SEXUAL SELECTION AND THE GENETIC MATING SYSTEM OF WILD TURKEYS

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Abstract. Molecular measures of parentage provide important insights into the opportunity for sexual selection; in birds, such studies have been conducted almost exclusively on pair-bonded passerines. Here I employ a multitiered parentage analysis involving 10-locus microsatellite genotypes to characterize the genetic mating system of a population of Wild Turkeys (*Meleagris gallopavo*), a promiscuous species in which males and potentially females have been thought to mate multiply. Young in almost half of nests (48%, $n = 15$) were each apparently the product of a single male and female parent. Fourteen broods (45%) resulted from multiple paternity; seven contained eggs from multiple females, four of which appeared to be cases of quasi parasitism, in which the offspring of the brood parasitic female were fathered by the same male that sired at least one of the host females' offspring. Bateman gradients for males and females indicate that males experience a significantly greater gain in reproductive success from additional mates; the trend for females to benefit from multiple matings disappeared when the small "clutches" of parasitic females were excluded from the analysis. Of the components of variance in male fitness, number of mates was the most important determinant of male reproductive success. Somewhat surprisingly, when considering only reproductively successful males, the proportion of a female's offspring that a male sired also explained a substantial proportion of the total variance in male reproductive success. Incomplete sampling of offspring could mean that these estimates, particularly the importance of mate number, may be underestimated. Regardless, these results suggest that multiple mating by females may be an important and overlooked component of sexual selection in species with lek-like mating systems, and that selection may act independently on males to attract more mates and increase their share of paternity with those mates.

Key words: Bateman gradient, brood parasitism, kin selection, microsatellite, opportunity for selection, polyandry, polygyny.

Selección Sexual y el Sistema de Apareamiento Genético de *Meleagris gallopavo*

Resumen. Las medidas moleculares de paternidad proveen información importante sobre las oportunidades para la selección sexual. En las aves tales estudios han sido llevados a cabo de manera casi exclusiva con paserinos que mantienen vínculos de pareja. En el presente estudio empleo un análisis de paternidad de múltiples niveles utilizando genotipos basados en 10 sitios microsatelitales para caracterizar el sistema de apareamiento genético de una población de *Meleagris gallopavo*. Esta es una especie promiscua en la cual los machos, y potencialmente las hembras, se aparean de manera múltiple. Casi la mitad de los nidos (48%, $n = 15$) fueron el producto de una madre y un padre. Catorce nidos (45%) fueron el resultado de paternidad múltiple, siete contenían huevos de múltiples hembras y, de estos siete, cuatro aparentan ser casos de quasi-parasitismo en el cual las crías de la hembra parasítica eran del mismo padre que al menos una de las crías de la hembra huésped. Los gradientes de Bateman para machos y hembras indican que los machos obtienen un aumento significativamente mayor en el éxito reproductivo cuando se aparean con más parejas; la tendencia en la cual las hembras obtenían beneficios del apareamiento múltiple desapareció cuando se excluyeron del análisis las puestas pequeñas de las hembras parasíticas. Al examinar los componentes de varianza en la aptitud biológica de los machos, el componente más importante del éxito reproductivo de los machos fue el número de parejas. Al considerarse solamente los machos que tuvieron éxito reproductivo, la proporción de crías de la hembra que el macho engendró también explicó una porción substancial de la varianza en el éxito reproductivo total de los machos. El muestreo incompleto de las crías podría significar que estos estimados pueden ser subestimaciones, en particular la importancia del número de parejas. Sin embargo, estos resultados sugieren que el apareamiento múltiple de hembras podría ser un componente importante y frecuentemente desapercibido de la selección sexual en especies con sistemas de apareamiento tipo lek y que la selección podría actuar independientemente sobre los machos para atraer más parejas y para incrementar la proporción de crías engendradas con esas parejas.

INTRODUCTION

Mating systems describe the social and genetic associations of individuals related to reproduction (Emlen and Oring 1977) and are particularly relevant for understanding evolutionary processes. While they are relevant to a variety of evolutionary phenomena (e.g., effects on genetic drift through changes in effective population size; Wright 1931), mating systems are most frequently considered when attempting to understand patterns of sexual selection (Emlen and Oring 1977, Møller 1992, Arnold and Duvall 1994, Ligon 1999, Shuster and Wade 2003). The opportunity for sexual selection (I_s) is the upper bound for the potential action of sexual selection in a given system (Wade and Arnold 1980, Shuster and Wade 2003); this value depends upon the variance in male reproductive success (Arnold and Wade 1984). Key aspects of mating systems such as the number of mates per male and the prevalence of multiple mating by females largely determine I_s (Shuster and Wade 2003).

Given the widespread interest in sexual selection in birds, it is somewhat surprising that direct measures of I_s are relatively uncommon compared to the growing number of species for which molecular parentage data are known (for reviews see Woolfenden et al. 2002, Freeman-Gallant et al. 2005, Hauber and Lacey 2005, Whittingham and Dunn 2005, Albrecht et al. 2007). Existing studies have typically focused on pair-bonded passerines, frequently with the purpose of exploring the relative importance of extra-pair and within-pair offspring in determining the variance in male reproductive success (Webster et al. 1995, 2007). Including extra-pair young when calculating male fitness could reduce I_s if males face trade-offs between gaining offspring in other nests and loss of paternity in their own broods. Alternatively, if males that produce more extra-pair young also generate more within-pair offspring, variance in reproductive success will tend to increase (Webster et al. 1995, Freeman-Gallant et al. 2005). Empirical studies have found that, while the inclusion of information on molecular paternity always increases estimates of the opportunity for selection compared to estimates based only upon the fecundity of social mates, the importance of extra-pair offspring can vary dramatically, even across years in the same population (Freeman-Gallant et al. 2005). Comparative studies are now beginning to examine across bird species how ecological and behavioral correlates can influence the opportunity for selection through changes in number of extra-pair young (Whittingham and Dunn 2005, Albrecht et al. 2007).

Molecular measures of I_s in polygynous or promiscuous bird species with non-resource-based mating systems are even less common than for pair-bonded species (Woolfenden et al. 2002); this is particularly surprising given that mating systems such as leks are touted as ideal for studying sexual selection (Höglund and Alatalo 1995). In these systems, males are often highly ornamented, females may be relatively free to mate with preferred males, and females are thought to base their mating decisions on obtaining superior genes for their offspring rather than for direct benefits to themselves or their offspring (Höglund and Alatalo 1995). Leks often prove amenable to measuring mating success, and in some cases, paternity studies have suggested strong or perfect concordance between observed female mating behavior and paternity (Semple et al. 2001, DuVal 2007, Lebigre et al. 2007, Reynolds et al. 2007).

