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Low Extra-Pair Paternity In White-Tailed Ptarmigan

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LOW EXTRA-PAIR PATERNITY IN WHITE-TAILED PTARMIGAN

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Abstract. The White-tailed Ptarmigan (*Lagopus leucurus*) is one of the few socially monogamous species within the highly polygynous grouse subfamily (Tetraoninae). I found White-tailed Ptarmigan in Glacier National Park, Montana, to be nearly genetically monogamous. Of 58 chicks with putative fathers identified, three were the result of extra-pair copulations (5%). Three of 18 clutches (17%) contained extra-pair offspring. I suggest that White-tailed Ptarmigan males are able to guard their females effectively from extra-pair copulations because of high visibility in their habitat and their ability to forage alongside their mate. The three extra-pair offspring were sired by unknown males.

Key words: Lagopus leucurus, mate guarding, monogamy, paternal care, paternity, White-tailed Ptarmigan.

Baja Paternidad Extra-Pareja en *Lagopus leucurus*

Resumen. *Lagopus leucurus* es una de las pocas especies socialmente monógama dentro de la subfamilia Tetraoninae que se caracteriza por ser altamente polígina. En el ''Glacier National Park,'' Montana, encontré que los individuos de *L. leucurus* eran casi completamente monógamos en términos genéticos. De 58 polluelos con padres putativos, tres (5%) fueron el resultado de copulaciones extra-pareja. Tres de 18 nidadas (7%) presentaron hijos extra-pareja. Sugiero que los machos de *L. leucurus* son capaces de proteger efectivamente a sus hembras para evitar copulaciones extra-pareja debido a la alta visibilidad del hábitat en que se encuentran y a la habilidad de forrajear junto con la hembra. Los tres hijos de origen extra-pareja no fueron engendrados por machos que estaban en pareja.

Over 90% of bird species are socially monogamous. Recently, however, avian behaviorists have become aware of the disparity between social and genetic mating systems (Gladstone 1979), especially since the advent of genetic fingerprinting techniques that allow rates of extra-pair paternity (EPP) to be measured (Burke and Bruford 1987, Quinn et al. 1987, Wetton et al. 1987). This disparity varies from extreme in, for example, the Superb Fairy Wren (*Malurus cyaneus*; 69% EPP; Dunn and Cockburn 1996) to nonexistent in the Common Loon (*Gavia immer*; 0%; Piper et al.

1997). The rate of EPP can also vary among congeners (e.g., 3% vs. 36% in two species of *Acrocephalus*; Schultz-Hagen 1993, Hasselquist et al. 1996), and can even vary among populations within species (Lifjeld et al. 1991, Gelter and Tegelström 1992).

Several hypotheses have been posed to explain interspecific and intraspecific variation in EPP, such as variation in breeding density (Birkhead and Møller 1992), breeding synchrony (Birkhead and Biggins 1987, Stutchbury and Morton 1995), and genetic variability (Petrie et al. 1998). Classic parental investment theory suggests that paternity may be related to male parental care (Trivers 1972). For example, Piper et al. (1997) hypothesized that the need for biparental care in large nonpasserines might favor the evolution of paternity guards that ensure genetic monogamy. Comparisons among closely related species are needed to help distinguish among hypotheses for variation in extra-pair paternity.

Only four species within the highly polygynous grouse (Tetraoninae) are socially monogamous. Of these four, only the genetic mating system of the Willow Ptarmigan (*Lagopus lagopus*) has been assessed. Freeland et al. (1995) found socially monogamous Willow Ptarmigan to have a low (4%) rate of extra-pair paternity.

Like Willow Ptarmigan, the White-tailed Ptarmigan (*L. leucurus*) has highly variable breeding densities (1–4 breeding pairs per km^2) and breeds from the middle of May through the middle of July (Braun et al. 1993, Hannon et al. 1998). Willow Ptarmigan males, however, are unique among grouse in providing extensive parental care. Willow Ptarmigan males defend nest and chicks, and will assume full responsibility for a brood if the female cannot (Martin 1984, Martin and Cooke 1987); yet, paternal care does very little to augment annual production (Martin and Cooke 1987). White-tailed Ptarmigan males defend females during incubation recesses early on, provide less defense as incubation continues, then join flocks late in the incubation period and rarely provide nest or brood defense (Schmidt 1988, K. Martin, pers. comm.). Both Willow and White-tailed Ptarmigan males spend much of their time accompanying their mates before incubation and during incubation recesses (Braun et al. 1993, Artiss and Martin 1995, Hannon et al. 1998, Artiss et al. 1999). Up to 26% of male ptarmigan are unmated "floaters" in some seasons (Hannon and Martin 1996). In this study I examined the genetic breeding system of White-tailed Ptarmigan for comparison with Willow Ptarmigan. I also attempted to assign genetic sires to extra-pair young.

