High frequency of polyandry in a lek mating system

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The adaptive significance of polyandry by female birds in the absence of direct benefits remains unclear. We determined the frequencies of polyandrous mating and multiple paternity in the ruff, a lekking shorebird with a genetic dimorphism in male mating behavior. More than half of female ruffs mate with, and have clutches fertilized by, more than one male. Individual females mate with males of both behavioral morphs more often than expected. Polyandrous mating was more likely following copulation interference, but interference was uncommon. The multiple paternity rate of ruffs is the highest known for avian lekking species and for shorebirds. The general hypothesis that pair-bond constraints are the major selective factor favoring multiple mating in birds does not predict our findings. Active genetic diversification, which has been widely dismissed as a functional explanation for polyandrous mating in birds, may apply with respect to the behavioral polymorphism in ruffs because of a Mendelian genetic basis for male behavioral morph determination and aspects of male–male cooperation and female choice. However, rates of multiple paternity in other species of lekking birds are higher than generally realized, and the potential benefits of diversification in general deserve further consideration. *Key words:* alternative mating behavior, female choice, leks, multiple paternity, *Philomachus pugnax*, polyandry, ruffs, sperm competition. *[Behav Ecol 13:209–215 (2002)]*

Females often copulate with several males during a breeding attempt, but the adaptive significance of polyandry, if any (Halliday and Arnold, 1987), often appears enigmatic (Birkhead and Møller, 1992; Jennions and Petrie, 2000; Petrie and Kempenaers, 1998; Westneat et al., 1990; Yasui, 1998). Female birds clearly benefit when polyandry increases their access to resources or paternal care provided by males, or their likelihood of obtaining future mates (e.g., Galapagos hawks, *Buteo galapagoensis*: Faaborg et al., 1980; dunnocks, *Prunella modularis*: Hatchwell and Davies, 1990; spotted sandpipers, *Actitis macularia*: Colwell and Oring, 1988; Lank et al., 1985). Polyandrous mating appears to increase offspring fitness in several groups of animals (e.g., adders, *Vipera berus*: Madsen et al., 1992; guppies, *Poecilia reticulata*: Evans and Magurran, 2000; bumble bees, *Bombus terrestris*: Baer and Schmid-Hempel, 1999), but the mechanisms producing the increases are unclear (Jennions and Petrie, 2000).

In pair-bonded species, including many birds, certain females may attempt to improve the genetic content of their offspring through extrapair copulations, despite potential retaliation from their social mates (Birkhead and Møller, 1992; Westneat et al., 1990). Many published studies of birds document nonrandom choice of extrapair mates, or second mates in non–pair-bonded species, which suggests choice for particular phenotypes potentially related to good genes (Birkhead, 1998; Jennions and Petrie, 2000). There are exceptions to this pattern, however, and experimental demonstrations are few

(see Hillgarth, 1990). One alternative hypothesis is that genetic diversification of offspring per se is favored. Although genetic diversification is a universal consequence of polyandry, it has widely been assumed to be inapplicable for birds in general (Westneat et al., 1990).

In lekking species, females choose mates without risking the loss of support from males, which provide no support to begin with. In the absence of this cost, if polyandry is advantageous, we would expect to find higher rates of polyandry among lekking than among pair-bonded species. Alternatively, because many females may readily mate with the best male at a lek, there may be no benefit from copulating with several males, in contrast to the pair-bonded situation. In many species of lekking grouse, females do have low rates of copulation and are overwhelmingly monogamous (Alatalo et al., 1996), as predicted by this latter logic. This was previously assumed to be a general pattern for lekking birds (Birkhead, 1998; Birkhead and Møller, 1992; Birkhead et al., 1987; Höglund and Alatalo, 1995). However, females in some lekking species of other groups of birds were more likely to be polyandrous when their mate choice was constrained by interference from males (Trail, 1985) or if males were temporarily monopolized by other females (Petrie et al., 1992). Polyandry in lekking species may also occur if assessment criteria are subject to error (Yasui, 1998), and in less well-understood situations (see Lanctot et al., 1997).