The Wild Turkey (*Meleagris gallopavo*) is a promiscuous species with a complex and variable social structure (Watts and Stokes 1971, Eaton 1992, Healy 1992). Turkey populations are found in a variety of habitats across North America and exhibit different social mating systems throughout their range. All populations share important similarities with lekking species in that only females provide parental care, and there is no social bond between males and females. The Eastern form of the species (*M. g. silvestris*) is typically described as exhibiting harem defense or male dominance polygyny, with males forming dominance hierarchies that determine their access to mobile groups of females (Eaton et al. 1976, Williams and Austin 1988). Populations of the Rio Grande subspecies (*M. g. intermedia*), on the other hand, may at times adopt a lek-like mating system and may additionally contain multimale coalitions that cooperatively court and defend female groups (Watts and Stokes 1971, Logan 1973). These striking differences in organization may be partly determined by habitat-dependent spacing patterns of males and females (similar to interspecific patterns in grouse; Wiley 1974), with the larger male aggregations in more open landscapes, and smaller groups in landscapes more dominated by forest (Watts and Stokes 1971). Local population density may also be a crucial mating system determinant, as population collapses have resulted in loss of multimale coalitions (Smith 1977, Balph et al. 1980), while, anecdotally at least, population increases of *M. g. silvestris* have coincided with the appearance of male-male coalitions in some areas where they were not previously described (S. Vehrencamp and J. Bradbury, Cornell University, pers. comm.; A. B. Clarke, State University of New York at Binghamton, pers. comm).

The stunning physical appearance and dramatic courtship behaviors of male turkeys suggest that their phenotype is the product of sexual selection. Adult males are twice as heavy as females and show a variety elaborated traits including colorful iridescent plumage and unique feather-like structures, spurs, and remarkable dermal ornaments that can quickly change in both size and color during interactions with conspecifics (Eaton 1992, Pelham and Dickson 1992). Sexual selection may act on these traits through both female mate choice and competition among males. Laboratory studies of mate choice have demonstrated that females prefer males with longer frontal wattles, or snoods (Buchholz 1995). Variation in snood length has been tied to male parasite loads as well as MHC genotype (Buchholz et al. 2004). Experimentally created variation in

parasite load can also affect the expression of iridescent plumage in subsequent molts, although the importance of plumage color in female choice has yet to be explored in this species (Hill et al. 2005). Snood length also relates positively to male dominance (Buchholz 1997), as does spur morphology (Badyaev et al. 1998). Male dominance status likely helps determine male access to females, both within cooperative coalitions and in the population as a whole (Watts and Stokes 1971, AHK, unpubl. data). It therefore appears that both inter- and intrasexual interactions combine to determine the distribution of male reproductive success.

Here I describe the genetic mating system of a population of Wild Turkeys in central California. I begin by using a multitiered parentage analysis to assign parentage to offspring sampled during three years of this study. I go on to compare the opportunity for sexual selection in males and females by measuring the variance in reproductive success and Bateman gradients—the relationship between mating success (i.e., number of mates) and reproductive success (i.e., number of offspring identified in the parentage analyses)—for both sexes. Both the putative mating system of this species and the conspicuous dimorphism and dichromatism lead to the expectation that the opportunity for sexual selection should be much higher in males than in females. I also use the patterns of maternity and paternity to further partition the variance in male reproductive success by measuring its components, including mate number, mate fecundity, and share of paternity.

METHODS

FIELD METHODS

My study was conducted at and around the Hastings Natural History Reservation in Carmel Valley, Monterey County, California. The study population originated from multiple translocation events, principally of Rio Grande Wild Turkeys (*M. g. intermedia*—the same subspecies studied by Watts) but possibly descended from other subspecies as well (Watts 1969, Watts and Stokes 1971, Roberson 2002). From 1999 through 2004, I captured a total of 126 immature and adult turkeys (51 males, 75 females) using walk-in traps or drop nets. Turkeys were individually marked using patagial wing tags, and a subset ($n = 8$ males, $n = 68$ females) were outfitted with backpack-style radio-transmitters. After taking approximately 100 μl of blood from the brachial vein for genetic analyses and storing it in 1 ml of Longmire's blood storage buffer (Longmire et al. 1988), birds were released at the site of capture. All methods were approved by both the University of California Berkeley and the California Department of Fish and Game.

With 1–2 assistants per year, I attempted to visually relocate radio-tagged birds at least two times per week in January, February, and June, and daily from March–May in order to identify female nesting attempts and observe courtship behav-

ior and male-male associations. Nests were monitored daily without flushing the incubating females. Genetic samples of offspring were obtained by salvaging the contents of failed or abandoned nests, by collecting the eggshell membranes in nests from which young had hatched, and by manually capturing, taking blood from, and releasing flightless poults within 48 hr of their leaving their nests. Poults sampled together likely represented nestmates, since in no cases were females with similar-aged poults observed nearby; furthermore, these sets of offspring did not seem more likely to contain chicks from multiple mothers than did sets of samples collected through other means (AHK pers. obs). Additionally, in 2001–2003, I collected the first 6–10 clutches in each breeding season by flushing females and removing their eggs on the first or second day of incubation. Females were then allowed to renest, and did so in virtually all cases. The collected clutches were incubated in the lab for 1–2 weeks and sampled when they contained sufficient tissue for reliable genetic analysis. Both eggshell membranes and embryonic tissue will yield offspring and not maternal DNA, provided that eggs have incubated for more than a few days (Pearce et al. 1997, Strausberger and Ashley 2001). In all, I had approximately half of males and females in the population marked in any given year, but at least half of tracked females likely nested on private property where I could not monitor their nests. As a result, the samples of nests likely reflect ≤25% of all nests in the population.

GENOTYPING

Genomic DNA was extracted from blood and tissue samples using Qiagen DNeasy tissue extraction kits (Qiagen Inc., Valencia, California) and then diluted to a concentration of 20 μg ml^{-1}. Adults and offspring were genotyped at 10 dinucleotide microsatellite loci identified in previous studies of wild or domestic turkeys (Donoghue et al. 1999, Reed et al. 2000, Mock et al. 2002; Table 1). An 11th locus (tum 17) was discarded from further analyses when Bonferroni-corrected linkage disequilibrium tests conducted using GENEPOP (Raymond and Rousset 1995) revealed its apparent linkage with two other loci (tum 23 and mnt 1).

To generate fluorescently labelled PCR product, single-locus reactions included one primer of each primer pair with an attached fluorescent tag. Reactions were 7.5 μl in total volume, with 0.75 μl 10× PCR buffer, 0.15 μl each of 40 nM dNTPs and 10 μM forward and reverse primers, 0.075 μl of 5 U μl^{-1} *Taq*, and 1.26 μl 20 μg ml^{-1} genomic DNA. Locus tum 50 required an additional 0.15 μl of 25 mM MgCl$_2$. Reaction conditions were 4 min at 94°C; followed by 30 cycles of 1 min at 94°C, 1 min at the annealing temperature (Table 1), and 1 min at 72°C; and finally, a 10 min extension phase at 72°C.

Products from PCR of different loci were often mixed (Table 1) when loaded on 96-well plates for visualization on an ABI 3730 automated sequencer. Each plate contained one negative control as well as two positive controls (i.e., PCR from

TABLE 1.   Properties of the 10 microsatellite loci used for parentage analyses of Wild Turkeys at the Hastings Natural History Reservation, Monterey County, CA. Characteristics are based upon complete genotypes from all 126 turkeys $\geq$ 1 year old. Het (obs), Het (exp), Excl (1), Excl (2) and Null refer to the observed per locus heterozygosity, expected per locus heterozygosity, probability of exclusion for first-parent analyses, probability of exclusion for second-parent analyses, and maximum proportion of null alleles, respectively, as determined by CERVUS 2.0 (Marshall et al. 1998). No locus showed significant deviation from Hardy-Weinberg equilibrium. Products of single-locus PCR were mixed and visualized together when possible; superscripts (d–h) denote typical combinations of loci.

