

Phenotypic correlates and survival consequences of male mating success in lek-mating greater prairie-chickens (*Tympanuchus cupido*)

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Abstract Female choice and male–male aggression are two modes of sexual selection that can lead to elaboration of male morphological and behavioral traits. In lek-mating species, male mating success is often strongly skewed, and it is puzzling why variation in male traits is still observed given directional female choice. If male traits correlated with reproductive success are honest signals of male quality, there may be survival costs associated with the expression of those traits. In this study, we examined whether morphological, behavioral, and territorial traits are correlated with male mating success and survival in the lek-mating greater prairie-chicken (*Tympanuchus cupido*). We introduce a novel application of multinomial discrete choice models for analysis of female mate choice behavior. We found that behavioral and territorial attributes showed 6.5 times more variability among males than morphological traits. Both display and aggressive behaviors were strong predictors of male mating success, suggesting that both female choice and male–male aggression were important in determining mating success among male greater prairie-chickens. Moreover, annual survival of male prairie-chickens was independent of mating success and male traits. Females appear to be choosing males based on behavioral traits where large variation exists between males (coefficient of variation >30%). Behavioral traits were the

most important factor in determining mating success of male prairie-chickens, but the mechanism underlying this relationship is unknown. In the future, experimental manipulations of male hormones or parasite loads could bridge the proximate mechanisms and ultimate consequences of factors mediating male mating success in lek-mating grouse.

Keywords Galliformes · Life history trade-off · Mate choice · Reproduction · Sexual selection

Introduction

Sexual selection is an important driver of evolutionary change and leads to elaboration of male traits, including morphology, behavior, and territory attributes. The intensity of sexual selection may be particularly high in lek-mating species because male mating success is often strongly skewed, and a subset of males receive the majority of copulations (Bradbury and Gibson 1983; Wiley 1991). Lek-mating is a rare mating system but is found in a variety of taxa, including insects, birds, and mammals (Bradbury 1981; Höglund and Alatalo 1995). In lek-mating species, aggregated males perform displays at a communal display site (Wiley 1991). Females visit display sites to obtain indirect benefits, such as good genes for offspring, and possibly direct benefits, such as reductions in copulation disturbance, transmittal of parasites, predation risk, or the cost of searching for a mate (Reynolds and Gross 1990; Gratson et al. 1991; Höglund et al. 1992a, b; but see Sæther et al. 1999). In most cases, females do not obtain food or nesting sites through mate choice, so they must select mates based on male traits alone.

Three important factors affecting male mating success in lek-mating birds include morphology, behavior, and terri-

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torial position (Balmford 1991; Fiske et al. 1998). In lek-mating greater sage-grouse (*Centrocercus pugnax*), females choose males based on their display characteristics, but aggressive behaviors, territory position, and physical size have little or variable effects on female choice (Gibson and Bradbury 1985; Gibson et al. 1991; Gibson 1996; Spurrier et al. 1994). In black grouse (*Tetrao tetrix*), univariate analyses indicate that successful males are heavier, have larger combs (fleshy areas above the eyes), invest more in display and aggressive behaviors, and hold territories closer to the center of the lek than unsuccessful males (Alatalo et al. 1991, 1996b; Höglund et al. 1997; Rintamäki et al. 2000). However, male traits may be correlated, and some male traits may be less important predictors of mating success in multifactor analyses (Höglund and Alatalo 1995; Alatalo et al. 1996b).

If male traits are honest signals of male quality, they should be costly to produce and maintain (Wiley 1991; Jennions et al. 2001). Steroid hormones, such as testosterone, may be a proximate mechanism that mediates variation in male traits. If high testosterone levels enhance male traits at the cost of suppressing the immune system (Mougeot et al. 2004; Redpath et al. 2006), elaborate male traits should be correlated with reduced survival (natural vs sexual selection trade-off; Jennions et al. 2001). On the other hand, males may vary in their expression of sexually selected traits relative to their ability to bear the costs of producing the trait (Jennions et al. 2001). In this case, condition, male traits, and survival should be positively correlated. However, the links among male traits, mating success, and survival are usually not examined in concert.

In this field study, we examined how male mating success correlates with male traits and survival in greater prairie-chickens (*Tympanuchus cupido*), a lek-mating species of prairie grouse. We improve on past work in three ways: (1) We describe the first quantitative field study of female mate choice in greater prairie-chickens; (2) we examine the survival consequences of sexually selected traits; and (3) we present a new application of multinomial discrete choice (MDC) models to studies of mate choice. Past studies of the reproductive behavior of greater prairie-chickens have not simultaneously quantified how male behavior, morphology, and territory attributes affected male mating success (Ballard and Robel 1974; Hamerstrom and Hamerstrom 1973; Robel 1966, 1970; Robel and Ballard 1974). In these studies, aggressive males in the center of the lek tended to receive more copulations, but the roles of morphology and age on male mating success have not been addressed. We also determined if reduced survival was a consequence of increased mating success. The link between male traits, mating success, and survival has only been examined in one other lek-mating species of grouse but was limited to males greater than 2 years old (Alatalo et al.

1991). MDC models have not been used previously in studies of mate choice. This statistical method improves upon logistic regression and other procedures because mating success is not assumed to be normally distributed among males and it controls for repeated observations of males in multiple years. The objectives of our study were threefold: (1) to quantify mating skew among male greater prairie-chickens, (2) to investigate morphological, behavioral, and territorial correlates of male mating success simultaneously using MDC models, and (3) to examine the relationship between male mating success and annual survival.