The ruff (*Philomachus pugnax*) is a lekking species in which females mate relatively frequently (Petrie and Kempenaers, 1998). The ruff is also unique among all birds in having a genetic dimorphism in male mating behavior. Two male morphs differ in both plumage and behavior, with darker plumaged, "independent" males defending adjacent small mating courts (ca. 1–1.5m²), and lighter plumaged, nonterritorial "satellite" males displaying with independents on the independents' courts (Hogan-Warburg, 1966; van Rhijn, 1991). The morph ratio is about 84% independents to 16% satellites over the entire breeding range from northern Europe to eastern Siberia (van Rhijn, 1983, 1991; Widemo,

1998). Genetically, independent males are homozygous recessive at the behavior locus, and 90% of satellites are heterozygotes (Lank et al., 1995).

In this article, we describe the mating patterns of wild female ruffs, called "reeves," with respect to male interference and male morph. We examined the rates of multiple paternity of clutches using DNA markers. We discuss our findings with respect to proximate and ultimate hypotheses regarding the causes and significance of polyandry in female birds.

METHODS

We studied reeves mating along the south and east shoreline of Liminganlahti (ca. 60°50′ N, 25°20′ E), about 30 km south-southwest of Oulu, Finland, during May and June of 1984–1987 and 1989–1990. We made daily observations throughout these breeding seasons from blinds located 15–30 m from leks, observing birds with binoculars and through 20–60× spotting scopes (Lank and Smith, 1987).

We recorded the mating behavior of females. A lek visit began when a reeve arrived and ended when she left. We tabulated mating behavior, including female crouches (Hogan-Warburg, 1966; Shepard, 1975), attempted copulations by males, apparently successful copulations, and copulation interference by other males. We scored a "mating attempt" when a female crouched, and a "mating" when a male mounted her. We tallied a "mating visit" when a female mated one or more times. "Multiple mating" means copulating more than once, with one or more male(s). We tallied the number of independent and satellite males present during each mating visit.

We used data from individually identifiable reeves to examine the timing of lek visitation relative to egg laying, mating behavior between successive visits, and mating behavior over an entire nesting attempt and season. Most identifiable reeves (83%) were captured and color-banded in years before the lek visits reported here, but we also include data from 10 unbanded females with extremely distinctive plumage characteristics. Because individual reeves may mate at several locations (including off the lek; Lank and Smith, 1987), matings occur throughout the long arctic days, and our observation schedules differed within and among years, our mating histories are incomplete, and our direct tallies of polyandrous mating rates are thus minimal.

Nearby males may interfere with mating attempts. Neighbors may threaten from their courts or charge, and neighbors and court co-occupants of either morph may attack a copulating pair. We scored mating interference only when there was physical contact and tallied the morph of the interfering male.

We searched intensively for nests in suitable habitat within approximately 2 km of lek sites, starting about a week after the first peak of mating. We found nests that survived to hatch laid by 13 out of 61 reeves identified at leks. We used the hatch dates from these nests, plus egg-laying and incubation periods determined for wild and captive birds, to estimate the time of lek visits and mating relative to egg-laying (wild: 5–7 days to lay 4 eggs and 22 days to hatch: Andersen, 1944; Kondrat'yev, 1982; captivity: 5–6 and 22.3 days: Lank and Smith, unpublished data).

In 1987, 1989, and 1990, we collected blood samples from 9, 25, and 15 males, respectively, at leks under observation, from females trapped on nests ranging from 20 to 1500 m from the leks, and from offspring from these nests. In 1987, blood samples were taken from newly hatched chicks in the field. In 1989 and 1990, we collected clutches, incubated the eggs, and took blood samples from hatching young. DNA isolated from embryos of a few unhatched eggs was also used.
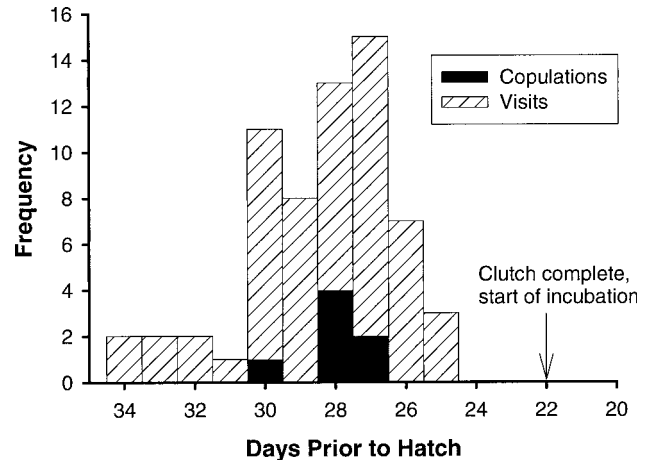
Figure 1
The pooled temporal distribution of visits to leks and matings by 13 female ruffs relative to the onset of incubation.