Locus	Annealing temperature (°C)	Number of alleles	Size range (base pairs)	Het (obs)	Het (exp)	Excl (1)	Excl (2)	Null
btm1[a,d]	57	11	108–143	0.833	0.865	0.563	0.723	−0.014
btm2[a,d]	58	7	185–212	0.770	0.805	0.426	0.604	−0.020
btm7[a,e]	52	13	127–170	0.904	0.882	0.606	0.756	−0.017
mnt1[b,f]	57	7	119–145	0.571	0.585	0.196	0.370	−0.018
rht0003[a,g]	52	6	196–249	0.849	0.865	0.584	0.738	−0.005
rht0011[a,g]	55	19	138–163	0.643	0.619	0.213	0.376	−0.020
rht0016[a,g]	54	12	91–139	0.857	0.844	0.520	0.687	−0.010
tum12[c,f]	56	7	198–258	0.714	0.743	0.339	0.517	−0.012
tum23[c,d]	59	6	151–162	0.595	0.606	0.201	0.368	−0.003
tum50[c,h]	52	12	124–145	0.698	0.705	0.333	0.525	−0.004

[a] Donoghue et al. 1999.
[b] Reed et al. 2000.
[c] Mock et al. 2002.

DNA of the same two individuals was included in each visualization). All adults were genotyped $\geq$2 times, and genotypes were complete at virtually all (>0.999) loci. Offspring genotypes were complete at 0.98 of loci. Individuals were rerun if allelic assignments were questionable or did not match the genotype of the incubating female. If additional PCR and scoring runs did not yield a clear genotype, ambiguous loci were omitted from that individual's genotype, and only offspring with $\geq$8 typed loci were included in subsequent parentage analyses.

PARENTAGE ASSIGNMENT

General comments.   In order to most accurately estimate rates of multiple maternity and paternity, it is necessary to attribute parentage to all offspring in a nest. Unfortunately, due to a variety of factors, including the presence of many unsampled fathers, the most successful fathers necessarily having genetically similar males among the set of candidate fathers (Krakauer 2005a), and some mutation or scoring errors, no single analysis technique could reconstruct parentage for entire broods. Elsewhere I have presented data on a more conservative set of paternity assignments based exclusively on the most strict analysis parameters (Krakauer 2005a). Here I use a combination of analysis techniques, including some with more relaxed assignment criteria, for the purpose of assigning parentage to entire nests. My strategy, as described below in detail, was to use different criteria to 1) assign maternity to incubating females, 2) assign, with a high degree of certainty, paternity in a subset of offspring to sampled fathers, 3) to assign paternity in additional offspring to males that were assigned paternity to offspring in their nest in step 2, and

finally, 4) manually reconstruct and compare the genotypes of unsampled males that were putative fathers of the remaining offspring. A similar multicomponent method was recently employed to describe mating patterns in Black Grouse (Lebigre et al. 2007). My results are generally concordant with independently calculated estimates of nestmate relatedness (mean nestmate $r = 0.36 \pm 0.23$; Krakauer 2005b). Any biases introduced by this strategy are likely to minimize the number of adults determined to contribute genetically to a given nest. The numbers of different mothers and fathers identified should therefore be considered minimum estimates.

Assigning maternity.   I began with the a priori assumption that the marked female found incubating a given clutch was in fact the genetic mother of offspring from that nest. I therefore used only an exclusion criterion for assigning maternity—the incubating female was assigned maternity to an offspring if she matched it at $\geq$9 of the 10 loci. I chose this threshold rather than requiring 10 out of 10 concordant loci in order to reduce the frequency of false identification of offspring as resulting from brood parasitism due to repeated misscoring or marker mutation at a single locus. The chance that an unsampled female would match the marked female exactly was small; given the conservative assumptions that a mother possessed the most common alleles at each locus and that there were 100 unsampled females in a given year, the chance that an unsampled female would match a marked female at nine loci was less than 0.03.

Assigning paternity.   I used the same two-stage process to assign paternity that I employed previously in order to minimize errors of incorrect assignment (Krakauer 2005a). First, I employed stringent criteria to identify all father-offspring pairs

in which I had high confidence based upon maximum likelihood analyses in CERVUS (Marshall et al. 1998). I performed separate analyses for each year of the study (2001–2003); this allowed me to account for interannual variability when estimating two CERVUS input parameters: the number of candidate males and the identity of sampled males. The number of candidate males was determined by simple counts of the several large, stable winter flocks conducted in January and February (prior to the breeding season). These censuses yielded counts of 15, 49, and 40 adult males for 2001, 2002, and 2003 respectively; the increased number of candidate fathers after 2001 reflects the expansion of the study area in 2002. The numbers of sampled males were eight, 28, and 33 for 2001, 2002, and 2003, respectively, and included tagged males ≥ 2 years old (juvenile one-year-old males do not mate in the wild; Healy 1992; AHK unpubl. data) plus any males captured in subsequent years who would have been in their third year during that season. Analysis parameters common to all years included using background allele frequencies calculated from all 126 individuals ≥ 1 year old, offspring genotypes complete at 98% of loci, and rates of typing or scoring errors of 2%. In order for a male to be assigned paternity, he needed to meet both the strict 95% likelihood level as well as be the only male sampled that represented a perfect genotypic match.

Typically, these conservative criteria did not allow me to assign parentage to entire broods. Thus, I made a further assumption that once a male was assigned by the previous strict criteria to any offspring in a given nest, he was more likely to be the father of additional eggs in the nest (i.e., that each egg is not necessarily an independent event). Therefore, if a male was assigned paternity in a nest and was consistent (i.e., had at most one mismatched locus) with other offspring in the nest, he would be designated as the father for those additional offspring that did not meet the previous likelihood- and exclusion-based criteria. This assumption seems justifiable given the ability of female turkeys to store sperm (Hale 1955, Birkhead and Biggins 1998) and the observation from other species that patterns of male reproduction are best explained if clutches, rather than individual eggs, can be considered independent events (Haydock and Koenig 2002, Lebigre et al. 2007). Moreover, while this method would fail to detect paternity by males of similar genotypes, my previous analyses found no evidence that more than one related male in a coalition obtained paternity (Krakauer 2005a).

An additional challenge stems from offspring originating from roughly half of sampled nests in this study that were sired by unsampled males. Although a software package exists to reconstruct parental genotypes (GERUD; Jones 2001), it is not tolerant of datasets with missing data, mutations, or scoring errors. Instead, I manually reconstructed the paternal genotypes of these young by subtracting the allelic contribution of the mother from offspring genotypes and tallying the remaining paternal alleles at each locus. Multiple mating by

females was inferred from the presence of >2 paternal alleles at ≥ 2 loci, which would be extremely unlikely to occur due to mutation (Laloi et al. 2004). This criterion for detecting multiple paternity is effectively the same as the relaxed exclusion criterion I used above when assigning offspring to males who were assigned paternity to other offspring in the nest, since that method also requires >1 mismatch to detect additional fathers.