Materials and methods

Overview

We observed greater prairie-chickens at lek sites between mid-March and mid-May, 2003–2006. All leks were located on cattle-grazed pastures in Riley and Geary Counties in northeast Kansas, USA (39°05'N, 96°34'W). Three leks were observed in 2003 (Konza North, Konza South, and Rannell), and we expanded our sampling effort to four leks in 2004–2006 (Poole). In this study, we restricted our mate choice analyses to observational data from three leks in 2003, four leks in 2004, and two leks in 2005. We did not include data from leks that were manipulated as part of a separate field study (Nooker 2007). Leks were visited in 2006 to determine annual return rates only.

Trapping and morphometrics

Birds were trapped at lek sites using walk-in funnel traps (Hamerstrom and Hamerstrom 1973, Toepfer et al. 1987). Males and females were given a unique combination of colored leg bands and tail markings using non-toxic permanent markers to aid in individual identification. Seven morphometric measurements were recorded during handling: body mass (± 1 g), four linear measurements of body size (lengths of tarsus plus the longest toe, anterior to posterior length of keel, flattened wing length, length of tail as measured from the middle retrices; ± 1 mm for all), and two sexually dimorphic ornaments (comb area, measured as length \times height, ± 1 mm²; pinnae length, feathers behind head erected during display, ± 1 mm). Principal components analysis (PCA) was not performed on morphometric data because these seven variables were weakly correlated ($|r| < 0.35$, $P > 0.16$). We determined age class as second-year (SY) or after-second-year (ASY) from the shape, coloration, and wear of the outermost two primaries (numbers 9 and 10; Schroeder and Robb 1993). In SY birds, the outer

two primaries 9 and 10 are retained from juvenile plumage and appear tapered with light brown dots on the leading edge extending to the tip, resulting in contrast with the coloration and wear of primaries 1 through 8. The outer primaries of ASY birds have truncate tips, light brown dots on the leading edge that terminate >2 cm from the tip, and do not contrast with the inner primaries.

Behavioral observations

Male greater prairie-chickens perform ritualized courtship and territorial behaviors on small territories at lek sites (Schroeder and Robb 1993). Courtship displays consist of rapid foot-stomping with tail fanning and raising of the pinnae feathers above the head. Displays culminate with the inflation of air sacs, a low three-note ‘boom’ vocalization, and flicking of the tail and wing feathers. Flutter-jumps are a courtship display that consists of short flights (~3 m) and a ‘clucking’ vocalization and are used to attract females when they are near the lek or on another male’s territory. Display behaviors are performed by unaccompanied males or can be directed at females. Territorial boundary disputes consist of two males facing each other at the territory boundary, frequently exchanging dry ‘neh’ calls. Fights often escalate to physical combat with males striking or pulling feathers from each other with their wings, beaks, and feet. Aggressive behavior is easily distinguished from display behavior because aggressive behavior is directed at competitors and causes an obvious response in the adjacent territorial male. Males rarely boom during aggressive behavior.

Blinds were placed ~6 m from the edge of each lek. Grid stakes were placed at 6-m intervals and did not interfere with the movement of males or females. To control for the possible effects of observer, time of day, and weather, observers were rotated among leks, the order that males were observed was varied systematically, and all observations were conducted during the peak period of activity (30 min before sunrise to 3 h after sunrise) on days without rainfall. Males were observed every other day on average to quantify display and aggressive behaviors. The behavior of individual males was recorded with continuous 10-min focal observations. Time spent in each of three main behavior categories (display, fighting, and other) was calculated. Other behaviors included preening, foraging, and roosting. Tallies were taken of the numbers of four types of discrete behaviors: fights, males approached, boom vocalizations, and flutter-jump displays. Female presence or absence on the lek during the observation period was recorded for every focal observation.

Position of males relative to grid stakes and copulations were recorded during focal observations and periodic scans of the lek. Territorial positions of males were only recorded

if associated with a boom vocalization or a territorial boundary dispute. When a pair attempted to copulate, adjacent males sometimes disrupted the copulation attempt. We determined that a copulation attempt was successful if females vigorously shook their wings and body feathers, preened their vent, and departed the lek shortly after mating (Schroeder and Robb 1993). Unsuccessful copulations occurred when a female solicited a male, and the male was able to put at least one foot on her back before being interrupted by intruding males. After unsuccessful copulations, females did not shake, remained on the lek, and usually continued to solicit males.

Statistical analyses

Statistical analyses were conducted in JMP IN (Ver. 4.0.4, SAS Institute 2003), except where otherwise noted. Sample sizes varied among analyses because it was not possible to measure every attribute for all males. Descriptive statistics are presented as mean \pm 1 SD unless otherwise indicated. To eliminate pseudoreplication in our descriptive statistics, we selected one record at random for each male observed in multiple years. The coefficient of variation (CV) was calculated as SD/mean.

Two indices of mating skew were calculated: λ and B . λ values of male mating skew allow the intensity of sexual selection to be quantified and compared across leks regardless of lek size (Kokko and Lindström 1997). This index varies from 0 to 1 where $\lambda=0$ indicates random mating and $\lambda=1$ indicates one male obtaining all the matings. λ values have been widely reported for lek-mating animals, but inference is hampered because variance of lambda cannot be calculated. The binomial skew index (B) improves upon λ values because confidence intervals can be calculated, facilitating statistical comparisons. B values are based on the observed variance in a group corrected by the expected variance if each member had an equal probability of gaining a copulation (Nonacs 2000). We calculated both λ and B values (including 95% confidence intervals and P values for B values) for male mating skew with Skew Calculator 2003 PC (Nonacs 2003). Because lek size was stable among years (± 1 –2 males), mean skew per lek was calculated to determine if leks exhibited different overall skew. The only value presented for Poole lek is from 2005 because only one copulation was observed in 2004.