Although all broods considered in this analysis initially had 4 eggs, we obtained DNA data from a mean of 3.0 chicks per brood (range 2–4).

We analyzed DNA extracted from samples using one of two techniques. The 1987 samples ($n = 4$ broods) were probed with multilocus DNA probes (Jeffreys 33.15 and 33.6; Bruford et al., 1998; Jeffreys et al., 1985), and the 1989 and 1990 samples ($n = 30$ broods) were analyzed using five single-locus minisatellite probes developed from the ruff genome (Hanotte, Bailey, and Burke, unpublished data; Lank et al., 1995). We categorized each brood as having single versus multiple paternity using one of three criteria: (1) a single father was identified for all chicks in a brood, or more than one father was assigned; (2) for the single-locus analyses only, if no father was identified for broods of three or more offspring, single paternity was scored if the offspring shared not more than two nonmaternal allele(s) for each of the five probes tested, whereas multiple paternity was scored if three or more different paternal alleles occurred at two or more loci; (3) for the single-locus analyses only, if no father was identified for broods of two offspring, multiple paternity was scored if the brood did not share paternal alleles at any of the five loci. Using these criteria, the probability of misclassification as multiple paternity is, for case 2, estimated as 10^{-5}, found from binomial expectation based conservatively on an expected mean mutation rate for minisatellite loci of 10^{-3} (Jeffreys et al., 1988) and, in case 3, equal to the probability that a heterozygote father for all five probes will transmit a different allele to each offspring for all five probes ($p = .03$ or less because two fathers could share alleles at some loci). These criteria are conservative and will underestimate the rate of multiple paternity. For offspring of known fathers (Lank et al., 1995), we tallied paternity by morph.

We determined the proportion of independent and satellite males in our local area by surveying ruffs throughout one of our study sites daily in 1986 and 1987 (Lank and Smith, 1987) and assigning a behavioral morph to each male based on his behavior or plumage coloration (Hogan-Warburg, 1966). Surveying decreased potential biases in morph ratio estimates based only on data from leks (see Widemo, 1998).

RESULTS

Mating patterns

Individually identified reeves visited leks between 25 and 34 days before their eggs hatched (Figure 1). Allowing 5 days for

Table 1

Frequency of mating for monogamous and polyandrous reeves within and between mating visits

	Within single mating visit		Between mating visits	
	Matings (mean ± SE)	n visits	Matings/visit (mean ± SE)	n reeves
Single mating	1.0	187		
Multiple mating				
1 Male	2.9 ± 0.2	81	1.5 ± 0.3	3
2 Males	2.7 ± 0.2	21	2.0 ± 0.7	6
3 Males	3.3 ± 0.3	3		
Uncertain		3		

laying and 22 for incubation (see Methods), reeves visited the lek for about 1 week before laying their first egg. Females mated on about 1 lek visit in 10 (Lank and Smith, unpublished data), concentrated 1–4 days before the start of laying. Although identifiable reeves nested as close as 20 m to a lek, we never saw visits during incubation.

During single mating visits, 37% of reeves mated multiply (Table 1). Among these, 24% mated polyandrously, including three trigamous reeves. The mean number of matings per visit did not differ between multiply mating monogamous and polyandrous females (Table 1; $t = 0.31$, df = 103, $p = .76$). Thus, polyandry within visits did not occur simply because certain multiply mating females copulated more often than others.

