies all predictions of the Hamilton and Zuk hypothesis. Males without malaria are preferred as mates, and breeding males that carry a malarial infection breed late in the lekking season when potential for producing a successful brood is minimal. A malaria infection reduces lek attendance, a cue females use in mate selection. Temporal variation in prevalence may indicate presence of a dynamic and changing host-parasite relationship. My data also suggest sage grouse have a heritable resistance to malaria as prevalence in yearling birds decreases as females become more selective.

Breeding males with lice secured significantly fewer copulations and bred later in the lekking period. Both results indicated a negative relationship between individual fitness and parasite presence. I also observed significant temporal and spatial variation in prevalences. Bill length was negatively correlated with presence of lice in these populations, suggesting an inability to effectively remove or control the parasite population. But, unlike effects of malaria on sage grouse mate choice, which influences both attendance rate and timing of attendance (Johnson and Boyce 1991; Deibert and Boyce unpubl. data), only the presence of hematomas on the gular sacs (Spurrier et al. 1991) negatively influence female mate choice. I was also unable to find evidence of

heritable resistance to lice, potentially because lice which infest sage grouse do not penetrate the host's skin.

Females may also select against both parasites on a regional level. Movement between leks during the breeding season allows females to examine many individual males, and possibly assess prevalence of malaria and lice on each lek. Female preference for uninfected males may result in selection of leks with a low parasite prevalence. This is presumably advantageous because it increases the probability of encountering an acceptable, uninfected male.

My data on malaria and sage grouse mate selection offer evidence in support of the Hamilton and Zuk hypothesis. It may also indicate that parasite-host interactions may offer a resolution to the lek paradox by maintaining variation for traits under intense sexual selection. However my data only partially support this hypothesis for lice and sage grouse. Lice do influence sage grouse mate selection. But my data are consistent with the parasite avoidance hypotheses (Borgia and Collis 1990).

Table 1. Definition of abbreviations used in the text and tables.

	Definitions
I	Intensity of female choice at year t
W_f	Fitness for parasite-free male breeders
W_p	Fitness for parasitized male breeders
W_r	Relative fitness of parasite free males at year t
Y_a	Change in parasite prevalence in all birds from year t to year t+1
Y_m	Change in parasite prevalence in all males from year t to year t+1
Y_{aj}	Change in parasite prevalence between all adult birds at year t and all yearling birds at year t+1
Y_{jj}	Change in parasite prevalence between all yearling birds at year t and all yearling birds at year t+1
Y_{am}	Change in parasite prevalence between all adult males at year t and all yearling males at year t+1
Y_{jm}	Change in parasite prevalence between all yearling males at year t and all yearling males at year t+1

Table 2. Morphological comparisons between adult male breeders and non-breeders. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between breeders and non-breeders. (+ indicates characteristic was larger in breeders, - indicates characteristic was smaller in breeders).

Characteristic	N	Average of all adult males	Difference breeder vs. non-breeder
Body mass	328	3011 g ± 336	+8.3 g
Total length	328	747 mm ± 36.5	+6.2 mm
Tail length	328	316 mm ± 25.8	+0.1 mm
Wing length	328	318 mm ± 15.1	+2.2 mm
Keel length	328	148 mm ± 17.3	-0.6 mm
Tarsus length	328	68.9 mm ± 2.9	+0.5 mm
Toe length	328	68.7 mm ± 3.3	+0.6 mm
Comb length	328	24.8 mm ± 2.2	+0.4 mm
Bill length	328	39.1 mm ± 1.8	+0.2 mm
Bill depth	328	22.2 mm ± 1.9	-0.3 mm
Condition index	216	0.1 g/mm^3 ± 0.04	+0.001 g/mm^3
No. tail feathers	154	17.8 ± 2.5	-0.7
Tail asymmetry	154	38.3%	P=0.99

Table 3. Hematocrit and color comparisons between adult male breeding and non-breeding sage grouse. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between breeders and non-breeders. (+ indicates characteristic was larger in breeders, - indicates characteristic was smaller in breeders).

	N	Average of all adult males	Difference breeder vs. non-breeder
Hematocrit	328	0.56 ± 0.13	-0.088**
Gular sac color			
Hue	289	7.50 ± 2.6	+0.5
Chroma	289	6.88 ± 0.6	-0.02
Color	289	9.02 ± 0.6	-0.06
Comb color			
Hue	305	8.13 ± 2.1	-0.09
Chroma	305	6.20 ± 0.6	-0.03
Color	305	7.08 ± 1.4	-0.06

Table 4: Tag comparisons between adult male breeding and non-breeding sage grouse. Percents are for all males captured, and are included for comparison. Except for the presence of tags no significant differences (ns) were detected between breeders and non-breeders. (*** = statistical significance at $P<0.001$).

Tag Characteristic	N	Percent of all adult males	Difference breeder vs. non-breeder
Tag color	328	not tested	$P=0.65$
Tag symmetry	328	23.6	$P=0.89$
Tag presence	1089	17.1	$P<0.001$

Table 5. Morphological comparisons between adult male sage grouse with and without malaria. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between males with and without malaria. (ns indicates no significant difference between groups, * = $P<0.05$, + indicates characteristic was larger in males without malaria, - indicates characteristic was smaller in males without malaria).

Characteristic	N	Average of all adult males	Difference malaria vs. no malaria
Body mass	328	3011 g ± 336	+38.9 g
Total length	328	747 mm ± 36.5	-0.1 mm
Tail length	328	316 mm ± 25.8	+5.6 mm*
Wing length	328	318 mm ± 15.1	+0.9 mm
Keel length	328	148 mm ± 17.3	+2.4 mm
Tarsus length	328	68.9 mm ± 2.9	+0.1 mm
Toe length	328	68.7 mm ± 3.3	+0.1 mm
Comb length	328	24.8 mm ± 2.2	+0.3 mm
Bill length	328	39.1 mm ± 1.8	+0.04 mm
Bill depth	328	22.2 mm ± 1.9	-0.3 mm
Condition index	216	0.1 g/mm^3 ±.04	-0.002 g/mm^3
No. tail feathers	219	17.8 ± 2.5	-0.7
Tail asymmetry	219	38.3%	P=0.99

Table 6. Hematocrit and color comparisons between adult male sage grouse with and without malaria. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between birds with and without malaria. (+ indicates characteristic was larger in males without malaria, - indicates characteristic was smaller in males without malaria).

	N	Average of all adult males	Difference malaria vs. no malaria
Hematocrit	328	0.56 ± 0.13	+0.03
Gular sac color			
Hue	289	7.50 ± 2.6	-0.7
Chroma	289	6.88 ± 0.6	-0.05
Color	289	9.02 ± 0.6	+0.1
Comb color			
Hue	305	8.13 ± 2.1	-0.1
Chroma	305	6.20 ± 0.6	-0.3
Color	305	7.08 ± 1.4	+0.1

Table 7. Morphological comparisons between adult male sage grouse with and without lice. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between males with and without lice. (ns indicates no significant difference between groups, * = $P<0.05$, ** = $P<0.01$, *** = $P<0.001$, + indicates characteristic was larger in males without lice, - indicates characteristic was smaller in males without lice).

Characteristic	N	Average of all adult males	Difference lice vs. no lice
Body mass	328	3011 g ± 336	-50.9 g*
Total length	328	747 mm ± 36.5	-12.4 mm**
Tail length	328	316 mm ± 25.8	-2.7 mm
Wing length	328	318 mm ± 15.1	+1.0 mm
Keel length	328	148 mm ± 17.3	+2.6 mm
Tarsus length	328	68.9 mm ± 2.9	-0.7 mm*
Toe length	328	68.7 mm ± 3.3	-0.5 mm
Comb length	328	24.8 mm ± 2.2	+0.4 mm
Bill length	328	39.1 mm ± 1.8	+0.9 mm***
Bill depth	328	22.2 mm ± 1.9	+0.1 mm
Condition index	216	0.1 g/mm^3 ± .04	-0.01 g/mm^3
No. tail feathers	219	17.8 ± 2.5	-0.07
Tail asymmetry	219	38.3%	P=0.995

Table 8. Hematocrit and color comparisons between adult male sage grouse with and without lice. Averages are values for all males captured, and are included for comparison. Reported values are the average difference between birds with and without lice. (+ indicates characteristic was larger in males without lice, - indicates characteristic was smaller in males without lice).

	N	Average of all adult males	Difference lice vs. no lice
Hematocrit	328	0.56 ± 0.13	-0.0003
Gular sac color			
Hue	289	7.50 ± 2.6	+0.02
Chroma	289	6.88 ± 0.6	-0.01
Color	289	9.02 ± 0.6	-0.02
Comb color			
Hue	305	8.13 ± 2.1	+0.2
Chroma	305	6.20 ± 0.6	-0.1
Color	305	7.08 ± 1.4	-0.1

Table 9: Number and dates of copulations by adult male sage grouse with and without malaria, and adult males with and without lice. Males without lice secured significantly more copulations than males with lice. Parasite-free breeders secured significantly more copulations prior to the peak of hen attendance than after, a difference not observed between breeders with parasites. Data are pooled over the 4 years of study.

	With Malaria	Without Malaria	With Lice	Without Lice
No. copulations	27	101	19	108
No. cops. before peak of hen attendance	8	73	9	76
No. cops. after peak of hen attendance	18	24	10	32

Table 10: Malarial prevalence of breeding and non-breeding male sage grouse, males and females, during the years of sampling. Prevalence was not statistically different between breeders and non-breeders; but females had a lower prevalence than males. Numbers in parentheses indicate sample size.

Year	Breeding Males	Non-breeding Males	All Males	Yearling Males	Females
1987	0% (8)	35.1% (97)	32.4% (105)	34.6% (26)	no data
1988	27.8% (18)	34.7% (72)	30.0% (100)	15.4% (13)	0% (117)
1989	33.3% (9)	12.7% (63)	15.3% (72)	25.0% (28)	15.4% (13)
1990	33.3% (3)	23.7% (59)	24.2% (62)	23.8% (21)	14.3% (14)
Total	23.7% (38)	27.8% (291)	26.5% (339)	26.1% (88)	2.8% (144)

Table 11. Male malaria prevalence (%) for all years on northern and southern leks. Prevalences were statistically different between all years. Prevalence was highest on southern leks in 1987 and 1988, and lowest on southern leks in 1989 and 1990. Numbers in parentheses indicate sample size. Northern leks include North lek, Cordingly, Windmill Dam, and South Fetterman. Southern leks include Long Lake, Viewpoint, Mud Springs, and Sybille Springs.

Year	Northern leks	Southern leks	All leks
1987	17.0 (41)	37.0 (73)	29.8 (114)
1988	12.5 (32)	32.8 (64)	26.0 (96)
1989	22.2 (9)	17.6 (19)	18.0 (100)
1990	31.8 (22)	20.0 (60)	23.2 (82)
Average all years	19.2 (104)	26.4 (288)	24.5 (392)

Table 12. Louse prevalence of breeding and non-breeding male sage grouse, males and females, during the years of sampling. Prevalence was not statistically different between breeders and non-breeders; but females had a lower prevalence than males. Numbers in parentheses indicate sample size.

Year	Breeding Males	Non-breeding Males	All Males	Females
1987	37.5% (8)	43.3% (97)	40.1% (105)	30.0% (30)
1988	33.3% (18)	33.8% (74)	33.7% (92)	0.9% (118)
1989	10.0% (10)	27.0% (63)	24.7% (73)	0.0% (11)
1990	0.0% (3)	28.8% (59)	27.4% (62)	0.0% (14)
Total	25.6% (39)	34.5% (293)	33.4% (332)	5.8% (173)

Table 13. Male louse prevalence (%) for all years on northern and southern leks. Prevalences were statistically different between years and leks. Prevalence was highest on northern leks in 1987 and 1988, and lowest on northern leks in 1989 and 1990. Numbers in parentheses indicate sample size. Northern leks include North lek, Cordingly, Windmill Dam, and South Fetterman. Southern leks include Long Lake, Viewpoint, Mud Springs, and Sybille Springs.