VARIANCE IN REPRODUCTIVE SUCCESS

Nesting rates in adult female turkeys range from 75% to 100% (Vangilder 1992), suggesting that optimally, one could obtain parentage data from the nesting attempts of a majority of females in a population. Due to the undersampling of nests in this study ($\leq 25\%$) and the inevitable overestimation of variance as a result, I excluded nonbreeding females when calculating $I_{s, females}$. In contrast, male reproduction may be highly skewed; males may fail to breed, or subordinate members of coalitions may forego breeding in order to help a dominant display partner (Watts 1969, Watts and Stokes 1971, Krakauer 2005a). For this reason, I included all potentially breeding males in calculations of $I_{s, males}$. Although the undersampling of nests could lead to the overestimation of $I_{s, males}$, this error is not likely to be as severe as for females; moreover, an estimate of $I_{s, males}$ is necessary for estimating the components of variance as described below.

I also calculated the standardized variance for breeding males only. While the presence of nonbreeding individuals is clearly important in determining the overall variance in reproductive success, their inclusion can obscure patterns of variance within breeding individuals (Hauber and Lacey 2005). Excluding nonbreeding birds also allowed me to compare the opportunity for sexual selection in male and female breeding turkeys since I was not able to estimate the variance among females in the absence of this restriction. Due to the relatively low numbers of nests examined in any given year, annual data were pooled across years (Woolfenden et al. 2002); interannual variation is clearly important (Freeman-Gallant et al. 2005) but could not be considered in the present study except in the analysis of males that included nonbreeding individuals because of insufficient sample size in individual years. If two nests from the same female were sampled in the same year, the first nest was included if I collected the entire clutch prior to incubation; otherwise, the nest with the most samples was used in this analysis. This resulted in a total of 24 nests ($n = 7, 11,$ and 6 in 2001, 2002, and 2003, respectively) and a total of exactly 200 sampled offspring. Although there is the potential for pseudoreplication when using repeated nests from the same female in different years, I found no occurrences of a female mating with the same male across years, and no single male fathered the most offspring in sampled nests in more than one year. Moreover, for females sampled in multiple years, mate number and clutch size were uncorrelated across years

(mate number: $r_s = -0.29$, $P = 0.48$, $n = 8$; clutch size: $r_s = -0.33$, $P = 0.42$, $n = 8$).

I calculated the standardized variance in reproductive success (I_s; Arnold and Duvall 1994, Shuster and Wade 2003) for both males and females by dividing the sex-specific variance in reproductive success by squared mean reproductive success. I also calculated Bateman gradients (Bateman 1948, Arnold and Wade 1984, Woolfenden et al. 2002) for both males and females as the slope of the least squares linear regression of reproductive success against mating success. These regressions did not include nonbreeding individuals. Brood parasitic females often were represented by a single egg in my sample and therefore could not exceed one genetic mate. Since these low-fecundity individuals had the potential to bias the slope of the female Bateman gradient by virtue of their low reproductive success, I also calculated the Bateman gradient for only the nonparasitic (i.e., incubating) females.

To examine the components of variance in male reproductive success, I followed the methods used in passerine studies (Webster et al. 1995, Freeman-Gallant et al. 2005). Because there are no pair bonds in turkeys, there is no distinction between within-pair and extra-pair offspring, so I did not calculate separate within-pair and extra-pair terms. Therefore, I considered only the variance explained by mate number (M), female fecundity (N), and proportion of the female's eggs that a male sired (P). I also considered the covariances between these terms, which signify correlations between mating success and mate fecundity, mating success and share of paternity with mates, and mate fecundity and paternity share. These components of male reproductive variance were computed arithmetically (Webster et al. 1995) in Microsoft Excel (Microsoft Corporation, Redmond, Washington). Individuals that did not sire offspring ($M = 0$) were not included in calculations of N or P to avoid overestimating the variance explained by these parameters (Arnold and Wade 1984, Webster et al. 1995, Freeman-Gallant et al. 2005). While this analysis provides the percent of the total standardized variance explained by each term, it does not indicate whether these associations are statistically significant. Therefore, I also calculated Spearman rank correlations of reproductive success and the three main variables (M, N, and P), as well as pairwise correlations among M, N, and P (Freeman-Gallant et al. 2005). Throughout the results, means are presented ±SD.

RESULTS

SAMPLING AND ASSIGNMENT

I collected tissue from a total of more than 40 nests. When excluding nests from which no maternal DNA was available or no offspring DNA could be recovered, the sample of clutches dropped to 31 nests from 16 different known females (range: 1–4 nests per female), with a total of 250 sampled and genotyped offspring (mean: 8.1 samples per nest). This value is somewhat lower than published clutch sizes (range: 8.5–12.7 eggs per nest; Vangilder 1992) as a result of infertile eggs that failed to yield embryonic tissue as well as inclusion in the sample of nests that were partially depredated or from which young had hatched. Twenty-one of the 31 sampled nests contained complete clutches collected at the onset of incubation ($n = 183$ offspring), while the remaining 10 nests, from which DNA was obtained from a combination of salvaged nest material, blood from chicks, or both, may have contained partial samples of the nest ($n = 67$ offspring).

Among offspring with one or fewer allelic mismatches to the incubating female, 217 matched at all loci, and 20 were inconsistent at one locus, while the majority of the 13 offspring identified as resulting from brood parasitism exhibited more than two loci incongruent with the incubating female. Paternity of 75 out of 250 offspring was assigned to a sampled male by the combination of exclusion and likelihood criteria. An additional 35 of the 250 offspring (totaling 110) were assigned paternity to sampled males that were identified as fathers of one or more nestmates by the combination of likelihood and exclusion criteria. All but six of these 35 additional offspring were consistent at all 10 loci with the genotype of a father assigned to one of these initial 75 offspring, and the remaining six were consistent at nine of 10 loci. The proportion of offspring that mismatched their putative father at one locus (six out of 110, 5.4%) was similar to that found in the maternity analysis described above (20 out of 237, 8.4%). The remaining 140 offspring appeared to be sired by unsampled males, and the paternal genotypes of these males were manually reconstructed.

PARENTAGE ANALYSES

In close to half of sampled nests (15 out of 31, 48%) genotypes of broods were consistent with each having a single mother and father. Although the majority of nests contained eggs laid entirely by the incubating females, multiple maternity was detected in 23% (7 out of 31) of nests, representing a total of 5% (13 out of 250) of offspring. Nests containing offspring resulting from brood parasitism had an average of 1.9 ± 1.1 (range: 1–4) foreign offspring per nest. Quasi parasitism, in which nestmates from different mothers share paternity, was found in four of the seven nests containing eggs from multiple females; in two of these nests, all offspring were fathered by the same male. The nesting status of most brood parasitic females was unknown, although at least one marked female laid parasitically and incubated eggs in her own nest in the same season.

Multiple paternity occurred more frequently than multiple maternity. Paternity by two or more males was detected in 45% (14 out of 31) of nests, and these extra-paternal offspring accounted for 12% (29 out of 250) of all young. Clutches containing offspring with multiple paternity had an average of 2.1 ± 0.9 (range: 1–5) extra-paternal eggs per nest. Of the

14 nests containing offspring with multiple genetic fathers, 12 resulted from multiple mating by a female, while in two nests, an incubating female and parasitic female each mated with different males. Only one nest required three fathers to explain the array of paternal alleles in its offspring; this nest resulted from multiple mating by the incubating female combined with parasitic eggs fathered by a third male.