METHODS

Data were collected May–September 1996–1998 from a population of White-tailed Ptarmigan in the Logan Pass area and from 1997–1998 in the Piegan Pass and Morning Eagle Falls areas of Glacier National Park, Montana (48°41′N, 113°43′W). The three study sites were 2–4 km apart with no movement of known individuals among sites (DPB, unpubl. data). I searched the Logan Pass area more thoroughly and more often (once per week) than the other two areas (twice per month). Searches consisted of systematically walking the study area while playing taped male challenge calls during and chick distress calls after the breeding season (Braun et al. 1973) in an effort to observe all individuals in the Logan Pass area.

Social mating status was determined by observation. Males observed with a female prior to or during incubation were considered the putative father of the offspring in the female's clutch. On one occasion, a male was seen flying back and forth between two females at approximately 5-min intervals, apparently guarding them, while they were off the nest during the incubation period. This trio was considered polygynous. Males who were observed alone before 16 July were considered unmated (Choate 1963). Females found before 16 July or brooding chicks within seven days of hatching were considered breeding females (Choate 1963). Because observations were made once weekly on Logan Pass but less often in other locations, I made mating status classifications only at Logan Pass. I assumed that chicks observed with a female were her offspring, due to the lack of evidence for egg dumping in this species (Braun et al. 1993).

I captured adults using a noose-pole (Zwickel and Bendell 1967), banded each with a colored, numbered band, and took three contour feathers as a DNA sample (Pearce et al. 1997). I captured chicks using a large insect net and removed two developing feathers. All chicks in each brood were captured. In three cases where nests were located, I used vascularized eggshell membranes as a source of chick DNA (Pearce et al. 1997). I prepared two feathers from each individual for DNA extraction by removing the vanes, slicing the shaft (calamus and the bottom two-thirds of the rachis) into fourths lengthwise, and then chopping the slices into 5-mm pieces (Pearce et al. 1997). Vascularized chorioallantois egg membranes were removed from the shell and broken into pieces (Pearce et al. 1997). The eggshell membrane or feather pieces from each individual were then ground with an epi-pestle and sterile sand in 500 μL of 2% CTAB solution for DNA extraction (Soltis et al. 1991) and incubated for 2 hr at 65°C. I used two chloroform extractions and precipitated DNA using ammonium acetate and isopropyl alcohol overnight at 0°C. The precipitated DNA was resuspended in 40 μL TE buffer, and 1 μL resuspended DNA was used per PCR reaction.

Three microsatellite DNA loci (LLST1, Piertney and Dallas 1997; LLST3 and LLST7 Piertney et al. 1998) were amplified in 10-μL PCR reactions containing 1 U Sigma Taq DNA Polymerase, 10 mM Tris-HCl (pH 9.0 at 25°C), 50 mM KCl, 1% Triton X-100®, 5% DMSO, 2 mM MgCl$_2$, 0.25 μM each primer, 0.1 mM each dNTP, and 1.5 μCi ^{35}S-labeled dATP. These reactions were conducted in a thermal cycler with an initial denaturation of 2 min at 96°C, followed by 34 cycles of 96°C for 1 min, 2 min at annealing temperature, and 72°C for 2 min. The cycling profile concluded with a 7-min extension at 72°C. Annealing temperatures of 59°C for LLST1 and LLST3 and 60°C for LLST7 were used. Amplification products were visualized on a 6% polyacrylamide gel using autoradiography and scored visually for size using an M13 bacteriophage sequence as a size standard.

For each individual I determined the genotype at

TABLE 1.   White-tailed Ptarmigan demographic data from Logan Pass, Montana 1996–1998, and Piegan Pass and Morning Eagle Falls, Montana, 1997–1998, showing breeding season numbers and extra-pair young (EPY). Mated males includes all males found with a female before 16 July (Choate 1963); unmated males includes all males located alone before that date. Breeding season total includes mated males, unmated males, and females found before 16 July or brooding on Logan Pass within seven days of hatch (Choate 1963). Because Piegan Pass and Morning Eagle Falls were not intensively surveyed, mated males, unmated males, and breeding season totals were not determined for those areas.