Year	Northern leks	Southern leks	All leks
1987	51.0 (49)	36.4 (88)	41.6 (137)
1988	32.1 (53)	12.6 (159)	17.5 (212)
1989	7.7 (13)	31.6 (98)	28.8 (111)
1990	17.9 (28)	30.4 (69)	26.8 (97)
Average all years	33.6 (143)	25.1 (414)	27.3 (557)

Table 14. Power analyses results and effect size ranges for morphological comparisons between breeding and non-breeding males. Top values are for non-breeders, bottom values are for breeders. All analyses, except color, were conducted with a t-test and an alpha value of 0.05. Color components were analyzed with a multiple linear regression. Low power was a result of small effect sizes. Necessary effect sizes to obtain a power of ≥ 0.95 were within the range of differences observed between breeders and non-breeders.

	Actual Power	Effect Size Difference	Necessary Effect Size	Observed Range
Body				2060-3800 g
Mass	0.04	8.3 g	167.0 g	2500-3600 g
Total				641-892 mm
Length	0.28	6.2 mm	19.0 mm	673-820 mm
Wing				288-395 mm
Length	0.20	2.2 mm	9.0 mm	299-389 mm
Tail				229-400 mm
Length	0.01	0.1 mm	14.0 mm	237-375 mm
Keel				106-220 mm
Length	0.06	0.6 mm	9.5 mm	122-187 mm
Tarsus				60-78 mm
Length	0.23	0.5 mm	1.8 mm	62-76 mm
Toe				56-77 mm
Length	0.27	0.6 mm	2.1 mm	57-83 mm
Bill				32-44 mm
Length	0.20	0.2 mm	1.0 mm	36-45 mm
Bill				16-41 mm
Depth	0.23	0.3 mm	1.2 mm	18-30 mm
Comb				19-36 mm
Length	0.27	0.4 mm	2.2 mm	22-32 mm
				0.03-0.22
Condition	0.01	0.001 g/mm	0.02 g/mm	0.04-0.16
Tail				6-23
Feathers	0.52	0.68	1.4	14-20

Table 14 (continued).

	Actual Power	Effect Size Difference	Necessary Effect Size	Observed Range
Gular Sacs				
				3.7 - 9.8
Hue	0.01	0.53	1.60	3.7 - 9.5
				5.9 - 7.5
Chroma	0.02	0.01	0.36	5.9 - 7.2
				6.3 - 9.3
Color	0.36	0.22	0.50	6.3 - 9.3
Combs				
				3.3 - 9.8
Hue	0.04	0.09	1.30	3.7 - 9.8
				5.9 - 8.0
Chroma	0.05	0.03	0.40	5.9 - 7.5
				6.3 - 14.3
Color	0.04	0.06	0.80	6.3 - 9.2

Table 15. Power analyses results and effect size ranges for morphological comparisons between all adult males with and without malaria infections. Top values are for non-infected males, bottom values are for infected males. All analyses, except color, were conducted with a t-test and an alpha value of 0.05. Color components were analyzed with a multiple linear regression. Low power was a result of small effect sizes. Necessary effect sizes to obtain a power of ≥ 0.95 were within the range of differences observed between males with and without malaria.

	Actual Power	Effect Size Difference	Necessary Effect Size	Observed Range
Body				2060-3650 g
Mass	0.15	38.9 g	145 g	2100-3800 g
Total				625-892 mm
Length	0.004	0.12 mm	17.5 mm	650-826 mm
Wing				288-389 mm
Length	0.07	0.90 mm	7.5 mm	288-395 mm
Keel				106-205 mm
Length	0.22	2.42 mm	8 mm	126-220 mm
Tarsus				60-78 mm
Length	0.05	0.13 mm	1.8 mm	62-76 mm
Toe				60-77 mm
Length	0.05	0.13 mm	1.7 mm	56-83 mm
Bill				23-44 mm
Length	0.02	0.04 mm	0.95 mm	35-43 mm
Bill				18-41 mm
Depth	0.20	0.25 mm	0.9 mm	16-26 mm
Comb				19-36 mm
Length	0.24	0.33 mm	1.0 mm	20-29 mm
Condi-				0.04-0.22 g/mm
tion	0.05	0.002 g/mm	0.018 g/mm	0.03-0.17 g/mm
Tail				4-20
Feathers	0.47	0.72	1.5	11-23
Hemato-				0.15-0.85
crit	0.34	0.03	0.07	0.14-0.76

Table 15 (continued).

	Actual Power	Effect Size Difference	Effect Size	Observed Range
Gular Sacs				
				3.7 - 9.6
Hue	0.28	0.69	1.25	3.7 - 9.8
				5.9 - 7.3
Chroma	0.10	0.05	0.27	5.9 - 7.5
				6.3 - 9.3
Color	0.32	0.14	0.34	6.3 - 9.3
Combs				
				3.3 - 9.8
Hue	0.08	0.14	1.0	3.3 - 9.8
				5.9 - 8.0
Chroma	0.09	0.05	0.28	5.9 - 8.0
				6.3 - 14.3
Color	0.10	0.12	1.6	6.3 - 14.3

Table 16. Power analyses results and effect size ranges for morphological comparisons between al adult males with and without lice. Top values are for uninfected males, bottom values are for infected males. All analyses, except color, were conducted with a t-test and an alpha value of 0.05. Color components were analyzed with a multiple linear regression. Low power was a result of small effect sizes. Necessary effect sizes to obtain a power of ≥ 0.95 were within the observed range of differences between males with and without lice.

	Actual Power	Effect Size Difference	Necessary Effect Size	Observed Range
				288-395 mm
Wing Length	0.15	1.0 mm	6.5 mm	288-365 mm
				229-400 mm
Tail Length	0.13	-2.7 mm	11.0 mm	231-395 mm
				110-189 mm
Keel Length	0.27	2.6 mm	7.5 mm	106-220 mm
				61-77 mm
Toe Length	0.24	0.5 mm	1.5 mm	56-83 mm
				20-33 mm
Comb Length	0.40	0.4 mm	1.0 mm	19-36 mm
				17-31 mm
Bill Depth	0.15	0.1 mm	0.9 mm	16-41 mm
Num. Tail				4-23
Feathers	0.03	0.07	1.3	10-23
				0.14-0.85
Hematocrit	0.002	0.0003	0.08	0.15-0.76
Gular Sacs				
				3.7 - 9.8
Hue	0.01	0.02	1.2	3.7 - 9.5
				5.9 - 7.5
Chroma	0.02	0.01	0.26	5.9 - 7.2
				6.3 - 9.3
Color	0.04	0.02	0.29	6.3 - 9.3

Table 16 (continued).

	Actual Power	Effect Size Difference	Necessary Effect Size	Observed Range
Combs				
				3.3 - 9.8
Hue	0.15	0.14	0.95	3.3 - 9.8
				5.9 - 8.0
Chroma	0.46	0.14	0.28	5.9 - 8.0
				6.3 - 14.3
Color	0.10	0.12	0.70	6.3 - 14.3

Table 17. Summary of power analyses results and effect size variations for all comparisons. A chi-square test was used for all analyses, except lek attendance and strutting frequency, with an alpha value of 0.05. Lek attendance and strutting frequency were analyzed via a t-test, and an alpha value of 0.05.

	Power	Effect Size Variation	Resulting Power	Comments
Breeders & Non-breeders				
Tag Color	0.31	Change in 1 tag color per lek	0.51	Change of 2 colors per lek is significant
Tag Symmetry	0.03	Change of 3 sets of tags between groups	0.35	Change of 4 sets becomes significant
Tail Symmetry	0.09	Change of symmetry in 3 birds	0.43	If change by 4 birds, becomes significant
Malaria, breeders vs. non-breeders	0.33	One less infected breeder	0.40	Change of 2 becomes significant
Louse prev., breeders vs. non-breeders	0.33	Change rate for 1 bird per group	0.43	Change of 2 birds per group becomes significant
Lice & No Lice				
Strutting frequency	0.26	Change of 4.2 struts/5 min. interval	0.95	Low power due to small effect size
Lek attendance	0.03	Change of 0.14 in prop. days attended	0.95	Low power due to small effect size

Table 17 (continued).

	Power	Effect Size Variation	Resulting Power	Comments
Malaria & No malaria				
Tail Symmetry	0.15	None	--	Any change becomes significant
Prevalence rates across years	0.53	Change in status for one bird per year	none	Becomes statistically significant
Prev. rates between adult and yearling males	0.02	Change in status for 7 yearlings	none	Becomes statistically significant
Number of copulations	0.20	Change of 4 copulations between groups	0.46	Change of 5 becomes significant

Table 18. Summary of intensity of female choice and relative fitness of un-parasitized breeders. Values are for all birds captured. (* = leks with 5 or more observed copulations, MS = Mud Springs, LL = Long Lake, NL = North Lek, VP = Viewpoint, SS = Sybille Springs).

Year	Lek	W_r	*I* malaria	*I* lice
1987	MS	0.00	0.25	0.31
1987	NL*	2.00	0.06	0.49
1987	SS	2.00	0.50	-0.63
1987	LL*	0.00	0.39	0.25
1988	MS*	-0.12	-0.38	-0.45
1988	NL*	2.00	0.06	0.12
1988	SS*	2.00	0.66	0.11
1988	LL	-2.00	-0.85	0.08
1988	VP	0.00	0.00	-0.25
1989	MS	2.00	0.13	0.14
1989	NL*	1.33	0.06	0.00
1989	SS*	-2.00	-0.61	0.61

Table 19. Summary of intensity of female choice and relative fitness of un-parasitized breeders. Values are for male sage grouse only. (* = leks with 5 or more observed copulations, ** = no yearling males captured, MS = Mud Springs, LL = Long Lake, NL = North Lek, VP = Viewpoint, SS = Sybille Springs).

Year	Lek	W_r	*I* malaria	*I* lice
1987	MS	0.00	0.25	0.34
1987	NL*	2.00	0.06	0.39
1987	SS	2.00	0.50	-0.56
1987	LL*	0.00	0.39	0.28
1988	MS*	-0.12	-0.25	-0.37
1988	NL*	2.00	0.12	0.29
1988	SS*	2.00	0.10	0.20
1988	LL	-2.00	-0.40	0.21
1988	VP	0.00	0.00	-0.14
1989	MS	2.00	0.12	0.22
1989	NL*	1.33	0.12	0.00
1989	SS*	-2.00	-0.57	0.67

Table 20. Summary of regression results for malaria. Both intensity of female choice (I) and relative fitness of un-infected breeders (W_r) at year t were independent variables. Regressions used prevalence data for all birds and for males only. The (+) and (-) marks designate if the slope is positive or negative, and values in parentheses are the statistical power of the analyses. (n.s.= correlation between variables was not significant, * northern populations consisted of North and Cordingly leks, southern populations consisted of Mud Springs, Sybille Springs, Long Lake, and Viewpoint leks).

All Birds			Five or more Copulations		N and S Populations*	
	I	W_r	I	W_r	I	W_r
Y_a	n.s. (0.04)	n.s. (0.17)	n.s. (0.12)	P<0.05 (+)	n.s. (0.18)	n.s. (0.07)
Y_{ij}	n.s. (0.21)	n.s. (0.06)	n.s. (0.00)	n.s. (0.16)	P<0.01 (-)	n.s. (0.21)
Y_{aj}	n.s. (0.11)	n.s. (0.09)	n.s. (0.00)	n.s. (0.14)	P<0.01 (-)	P<0.05 (-)
Male Y_m	P<0.01 (+)	P<0.01 (+)	P<0.02 (+)	P<0.02 (+)	n.s. (0.08)	n.s. (0.23)
Y_{jm}	n.s. (0.11)	n.s. (0.28)	n.s. (0.16)	n.s. (0.23)	n.s. (0.67)	n.s. (0.46)
Y_{am}	n.s. (0.21)	n.s. (0.48)	n.s. (0.21)	n.s. (0.23)	n.s. (0.57)	n.s. (0.41)

Fig. 1. Location of sage grouse study area near Laramie, Wyoming.