VARIANCE IN REPRODUCTIVE SUCCESS

When considering all potentially breeding males in the population, the standardized variance in reproductive success was $I_{s,males} = 5.2$, with annual estimates ranging from 2.6 to 6.5. However, when considering only individuals that sired at least one offspring, this value dropped to $I_{s,males} = 0.7$. Individual males assigned paternity fathered offspring with up to four females in a given year (1.3 ± 0.7), and male reproductive success increased significantly with number of mates (slope = 6.3 offspring per additional mate, $P < 0.001$; Fig. 1A). Females showed a smaller standardized variance in their reproductive success, with $I_{s,females} = 0.2$, which was significantly less than that of males ($F_{27,29} = 4.0$, $P < 0.001$). Females mated with an average of 1.2 ± 0.4 males. Although the trend in the Bateman gradient for females was for reproductive success to increase with mating success (slope = 2.3 offspring per additional mate, $P = 0.07$; Fig. 1B); it had a significantly smaller slope than did the male gradient ($t_{54} = 6.4$, $P < 0.0001$). The association between mating success and reproductive success disappeared altogether when the six parasitic females were removed from calculations of the gradient (slope = 0.7 offspring per additional mate, $P = 0.42$).

A more detailed examination of the components of variance of male mating success appears in Table 2. When considering all potentially breeding males in the analysis, mate number (M) accounted for 74% of the total standardized variance in male reproductive success and was significantly correlated with reproductive success ($r_s = 0.90$, $P < 0.001$, $n = 105$). No other parameter or covariance term explained more than 7% of the variance, although paternity share (P) showed a significant correlation with reproductive success ($r_s = 0.77$, $P < 0.001$, $n = 28$), and M and N (female fecundity) were negatively correlated with each other ($r_s = -0.43$, $P = 0.02$, $n = 28$). No other terms showed significant correlations: (reproductive success with N: $r_s = 0.13$, $P = 0.50$, $n = 28$; M and P: $r_s = 0.14$, $P = 0.48$, $n = 28$; N and P: $r_s = -0.20$, $P = 0.31$, $n = 28$).

When limiting this analysis to reproductively successful males (Table 2), M still explained more of the variation in male reproductive success than any other term, but P also explained a substantial proportion of the total variance. Mating success and reproductive success were still correlated ($r_s = 0.39$, $P = 0.04$, $n = 28$, also significant using parametric statistics as shown by the Bateman gradient above). The remaining nonparametric correlations did not change, since nonbreeding
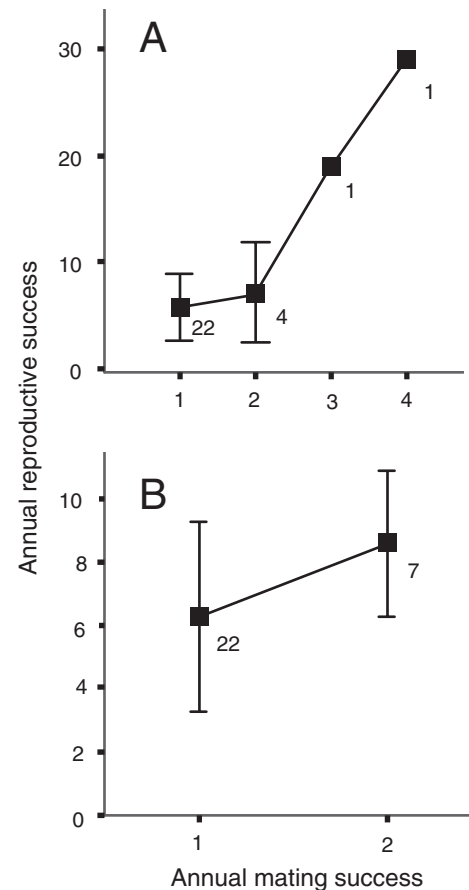

FIGURE 1. Bateman gradients—the relationship between reproductive success (i.e., number of offspring) and mating success (i.e., number of mates)—for (A) male and (B) female Wild Turkeys at the Hastings Natural History Reservation, Monterey County, CA in 2001–2003. Graphs display mean ± SD offspring for individuals obtaining a given number of mating partners; number of individuals appears next to each point.

individuals were already excluded from the terms involving N and P that were nested within M. The most important of the three interaction terms was the covariance between male mating success (M) and fecundity of those mates (N), accounting for -14% of the variance. This negative value suggests that the covariance between M and N constrains the total variance in male reproductive success.

DISCUSSION

THE GENETIC MATING SYSTEM OF THE WILD TURKEY

Mating systems such as leks have long been powerful for understanding sexual selection (Höglund and Alatalo 1995), yet the difficulty in measuring reproductive success in lekking species implies that the full potential of

TABLE 2.   Partitioning of variance in male reproductive success (I_s) in Wild Turkeys at the Hastings Natural History Reservation, Monterey County, CA in 2001–2003. Standardized variance in reproductive success was calculated both with ($I_{s,males} = 5.2$) and without ($I_{s,males} = 0.7$) nonbreeding individuals. Spearman rank correlations were calculated between reproductive success and its three component variables (mating success [M], female fecundity [N], and share of paternity [P]), as well as between those three variables (shown as covariances). Those correlations significant at $P < 0.05$ are indicated by an asterisk.

Component of variance	All males ($n = 104$)			Breeding males only ($n = 28$)		
	Variance	Standardized variance	Percent of total	Variance	Standardized variance	Percent of total
Mate number (M)*	14.2	3.84	74	15.4	0.30	44
Mate fecundity (N)	0.34	0.09	2	4.7	0.09	13
Paternity share (P)*	0.83	0.22	4	11.5	0.22	33
Covariance (M,N)*	−1.4	−0.37	−7	−5.0	−0.10	−14
Covariance (M,P)	0.60	0.16	3	2.2	0.04	6
Covariance (N,P)	−0.15	−0.04	−1	−2.1	−0.04	−6
Remainder	4.8	1.3	25	8.3	0.16	24
Total standardized variance (I_s)	19.3	5.2	100.0	35.0	0.69	100.0

studying such systems is rarely realized. The difficulty in finding nests of these species has limited our ability to sample offspring even when candidate parents can be identified. As a result, few lekking studies have obtained the level of parentage assignment typical of studies of many socially monogamous passerine systems. Even with far from complete samples of parents or offspring, I was able to use a multitiered approach based on biologically plausible assumptions (Lebigre et al. 2007) in order to provide, to my knowledge, the first description of the genetic mating system of the Wild Turkey.

Conspecific nest parasitism by turkeys has been documented using criteria such as abnormally large clutches (Bailey and Rinell 1967) to nest attendance by multiple females (Williams and Austin 1988) and oviposition patterns inconsistent with a single incubating female (Williams and Austin 1988). This study presents genetic evidence that female turkeys may incubate eggs that are not their own. Moreover, it provides an estimate of the frequency of multiple maternity in a turkey population ($n = 7$ out of 31 nests). The presence of multiple females at a single nest was observed at only one of the seven nests containing extra-maternal eggs, indicating that rates of nest parasitism based solely on clutch sizes or abnormal laying patterns may underestimate this phenomenon. The observation of one female that laid parasitically and incubated her own eggs at another nest raises the possibility that female turkeys can pursue both nesting and parasitic tactics to increase their reproductive success.