The six behavioral variables (% time displaying, % time fighting, and number of boom vocalizations, flutter-jump displays, fights, and males approached) were correlated. Of 15 pairwise correlations, 11 were statistically significant ($|r|>0.44$; $P<0.01$). Thus, we used PCA to obtain two principal components of behavior that were orthogonal. The Kaiser criterion (eigenvalues ≥ 1) was used to select

the number of principal components to retain for use in our analysis (Kaiser 1960). Female presence has a large effect on male behavior in other species of lek-mating grouse (Wiley 1991; Höglund et al. 1997). To minimize variation among focal observations and to control for female presence, principal component scores were calculated for each observation session, separated by female presence or absence, and averaged for each male to obtain four behavior scores for each male (PC1 and PC2 in the presence of females and PC1 and PC2 in the absence of females). Changes in behavior with respect to female presence were analyzed using a matched pairs analysis of each male.

Territorial positions of males were plotted in ArcView (Ver. 3.3; Environmental Systems Research Institute, St. Charles, MO, USA). Using the Animal Movement extension (Hooge et al. 1999), we obtained 95% kernel estimates of territory size from positions of each male and lek size from the pooled positions of all males ($\pm 0.1 \text{ m}^2$). Centroids of the 95% kernel estimates were determined using the XTools extension (Delaune 2003). Distance to lek center was defined as the distance between the centroid of each males' range to the centroid of the entire lek ($\pm 0.1 \text{ m}$).

Annual survival was estimated from return rates of male prairie-chickens to lek sites. Return rates are the product of multiple probabilities including true survival (S), site-fidelity (F), and encounter rate (p ; Sandercock 2006). Our live encounter data indicated that F and p were close to unity (see "Results"), and we interpret return rates as estimates of true survival for male greater prairie-chickens. The SE of survival was calculated using the formula:

$$SE(\hat{S}) = \sqrt{\frac{\hat{S}(1 - \hat{S})}{N}}$$

Where \hat{S} =annual survival and N =sample size of males. Logistic regression was used to analyze annual survival rates in JMP IN (Ver. 4.0.4, SAS Institute 2003). Predictor variables included number of successful copulations received, mass, comb size, aggressive and display behavior when females were present, and distance to the lek center.

The discrete choice model

Studies correlating mating success with male traits are complicated in lek-mating species because male mating success is highly skewed and males may be observed in multiple years. Previous studies have often used Pearson correlations or multiple regression to examine the effects of male traits on mating success (Höglund and Lundberg 1987; Hill 1991; Shorey 2002). Data on mating success among males in a lek frequently violate both the assump-

tions of normality and independence that underlie correlation and regression analyses. These problems can be avoided by using logistic regression to compare unsuccessful (0 copulations) and successful males (≥ 1 copulation; Gibson and Bradbury 1985; Höglund et al. 1997). However, use of a binomial response variable reduces the power to detect differences because males that received one or multiple copulations are pooled, and it still does not address the lack of independence in responses among males in a lek. An additional complication is that some males may be observed in more than one year, leading to possible pseudoreplication (Hurlbert 1984).

Discrete choice models provide a possible solution to sampling issues by testing how an individual chooses among a defined set of choices (Buskirk and Millspaugh 2006; Cooper and Millspaugh 1999; Moore and Swihart 2006). Discrete choice models use multinomial distributions to describe how females choose a mate from among a group of males in a lek, thereby making the choice of the female the unit of measurement, not the individual males. Each copulating female increases the copulation count of exactly one male so that features such as skewed mating success among males and dependence among males' counts arise naturally from the model.

Three assumptions of the discrete choice model include choices are equally accessible to the individual, the individual gains a 'benefit' from making the choice, and the 'benefit' is a function of the attributes of the resource (sensu 'satisfaction' in Cooper and Millspaugh 1999). These three assumptions are likely to be met with respect to lek-mating prairie-chickens. First, forced copulations do not occur, and females have the ability to choose any male on a lek regardless of previous matings by that male. There is no evidence that male prairie-chickens will refuse to mate with a soliciting female, although this may be an issue for other lek-mating birds (Sæther et al. 2001). Second, females may gain indirect benefits of good genes for their offspring and possibly direct benefits such as avoiding harassment or reduced search costs (Reynolds and Gross 1990). Last, female benefits will be a function of male traits such as morphology, behavior, or territory position in lek-mating grouse.

Correlates of female choice were analyzed using a conditional logit MDC model (Proc MDC, SAS Ver. 9.1, SAS Institute 2003). The utility of a choice (U) in benefiting the individual is modeled as:

$$U_{ij} = x_{1,ij}\beta_1 + x_{2,ij}\beta_2 + \dots x_{n,ij}\beta_n + \varepsilon_j$$

where female i chooses male j , β_n is the slope coefficient for explanatory variables, and ε is the error term (SAS Institute 2003). In this study, each lek represents a different set of choices (males) from which the females choose,

which are represented in the model by different sets of values for the characteristics, x_1, \dots, x_n .