Among identifiable females with two or more mating visits, six of nine were polyandrous (Table 1); one of these was also polyandrous within a visit. Seven additional females attempted to mate on two or more visits, but failed on one or both. Six of these seven would have been polyandrous had they mated on both visits. Thus, 12 of 16 females attempted to be polyandrous between visits. Four of the six successfully polyandrous females clearly switched mates, since both chosen males were present on both mating visits. One female mated with two different satellites, each of which was present on only one visit. The sixth female mated with independent males on two leks approximately 1.4 km apart. Finally, we observed four additional females mating before laying two separate clutches. One changed mates, two remated with their original male, and one remated with her original male but also mated with a second male. Although these samples are small, they suggest that a majority of females change males within or between clutches.

Mating histories of individuals

We compiled lek visit histories for 61 individually identifiable reeves. We observed 1–13 visits over 1–7 days before single nesting attempts (Table 2). We saw no mating attempts for 27 of these females. Assuming that these females did mate at least once, we missed about half or more of the matings at our sites. The females we observed attempting to mate did so 3.3 times, on average, ranging up to 13. Seventy-four percent of this group (25/34) made more than one mating attempt, and 38% did so with more than one male. Thus, among all females we observed crouching or mating more than once, 52% (13/25) did so with more than one male. Two females attempted to mate with five different males. There was no significant difference between the mean number of lek visits or number of mountings by males for multiply mating monogamous and polyandrous females (visits: 4.0 vs. 5.0, $t = 0.79$, df = 23, $p = .45$; matings: 1.9 vs. 2.8, $t = 0.81$, df = 17.3, $p = .43$). However,

Table 2

Number of days visiting leks, lek visits, and mating attempts for females of different mating categories (mean ± SE)

Matings	Days visiting	Visits	Mating attempts	n
None	1.6 ± 0.2	2.2 ± 0.4	0	27
1	2.2 ± 0.4	3.6 ± 0.8	1	9
>1 Monogamous	2.2 ± 0.4	4.0 ± 1.1	3.0 ± 0.4	12
>1 Polyandrous	2.8 ± 0.4	5.0 ± 0.7	5.2 ± 1.0	13
2 Males	2.6 ± 0.4	4.5 ± 0.6	4.5 ± 1.2	10
3 Males	2	3	10	1
5 Males	4.0 ± 1.0	8.5 ± 2.5	6.5 ± 0.5	2

the number of mating attempts by females may have been higher for polyandrous females (3.0 vs. 5.2, $t = 2.04$, df = 14.6, $p = .06$).

Mating interference

Intruding males or court co-occupants interfered with matings during 11.3% of the 612 copulation attempts we observed. To compare rates of male interference during multiply mating monogamous versus polyandrous mating visits, we classified visits as interfered with only if the interference occurred before a mate switch or before the last mating attempt during that visit. Interference was more frequent for females subsequently mating polyandrously than for monogamous females who mated multiple times (7/72 for monogamous visits versus 8/23 for polyandrous visits; $\chi^2 = 8.23$, df = 1, $p = .004$). In half (4/8) of the polyandrous cases, the female subsequently mated with the interfering male. Interference occurred at a similar rate during mixed-morph polyandrous mating visits (6/14) as those with independents only (2/9; Fisher's Exact test, $p = .38$).

Multiple paternity rates

We determined single versus multiple paternity for 34 broods (Table 3). Exactly half had multiple paternity, including three with three fathers. The average brood thus had at least 1.6 fathers. Similar results were obtained in all 3 years and with both paternity assessment techniques. We did not detect a higher frequency of multiple paternity when more samples per brood were obtained. Nonetheless, the true multiple paternity rate is likely to be higher than 50% because we obtained data for only 3.0 of the 4 chicks per brood, on average. With data from two of four chicks, we have a 50% chance of having missed multiple paternity had it occurred, and we had a 30% chance of missing additional fathers from three chick

Table 3

Frequencies of multiple paternity among broods with different brood sizes (multiple paternity/total)

Year	Sample size obtained per brood of 4			All
	2	3	4	
1987	1/1	—	1/3	2/4
1989	2/5	5/9	2/2	9/16
1990	1/3	4/7	1/4	6/14
Total	4/9	9/16	4/9	17/34

Three broods had three fathers.