This study also provides the first estimate for the rate of multiple paternity in a free-ranging population of Wild Turkeys. Although multiple mating by females was common, since only successful fertilizations were detected, it is possible that an even greater number of females copulated with more than one male. Turkeys exhibit many "fast" life history traits, such as high adult mortality, high fecundity, and low (i.e., no) paternal care, with pair-bonded species also possessing high rates of multiple paternity (Arnold and Owens 2002). The accumulation of paternity data from additional species with

lek or lek-like mating systems will reveal whether these correlations between life history and genetic mating system are common across birds, or whether the presence or absence of a pair bond is the most important factor in determining rates of multiple mating (Lank et al. 2002).

These mating system data are crucial for understanding population processes in Wild Turkeys. First of all, the high levels of multiple mating by females indicate that turkeys are promiscuous rather than strictly polygynous; thus, the impact to the mating system should be to raise the effective population size, N_e, (Wright 1931, Sugg and Chesser 1994). Therefore, female promiscuity may help to explain the surprisingly high level of genetic diversity present in introduced turkey populations where genetic bottlenecks might be expected (Boone and Rhodes 1996, Mock et al. 2002, Mock et al. 2004). Secondly, the mating system determines the distribution of relatives and nonrelatives among offspring in a population. This distribution is not only important for determining where males are likely to encounter relatives when establishing reproductive coalitions, but also affects the relative fitness benefits of alternative kin recognition mechanisms (Krakauer 2005b, AHK unpubl. data).

OPPORTUNITY FOR SEXUAL SELECTION

Sex differences in reproductive variance. Given the extreme sexual dimorphism and dichromatism clearly evident in turkeys, one might expect to find strong evidence for sexual selection in this species. A comparison of estimates of $I_{s,males}$ and $I_{s,females}$ based upon individuals that apparently bred supports this prediction. More complete sampling would likely reveal higher opportunity for sexual selection. For females, high rates of nesting (75%–100% for adults; Vangilder 1992) would suggest that my estimate of standardized variance in reproductive success may be a reasonable approximation for all females in the population. In contrast, I calculated $I_{s,males}$ for all males based upon genetic paternity data; this value was much higher than when only detected breeding

individuals were considered. Many of these males identified as nonbreeding probably did not breed; for example, approximately 25% of adult males at Hastings were nonbreeding subordinate members of reproductive coalitions. However, other males did breed but were missed in paternity analyses due to limited nest sampling. If offspring in the unsampled nests were fathered by males previously identified from the sampled nests, my measurement would likely be an underestimate of $I_{s,males}$, as the reproductive success of a few males would increase even more relative to others in the population. Alternatively, if additional fathers were detected by more thorough nest sampling, the standardized variance could decrease. In reality, all of these processes are likely to have occurred, suggesting that the effects of nonbreeding males and unsampled nests may to some extent offset each other and that my estimate of $I_{s,males}$ could be a reasonable approximation of the true opportunity for selection on males. While the difficulty in collecting samples of offspring precluded better estimates of standardized variance, this is one of the few avian studies to calculate the opportunity for sexual selection based on genetic estimates of I_s for both males and females, and in particular, is among the first to do so in a bird species without pair bonds.

Components of variance of male reproductive success. This study is among the first in nonterritorial birds to partition $I_{s,males}$, the opportunity for selection in males, in this manner. Not surprisingly, mating success (M) explained the largest share of variance in reproductive success, both when variance estimates included nonbreeding birds ($M = 0$) and in a separate analysis considering variation in annual reproductive success of breeding individuals only ($M > 0$). To the extent that the limited sampling of nests may have created an artificial limit for the maximum number of nests in which a male sired offspring, the variance attributable to M may have been underestimated. In lekking or lek-like systems, mate number has long been assumed to be the best proxy for male reproductive success and, in the absence of molecular data on parentage, is often used to infer patterns of sexual selection (Watts and Stokes 1971, Höglund and Alatalo 1995). Here I provide further evidence that mating success typically does reflect the general pattern of reproductive success in polygynous species.

Unexpectedly, the proportion of a female's clutch that a male sired (P) explained almost as much variance as did the number of females he mated with, when only breeding males were considered. Given the relatively large proportion of nests containing offspring sired by multiple males, sperm competition must occur frequently in wild turkeys. Interest in multiple mating in lekking birds traditionally has focused on the question of why females seek copulations with additional mates when they presumably have free choice to mate with a preferred male (Höglund and Alatalo 1995, Lank et al. 2002, but see Saether et al. 2001). My estimate of the frequency of multiple paternity in turkey nests falls close to those reported for two lekking shorebirds with relatively low variance

in male reproductive success (Buff-breasted Sandpipers: 40%; Lanctot et al. 1997, Ruffs: 50%; Lank et al. 2002) but interestingly were greater than estimates published for two lekking galliforms (Greater Sage-Grouse: 20%, Semple et al. 2001; Black Grouse: 4%–19%, Alatalo et al. 1996, Lebigre et al. 2007). My findings indicate that in lekking species exhibiting multiple paternity, there could be strong selection on males to maximize their share of paternity, an otherwise overlooked area of competition.

While sperm performance and sperm storage have been examined in domestic turkeys (Hale 1955, Birkhead and Biggins 1998, Donoghue et al. 1998, 1999), we know nothing about the factors determining paternity in multiply mated female turkeys in the wild. The covariance between mating success and proportion of young sired was small, which implies that M and P are not positively related, nor do males face a trade-off between mate number and share of paternity. This suggests that in polygynous species where females mate multiply, selection could act on separate components of male courtship and reproduction. Unlike males of true lekking species, male turkeys have the opportunity to mate guard (Watts and Stokes 1971, Healy 1992); their reproductive success could therefore be the product of their ability to search for or attract distant females, compete with other males to copulate with these females, and to decrease the likelihood that females will mate again with other males. The importance of P and its independence from M could also result from physiological adaptations related to sperm competition. For example, selection could act on different aspects of sperm competition, such as sperm quality, ejaculate quantity, or female-mediated fertilization success (Pizzari and Birkhead 2000, Pizzari et al. 2004, Cornwallis and Birkhead 2007).

In this study, female fecundity (N) was not an important determinant of male reproductive success, as has recently been shown in some socially monogamous passerines (Webster et al. 2007). However, this finding should be considered cautiously, particularly given the limited number of sampled nests and the manner in which genetic material from offspring was collected. Despite the fact that the various methods of offspring sampling should be arbitrary with respect to the mating behavior of the females involved, the presence of incomplete clutches did add additional noise to estimates of N.