Each successful copulation was considered an independent choice of a female among the males at a lek. Studies of other lek-mating grouse indicate that females may copy choices of prior-mating females (Gibson et al. 1991; Gibson 1996; but see Spurrier et al. 1994). To test for a possible role of female mate choice copying in greater prairie-chickens, we modified the best fit MDC model ($\Delta\text{AIC}=0$) to examine correlates of female choice with respect to female mating order (a =first-mated or only females to copulate on a given day; b =females that copulated subsequently). We partitioned the model as follows:

$$U_{ij} = x_{1-a}\beta_{1-a} + x_{2-a}\beta_{2-a} + \dots + x_{n-a}\beta_{n-a} + x_{1-b}\beta_{1-b} \\ + x_{2-b}\beta_{2-b} + \dots + x_{n-b}\beta_{n-b} + \varepsilon_j$$

where x_{1-a} and x_{1-b} are the contributions of x_1 of first- and second-mated females, respectively. The resulting model AIC was compared to the best fit MDC model to determine model support. The paired estimates (x_{1-a} and x_{1-b} , for example) were also compared using a Z-statistic to determine if first- and second-mated females used different male traits to choose a mate.

In general, female prairie-chickens visited lek sites for short periods, were rarely available for capture, and a majority of the copulations were with unbanded females. Nevertheless, we expected pseudoreplication among females to be low for three reasons. First, we included only successful copulations in our analyses. Second, annual survival of females is low (51–59%, Hamerstrom and Hamerstrom 1973; 28–42%, Nooker 2007), and turnover of females was expected to be high. Last, behavioral and genetic data indicate that in lek-mating species of grouse, females typically copulate only once to fertilize the entire clutch and do not copulate again unless to fertilize a re-nesting attempt (Alatalo et al. 1996a; Semple et al. 2001; Gregory and Nooker, unpublished data). However, multiple mating by females does occur infrequently (10–20%), and we predict that multiple mating may slightly enhance previously existing trends. We only included one copulation if we saw a banded female mate multiple times, but we are unable to control for this among unbanded females due to the limitations of our data.

In the global discrete choice model, male characteristics hypothesized to be linked to female choice included four behavioral indices (PC scores of display and aggression with and without females), five measurements of body size (mass, tarsus, keel, wing, and tail), two ornaments used in display (comb and pinnae), age class (SY or ASY, coded as 0 and 1), and two territory measurements (distance to lek center and size). Morphometric and territory measurements were standardized before analysis (mean=0, SD=1), so

slope coefficients would be directly comparable with our PC scores for components of behavior. Sequential elimination of terms was used to simplify the model, and the resulting models were evaluated using an information-theoretic approach (Burnham and Anderson 2002). Additional models where variables were added and subtracted from the minimum-AIC model were also considered. In all, 51 models were considered. Akaike weights (w_i), model-averaged estimates ($\hat{\theta}_\alpha$), and weighted unconditional standard error [$\text{SE}(\hat{\theta}_\alpha)$] were calculated using formulae in Burnham and Anderson (2002; Eqs. 4.1 and 4.9).