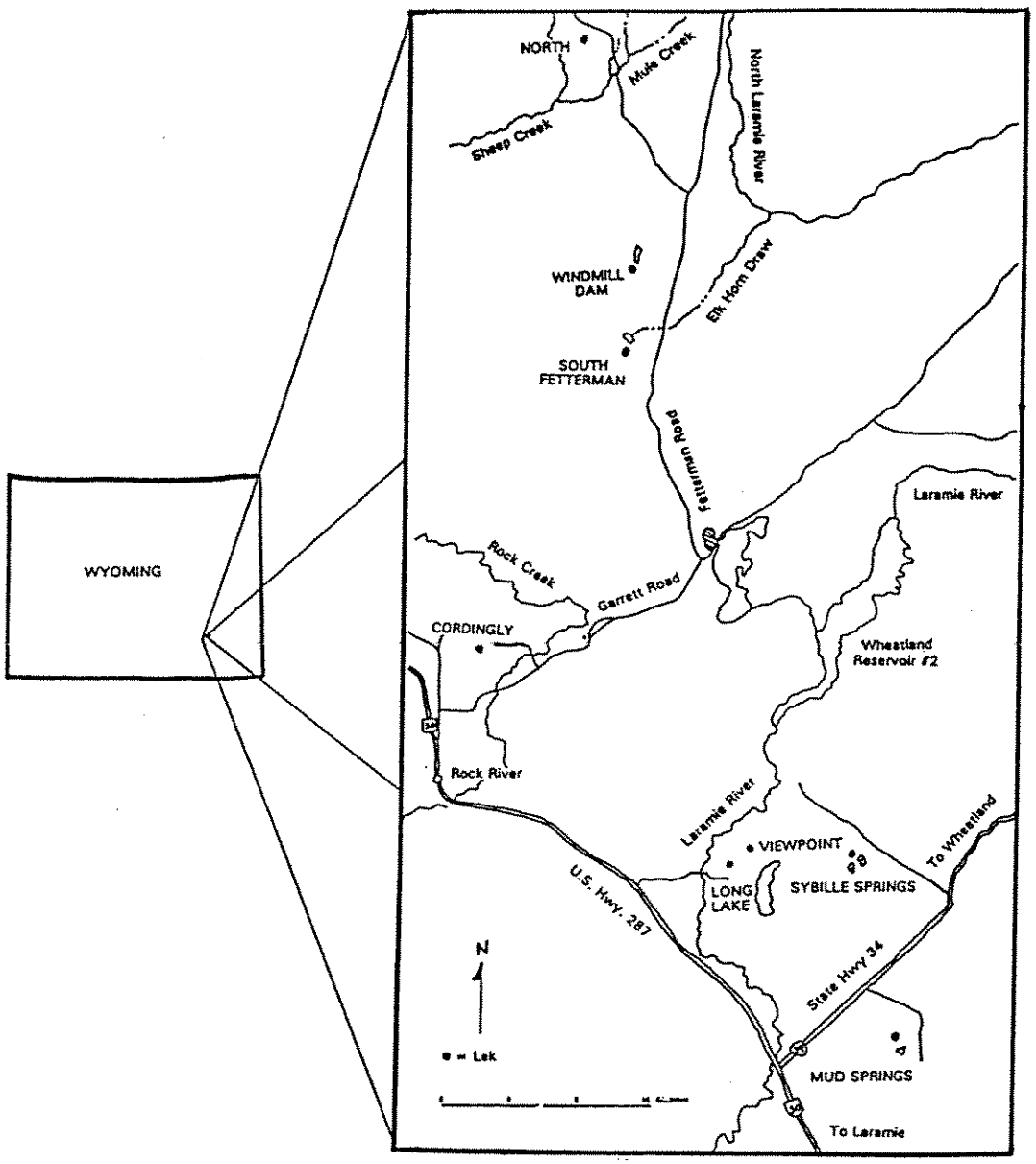

WYOMING
NORTH
Mule Creek
Sheep Creek
North Laramie River
WINDMILL DAM
Elk Horn Draw
SOUTH FETTERMAN
Fetterman Road
Laramie River
Rock Creek
Garrett Road
CORDINGLY
Wheatland Reservoir #2
Rock River
Laramie River
VIEWPOINT
To Wheatland
U.S. Hwy. 287
LONG LAKE
SYBILLE SPRINGS
N
State Hwy 34
● = Lek
MUD SPRINGS
To Laramie

Fig. 2. Difference in number of behavioral observations for all years. Observations in 1987 and 1988 occurred more frequently before the peak of hen attendance, while observations in 1989 and 1990 occurred more frequently after the peak of hen attendance.

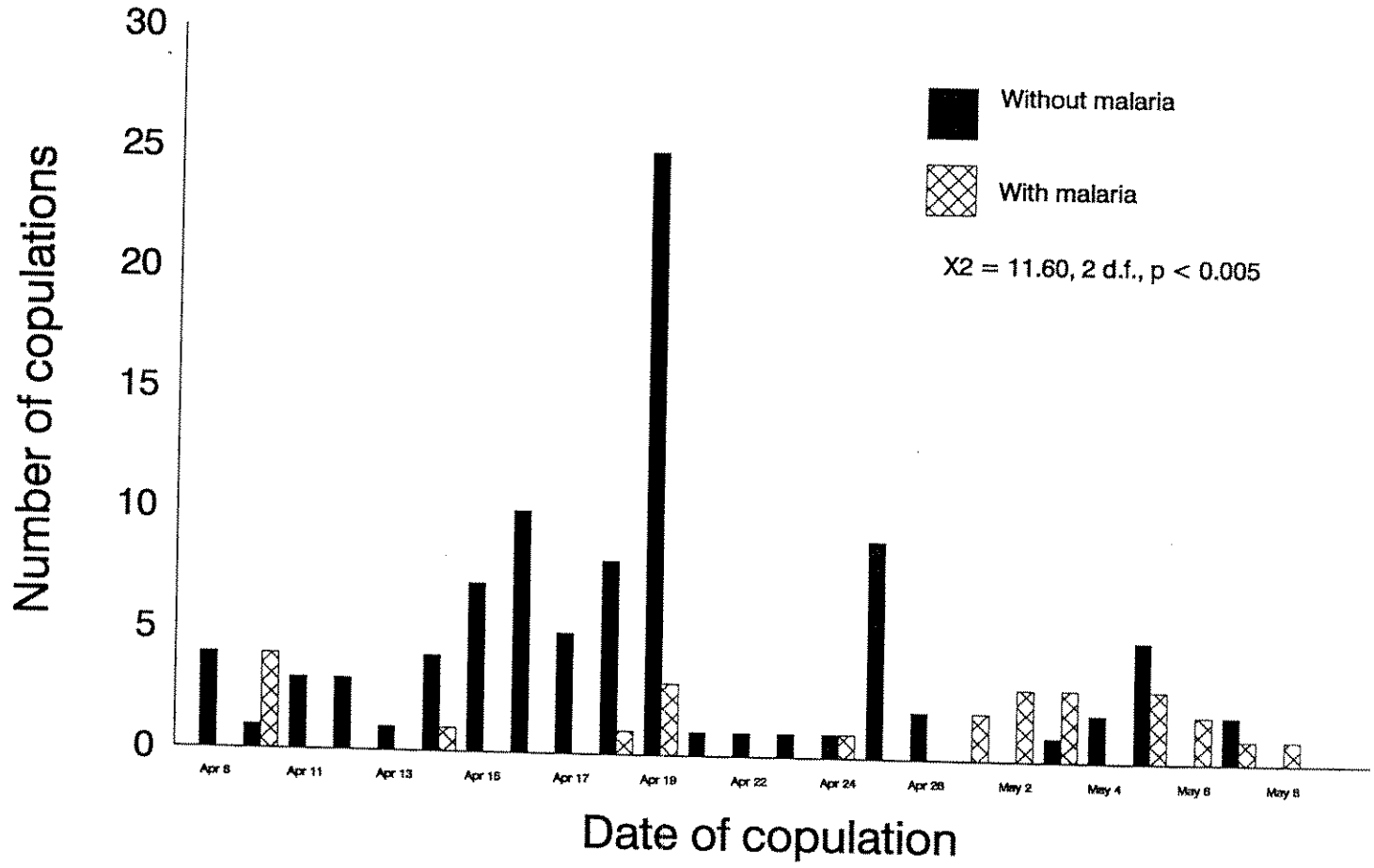

Number of copulations
30
25
20
15
10
5
0
Without malaria
With malaria
X2 = 11.60, 2 d.f., p < 0.005
Apr 8
Apr 11
Apr 13
Apr 15
Apr 17
Apr 19
Apr 22
Apr 24
Apr 26
May 2
May 4
May 6
May 8
Date of copulation

Figure 3. Change in prevalence in all birds (Y_a) and males only (Y_m) at year t+1 minus prevalence at year t versus relative fitness of malaria-free breeders at year t (W_r). The positive slope indicates that change in malaria prevalence over time increases as the relative fitness of un-parasitized breeders increases.

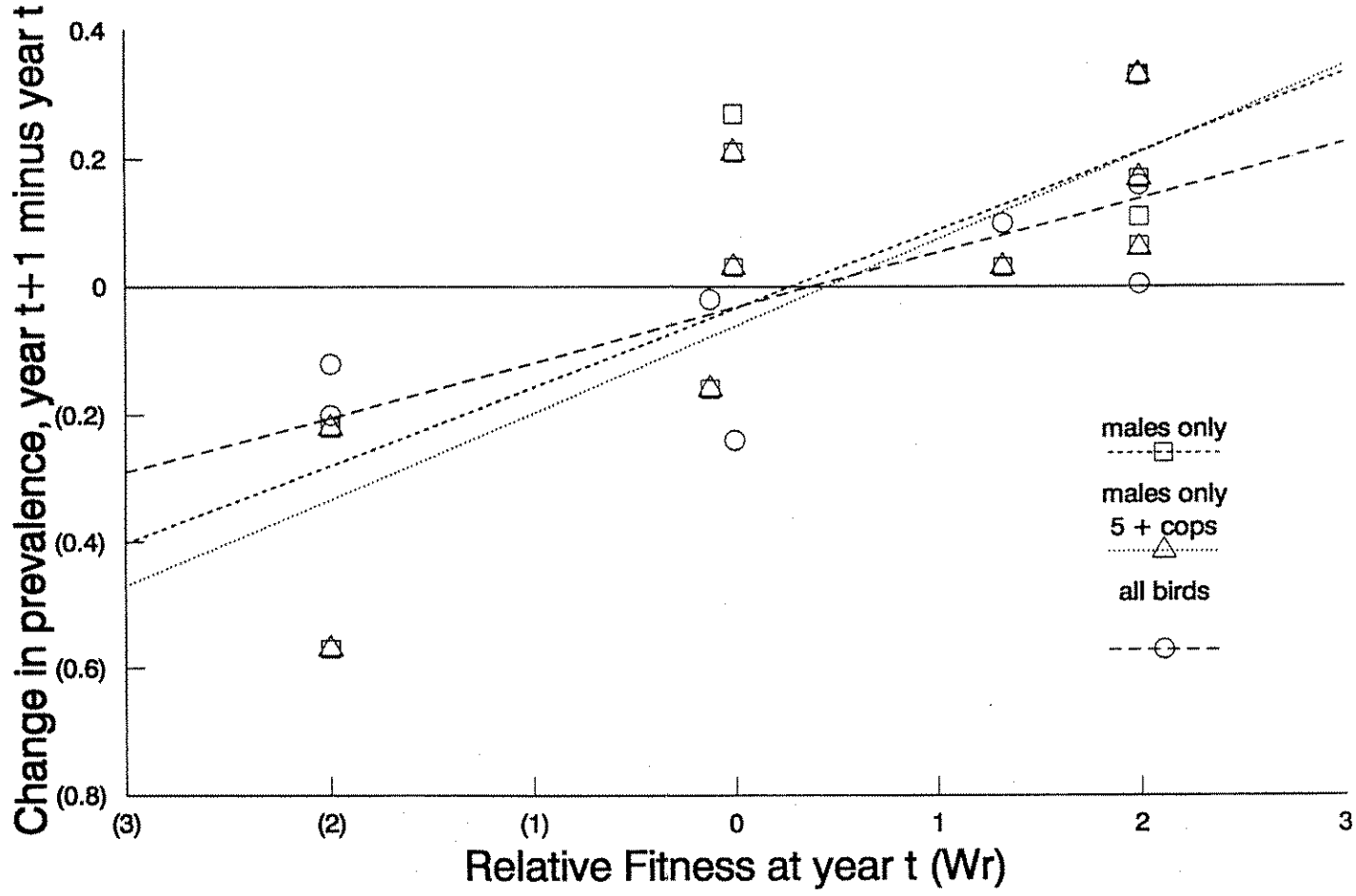

Change in prevalence, year t+1 minus year t
0.4
0.2
0
(0.2)
(0.4)
(0.6)
(0.8)
(3)
(2)
(1)
0
1
2
3
Relative Fitness at year t (Wr)
males only
males only
5 + cops
all birds

Figure 4. Change of malaria prevalence in male sage grouse from year t+1 to year t (Y_m) and intensity of female choice at year t (I) for all data and for sample sizes of greater than 5 copulations.