While the covariance between mate number and female fecundity explained a much lower proportion of the overall variance in male reproductive success than did mate number or paternity share alone, M and N were significantly and negatively correlated. Although inferences involving N should be considered cautiously since clutch size varied with collection method and because of the modest sample size, this result does raise an interesting possibility that a trade-off between mate number and female fecundity could act to constrain sexual selection in this species. One source of the negative covariance between these parameters may be quasi parasitism; in four

cases, a male was identified as both the father of at least part of an incubating female's clutch as well as the father of parasitic eggs in that same nest. Since the mean parasitic clutch size was <2 eggs, males that fathered these clutches had one clutch that was particularly small, and if they also mated with the incubating females, having two clutches would put them above the mean number of mates. Other processes could also lead to negative covariance between M and N, especially if certain males are more likely to mate with low-fecundity females. For example, younger females could have different preferences than older females (Coleman et al. 2004), or groups of younger females could copy the preference of an older female (Gibson et al. 1991).

In lek or lek-like systems, it has traditionally been difficult to collect enough parentage data to examine the importance of various components of fitness in the framework of the opportunity for selection. However, just as it has for studies of socially monogamous birds, this method will provide key insights into how sexual selection operates in polygynous species. This approach incorporates components of fitness other than mating success, meaning that the importance of factors such as female quality and multiple mating by females are explicitly examined. Additionally, comparative studies will become more informative, as researchers can investigate not only whether sexual selection is stronger in one population or species than another, but go on to measure how the opportunity for selection may differ across various fitness components. Given the dramatic variation in habitat, population density, and mating system of Wild Turkeys across North America, future research on this species may continue to illustrate the value of the opportunity for selection approach, as measures of paternity from additional populations become available.

ACKNOWLEDGMENTS

LITERATURE CITED

ALATALO, R. V., T. BURKE, J. DANN, O. HANOTTE, J. HÖGLUND, A. LUNBERG, R. MOSS, AND P. T. RINTAMÄKI. 1996. Paternity, copulation disturbance and female choice in lekking Black Grouse. Animal Behaviour 52:861–873.

ALBRECHT, T., J. SCHNITZER, J. KREISINGER, A. EXNEROVÁ, J. BRYJA, AND P. MUNCLINGER. 2007. Extra-pair paternity and the opportunity for sexual selection in long-distant migratory passerines. Behavioral Ecology 18:477–486.

ARNOLD, K. E., AND I. P. F. OWENS. 2002. Extra-pair paternity and egg-dumping in birds: life history, parental care, and the risk of retaliation. Proceedings of the Royal Society of London Series B 269:1263–1269.

ARNOLD, S. J., AND D. DUVALL. 1994. Animal mating systems: a synthesis based on selection theory. American Naturalist 143:317–348.

ARNOLD, S. J., AND M. J. WADE. 1984. On the measurement of natural and sexual selection: applications. Evolution 38:720–734.

BADYAEV, A. V., W. J. ETGES, J. D. FAUST, AND T. E. MARTIN. 1998. Fitness correlates of spur length and spur asymmetry in male Wild Turkeys. Journal of Animal Ecology 67:845–852.

BAILEY, R. W., AND K. T. RINELL. 1967. Events in the turkey year, p. 73–91. In O. H. Hewitt [ED.], The Wild Turkey and its management. The Wildlife Society, Washington, DC.

BALPH, D. F., G. S. INNES, AND M. H. BALPH. 1980. Kin selection in Rio Grande Turkeys: a critical assessment. Auk 97:854–860.

BATEMAN, A. J. 1948. Intra-sexual selection in Drosophila. Heredity 2:349–368.

BIRKHEAD, T. R., AND J. D. BIGGINS. 1998. Sperm competition mechanisms in birds: models and data. Behavioral Ecology 9:253–260.

BOONE, M. D., AND O. E. RHODES JR. 1996. Genetic structure among subpopulations of the Eastern Wild Turkey (Meleagris gallopavo silvestris). American Midland Naturalist 135:168–171.

BUCHHOLZ, R. 1995. Female choice, parasite load and male ornamentation in Wild Turkeys. Animal Behaviour 50:929–943.

BUCHHOLZ, R. 1997. Male dominance and variation in fleshy head ornamentation in Wild Turkeys. Journal of Avian Biology 28:223–230.

BUCHHOLZ, R., M. D. JONES DUKES, S. HECHT, AND A. M. FINDLEY. 2004. Investigating the turkey's "snood" as a morphological marker of heritable disease resistance. Journal of Animal Breeding and Genetics 121:176–185.

COLEMAN, S.W., G. L. PATRICELLI, AND G. BORGIA. 2004. Variable female preferences drive complex male displays. Nature 428:742–745.

CORNWALLIS, C. K., AND T. R. BIRKHEAD. 2007. Experimental evidence that female ornamentation increases the acquisition of sperm and signals fecundity. Proceedings of the Royal Society of London Series B 274:583–590.

DONOGHUE, A. M., D. R. HOLSBERGER, D. P. EVENSON, AND D. P. FROMAN. 1998. Semen donor selection by in vitro sperm mobility increases fertility and semen storage in the turkey hen. Journal of Andrology 19:295–301.

DONOGHUE, A. M., T. S. SONSTEGARD, L. M. KING, E. J. SMITH, AND D. W. BURT. 1999. Turkey sperm mobility influences paternity in the context of competitive fertilization. Biology of Reproduction 61:422–427.

DUVAL, E. H. 2007. Adaptive advantages of cooperative courtship for subordinate male Lance-tailed Manakins. American Naturalist 169:423–432.

EATON, S. W. 1992. Wild Turkey. In A. Poole, P. Stettenheim, and F. Gill [EDS.], The birds of North America, No. 22. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC.

Eaton, S. W., F. W. Evans, J. W. Glidden, and B. D. Penrod. 1976. Annual range of Wild Turkey in southwestern New York. New York Fish and Game Journal 23:20–33.

Emlen, S. T., and L. W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215–223.

Freeman-Gallant, C. R., N. T. Wheelwright, K. E. Meiklejohn, S. L. States, and S. V. Sollecito. 2005. Little effect of extra-pair paternity on the opportunity for sexual selection in Savannah Sparrows (*Passerculus sandwichensis*). Evolution 59:422–430.

Gibson, R. M., J. W. Bradbury, and S. L. Vehrencamp. 1991. Mate choice in lekking Sage Grouse revisited: the roles of vocal display, female site fidelity, and copying. Behavioral Ecology 2:165–180.

Hale, E. B. 1955. Duration of fertility and hatchability following natural matings in turkeys. Poultry Science 34:228–233.

Hauber, M. E., and E. A. Lacey. 2005. Bateman's principle in cooperatively breeding vertebrates: the effects of non-breeding alloparents on variability in female and male reproductive success. Integrative and Comparative Biology 45:903–914.

Haydock, J., and W. D. Koenig. 2002. Reproductive skew in the polygynandrous Acorn Woodpecker. Proceedings of the National Academy of Sciences USA 99:7178–7183.

Healy, W. M. 1992. Behavior, p. 46–65. *In* J. G. Dickson [ed.], The Wild Turkey: biology & management. Stackpole Books, Mechanicsburg, PA.

Hill, G. E., S. M. Doucet, and R. Buchholz. 2005. The effect of coccidial infection on iridescent plumage coloration in Wild Turkeys. Animal Behaviour 69:287–294.

Höglund, J., and R. V. Alatalo. 1995. Leks. Princeton University Press, Princeton, NJ.