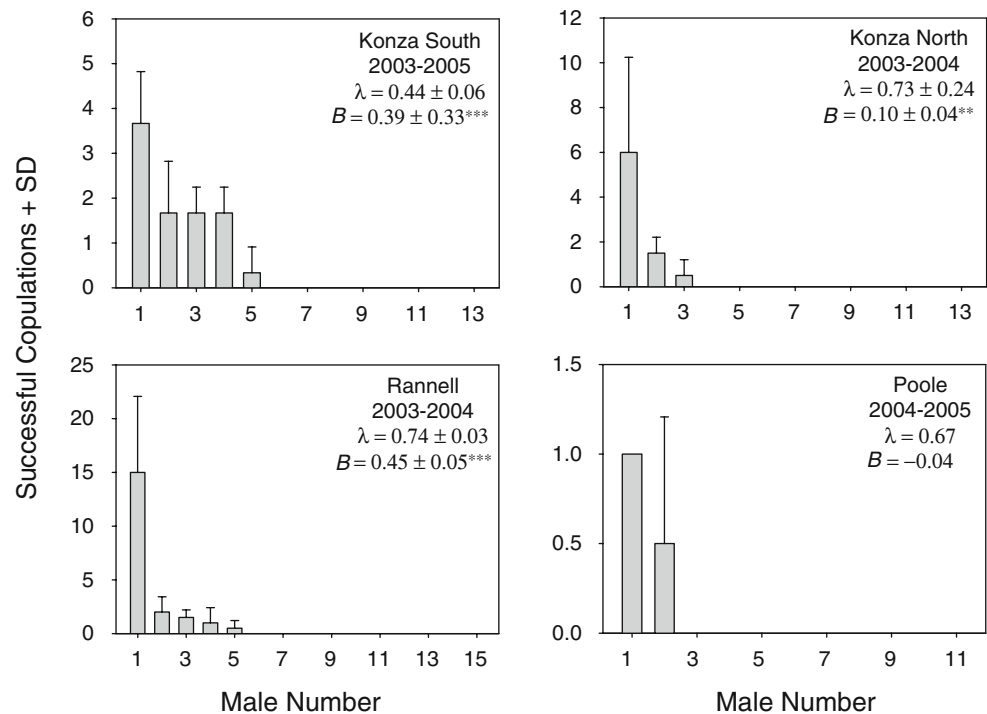
Results

Male mating success

Over 3 years and 263 mornings of observations, 108 males were observed at four lek sites of greater prairie-chickens (9 lek-years). On average, 2.3 ± 2.9 females visited a lek each morning (range, 0–18; $n=263$ mornings). Less than half of all copulation attempts were successful (44.5% of 191 copulation attempts). Therefore, successful copulations were relatively infrequent events, occurring at an average rate of 9.6 ± 7.5 successful copulations per lek per season. Lek size varied slightly among leks (10–14 territorial males per lek), but male attendance was consistently high during the observation period with $92.4 \pm 14.6\%$ of all territorial males attending per day ($n=263$ mornings). Male mating success was strongly skewed overall ($\lambda=0.62 \pm 0.17$; B value= 0.24 ± 0.22 , $P<0.001$) and at most lek sites (Fig. 1). λ values for male mating skew ranged from 0.38 to 0.90 (Fig. 1), and B values ranged from -0.04 to 0.63 (Fig. 1). B values indicated that mating was skewed on Konza South and Rannell's leks in all years of the study (Konza South, 2003: mean 0.63, 95% CI 0.26 to 0.81, $P<0.001$; 2004: mean 0.16, 95% CI 0.00 to 0.52, $P=0.02$; Rannell's 2003: mean 0.42, 95% CI 0.21 to 0.68, $P<0.001$; 2004: mean 0.49, 95% CI 0.30 to 0.69, $P<0.001$). Mating skew varied among years on the Konza South lek (2003: mean B value 0.10, 95% CI -0.15 to 0.41, $P=0.08$; 2004: mean 0.06, 95% CI -0.10 to 0.26, $P=0.06$; 2005: mean 0.14, 95% CI 0.03 to 0.34, $P=0.004$) but was significant overall (Fig. 1). Only two copulations were observed by two different males on the Poole lek in 2005, resulting in a negative and non-significant B value (-0.04 , 95% CI -0.46 to 0.00, $P=1.0$; Fig. 1). Overall, 18.5% of males obtained 87.2% of all successful copulations ($n=108$ males; 85 copulations).

Of 85 successful copulations, 84.7% involved unbanded females. Of ten color-banded females observed to copulate, eight females copulated once and two females mated multiple times. One female copulated successfully with the same male three times in the span of 4 days. The other

Fig. 1 Mating success of male greater prairie-chickens observed at four leks from 2003 to 2005 near Manhattan in northeast Kansas. *Bars and whiskers* represent means and SD. λ and B values are means and SD per lek. Males are ranked on the x -axis based on the number of copulations they received. *Bars* for the Poole lek include data from 2004 to 2005, but the λ and B values were calculated for 2005 only. Significance levels for B values indicated by *asterisks* (* $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$)



female copulated with two different males with a 1-month interval between copulations. The timing of the second copulation was consistent with a re-nesting attempt. We included only the first copulations in the MDC analyses.

Morphology

Of the 108 male-years of observation over 3 years, 67 males were captured and banded in the year of the

observation, 13 were recaptured in years after initial capture, 14 were resighted only after initial capture, and 14 were unbanded. Because males captured in multiple years were used only once to describe morphometrics, our analysis is based on 62 males (morphometrics were not obtained from five males). Most morphological characters showed relatively little variability (CV < 9%; Table 1). Excluding comb size, the mean CV in morphological characters was 4.8 ± 2.5%. Comb size exhibited the most

Table 1 Descriptive statistics for traits of male greater prairie-chickens observed at four leks near Manhattan, northeast Kansas during 2003–2005

Category	Male traits	Mean	SD	Number of males	%CV
Morphology	Mass (g)	1,033	63	62	6.1
	Tarsus (mm)	106	3	62	3.0
	Tail (mm)	96	5	60	5.0
	Keel (mm)	121	10	60	8.6
	Wing (mm)	230	4	62	1.4
	Pinnae (mm)	77	4	60	5.0
	Comb area (mm ²)	225	54	58	24.0
	Comb height (mm)	9	2	58	18.4
Behavior ^a	Comb length (mm)	26	2	61	9.4
	Time displaying (%)	52	15	78	29.5
	Time fighting (%)	29	14	78	49.0
	Boom vocalizations (number)	31	12	78	38.1
	Flutter jump displays (number)	3	3	78	100.9
	Fights (number)	4	2	78	42.2
	Males engaged (number)	2	1	78	33.3
Territory	Territory Size (m ²)	412	281	77	68.2
	Distance to lek center (m)	14	6	77	43.6

Males observed in multiple years are included once only.
^aQuantified during 10-min focal observations of males

variability, with a CV over three times greater than other morphological characters (Table 1).

Behavioral attributes

Over 3 years, 912 10-min focal observations were conducted for an average of 8.4 ± 3.3 observations per male each year ($n=108$ male-years). Behavior showed greater variability among males ($CV > 30\%$) than most morphological traits ($CV < 10\%$; Table 1). The first and second principal components of behaviors (PC1 and PC2) were extracted from a PCA of six behavioral traits and explained 74.8% of the variance in male behavior (Table 2). Loadings on PC1 were high and positive for number of booms and time in display but negative for time in fights, so we interpreted PC1 as an index of ‘display’ behavior. Loadings on PC2 were high and positive for number of fights and number of males engaged, so we considered PC2 an index of ‘aggressive’ behavior. In a matched pairs analysis, both male display and aggression were greater if females were present on the lek ($t_{98} < -9.1$, $P < 0.001$).