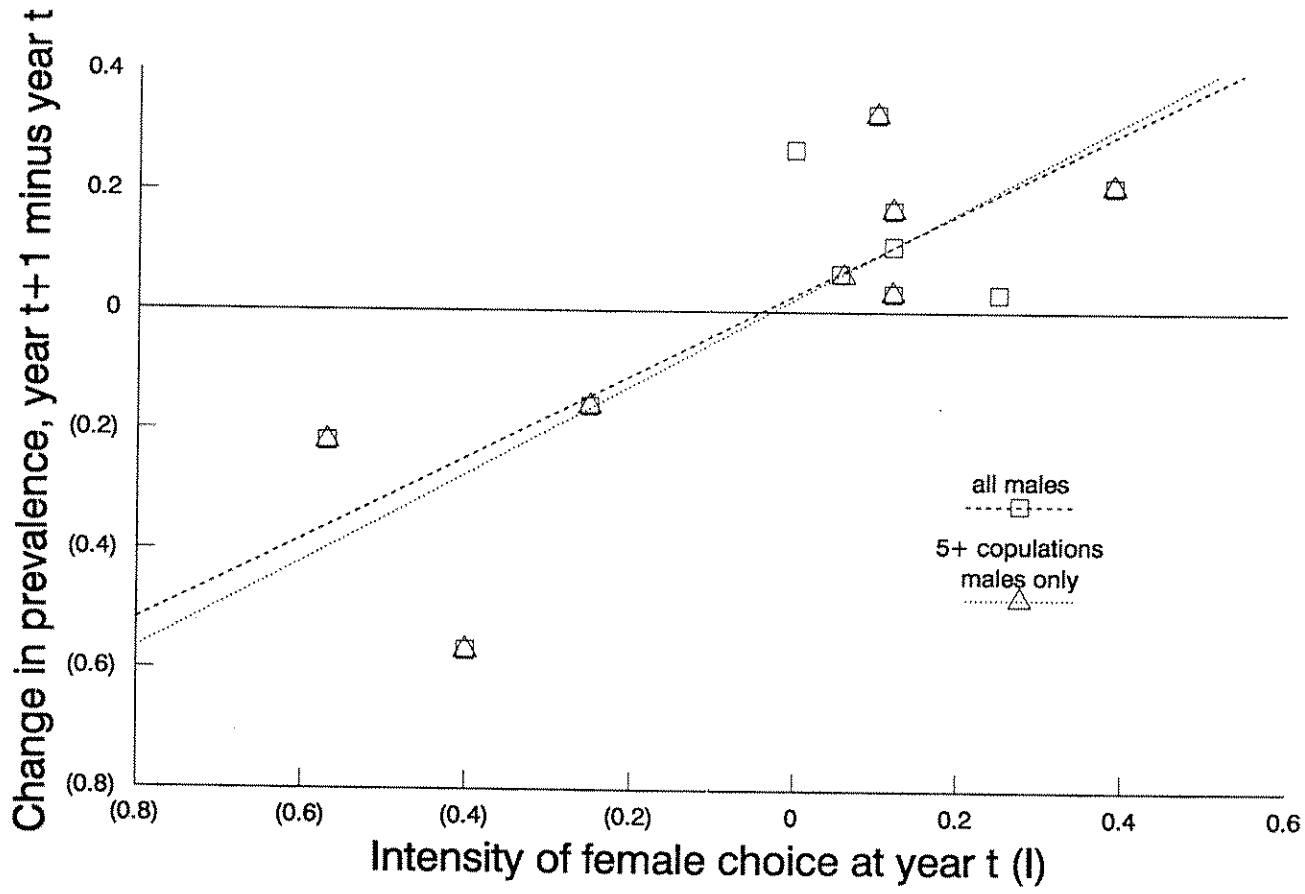

Change in prevalence, year t+1 minus year t
0.4
0.2
0
(0.2)
(0.4)
(0.6)
(0.8)
(0.8)
(0.6)
(0.4)
(0.2)
0
0.2
0.4
0.6
Intensity of female choice at year t (I)
all males
5+ copulations
males only

Figure 5. Change in yearling sage grouse malarial prevalence over time relative to yearling (Y_{jj}) and adult prevalences (Y_{aj}), and intensity of female choice at year t (I). Leks were grouped into northern and southern populations.

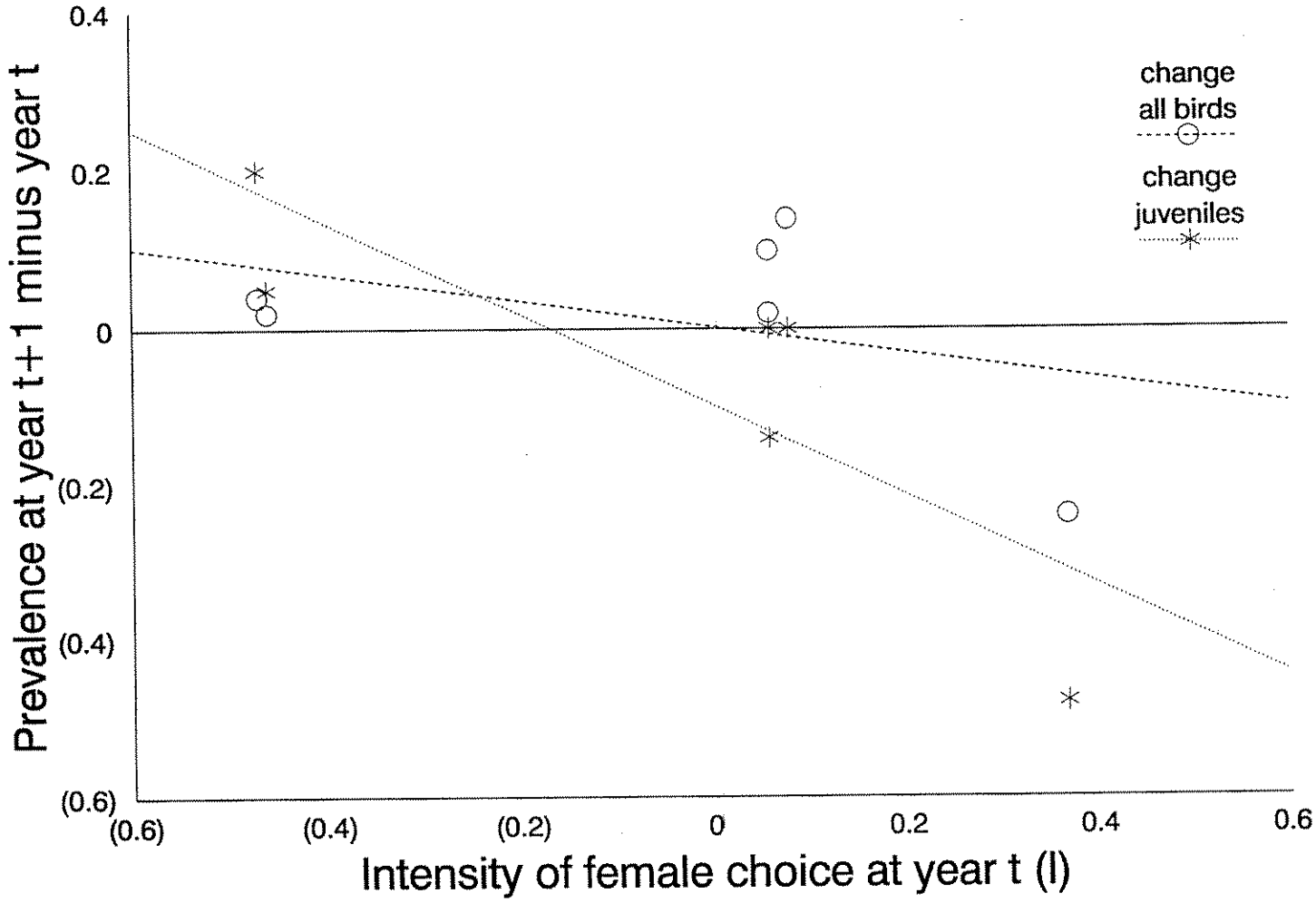
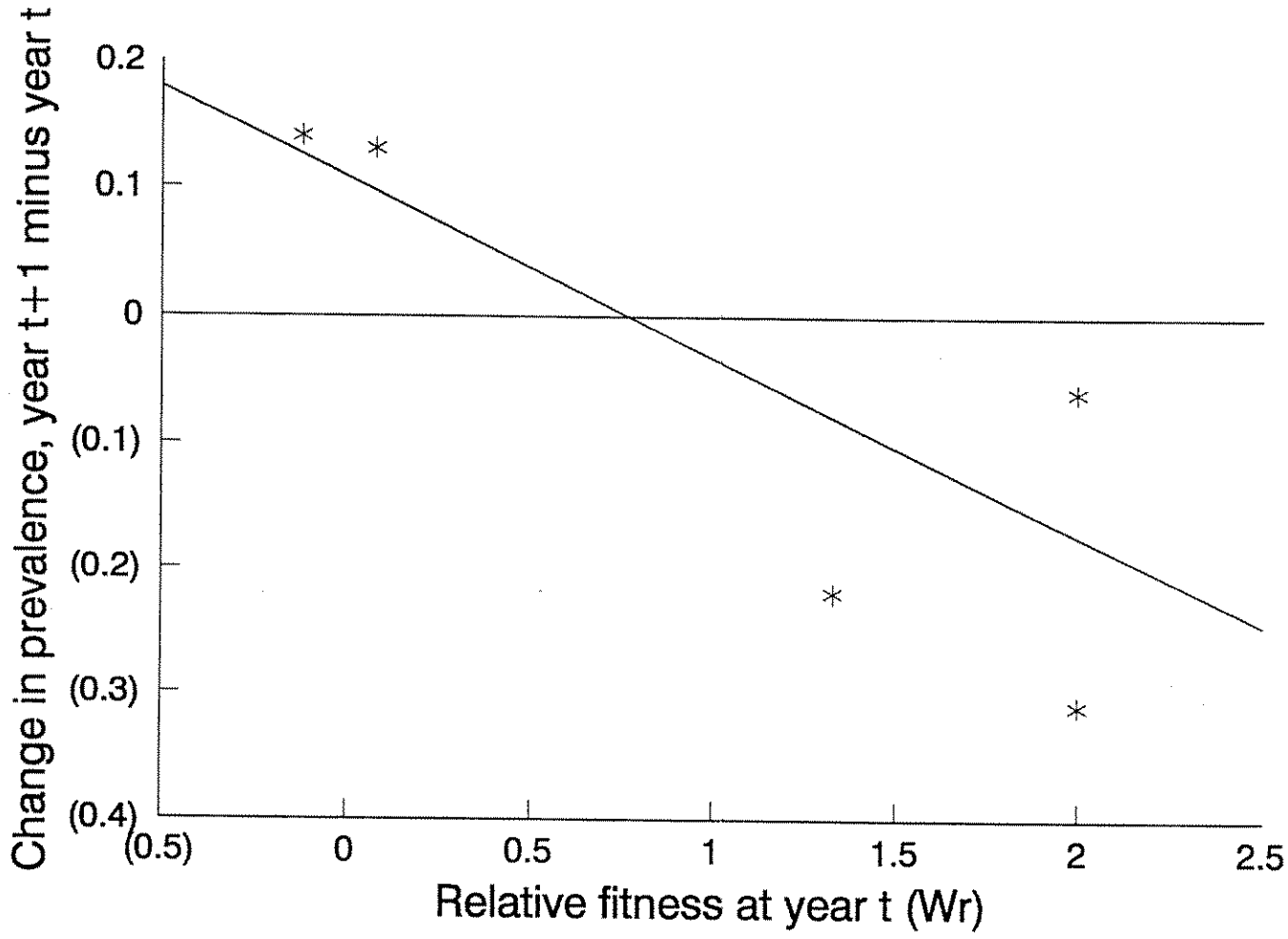

Prevalence at year t+1 minus year t
0.4
0.2
0
(0.2)
(0.4)
(0.6)
(0.6)
(0.4)
(0.2)
0
0.2
0.4
0.6
Intensity of female choice at year t (I)
change
all birds
change
juveniles

Figure 6. Change of yearling sage grouse malaria prevalence at year t+1 (Y_{jt}) relative to adult prevalence at year t (Y_{at}) and relative fitness of un-parasitized breeders (W_r). Leks were grouped into northern and southern populations.