Table 4

Copulation rate (mean ± SE) per mating visit type with respect to behavioral morph of male partner

	Male morph			
	Independent		Satellite	
Mating visit type	Rate	n	Rate	n
Single	1.0	130	1.0	51
Multiple				
Monogamous	3.0 ± 0.2	65	2.2 ± 0.2	10
Polyandrous				
Single	1.0	22	1.0	16
Multiple	3.0 ± 0.5	6	2.0 ± 0.0	2
Total single	1.0	152	1.0	67
Total multiple	3.0 ± 0.2	71	2.2 ± 0.2	12

broods. If we conservatively assume a mean of 1.6 fathers per brood, based on our incomplete sample, we expect that 3 of the 12 single-paternity clutches with incomplete information in Table 3 were multiply sired. Thus we estimate a multiple paternity rate of 59%.

Female mating behavior with respect to male morph

Reeves mating with independent males were more likely to mate multiply during a mating visit than those mating with satellites (Table 4; $\chi^2 = 8.11$, df = 1, $p = .004$). Among multiply mating females, those mating with independents copulated more often per mating visit than those mating with satellites (3.0 vs. 2.2, $t = 3.55$, df = 41.2, $p = .001$).

Polyandrous females mated nonrandomly with respect to male morph type. On surveys, we found the proportion of independent males to be 0.840 ± 0.006 in 1986 ($n = 24$ days) and 0.838 ± 0.006 in 1987 ($n = 16$ days), for an overall mean of 0.839. If reeves change mates randomly with respect to male morph, the binomial expectation is 0.70 independent male combinations, 0.27 both morphs, and 0.03 both satellites. Out of 23 reeves observed to mate polyandrously, 14 mated with both morphs, twice as many as expected (Table 5). In nine of these cases, females mated first with an independent, and in five cases first with a satellite.

Because the proportion of independent males at leks may differ from that in the general population, we calculated the proportion at the lek when a female mated with the second male. The morph ratio when independent–independent combinations occurred was 0.76 independents, and when independent–satellite switches occurred was 0.82, suggesting a slight overrepresentation of satellites at leks relative to our censuses. The two ratios did not differ significantly, so we used

the weighted mean of 0.80 as an expected value. Females still mated with both morphs significantly more often than expected by chance (Table 5).

We also looked at the mate choices of females seen to change mates between visits before laying a single clutch (Table 5). Two of six switched morphs. If we tally mating attempts rather than matings, seven of 12 polyandrous females attempted to mate only with independents, four attempted to mate with both morphs, and one attempted to mate with two satellites and no independents. The four females seen mating during two nesting attempts all remated with the same morph. One mated with the same independent male and one with the same satellite, one changed from one independent male to another, and one mated with the same independent male for both clutches but also mated with a second independent male on her second clutch.

We assessed the paternal morph ratios of clutches with known fathers. Two single-paternity broods were fathered by an independent and two by a satellite father. Three multiple-paternity broods were fathered by an independent and a male of unknown morph; one was fathered by two independent males and a third male of unknown morph; two were fathered by an independent, a satellite male, and a male of unknown morph; one was fathered by a satellite and a male of unknown morph; and three were fathered by two satellite males.

DISCUSSION

Most female ruffs are polyandrous

Half of the clutches analyzed demonstrated multiple paternity, and given our less than complete information (Table 3) and conservative assignment criteria (see Methods), we estimate 59% as a minimum estimate of the true rate of multiple paternity. It is difficult to quantitatively compare behavioral and genetic rates of polyandry because our behavioral data are substantially incomplete. However, just more than half of the individually recognizable females we saw attempting to mate more than once did so with more than one male (Table 2). Because only 8% of females mated polyandrously during single lek visits (Table 1), the preponderance of multiple paternity must be due to mate changes between mating visits, as occurred in six of the nine cases of mating during two visits that we did observe (Table 1).