Year	Mated males	Unmated males	Breeding females	Breeding season total	Putative fathers known		
					Broods	Chicks	EPY
Logan Pass							
1996	10	6	11	27	5	17	1
					2[a]	7	1
1997	8	5	10	23	4[b]	14[b]	1
1998	6	7	5	18	4	13	0
Piegan Pass and Morning Eagle Falls							
1997					2	8	0
1998					1	5	0
Totals					18	64	3

[a] One male attended two females and was considered the putative father of both broods.
[b] Two females sampled in 1996 produced two broods and six offspring in 1997. These broods and chicks were excluded from the EPY analysis.

each of the three microsatellite loci. Then, using the genotype of each chick and its putative mother, I was able to include or exclude the putative father as the sire. I assigned paternity to the putative father when his genotype was compatible with those of the chicks in the clutch with which he was associated. If the putative male was not the father, I examined all other males in the population for possible paternity. Exclusion probabilities were calculated using allele frequencies at each locus by Cervus software (Marshall et al. 1998). Because some females were not observed with a male before or during incubation, I could not assign putative fathers to their offspring. These offspring were omitted from the results.

RESULTS

During the three years of this study 64 chicks were genetically typed and attributed to both a putative father and mother (Table 1). Thirty-five males were fin-

TABLE 2.   Microsatellite loci, alleles, heterozygosity, and probability of paternity exclusion given the putative mother's genotype, for a population of White-tailed Ptarmigan in Glacier National Park, Montana. The hypervariable loci LLST3 and LLST7 yield a high probability of exclusion. Exclusion probabilities were calculated using Cervus software (Marshall et al. 1998).

MSAT loci	Number of alleles	Average heterozygosity	Probability of exclusion
LLST1	10	0.714	0.628
LLST3	43	0.899	0.908
LLST7	28	0.854	0.849
Total			0.995

gerprinted genetically in the study and classified as mated or unmated each year (Table 1). Total breeding-season birds on Logan Pass decreased during the three years of this study (Table 1). There were 16 socially monogamous pairs and one polygynous trio that produced offspring and for which putative fathers were known (Table 1).

Two ptarmigan pairs with offspring in 1996 had chicks again in 1997. The 1997 broods and offspring (six total) appear in Table 1, but are not included in calculations of extra-pair young (EPY) (below). Neither had EPY in either year.

All three loci were highly polymorphic, with heterozygosities ranging from 0.714 to 0.899 (Table 2). Individual total exclusion power ranged from 0.964 to 0.999 for the three loci combined and the average total exclusion power was 0.995. Of 58 chicks (64 with putative fathers minus 6 from resampled pairs), 55 matched the putative father at all three loci. Alleles of three chicks did not match the putative father at all three loci and were considered extra-pair young (5% of 58 chicks). Three of 18 clutches (17%) contained EPY. One of the EPY occurred in a polygynous trio in 1996 (1 of 7 chicks; 14%), and the other two were found in socially monogamous pairs (2 of 51 chicks; 4%) in 1996 and 1997 (Table 1). One male was cuckolded in two successive years, once as a member of the socially polygynous trio and once with a different mate in a socially monogamous pair.

One chick in a brood found about 30 days after hatching mismatched the attending female at two loci. The chick could not be matched up with any other pair, and may have been a result of egg dumping or after-hatch adoption.

Although all resident males sampled ($n = 35$) were typed at all three loci, none of the three EPY matched

a male at more than two loci; thus, I was unable to assign paternity to any of the EPY.

I observed two extra-pair copulation (EPC) attempts and one within-pair copulation during the three years of this study; all occurred at dusk. During both EPC attempts, an unbanded and unsampled flying male repeatedly landed next to or on a female. The social partner of the female chased the intruder away while vocalizing vigorously. Neither of the EPC attempts resulted in EPY.