Change in prevalence, year t+1 minus year t
0.2
0.1
0
(0.1)
(0.2)
(0.3)
(0.4)
(0.5)
0
0.5
1
1.5
2
2.5
Relative fitness at year t (Wr)

Appendix A: Change in prevalence data

Table 1. Summary of prevalence change in malaria from year t+1 to year t for all sage grouse captured. Negative change of prevalence values indicate that parasite prevalences at year t were greater than year t+1.

Year	Lek	Y_a	Y_{ij}	Y_{aj}
1987	MS	-0.10	-0.33	-0.25
1987	NL*	0.004	-0.14	-0.06
1987	SS	-0.44	-0.75	-0.50
1987	LL*	0.24	-0.39	-0.28
1988	MS*	-0.02	0.33	0.18
1988	NL*	0.16	0.00	-0.06
1988	SS*	0.43	0.50	0.44
1988	LL	-0.12	-0.11	-0.15
1988	VP	0.25	0.00	0.00
1989	MS	0.06	0.05	0.25
1989	NL*	0.10	0.00	-0.22
1989	SS*	-0.20	-0.25	-0.14

Table 2. Summary of prevalence change in lice from year t+1 to year t for all sage grouse captured. Negative change of prevalence values indicate that parasite prevalences at year t were greater than year t+1. (* = leks with 5 or more observed copulations by marked males, MS = Mud Springs, LL = Long Lake, NL = North Lek, VP = Viewpoint, SS = Sybille Springs).

Year	Lek	Y_a	Y_{ji}	Y_{aj}
1987	MS	-0.23	-0.33	-0.31
1987	NL*	-0.32	0.17	-0.05
1987	SS	-0.27	-0.50	-0.38
1987	LL*	-0.27	0.07	-0.33
1988	MS*	0.26	0.50	0.45
1988	NL*	-0.23	-0.50	-0.41
1988	SS*	0.50	0.70	0.59
1988	LL	0.04	0.20	0.01
1988	VP	-0.67	-0.50	-0.75
1989	MS	0.10	-0.06	0.10
1989	NL*	-0.20	0.20	-0.20
1989	SS*	-0.11	-0.20	-0.11

Table 3. Summary of prevalence change in malaria from year t+1 to year t for all male sage grouse only. Negative change of prevalence values indicate that parasite prevalences at year t were greater than year t+1. (* = leks with 5 or more observed copulations by marked males, ** = no yearling males captured; MS = Mud Springs, LL = Long Lake, NL = North Lek, VP = Viewpoint, SS = Sybille Springs).

Year	Lek	Y_m	Y_{im}	Y_{am}
1987	MS	0.03	-0.33	-0.25
1987	NL*	0.06	-0.14	-0.06
1987	SS	-0.40	-**	-**
1987	LL*	-0.21	0.00	0.11
1988	MS*	-0.16	0.40	0.12
1988	NL*	0.17	0.00	-0.12
1988	SS*	0.43	-**	0.46
1988	LL	-0.57	-0.50	-0.60
1988	VP	0.27	0.00	0.00
1989	MS	0.23	-0.02	0.26
1989	NL*	0.32	0.00	-0.29
1989	SS*	-0.21	-0.31	-0.18

Table 4. Summary of prevalence change in lice from year t+1 to year t for male sage grouse only. Negative change of prevalence values indicate that parasite prevalences at year t were greater than year t+1. (* = leks ≥ 5 copulations observed of marked males, ** = no yearling males captured, MS = Mud Springs, LL = Long Lake, NL = North Lek, VP = Viewpoint, SS = Sybille Springs).

Year	Lek	Y_m	Y_{im}	Y_{am}
1987	MS	-0.18	-0.33	-0.33
1987	NL*	-0.03	0.53	0.23
1987	SS	-0.24	**	*
1987	LL*	-0.16	0.25	-0.17
1988	MS*	0.27	0.60	0.45
1988	NL*	-0.41	-0.67	-0.41
1988	SS*	0.47	**	0.58
1988	LL	-0.09	0.02	0.01
1988	VP	0.77	**	**
1989	MS	-0.04	-0.16	0.02
1989	NL*	0.23	0.25	0.25
1989	SS*	-0.36	-0.28	-0.17

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GENETIC VARIATION IN SAGE GROUSE

(*CENTROCERCUS UROPHASIANUS*)

Sage grouse (*Centrocercus urophasianus*) have one of the most polygamous mating systems among birds. Both sexes gather on a lek, where a female will wander through strutting males for several days until she selects a mate. Only one or two males are chosen by all females attending the lek (Patterson 1952, Wiley 1973, Gibson and Bradbury 1986, Hartzler and Jenni 1988, Johnson and Boyce 1991). This asymmetrical mate selection occurs despite the presence of up to 300 males. In lekking systems females receive only sperm from their mate. Males do not provide nest defense, food, or parental care to their offspring. In species where clear economic benefits (e.g., nest defense) are gained by being choosy, mate choice mechanisms do not seem as well developed (Borgia 1979, Taylor and Williams 1982). Since males offer nothing but sperm, female sage grouse appear to be making mate choices based on a "good genes" assessment (Bradbury and Andersson 1987). However, such intense selection should eventually erode heritability of preferred characteristics. This is the lek paradox (Taylor and Williams 1982).

Expected effective population sizes (N_e) for lek mating systems appear to be small. Although population size and effective population size can be nearly equivalent in large, randomly mating populations, they differ dramatically when the sex ratio or mating system is skewed. In strongly polygamous species, such as elephant seals

(*Mirounga angustirostris*), effective population sizes approach four, regardless of total population size, as most copulations are captured by a single male (Futuyma 1979).

In 1982, Hamilton and Zuk proposed that condition and degree of development of secondary sexual characteristics may reflect resistance of a potential mate to parasites or pathogens. Their hypothesis assumes that parasite resistance is heritable, and therefore females may select mates so as to confer resistance to their offspring. Dynamic interactions between parasites and hosts act to maintain genetic variability for resistance, thereby preventing erosion of heritability for preferred traits (Hamilton and Zuk 1982). This hypothesis may offer an intriguing solution to the lek paradox (Taylor and Williams 1982) by maintaining genetic variation for traits under intense sexual selection (Boyce 1990; Kirkpatrick and Ryan 1991).

Sage grouse mate selection can be affected by the presence of parasitic infections among males. Three parasites that influence mate selection in Wyoming sage grouse are avian malaria (*Plasmodium pediocetii*), and two species of chewing lice (*Lagopoecus gibsoni, Goniodes centrocerci*, Order Phthiraptera) (Boyce 1990, Johnson and Boyce 1991, Spurrier et al. 1991, Deibert and Boyce unpubl. data). Males that carry either a malarial infection or a louse infestation are less preferred by females as mates. Breeding male sage grouse with lice secure fewer copulations than uninfected birds (Johnson and Boyce 1991, Deibert and Boyce unpubl. data), and breeders infected with either parasite secure copulations late in the lekking season when females are more likely to be in poor condition and/or are juveniles (Johnson and Boyce 1991). Juveniles ovulate fewer follicles, lay smaller clutches, and are less successful at

bringing off a brood (Wallestad and Pyrah 1974, Moller 1991). This suggests poor reproductive success for infected males, and amplifies the Darwin-Fisher mechanism of reproductive advantage for parasite-free males (Moller 1991). Female sage grouse were significantly less likely than males to harbor either parasite.

Effects of both avian malaria and chewing lice on sage grouse mate selection provide partial support of Hamilton and Zuk's "good genes" hypothesis. If sage grouse have a genetic resistance to either malaria or lice, the dynamic interaction between changing parasite virulence and host resistance may maintain genetic variation in their hosts despite a highly polygamous mating system and resultant low N_e.

The influence of parasites on sage grouse mate selection, and extreme polygamy of this species led me to initiate studies of genetic variation and mechanisms of mate selection. I found that despite low effective population sizes, sage grouse have high genetic variation, and frequencies of some alleles vary between birds with and without parasites. My results suggest that parasites may have the potential to maintain genetic variability for some alleles in sage grouse.

METHODS

My study was conducted on eight sage grouse leks in southeastern Wyoming, 25 to 100 km north of Laramie (Fig. 1), from 1987 through 1990. Birds were captured on or near leks by spotlighting and rocket netting during the breeding season (Giesen et al. 1982). Each bird was weighed, measured, and marked with a unique color combination of patagial tags for subsequent identification during behavioral

observations. Age was determined on the basis of plumage differences and primary feather molt sequence (Crunden 1963, Gill 1967). Gular sacs, combs, and the back of the head were examined for presence of lice (Ash 1960). One to 3 ml of blood were taken from the brachial vein and placed into a Beckman vacutainer with ACD solution to prevent clotting. Birds were then released at the site of capture.

Two smears were prepared from each blood sample and preserved in pure methanol. The slides were later stained with Giemsa, and examined under oil immersion (1000x) for presence of hematozoa (Hayworth et al. 1987). Ten fields (approximately 2000 - 3000 red blood cells) were examined per slide (Gibson 1990).

Mating behavior was observed for several days, from mid-March through mid-May. Observations began at first light and continued until one hour after sunrise. Information on breeding status, number of copulations, and total number of males and females attending the lek were recorded.

ENZYME RESOLUTION

The blood was centrifuged to pack red blood cells. Serum was decanted, and replaced with an equal volume of water. Enzymes were released from the cells with a sonicator. Samples were either immediately analyzed or stored at -80°C to prevent enzyme activity and degradation until analysis could be conducted.

Enzymes were resolved with horizontal starch gel electrophoresis. Each enzyme system was run on three to five buffer systems to optimize activity and resolution, and to detect polymorphisms. (Optimal buffer systems for sage grouse

enzymes are described in Appendix I). Since enzymes reflect gene loci, individual sage grouse were scored on each enzyme system, creating an allele profile for that bird. Blood samples collected in 1990 deteriorated prior to electrophoresis, and consequently were not included in any analyses.

For each enzyme resolved, I examined allelic frequencies to determine if the locus was in Hardy-Weinberg equilibrium. Using Chi^2 analysis, I also determined if there were allelic frequency differences between groups of birds. These groups were defined by observed dissimilarities and included breeders vs. non-breeders, birds with and without malaria, birds with and without lice, males and females, adults and juveniles, adult males and juvenile males, adult females and juvenile females, juvenile males and females, and adult males and females. Individual leks may be samples of a larger population, and probably do not reflect separate populations due to inter-lek migration. Therefore I also examined allelic frequency differences for northern and southern groups of leks. Population segregation was based on the presence of approximately 30 km of grassland that is unsuitable habitat for sage grouse between these groups of leks. Mixing of birds between these areas is possible, but unlikely given typical dispersal distances (Dunn and Braun 1985, Connelly et al. 1988). A power analysis was conducted on all non-significant results to determine the probability of a Type II error (Cohen 1988, Peterman 1990).

EFFECTIVE POPULATION SIZES

Effective population sizes were approximated for each lek and year using Wright's island model:

$$N_e = 4N_fN_m/(N_f+N_m+1),$$

where N_f = number of breeding females, and N_m = number of breeding males (Futuyma 1979). I presumed that all females which attended the lek bred, and determined N_f to be the number of females captured, plus the highest number of unmarked females observed on each lek, while N_m was the actual number of males observed copulating. Effective population sizes were then compared to genetic variation in sage grouse as determined by blood enzyme analysis. I also calculated N_e for northern and southern groups of leks.

RESULTS

EFFECTIVE POPULATION SIZES

Four to six leks per year had enough observations of marked individuals for calculation of effective population sizes. Number of breeding males per lek ranged from 1% to 16% of all males in attendance, with most leks averaging 5% (Table 1). In 1988, one male on North lek accounted for 88% of all observed copulations before he was injured by a golden eagle (*Aquila chrysaetos*). Numbers of breeding males were slightly higher in 1988 due to more attending males and the presence of second mating centers on several leks.

Effective population sizes for each lek were small (4-19) in comparison to the actual number of birds observed (29-254) (Table 1), and N_e was higher in southern leks during the four years of the study (Table 2). My estimates of N_e however may be lower than the actual N_e. The number of unmarked breeders used to calculate N_e was the maximum number of unmarked birds which copulated on one day. Therefore, I may have underestimated their actual numbers since different unmarked birds may have bred on other days. Copulations also occurred at night during the full moon (Johnson 1990) when I were unable to reliably identify marked and unmarked individuals.