Territory attributes

For 9 lek-years, an average of 911 ± 211 male positions per year per lek were obtained. The 95% kernel estimates of lek size ranged from 0.10 to 0.27 ha with a mean of 0.15 ± 0.06 ha ($n=9$ lek-years). The four leks were located on average 4.0 ± 2.0 km from each other (range, 1.0–7.3 km). For 108 males, 74.6 ± 34.8 positions per male per year were obtained. Males showed strong fidelity to lek territories within a breeding season, and territory size averaged 406.8 ± 277.0 m² (range = 107.9 - 2078.1 m², $n=77$). The two largest territories ($>1,200$ m²) were due to peripheral males shifting territorial positions around the edge of the

Table 2 Eigenvectors of a principal component analysis of male behavior from 912 10-min focal observations of 108 male greater prairie-chickens at two to four leks per year

Behavior	PC1 (Display)	PC2 (Aggression)
Percent time displaying	0.52	0.33
Percent time fighting	-0.52	0.08
Number of boom vocalizations	0.47	0.37
Number of flutter jump displays	0.34	0.06
Number of fights	-0.25	0.62
Number of males engaged	-0.26	0.60
Eigenvalue	2.75	1.73
Percent of variance explained	45.9	28.9

Observations were conducted during the breeding season (mid-March through mid-May) near Manhattan in northeast Kansas during 2003–2005. Principal component loadings >0.4 are in boldface.

lek during the mating season. Male territories were located on average 13.9 ± 6.2 m from the center of the lek ($n=77$). Territory attributes had CVs similar to behavioral traits (45–68%, Table 1).

Results of MDC model

To be included in the MDC analysis, males had to have a complete set of explanatory variables (behavioral, morphological, and territorial measurements). The MDC analysis was based on 62 successful copulations among 20 successful and 43 unsuccessful males where we had complete information for each male. Of the 51 models considered, 17 models had ΔAIC values ≤ 2 (Table 3). Male mating success was consistently linked to behavior and body mass as indicated by the inclusion of these variables in all the minimum-AIC models and by their large slope coefficients ($\beta > 0.55$, Fig. 2). Male behavior when females were present was the strongest predictor of mating success, but behavior when females were absent was also important. Male mating success increased if males were more aggressive ($\beta = 0.80$) but displayed less ($\beta = -0.80$) when females were absent. Of the seven morphological traits, body mass ($\beta = 0.55$) and comb size ($\beta = 0.24$) made the largest contributions toward mating success, but the magnitude of slope coefficients were less than half of the components of behavior (Fig. 2). Of the two territorial metrics examined, neither distance from the lek center nor territory size were correlated with mating success (Fig. 2).

Female mate choice copying

Opportunities for mate-choice copying among female prairie-chickens were limited. Of the 57 morning observation periods when successful copulations occurred, only one female copulated on 40 mornings (70.2%), and multiple females were observed copulating on only 17 mornings (29.8%). Of the subset of mornings where multiple females copulated, two or more females copulated with the same male on nine mornings (52.9%) and with different males on eight mornings (47.1%). At most, only 15 of the 85 successful copulations observed (17.6%) could be the result of mate-choice copying.

When the best fit MDC model ($\Delta AIC = 0$) was compared to a model that partitioned female choice between first- and subsequently mating females, the partitioned model had a $\Delta AIC = 8.6$ and a $w_i < 0.01$. Therefore, there is little evidence that females are copying the mating choices of previously mated females. A comparison of the parameter estimates indicated that first- and subsequently mated females used the same cues to select a mate (estimates considered: mass, tail length, comb size, and display and aggression with and without females; $Z < 1.63$; $P > 0.05$).

Table 3 Comparison of multinomial discrete choice models that had $\Delta AIC \leq 2$ examining the effects of male morphology, behavior, and territory attributes on mating success

Model	Morphology	Behavior	Territory	Deviance	<i>K</i> (number of parameters)	AIC	ΔAIC	w_i
1	mct	DAda	–	132.7	7	146.72	0.00	0.09
2	mctk	DAda	–	130.7	8	146.73	0.01	0.09
3	mk	DAda	–	134.8	6	146.77	0.05	0.09
4	mc	DAda	–	134.8	6	146.85	0.13	0.08
5	mck	DAda	–	133.0	7	146.99	0.27	0.08
6	mtk	DAda	–	133.2	7	147.16	0.44	0.07
7	mctr	DAda	–	131.3	8	147.29	0.57	0.07
8	mcr	DAda	–	133.4	7	147.39	0.67	0.06
9	mt	DAda	–	135.4	6	147.43	0.71	0.06
10	mctk	DAda	l	129.6	9	147.63	0.91	0.06
11	mk	DAda	l	133.9	7	147.93	1.21	0.05
12	mct	DAd	–	136.1	6	148.14	1.42	0.04
13	mp	DAda	–	136.3	6	148.27	1.55	0.04
14	mct	DAda	l	132.6	8	148.63	1.91	0.03
15	mctp	DAda	–	132.7	8	148.69	1.97	0.03
16	mctw	DAda	–	132.7	8	148.72	2.00	0.03
17	mctg	DAda	–	132.7	8	148.72	2.00	0.03

Data included 62 copulations among 20 successful and 43 unsuccessful males on four greater prairie-chicken leks between 2003 and 2005 in northeast Kansas. Model abbreviations are as follows: morphological variables (*m* mass at capture, *c* comb area, *t* tail, *k* keel, *r* tarsus, *p* pinnae, *w* wing, *g* age class); behavioral variables (*D* PC1, display with females; *A* PC2, aggression with females; *d* PC1, display without females; *a* PC2, aggression without females); and territory variables (*l* distance to center of lek, – no effect).