DISCUSSION

Males in the population of White-tailed Ptarmigan I studied in Glacier National Park, Montana, rarely lost paternity. This is the second of the four socially monogamous species within the Tetraoninae found to be nearly genetically monogamous (Freeland et al. 1995). Certainty of paternity does not appear to be related to the evolution of male parental care in ptarmigan. White-tailed Ptarmigan males provide little parental care yet have a low rate of extra-pair paternity (4%), similar to Willow Ptarmigan in which males provide comparatively much more care. The lack of a relationship between paternity and parental care is to be expected if the male investment in parental care has no effect on recruitment (Whittingham et al. 1992), which appears to be the case in Willow Ptarmigan (Martin and Cooke 1987).

Male birds are thought to increase their certainty of paternity by assurance techniques such as mate guarding (Birkhead and Møller 1992). This behavior presumably reduces opportunities for females to engage in EPCs. Mate guarding has been shown to be effective in mate removal experiments (Westneat 1994, MacDougall-Shackleton et al. 1996). However, in a meta-analysis of avian paternity studies, Møller and Ninni (1998) found no relationship between the intensity of mate guarding and paternity. Further, many descriptive studies have found a negative relationship between the intensity of mate guarding and paternity (Gowaty and Bridges 1991, Kempenaers et al. 1995, Schleicher et al. 1997). In this study, the intensity of mate guarding was not recorded; however, other studies of White-tailed Ptarmigan have described intense mate guarding prior to incubation and while the female is off the nest during incubation (Schmidt 1988, Artiss and Martin 1995). Freeland et al. (1995) suggested that mate guarding was important in reducing EPP in Willow Ptarmigan. Mate guarding throughout incubation in Willow Ptarmigan might also enhance male reproductive success by ensuring paternity in renesting attempts (Martin 1984) or by enhancing female foraging rates (Artiss et al. 1999).

The efficacy of mate guarding may depend on the physical ability of a male to remain close to his female. High visibility in alpine habitat, the low density of ptarmigan populations, and the sedentary nature of White-tailed Ptarmigan may limit the ability of males or females to engage in EPCs. Territorial ptarmigan males may not be willing to jeopardize the energetic investment in their territory by leaving their mates to seek EPCs themselves (Martin 1984, Hannon and Martin 1992). White-tailed Ptarmigan also do not need to trade off mate guarding for foraging, because they forage alongside their mates.

If male ptarmigan do enforce fidelity upon females through mate guarding, one would expect that males who are socially paired with two females would be less able to guard both mates, and therefore lose more paternity to cuckoldry, than socially monogamous males. Sample sizes for both studies were low, but Freeland et al. (1995) suggested that this was true in Willow Ptarmigan and this may also be true in the present study (the only polygynous trio was cuckolded, whereas the rate of EPY in monogamous pairs was 12% of clutches).

Breeding density has been proposed as an explanation for within and among species variation in EPO (Birkhead 1978, Møller 1987). The density hypothesis suggests that as density increases, so does the accessibility of extra-pair partners. The data presented here lend some support to this hypothesis. From 1996–1998 the number of White-tailed Ptarmigan present on Logan Pass during the breeding season decreased 33% from 27 to 18. Extra-pair offspring found on Logan Pass decreased as well (two in 1996, one in 1997, and none in 1998).

None of the three EPY found in this study could be assigned to any of the 35 resident males (both mated and unmated) sampled. Because mated male White-tailed Ptarmigan respond to tape-recorded vocalizations during the breeding season and unmated males often do not (making them more easily overlooked), it is possible that the EPY were sired by unmated rather than mated males. Unmated males have been found to engage in EPCs in other species, such as Willow Ptarmigan (Martin and Hannon 1988), Tree Swallows (*Tachycineta bicolor*; Barber and Robertson 1999) and Stitchbirds (*Notiomystis cincta*; Ewen et al. 1999). Because female White-tailed Ptarmigan are receptive to intruder males (Martin and Hannon 1988), the potential benefits of engaging in EPCs for mated male ptarmigan may be outweighed by the cost (i.e., lost paternity) of leaving their mates.

In conclusion, this study found a low number of EPY in White-tailed Ptarmigan in Glacier National Park. White-tailed Ptarmigan males provide less parental care than males of the closely related Willow Ptarmigan, yet have a similar rate of EPY. I suggest that extra-pair sexual activity may be constrained by male mate guarding, and that male ptarmigan may be physically able to guard against intruder males due to their high-visibility habitat and the lack of trade-offs such as the need to leave the female to forage.

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