GENETIC VARIATION

The genetic survey of blood enzymes included 26 enzyme systems, and gene products of 33 enzyme loci were detected. A total of 18 loci were monomorphic, and no activity was detected at 4 loci (malic enzyme, glutamate oxaloacetate transaminase, adenylate kinase, and adenosine deaminase). Aconitase had low activity, and could not be reliably scored. However, no variation was detected at that locus. Phosphoglucomutase-1, Ng, and a colorimetric esterase were polymorphic, but could not be scored in all individuals due to low activity. Two enzymes (colorimetric esterase-2 and creatine kinase) had such complex patterns of polymorphisms that genotypes could not be accurately scored using electrophoretic techniques.

Five polymorphic loci were scored from all individuals sampled (Table 3). The number of alleles at these loci ranged from two to four (Table 3), and heterozygosity ranged from 8% to 45% (Table 4). Based on these enzyme surveys, the proportion of

polymorphic loci in these sage grouse populations was 0.30, and individual heterozygosity averaged 8.4%. Using data for all birds sampled, genotypic distributions approximated Hardy-Weinberg expectations for only two (amino-peptidase slow, and colorimetric esterase) of the five polymorphic loci scored. The results were the same when all birds from southern leks only were examined. For the northern group of leks however, all loci, except phosphomanose isomerase, were in Hardy-Weinberg equilibrium (Table 5).

Of the 10 groups of birds compared, I found significant allelic frequency differences among only four (Table 6). Grouse infected with malaria were less likely to be heterozygous at the aminopeptidase-medium locus than uninfected birds (X^2 = 15.30, df = 5, P = 0.011) (Fig. 2). At the aminopeptidase-slow locus, adult males were more likely to be heterozygous than adult females (X^2 = 12.41, df = 2, P = 0.003) (Fig. 3). Adult males were less likely to be heterozygous for two of three allelic combinations at the colorimetric esterase-1 locus than females (X^2 = 11.16, df = 5, P = 0.049) (Fig. 4). Distribution of allelic frequencies between juvenile and adult males were also significantly different at the esterase locus, with juveniles more likely to be monomorphic for one of the three alleles (X^2 = 23.02, df = 5, P < 0.001) (Fig. 5).

Statistical analyses resulting in non-significant differences between groups had low power (Table 7). Manipulation of effect sizes for all comparisons, maintaining observed sample sizes, did not result in a power of greater than 0.73 before differences between groups became statistically significant. Therefore, my sample sizes were

insufficient to detect differences in allelic frequencies between groups, and I was unable to draw definitive conclusions regarding these comparisons.

DISCUSSION

EFFECTIVE POPULATION SIZES AND GENETIC VARIATION

As is characteristic of all lek mating systems, few male sage grouse were selected by females as mates, which resulted in low effective population sizes for leks. In a survey of 46 avian genetic variation studies, Nevo et al. (1984) estimated the average polymorphism was 0.30 ± 0.02, and average heterozygosity to be 0.051 ± 0.003. Thus, sage grouse in southern Wyoming appear to have average or above average levels of genetic variation despite small effective populations sizes.

Inter-lek migration for both male and female sage grouse has been estimated at 10%-15% in northern Colorado (Dunn and Braun 1985). If rates are similar in southern Wyoming migration may maintain genetic variation in this population of sage grouse. Very small migration rates can be sufficient to make adjacent sub-populations one panmitic unit (Wright 1931; Falconer 1989). Since distances among leks within the northern and southern groups are much less than 30 km, migration is probably not restricted. Migration may also "swamp" gene pools of the northern and southern groups of leks even though the distance separating them is sufficient to limit sage grouse dispersal (Dunn and Braun 1985; Connelly et al. 1988). There were several other leks within the northern and southern groups which were not sampled. Immigration from these leks may increase effective population sizes and help maintain

the observed genetic variation. Proximity of the northern group of leks to other groups is also unknown. But habitat is suitable for sage grouse in most of the surrounding area. The southern group of leks is relatively isolated, but at least one female sage grouse moved into this population from northern Colorado in 1989 (O. Meyers, pers. comm.). However, migration can be overridden by natural selection (Endler 1973; Mitton et al. 1989), particularly in lek mating systems (Taylor and Williams 1982).

Genetic variation in this population of sage grouse may also be maintained by selection for heterozygotes. I observed evidence of heterosis occurring between juvenile and adult males at one locus (colorimetric esterase-1). Heterosis may occur at other loci which I was unable to resolve or detect.

Another potential selective force maintaining genetic variation is coevolution of parasites and their hosts. As proposed by Hamilton and Zuk (1982), parasites may act to maintain host genetic variability through a genetic "arms race" of parasite virulence and host resistance. Sage grouse without malaria were less likely to be heterozygous at the amino-peptidase medium locus, suggesting a genetic basis for lack of malarial infections in some sage grouse. However, since some birds with malaria were heterozygous at this locus, it is unlikely that a genetic resistance to this parasite is controlled by a single locus. Perhaps the products of this heterozygous combination must work with other, unmeasured allelic products in providing a malaria resistance. A previous study of malaria in sage grouse found evidence for heritable resistance to this parasite (Deibert and Boyce unpubl. data), and resistance to malaria has been observed in some avian species (Bennett et al. 1993).

Comparisons of allele frequencies between birds with and without lice did not reveal any significant difference. However, I must interpret these results with caution due to the high probability of a Type II error. Additionally, the enzymes I was able to resolve for sage grouse may not be associated with presence of lice, and therefore may provide little information about any correlation between these two variables.

ALLELIC FREQUENCY DIFFERENCES

Few significant differences in allelic frequencies were observed between different groups of sage grouse at the five genetic loci measured. These results suggest that little selection is occurring on these five loci, and that the groups of sage grouse examined may actually be part of a much larger population.

As previously discussed, birds with malaria were less likely to be heterozygous at the amino-peptidase medium locus. But, this difference was not observed between males and females even though female sage grouse have a significantly lower prevalence of malaria (Deibert and Boyce, unpub. data). Male sage grouse are probably more susceptible to a malarial recrudescence earlier in the spring than females due to elevated testosterone and stress levels (Beaudoin et. al 1971, Folstad and Karter 1992). Since I sampled sexes simultaneously, I may have failed to accurately detect malaria in females if their recrudescence had not yet occurred.

Adult male sage grouse were more likely to be heterozygous at the amino-peptidase slow locus, and less heterozygous at the colorimetric esterase-1 locus than adult females suggesting differential selection on sexes. Male and female grouse rarely

associate, except in winter flocks and in their brief encounter on the lek (Patterson 1952). Inter-sexual differences in habitat association, predation, and energetic costs may provide a mechanism for differential selective forces. However, I was unclear which of these differences in life history, if any, provide the selective force on these particular loci.

Increased heterozygosity of adult males in comparison to juvenile males at the colorimetric esterase-1 locus suggests that heterozygous males may have an increased survival rate. The products of this locus may be sex-linked as the same heterozygote advantage was not observed among females.

Deviation from expected Hardy-Weinberg equilibrium for all birds at three loci (amino-peptidase medium, amino-peptidase fast, and phosphomanose isomerase) may be due to violation of any number of assumptions: 1) random mating, 2) no migration or mutations, 3) infinite population size, and 4) no selection (Futuyma 1979). Due to low rates of genetic mutation (Futuyma 1979, Mettler et al. 1988), it is improbable that my data reflects a violation of that assumption. Lack of differences between the observed allelic frequencies of northern and southern leks suggest that this sage grouse population may be very large. But, the assumption of random mating is obviously violated and no selection is highly improbable.

Given the intense sexual selection in sage grouse mating systems, it is surprising any loci are in Hardy- Weinberg equilibrium. Yet, this is true for amino-peptidase slow and colorimetric esterase-1 in all groups (all leks and northern and southern groups of leks) examined. Perhaps these loci are not under direct selection and migration is

sufficient to counteract the asymmetrical mate selection in this species. Reasons for differences between Hardy-Weinberg equilibrium results for northern and southern leks are unclear. However, it suggests that these two groups are under differential selective forces.

SUMMARY

Genetic variation of sage grouse in southern Wyoming approximates levels observed in other bird species despite apparent low effective population sizes. Migration may explain maintenance of this variation. My data also provide limited evidence of heterosis in males, inter-sexual differences in selective forces, and a heterozygote advantage against malaria at one locus. Both may also help maintain genetic variation in sage grouse. Differences in allelic frequencies between selected groups of birds may be the result of differential selective forces.

Table 1. Number and percent of all breeding males (marked and unmarked), all females (marked and unmarked), and N_e for each lek and year. (Leks - LL-Long Lake, CO-Cordingly, NL-North Lek, SS-Sybille Springs, MS-Mud Springs, VP-Viewpoint).

Year	Lek	Total Birds	Total Males	Male Breeders	% Males Breeding	Total Females	N_e
1987	LL	169	73	3	4.1	96	11.5
1987	NL	99	36	3	8.0	81	11.2
1987	SS	88	36	2	5.6	52	7.6
1987	MS	141	67	3	4.5	74	11.4
1988	LL	261	102	5	4.9	159	19.3
1988	NL	108	37	5	13.5	71	18.4
1988	SS	85	37	6	16.2	48	20.9
1988	MS	215	91	5	5.0	124	19.1
1988	VP	35	21	1	4.8	14	3.5
1988	CO	29	8	1	12.5	21	3.7
1989	LL	94	69	1	1.4	25	3.7
1989	NL	119	43	3	6.9	76	11.4
1989	SS	59	41	1	2.0	18	3.6
1989	MS	254	143	4	2.8	111	15.3
1989	VP	44	16	1	6.3	28	3.7
1990	NL	101	36	2	5.6	65	7.6
1990	SS	91	54	2	3.7	37	7.4
1990	MS	204	151	2	1.3	53	7.6

Table 2. Effective population sizes for northern and southern groups of leks and years. Northern leks included North (NL) and Cordingly (CO) leks, southern leks included Mud Springs (MS), Sybille Springs (SS), Long Lake (LL), and Viewpoint (VP) leks.

Year	Lek Group	Number Males	Males Breeding	Number Females	N_e
1987	south	176	8	222	30.1
1987	north	36	3	81	11.4
1988	south	251	17	345	64.6
1988	north	45	6	92	22.3
1989	south	269	7	182	26.8
1989	north	43	3	76	11.4
1990	south	205	4	90	15.2
1990	north	36	2	65	7.7

Table 3. Polymorphic loci scored of 33 measured in sage grouse.

(unk = unknown)

Polymorphic Blood Loci	# Alleles
1. Amino-peptidase - slow (APS)	2
2. Amino-peptidase - medium (APM)	2
3. Amino-peptidase - fast (APF)	4
4. Phosphomanose isomerase (PMI)	3
5. Colorimetric esterase-1 (EST-1)	3
6. Colorimetric esterase-2 (EST-2)*	unk
7. Creatine kinase (CK)*	unk

* Polymorphisms were too complex to reliably score in all individuals.

Table 4: Percentage of individuals heterozygous for each of 5 loci scored in sage grouse. Numbers in parentheses indicate sample size. (Leks - LL=Long Lake, SS=Sybille Springs, MS=Mud Springs, NL=North Lek, CO=Cordingly, SF=South Fetterman, WD=Windmill Dam, VP=Viewpoint, MCJ=Mule Creek Junction, BW=Broken Wing; Loci - APS=amino peptidase slow, APM=amino peptidase medium, APF=amino peptidase fast, PMI=phosphomanose isomerase, EST=colorimetric esterase-1).

Table 4.

Lek	Locus				
	APS	APM	APF	PMI	EST
LL	14.6 (123)	5.8 (120)	44.4 (124)	9.6 (104)	17.0 (112)
SS	20.0 (45)	3.6 (55)	40.7 (54)	20.4 (49)	11.5 (52)
MS	21.3 (89)	6.7 (89)	42.2 (90)	24.4 (82)	10.2 (88)
NL	34.9 (43)	9.7 (41)	55.8 (43)	24.4 (41)	18.2 (33)
CO	22.2 (18)	11.1 (18)	38.9 (18)	5.9 (17)	11.8 (17)
SF	13.0 (23)	12.5 (24)	29.2 (24)	4.5 (22)	8.7 (23)
WD	27.3 (11)	9.1 (11)	27.3 (11)	10.0 (10)	9.1 (11)
VP	12.5 (16)	12.5 (16)	68.8 (16)	0.0 (11)	31.3 (16)
MCJ	8.3 (12)	16.7 (12)	66.7 (12)	8.3 (12)	18.2 (11)
BW	10.5 (19)	14.3 (21)	50.0 (22)	40.9 (22)	4.8 (21)
Total	19.3 (394)	7.9 (407)	45.0 (414)	17.0 (370)	13.8 (384)

Table 5. Status of Hardy-Weinberg equilibrium for each locus. Northern leks included North lek and Cordingly, southern leks included Mud Springs, Sybille Springs, Long Lake, and Viewpoint leks. (Y - locus in Hardy-Weinberg equilibrium, N - locus not in Hardy-Weinberg equilibrium; Loci - APS=amino peptidase slow, APM=amino peptidase medium, APF=amino peptidase fast, PMI= phosphomanose isomerase, EST = colorimetric esterase-1).