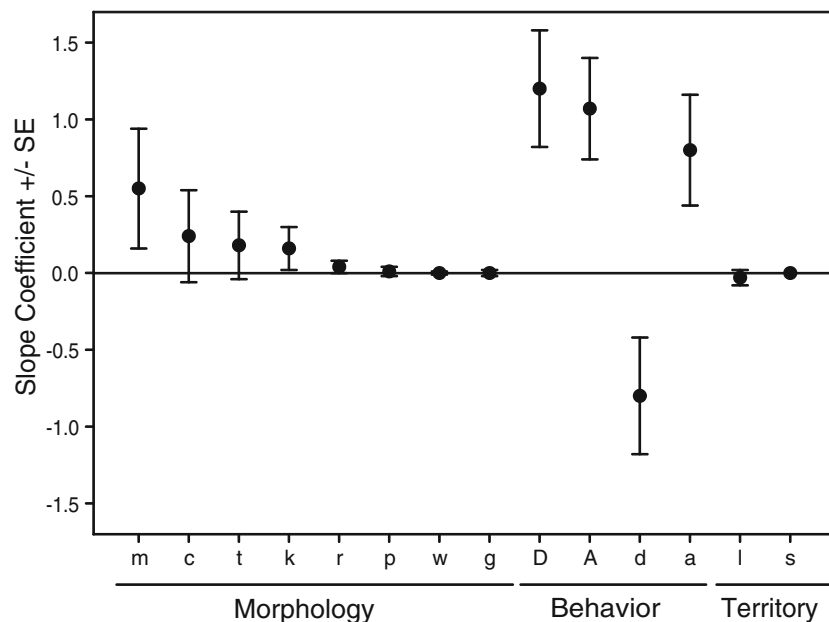


Fig. 2 Model-averaged estimates of the slope coefficients from a multinomial discrete choice model estimating the effect of male attributes on male mating success. Explanatory variables were standardized so slope estimates are directly comparable. Estimates of SE are unconditional and include uncertainty due to model selection. Data included 62 copulations among 20 successful and 43 unsuccessful male greater prairie-chickens from four leks between 2003 and

2005 near Manhattan in northeast Kansas. Abbreviations are as follows: eight morphological measurements (*m* mass at capture, *c* comb area, *t* tail, *k* keel, *r* tarsus, *p* pinnae; *w* wing, *g* age class); four behavioral variables (*D* PC1, display with females; *A* PC2, aggression with females; *d* PC1, display without females; *a* PC2, aggression without females); and two territory attributes (*l* distance to center of lek, *s* territory size)

Annual survival

Return rates were determined from 64 males, 31 of which returned at least once, for a total of 95 bird-years. Return rates are the product of true survival (S), site-fidelity (F), and encounter rate (p). The encounter rate of male prairie-chickens was at unity ($p=1$) because males were readily observed at leks and no males were overlooked for an intervening year between breeding seasons (i.e., bird banded at time t , not seen in $t+1$, but seen again at or after $t+2$). In our study area, only 1 of 108 males (0.9%) was detected at more than one lek. This bird did not establish a territory on the second lek he visited and was only sighted as a visitor on one occasion. From these observations, we conclude that once males established a territory on a lek, they were unlikely to emigrate to a new lek, and that F was also close to 1. Therefore, return rates are effectively an estimate of true survival for male greater prairie-chickens in our study population.

Annual survival of males was not related to the number of successful copulations received ($\chi^2=0.27$, $P=0.60$, $n=95$ bird-years), mass at capture ($\chi^2=0.98$, $P=0.37$, $n=80$), comb size ($\chi^2=0.47$, $P=0.49$, $n=75$), display behavior when females were present ($\chi^2=0.00$, $P=1.00$, $n=88$), aggressive behavior when females were present ($\chi^2=0.07$, $P=0.79$, $n=88$), or territory distance to lek center ($\chi^2=0.10$, $P=0.75$, $n=94$). Annual survival of males did not differ between age-classes (SY=57.8±7.4%, $n=45$; ASY=55.1±7.1%, $n=49$; Fisher's exact $P=0.84$). Overall, annual survival of males was 55.8±5.1% (±SE; $n=95$ bird-years).

Discussion

In this 3-year study of greater prairie-chickens, male mating success was strongly skewed, similar to other lek-mating grouse (Wiley 1991; Höglund et al. 1997). Behavioral traits were better predictors of male mating success than morphological and territorial attributes and showed the most variability among males. Unexpectedly, annual survival was not related to male mating success or male traits, suggesting that there is no trade-off between reproductive effort and survival in males.

The importance of behavioral traits in determining male mating success may be a general pattern that is common to lek-mating species of birds. Female greater prairie-chickens select males based on behavioral traits where variation may be adequate for mate choice decisions. In greater prairie-chickens, both display and aggressive behavior were important predictors of male mating success, contrary to previous studies of lek-mating birds where aggressive behavior did not correlate with mating success (Gibson and Bradbury 1985; Höglund and Lundberg 1987; Gibson

et al. 1991; Alatalo et al. 1996b; Shorey 2002). Aggression may be particularly important in male–male competition if males establish dominance hierarchies at lek sites (Alatalo et al. 1991; Höglund et al. 1997), but the importance of male–male competition might vary among species. In the absence of females, aggressive and display behavior of male prairie-chickens were positively and negatively correlated with mating success, respectively. We conclude that males that fight more but display less may be establishing dominance relationships in the absence of females, which females subsequently may use to select a mate (Bradbury and Gibson 1983).