If the probability that a female will mate with a new male is independent between mating visits and independent of her status as polyandrous or not within visits, females with one to four mating visits would have had polyandry rates of 8%, 70%, 90%, and 97%, respectively. Van Rhijn (1983) reported that a few distinctively plumaged reeves each mated on about three different visits.

We conclude that the majority of reeves are both behaviorally and genetically polyandrous. These are the highest rates

Table 5

Mating combinations of individual females with respect to male morph

	Ind + Ind	Sat + Ind	Sat + Sat	χ^2	p
Within visit					
Observed	9	14	0		
Expected (population ratio)	16.24	6.19	0.57	13.65	.003
Expected (lek ratio)	14.65	7.41	0.94	8.98	.030
Between visits					
Observed	3	2	1		

Ind = independent, Sat = satellite.

estimated for any lekking bird species (Lanctot et al., 1997; Wiley, 1991) and also the highest for any shorebird species (see references in Johnson and Briskie, 1999; see also semi-palmated plover, *Charadrius semipalmatus,* 4%: Zharikov and Nol, 2000; ringed plover, *Ch. hiaticula,* 0%: Wallander et al., 2001; great snipe, *Gallinago media,* 2/7 families: Bailey, Kålås JA, and Burke, unpublished data; Wilson's phalarope, *Phalaropus tricolour,* 0%: Delehanty et al., 1998; red-necked phalarope, *P. lobatus,* 6%: Schamel, 2000; western sandpiper, *Calidris mauri,* 5%: Blomqvist et al., in press).

Females fertilized eggs using stored sperm (Figure 1), and the sperm size of ruffs supports an evolutionary history of sperm competition and multiple paternity. In passerine birds (Briskie et al., 1997) and shorebirds (Johnson and Briskie, 1999), sperm size increases with higher rates of multiple paternity, and ruffs have the longest sperm of any shorebird yet measured (Johnson and Briskie, 1999; Lank et al., unpublished data).

Is female choice constrained by male interference?

Courtship interference occurred on 11% of mating attempts, similar to rates in Götland, Sweden (Widemo, 1997, 1998). This rate is low compared to that of multiple paternity, and mate changes between visits account for most of our estimated multiple-paternity rate. Thus, interference is not a proximal cause of most of the multiple paternity in ruffs. Nonetheless, a third of the polyandrous matings we observed during single lek visits were preceded by physical interference with a copulation attempt before the female mated with a second male, and multiply-mating reeves were more likely to be polyandrous after male–male interference, as also occurs in black grouse (*Tetrao tetrix;* Alatalo et al., 1996). This does not necessarily mean that female choice is substantially constrained by male interference (Sæther et al., 1999), but females may use interference in making mate-choice decisions (Avery, 1984). Females subsequently mated with interfering males in four of eight cases we observed. Such redirected mate choice has been reported for Guianan cock-of-the-rock *Rupicola rupicola* (Trail, 1985; Trail and Koutnik, 1986), but not in other lekking species in which interference was reported (e.g., Alatalo et al., 1996), including two lekking shorebirds (great snipe: Sæther et al., 1999; buff-breasted sandpiper, *Tryngites subruficollis*: Lanctot et al., 1997).

Do female ruffs actively genetically diversify their offspring?

Why is polyandry unusually frequent in ruffs relative to other lekking species and to related shorebirds? Several hypotheses seem inapplicable in this case. Neither good genes nor better genes (Birkhead, 1998; Jennions and Petrie, 2000), nor fertility insurance (Sheldon, 1994), nor inducing direct sperm competition and/or sperm selection by females (Yasui, 1997; but see Curtsinger, 1991) predict disproportionate cross-morph mating (Table 5). This intriguing observation is instead consistent with the hypothesis that females actively diversify their offspring with respect to male morph.