Leks	APS	APM	APF	PMI	EST
All	Y	N	N	N	Y
northern	Y	Y	Y	N	Y
southern	Y	N	N	N	Y

Table 6. Allelic frequency data (percentage) of alleles at three loci that showed statistically significant differences between groups. (Loci - APM=amino-peptidase medium (2 alleles), APS=amino-peptidase slow (2 alleles), EST=colorimetric esterase-1 (3 alleles)).

Comparison	Locus		Alleles 11	12	13	22	23	33	N
Mal. vs. no mal.	APM	M	1.5	4.6		93.9			263
		N	1.3	17.9		80.8			78
Adult males & females	APS	M	2.0	42.4		55.6			302
		F	1.4	20.5		78.1			73
Adult males & females	EST	M	0.5	9.0	0	88.2	2.4	0	211
		F	1.4	15.5	0	73.2	9.9	0	71
Adult vs. juvenile males	EST	A	0.3	33.3	0	64.6	1.7	0	288
		J	0	2.0	0	92.2	5.9	0	51

Table 7. Power analysis results for all non-significant allelic frequency comparisons. Manipulation of effect sizes, keeping sample sizes constant, did not result in a power of greater than 0.73 before results became statistically significant. Numbers in parentheses indicate sample sizes.

Group	Locus				
	APS	APM	APF	PMI	EST
Breeder vs. non-breeder	0.40 (222)	0.25 (226)	0.14 (227)	0.21 (214)	0.10 (213)
Lice vs. no lice	0.32 (382)	0.13 (385)	0.35 (391)	0.76 (347)	0.65 (365)
Malaria vs. no malaria	0.30 (339)	---*	0.45 (347)	0.64 (364)	0.31 (324)
All males vs. all females	0.26 (398)	0.25 (406)	0.16 (411)	0.49 (370)	0.22 (286)
Adults vs. juveniles	0.30 (380)	0.33 (388)	0.47 (395)	0.36 (356)	0.38 (368)
Adult males vs. juvenile males	0.23 (278)	0.21 (277)	0.48 (280)	0.28 (266)	---*
Adult females vs. juv. females	0.13 (108)	0.55 (110)	0.43 (115)	0.47 (90)	0.23 (106)
Juvenile males vs. juv. females	0.11 (87)	0.22 (90)	0.19 (95)	0.62 (80)	0.46 (86)
Adult males vs. adult females	---*	0.31 (297)	0.13 (303)	0.18 (276)	---*
Northern vs. southern leks	0.50 (398)	0.42 (405)	0.48 (370)	0.53 (370)	0.29 (386)

* Differences were statistically significant and power analysis was not necessary.

Figure 1: Location of sage grouse study area near Laramie, Wyoming.

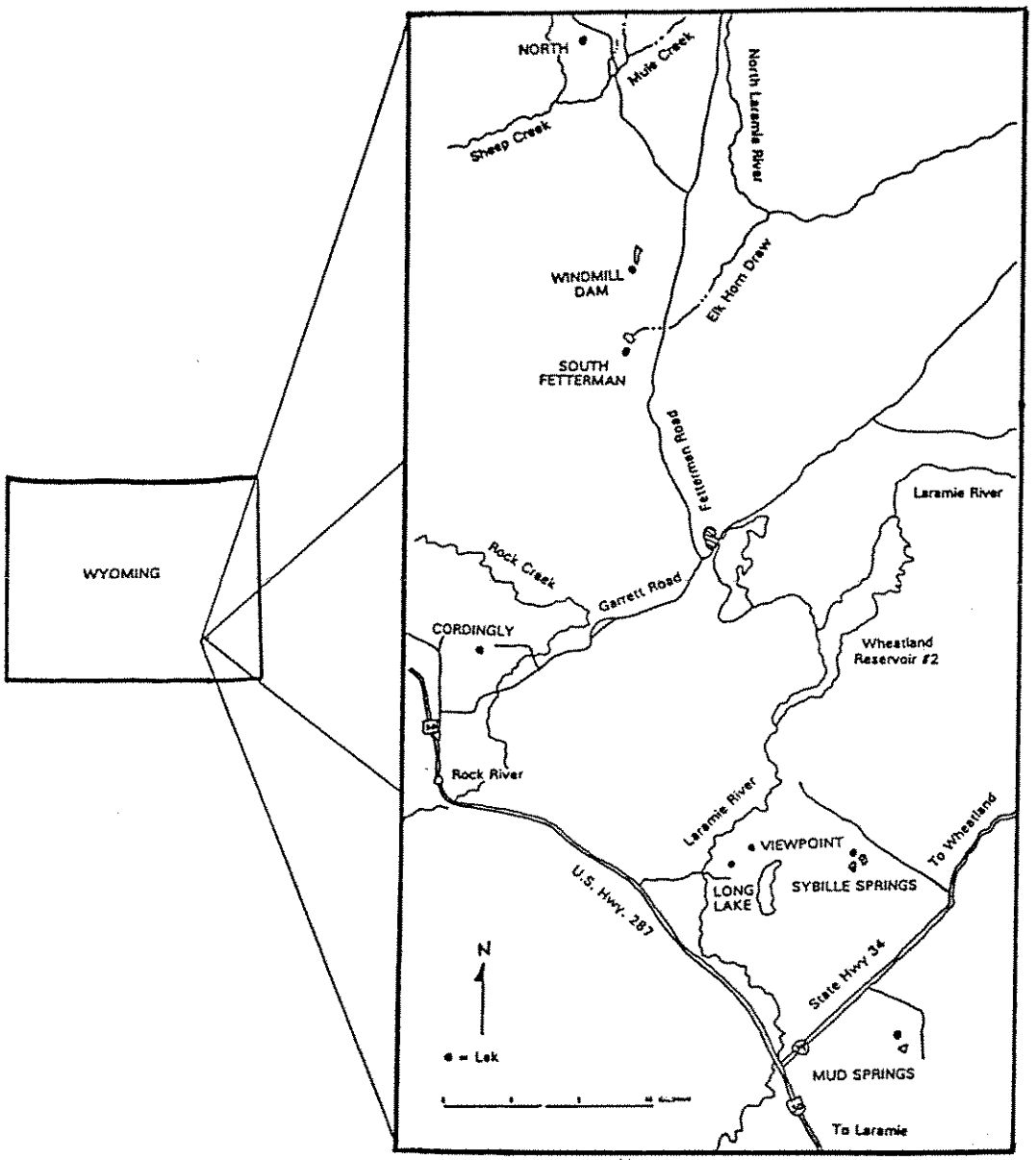

WYOMING
NORTH
Mule Creek
Sheep Creek
North Laramie River
WINDMILL DAM
Elk Horn Draw
SOUTH FETTERMAN
Fetterman Road
Laramie River
Rock Creek
Garrett Road
CORDINGLY
Wheatland Reservoir #2
Rock River
Laramie River
VIEWPOINT
To Wheatland
LONG LAKE
SYBILLE SPRINGS
U.S. Hwy. 287
N
State Hwy 34
● = Lek
MUD SPRINGS
To Laramie

Figure 2. Allelic frequency comparison of the amino-peptidase medium locus between birds with and without malaria. Data is presented in percentage of occurrence for each group.

Figure 2

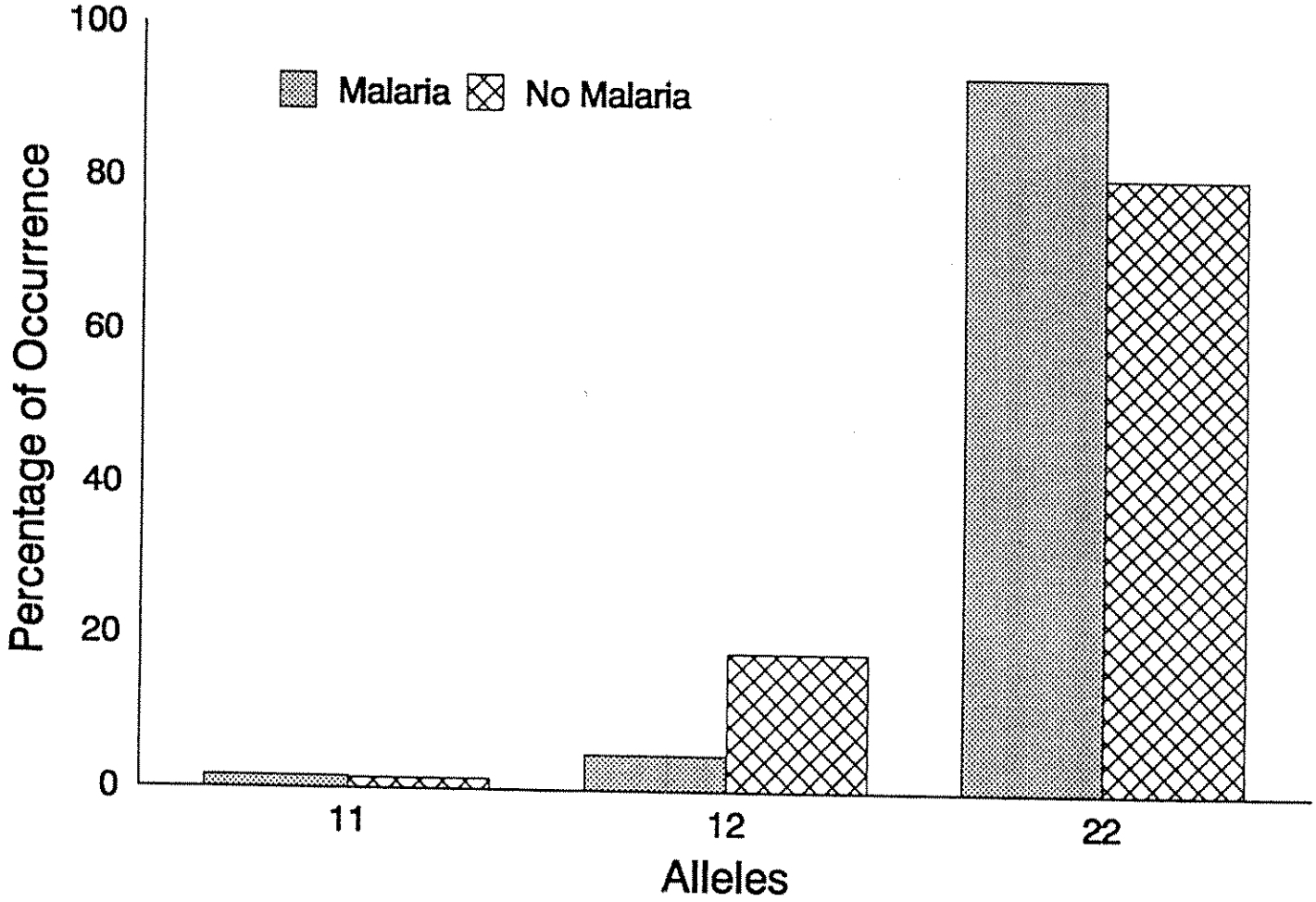

Malaria
No Malaria
Percentage of Occurrence
100
80
60
40
20
0
11
12
22
Alleles

Figure 3. Allelic frequency comparison of the amino-peptidase slow locus between male and female sage grouse. Data is presented in percentage of occurrence for each sex.