Morphological characters had low predictive power for determining male mating success in prairie-chickens, with the exception of comb size (Gratson et al. 1991). Comb size was the only morphological trait with high variation (CV=26%), and it was included in 71% of the 17 models with $\Delta\text{AIC}\leq 2$. The low predictive power of most morphological characters in mate choice may be a general feature of galliform birds (Alatalo et al. 1991; Beani and Dessi-Fulgheri 1995; Rintamäki et al. 1998; Hagelin and Ligon 2001; Parker and Ligon 2003). We propose three possible explanations. First, male plumage ornamentation is a primitive character in Galliformes with the cryptic female plumage being a derived estrogen-dependent character (Kimball and Ligon 1999). Given that female plumage is a derived character, natural selection for cryptically colored females may be more intense than sexual selection for larger, more elaborate male plumage, thereby limiting variation in size components of male morphology. Second, in a comparative analysis of grouse species, natural selection may be relatively more important than sexual selection in determining plumage ornaments (Bleiweiss 1997). Grouse living in similar habitats have more similar size-independent morphology, and mating system affected the size of both sexes equally (Drovetski et al. 2006), resulting in lower variation in the size of male morphology. Last, low CV values (mean <5%) among body size, plumage, and male ornaments, such as pinnae feathers, may suggest that these traits have been under strong selection in the past and are no longer condition-dependent indicators of male quality.

Previous studies of lek-mating birds have frequently emphasized a link between territory position and male mating success (Höglund and Lundberg 1987; Gratson et al. 1991; Alatalo et al. 1996b; Shorey 2002). We did not find territory size or position to be an important predictor of male mating success, despite high CV values (>46%) and contrary to previous studies of prairie grouse (Robel 1966; Robel and Ballard 1974; Gratson et al. 1991). Our results support the hypothesis that direct female choice via behavior may be more important than indirect female choice via territory attributes (Sæther et al. 2005).

The phenotypic traits of male prairie-chickens were ranked by CVs as follows: behavior > territory traits > morphology. When these CV values are compared to the traits used in female choice, our results suggest that females are using traits with high variability to select mates. Two caveats apply to our interpretation. First, CV values are typically used to compare the same metric in different habitats, but we are using CV values to compare different traits of the same individuals. Second, behavior can be affected by nutrition, weather, the presence of females, and other environmental factors (Bradbury et al. 1989, Höglund et al. 1997, West and Packer 2002), making behavior inherently more variable than the other phenotypic traits. However, we controlled for variability by taking multiple observations per male (average, 8.4 ± 3.3) and by only conducting behavioral observations on days without precipitation and during a narrow time period (within 3 h of sunrise). We also recorded and controlled for female presence in our analyses. Thus, variability could have contributed to the relevance of male behavior as an important phenotypic trait for female mate choice.

An unexpected result of our study was that male survival was not related to any of the traits examined (mating success, morphological, behavioral, or territorial traits), despite strong evidence from previous studies showing that male characteristics are often correlated with survival due to the effects of condition-dependence and trade-offs between natural and sexual selection (Jennions et al. 2001). Yearling males had slightly higher survival than adult birds, but the difference was not significant. A trend for higher survival among yearlings than adults has been reported in previous studies of greater and lesser prairie-chickens (Hamerstrom and Hamerstrom 1973, Hagen et al. 2005). Future work should determine if counteracting selective pressures may differentially affect males based on their mating success or behavior. For example, variation in predation among successful and unsuccessful males could arise from male position or dominance on and off the lek. If male traits are energetically costly (Vehrencamp et al. 1989), successful males may be better foragers than less successful males and could off-set the costs of enhanced traits with greater food intake. Parasite burden has been shown to vary with mating success and male traits (Höglund et al. 1992a, b) and may affect survival. In these examples, apparent survival would not vary with mating success due to multiple or compensatory selective pressures reducing the observed variation in survival.

In the future, research on the correlates of male mating success in lek-mating species will benefit from utilizing MDC models, quantifying the display and aggressive components of behavior, and determining the underlying physiological mechanisms mediating variation in male mating success and survival. MDC modeling is a useful

statistical method because it directly models the process of female mate choice. In addition, MDC models control for pseudoreplication of males observed in multiple years and eliminate the problem of the non-normal distribution of male mating success. Past studies link male mating success of lek-mating species to components of display but have not considered the role of aggressive behaviors. We were able to identify aggression as an important factor determining male mating success but were unable to examine the proximate causes. Variation in steroid hormones, such as testosterone, may underlie the variation in male traits and survival. Testosterone has been linked to aggression, comb size, and increased male mating success (Zuk et al. 1995a, b; Alatalo et al. 1996b). Moreover, male grouse with higher testosterone levels can have higher parasite loads, which may ultimately decrease survival (Redpath et al. 2006; Seivwright et al. 2005). A better understanding of the interactions among testosterone, parasite loads, mating success, and survival in a lek-mating species would link the proximate mechanisms and ultimate consequences of factors mediating male mating success.

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