Jones, A. G. 2001. GERUD 1.0: a computer program for the reconstruction of parental genotypes from progeny arrays using multilocus DNA data. Molecular Ecology Notes 1: 215–218.

Krakauer, A. H. 2005a. Kin selection and cooperative courtship in Wild Turkeys. Nature 434:69–72.

Krakauer, A. H. 2005b. The evolution of cooperative male courtship: kin selection and the mating system of the Wild Turkey *Meleagris gallopavo*. Ph.D. dissertation, University of California, Berkeley, CA.

Laloi, D., M. Richard, J. Lecompte, M. Massot, and J. Clobert. 2004. Multiple paternity in clutches of common lizard *Lacerta vivipara*: data from microsatellite markers. Molecular Ecology 13:719–723.

Lanctot, R. B., K. T. Scribner, B. Kempenaers, and P. J. Weatherhead. 1997. Lekking without a paradox in the Buff-breasted Sandpiper. American Naturalist 149:1051–1070.

Lank, D. B., C. M. Smith, O. Hanotte, A. Ohtonen, S. Bailey, and T. Burke. 2002. High frequency of polyandry in a lek mating system. Behavioral Ecology 13:209–215.

Lebigre, C., R. V. Alatalo, H. Siitari, and S. Parri. 2007. Restrictive mating by females on Black Grouse leks. Molecular Ecology 16:4380–4389.

Ligon, J. D. 1999. The evolution of avian breeding systems. Oxford University Press, New York.

Logan, T. H. 1973. Seasonal behavior of Rio Grande Wild Turkeys in western Oklahoma. Proceedings of the Annual Conference of the Southeast Association of Game and Fish Commissions 27:74–91.

Longmire, J. L., A. K. Lewis, N. C. Brown, J. M. Buckingham, L. M. Clark, M. D. Jones, L. J. Meincke, J. Meyne, R. L. Ratliff, F. A. Ray, R. P. Wagner, and R. K. Moyzis. 1988. Isolation and molecular characterization of a highly polymorphic centromeric tandem repeat in the family Falconidae. Genomics 2:14–24.

Marshall, T. C., J. Slate, L. E. B. Kruuk, and J. M. Pemberton. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. Molecular Ecology 7:639–655.

Mock, K. E., E. K. Latch, and O. E. Rhodes. 2004. Assessing losses of genetic diversity due to translocation: long-term case histories in Merriam's Turkey (*Meleagris gallopavo merriami*). Conservation Genetics 5:631–645.

Mock, K. E., T. C. Theimer, O. E. Rhodes, D. L. Greenberg, and P. Keim. 2002. Genetic variation across the historical range of the Wild Turkey (*Meleagris gallopavo).* Molecular Ecology 11:643–657.

Møller, A. P. 1992. Frequency of female copulations with multiple males and sexual selection. American Naturalist 139:1089–1101.

Pearce, J. M., R. L. Fields, and K. T. Scribner. 1997. Nest materials as a source of genetic data for avian ecological studies. Journal of Field Ornithology 68:471–481.

Pelham, P. H., and J. G. Dickson. 1992. Physical characteristics, p. 32–45. *In* J. G. Dickson [ed.], The Wild Turkey: biology & management. Stackpole Books, Mechanicsburg, PA.

Pizzari, T., and T. R. Birkhead. 2000. Female feral fowl eject sperm of subdominant males. Nature 405:787–789.

Pizzari, T., P. Jensen, and C. K. Cornwallis. 2004. A novel test of the phenotype-linked fertility hypothesis reveals independent components of fertility. Proceedings of the Royal Society of London Series B 271:51–58.

Raymond, M., and F. Rousset. 1995. GENEPOP. Version 1.2: Population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248–249.

Reed, K. M., M. C. Roberts, J. Murtaugh, C. W. Beattie, and L. J. Alexander. 2000. Eight new dinucleotide microsatellite loci in turkey (*Meleagris gallopavo*). Animal Genetics 31:140–141.

Reynolds, S. M., K. Dryer, J. Bollback, J. A. C. Uy, G. L. Patricelli, T. Robson, G. Borgia, and M. J. Braun. 2007. Behavioral paternity predicts genetic paternity in Satin Bowerbirds (*Ptilonorhynchus violaceus*), a species with a non-resource-based mating system. Auk 124:857–867.

Roberson, D. 2002. Birds of Monterey County. 2nd ed. Monterey Peninsula Audubon Society, Carmel, CA.

Saether, S. A., P. Fiske, and J. A. Kålås. 2001. Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird. Proceedings of the Royal Society of London Series B 268:2097–2102.

Semple, K., R. K. Wayne, and R. M. Gibson. 2001. Microsatellite analysis of female mating behavior in lek-breeding Sage Grouse. Molecular Ecology 10:1043–1048.

Shuster, S. M., and M. J. Wade. 2003. Mating systems and strategies. Princeton University Press, Princeton, NJ.

Smith, D. M. 1977. Social organization of Rio Grande Turkeys in a declining population. Ph.D. dissertation, Utah State University, Logan, UT.

Strausberger, B. M., and M. V. Ashley. 2001. Eggs yield nuclear DNA from egg-laying female cowbirds, their embryos and offspring. Conservation Genetics 2:385–390.

Sugg, D.W., and R. K. Chesser. 1994. Effective population sizes with multiple paternity. Genetics 137:1147–1155.

Vangilder, L. D. 1992. Population Dynamics, p. 144–164. *In* J. G. Dickson [ed.], The Wild Turkey: biology & management. Stackpole Books, Mechanicsburg, PA.

Wade, M. J., and S. J. Arnold. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. Animal Behaviour 28:446–461.

WATTS, C. R. 1969. Social organization of Wild Turkeys on the Welder Wildlife Refuge, Texas. Ph.D. dissertation, Utah State University, Logan, UT.

WATTS C. R., AND A. W. STOKES. 1971. Social order of turkeys. Scientific American 224:112–118.

WEBSTER, M. S., S. PRUETT-JONES, D. F. WESTNEAT, AND S. J. ARNOLD. 1995. Measuring the effects of pairing success, extra-pair copulations and mate quality on the opportunity for sexual selection. Evolution 49:1147–1157.

WEBSTER, M. S., K. A. TARVIN, E. A. TUTTLE, AND S. PRUETT-JONES. 2007. Promiscuity drives sexual selection in a socially monogamous bird. Evolution 61:2205–2211.

WHITTINGHAM, L. A., AND P. O. DUNN. 2005. Effects of extra-pair and within-pair reproductive success on the opportunity for selection in birds. Behavioral Ecology 16:138–144.

WILEY, R. H. 1974. Evolution of social organizations and life history patterns among grouse. Quarterly Review of Biology 49:201–227.

WILLIAMS, L. E., AND D. H. AUSTIN. 1988. Studies of the Wild Turkey in Florida. University Presses of Florida, Gainesville, FL.

WOOLFENDEN, B. E., H. L. GIBBS, AND S. G. SEALY. 2002. High opportunity for sexual selection in both sexes of an obligate brood parasitic bird, the Brown-headed Cowbird (*Molothrus ater*). Behavioral Ecology and Sociobiology 52:417–425.

WRIGHT, S. 1931. Evolution in Mendelian populations. Genetics 16:97–159.