Increased genetic diversification of offspring is a universal result of polyandrous mating by females, but it has been consistently dismissed as an unlikely ultimate explanation for polyandrous mating by female birds in general (e.g., Birkhead and Møller, 1992; Westneat et al., 1990; Williams, 1975; Yasui, 1998) and in specific cases (e.g., Ligon and Zwartjes, 1995; Petrie et al., 1992; Wagner et al., 1996; Westneat, 1992), and many authors do not even discuss the possibility (e.g., Kempenaers et al., 1992; Sheldon, 1994; but see Dunn et al., 1994; Strohbach et al., 1998; Taylor et al., 2000, for possible cases). Three common objections against its importance (Westneat

et al., 1990) may be less applicable for the specific trait of male behavioral morph. First, females will substantially increase the genetic diversity of their offspring through multiple mating, at least with respect to male morph. Male morph is a Mendelian rather than quantitative trait, with autosomal inheritance and a dominant satellite allele (Lank et al., 1995, 1999). Females can theoretically allocate their genetic and behavioral "male morph investment" only by mating with both morphs. Because 86% of females are homozygous recessive at the morph locus, they will produce only independents if they mate with independents, and approximately equal proportions of satellite and residents by mating only with a satellite. Second, a theoretical decrease in parental fitness through increased sib competition in mixed broods (Sherman, 1981) is less applicable in a precocial species with a small clutch size. Finally, because most reeves do pursue polyandrous matings, rather than only females whose partners are perceived as being of lower genetic quality (Birkhead, 1998; Jennions and Petrie, 2000; Westneat et al., 1990), an adaptive role for diversification per se is plausible.

What benefits might females obtain from diversification? The most intriguing theoretical possibility is half-sib cooperation among offspring (Yasui, 1998). Combinations of independent and satellite males apparently attract females to courts (van Rhijn, 1973; Widemo, 1998), thereby stabilizing the maintenance of the male dimorphism (Hugie and Lank, 1997). Co-display by independent and satellite brothers would decrease the fitness costs of sharing matings with a co-occupant. Although satellites track female movements among leks (Lank and Smith, 1987; van Rhijn, 1983, 1991) and among males within leks (Widemo, 1998), they also form temporary associations with particular independents (van Rhijn, 1991). If the frequency and payoff for half-sib associations were sufficiently high, this mechanism could offset a female's costs of pursuing polyandrous matings between morphs. Although the exceptionally cooperative males at long-tailed manakin display sites are unrelated (McDonald and Potts, 1994), genetic structure does exist among leks of black grouse (Höglund et al., 1999) and white-bearded manakins (*Manacus manacus;* Shorey et al., 2000), and kin-biased association at display sites was found among feral peacocks (*Pavo cristatus*) raised experimentally in non-sib groups (Petrie et al., 1999).

Polyandry in lekking species

Lekking species have been characterized as having low rates of multiple mating and multiple paternity (Birkhead, 1998; Birkhead and Møller, 1992; Birkhead et al., 1987), based primarily on the low mating rates of lekking grouse (Alatalo et al., 1996; Höglund and Alatalo, 1995; Wiley, 1991) and supported by the logic that multiple mating was unnecessary because highly attractive males were readily available to all females (Westneat et al., 1990). However, multiple paternity in several lekking species is more frequent than expected from this point of view. In white-bearded manakins, buff-breasted sandpipers, peafowl, the Guianan cock-of-the-rock, and ruffs, a quarter or more of females mated with more than one male (see Lanctot et al., 1997). Because females of lekking species do not face the potential cost of loss of male support, and search costs are low, the costs of polyandry may also be low. Given low costs, any of the many potential genetic benefits from polyandry (Jennions and Petrie, 2000), including sperm competition and/or sperm selection by females (Yasui, 1997) or more exotic direct benefits (e.g., Lombardo et al., 1999) may result in its spread. Höglund and Alatalo (1995) suggested that the most likely factor selecting against polyandrous mating in lekking species was avoidance of disease. Strongly skewed mating systems have tremendous potential for spread-

ing sexually transmitted diseases (Hamilton, 1990; Lombardo, 1998), and polyandry may pay with respect to the coevolution of disease resistance (Møller, 1997). For whatever reason, a female's mating rule in many lekking species may be not the oft-stated search for the highest quality male, but rather to seek several high quality mates.

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