Figure 3

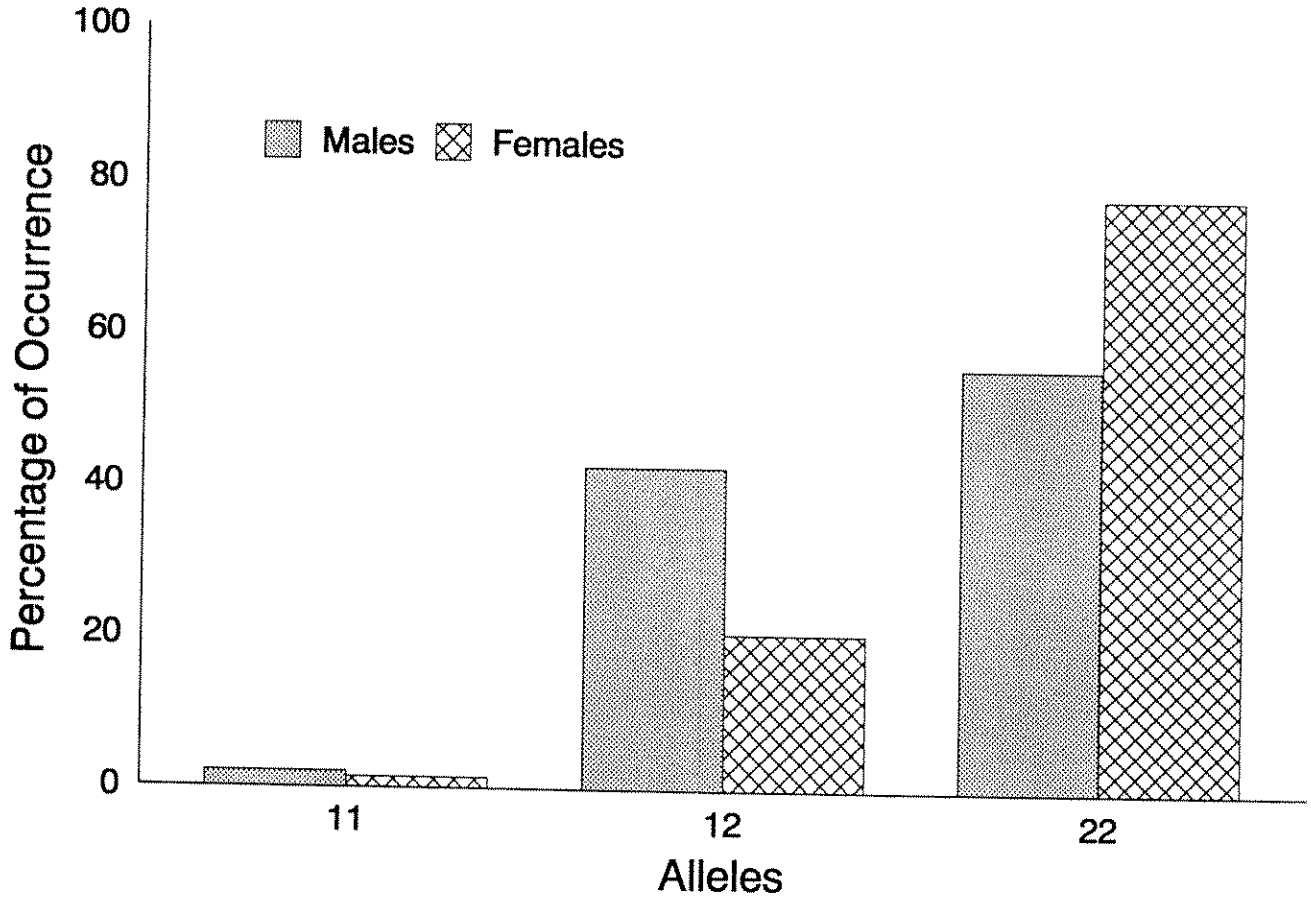

100
80
60
40
20
0
Percentage of Occurrence
Males
Females
11
12
22
Alleles

Figure 4. Allelic frequency comparison of the colorimetric esterase-1 locus between male and female sage grouse. Data is presented in percentage of occurrence for each sex.

Figure 4

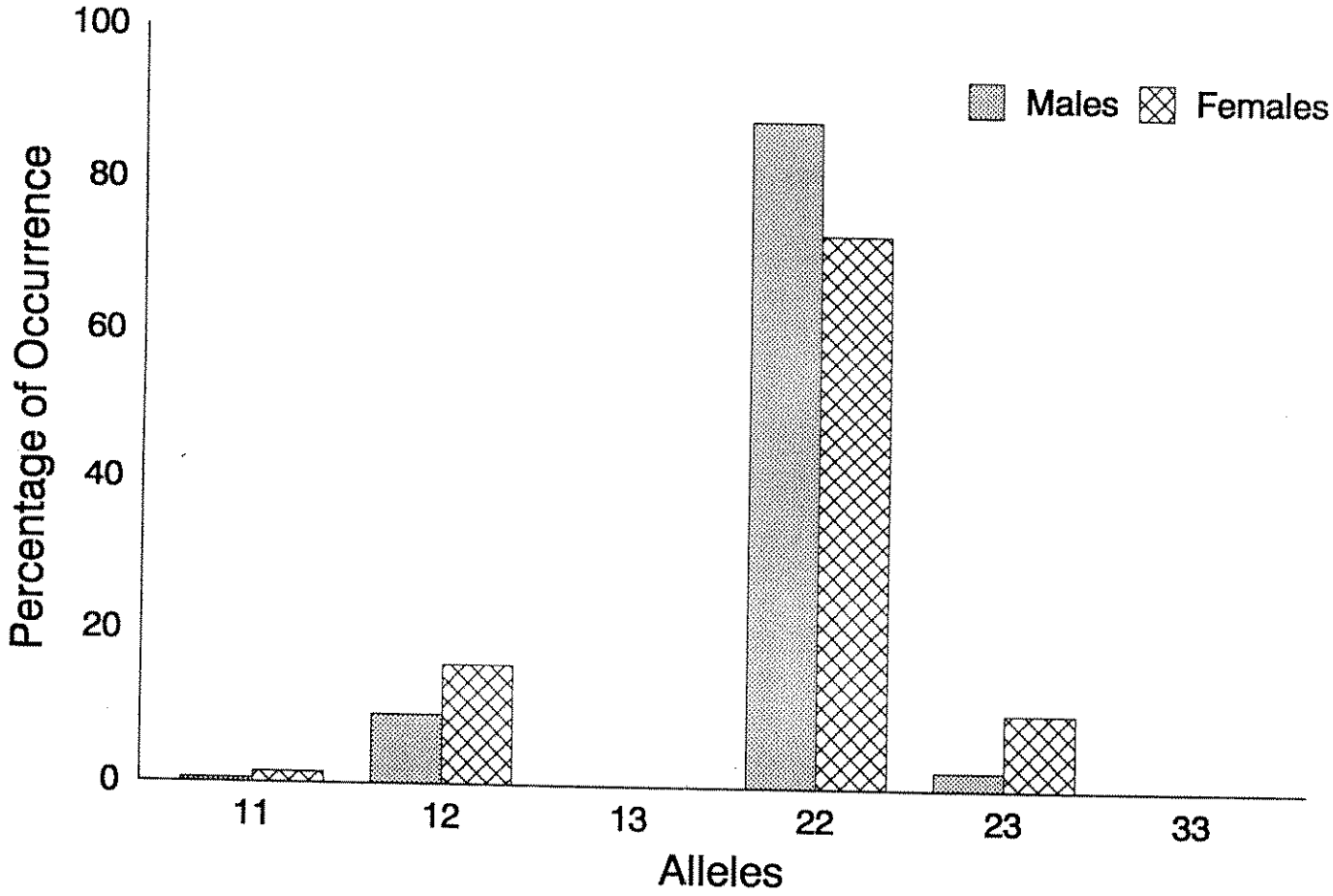
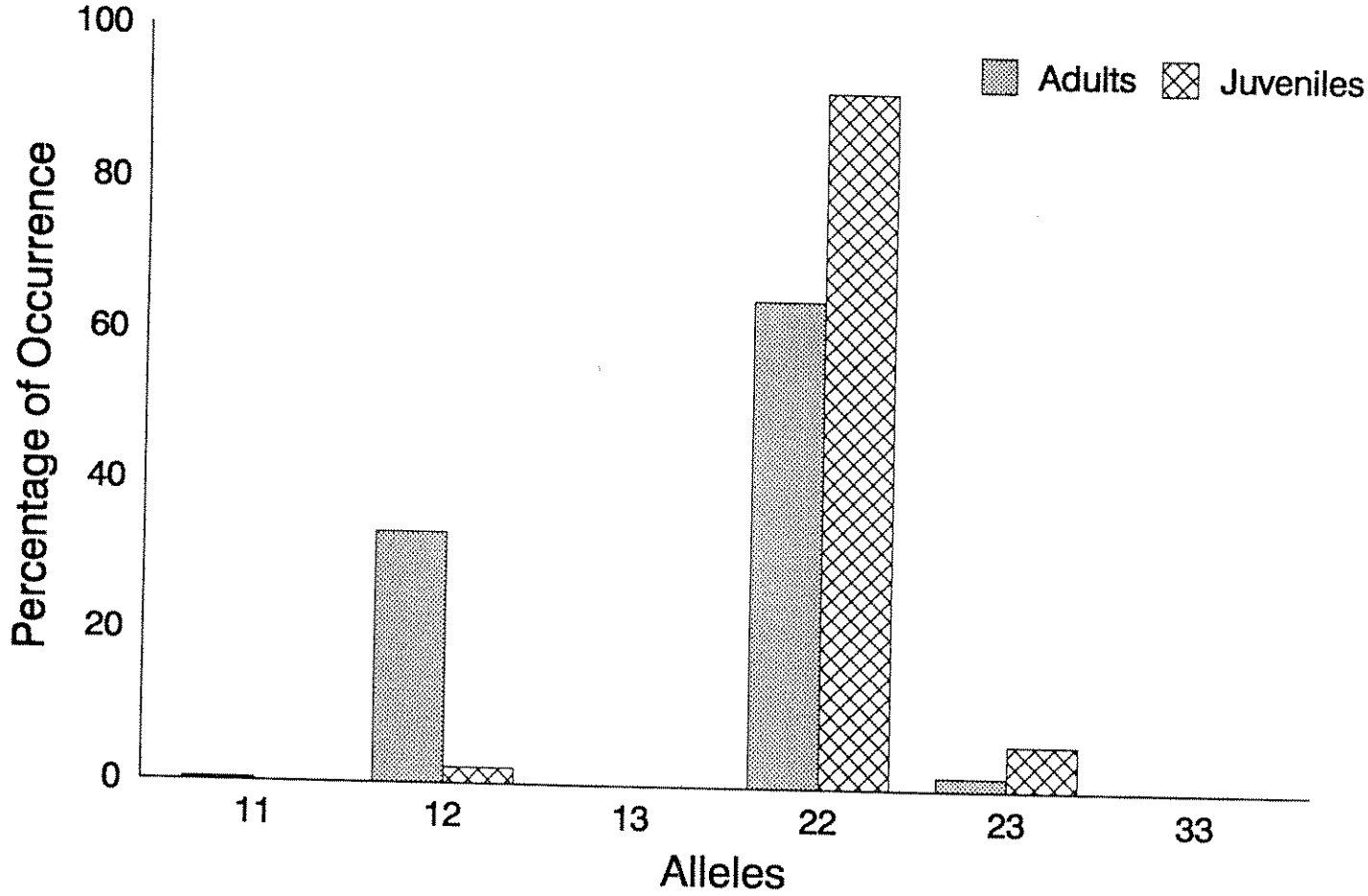

Percentage of Occurrence
100
80
60
40
20
0
Males
Females
11
12
13
22
23
33
Alleles

Figure 5. Allelic frequency comparison of the colorimetric esterase-1 locus between juvenile and adult male sage grouse. Data is presented in percentage of occurrence for each group.

Figure 5


Percentage of Occurrence
100
80
60
40
20
0
Adults
Juveniles
11
12
13
22
23
33
Alleles

Appendix 1: Buffer systems used to resolve sage grouse blood enzymes.

Alle I Buffer System (O'Malley et al. 1979)

For aminopeptidases slow and medium (APS and APM):

Gel:
0.03 M tris
0.005 M monohydrate citric acid
pH 8.5

Electrode:
0.06 M monohydrate lithium hydroxide
0.3 M boric acid
pH 8.1

Gel buffer is 99% gel, 1% electrode buffer

Alle II Buffer System (O'Malley et al. 1979)

For aminopeptidase fast (APF), phosphomanose isomerase (PMI) and colorimetric esterase-1 (EST):

Gel:
0.005 M histidine
pH 7.0

Electrode:
0.41 M sodium citrate

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