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Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis

Abstract The genetic parentage and pedigrees of 35 litters from 12 family groups of monogamous Alpine marmot (*Marmota marmota*) in the French Alps were analyzed using six hypervariable sequence repeat nuclear loci (microsatellites). All of the members of these family groups were sampled during a 5-year period. Hairs taken directly from animals served as a source of DNA for amplification of the loci. Our results indicate that the genetic mating system of the Alpine marmot is quite different from a strictly monogamous breeding system. Extra-pair paternity occurred in 11 of the 35 litters (31.4%). Of the 134 juveniles typed, 26 (19.4%) could be attributed to extra-pair copulation (EPC). We examine hypotheses which could explain the evolution of EPC and discuss the different patterns of extra-pair mating.

Key words Paternity exclusion · Extra-pair copulation · Monogamy · Hair · *Marmota marmota*

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Introduction

Monogamy, as a mating system (Wickler and Seibt 1983), implies that one male and one female mate exclusively with each other for at least one breeding event (Kleiman 1977; Wittenberger and Tilson 1980). In this mating system, male reproductive success is thought to be limited by the lack of opportunities to gain access to additional mates. Trivers (1972) argued that it would be adaptive for a male to pursue a mixed reproductive strategy by providing paternal care to the offspring of his mate while engaging in extra-pair copulation (EPC) to fertilize extra-pair females. Assessments of the efficiency of EPC are required to evaluate its effects on male reproductive success. If EPCs are successful in fertilizing ovocytes (resulting in extra-pair paternity, EPP), monogamous males that engage in EPC would increase their reproductive success without providing extra-pair paternal care. If extra-pair paternity is significant, the number of young raised by the female mating partner (Vehrencamp and Bradbury 1984) would no longer be an accurate measure of male reproductive success. To better understand the evolutionary consequences of EPC, EPP needs to be quantified.

Most bird species are assumed to be monogamous (Lack 1968) but EPC appears to be widespread among birds (Gladstone 1979; Westneat et al. 1990, Birkhead and Møller 1992 for reviews). The frequency of EPP varies from 0 (e.g., willow warbler *Phylloscopus trochilus*, Gyllensten et al. 1990) to more than 0.5 (e.g., superb fairy-wren *Malurus cyaneus*, Dunn and Cockburn 1996; see Birkhead and Møller 1992 for a review) suggesting that the measure of male reproductive success in monogamous species should be reconsidered.

In mammals, monogamy is restricted to less than 3% of species, and is observed primarily in primates, rodents and canids (Kleiman 1977). EPCs have been described in some species (*Proteles cristatus*, Richardson 1987; *Meriones unguiculatus*, Agren et al. 1989; *Hylobates syndactylus*, Palombit 1994; *H. lar*, Reichard 1995)

However, assessments of monogamy based on genetic data have been performed on only six mammals species (*Rhinolophus sedulus*, Heller et al. 1993; *Peromyscus polionotus*, Foltz 1981; *Peromyscus californicus*, Ribble 1991; *Peromyscus maniculatus*, Ribble and Millar 1996; *Lycaon pictus*, Girman et al. 1997; *Madoqua kirkii*, Brotherton et al. 1997). In all of these studies, EPP was absent or very scarce (Girman et al. 1997).

In the Alpine marmot *Marmota marmota*, a monogamous mating system has been inferred from observations on the social structure (Zelenka 1965; Barash 1976, Arnold 1990; Perrin et al. 1993). The social unit is the family group, which is composed of a resident pair, juveniles, yearlings, and subordinates of 2-, 3- or 4-year-olds. Home ranges may overlap slightly (Allainé et al. 1994) and there are some satellite individuals which live on the periphery of family groups. Although the resident pair defends the territory against intruders, the potential for EPC is, a priori, important because the resident male may be cuckolded by his own subordinate males, by satellite males, and by males of neighboring groups. Arnold (1990) used protein electrophoretic analyses to investigate the occurence of EPP. Only 5% of litters were not sired entirely by a resident male and 2% of juveniles carried alleles not found in the resident male. However, as noted by Arnold, these values may be an underestimate because results were derived from only two informative loci. Further developments in molecular genetics have provided new tools for paternal-exclusion analyses and paternity assessment, including DNA fingerprinting analyses (Jeffreys et al. 1985; Burke 1989; Packer et al. 1991; Ribble and Millar 1996; Travis et al. 1996), random amplified polymorphic DNA analyses (Neveu et al. 1996), and hypervariable microsatellite loci analyses (Morin and Woodruff 1992, Morin et al. 1994; Zhang et al. 1994; Craighead et al. 1995; Fredholm and Winterø 1996; Keane et al. 1997; Petri et al. 1997).

Here, we reexamined the mating system of the Alpine marmot using a nuclear DNA microsatellite method and hair samples (Taberlet and Bouvet 1992; Morin and Woodruff 1996; Taberlet et al. 1997), combined with long-term observations. Microsatellites are short tandem repeats of mono-, di-, tri-, or tetranucleotide sequence units, widely and randomly dispersed throughout eukaryotic genomes, and highly polymorphic (Bruford and Wayne 1993). Major advantages of using nuclear DNA microsatellite analysis include the easy interpretation of gels, Mendelian segregation of alleles and a high mutation rate. We quantified the frequency of EPP to analyze the consequences of EPC on the reproductive success of resident males. The adaptative significance of the occurence of EPC in the Alpine marmot is discussed.

Methods

Field data

The study site is located at an elevation of 2350 m in La Grande Sassière Nature Reserve, Vanoise National Park (French Alps).

Alpine marmot family groups are continuously distributed throughout this area. From 1992 to 1996, 214 different marmots were captured from 12 contiguous family groups using live traps. We also trapped some males from neighboring groups but we were unable to trap satellite males. We marked animals using metal eartags and fur dye for visual identification, and an electronic device (Transpondeur TROVAN) was injected under the neck skin to allow permanent identification of individuals.

Each year, observations were made during the activity period from 10 April to 30 September. Marmots were observed with binoculars and a 20–60× telescope from a distance of 80–200 m between 0800–1200 hours and 1600–2000 (2100) hours. This was done almost every day of the activity period to be sure that we captured all the family group members and to determine the dominant pair and the subordinates of all family groups. Copulations seemed to occur within burrows and were rarely seen, so we have little data on EPC. At the time of emergence, we determined the litter size and all the young were captured in the 48 h when they stay near the natal burrow.

We collected hair samples from all captured animals for genetic parentage analysis. They were stored in individual envelopes and kept dry in our laboratory at room temperature.

DNA extraction

DNA was extracted from ten hairs per individual (Goossens et al., in press) by cutting a 1-cm portion from the root end of the hair and placing it in 400 μl of a 5% Chelex-100 (Bio-Rad) suspension (Walsh et al. 1991). The samples were incubated at 56 °C for 5 h, and then in a boiling water bath for 8 min. Five microliters of each extract was added to each polymerase chain reaction (PCR).

DNA amplification and genetic typing

Six microsatellite DNA loci named SS-Bibl1, SS-Bibl4, SS-Bibl18, SS-Bibl20, SS-Bibl25 and SS-Bibl31 (Klinkicht 1993) (Table 1) were amplified with Ampli Taq Gold using primer sets labelled with FAM, HEX and TET fluorescent dyes in a Perkin Elmer Gene Amp PCR System 9600. Multiplexing on the gel was attempted with compatible microsatellite loci. We multiplexed combinations of three microsatellite primers with sufficiently different size ranges (SS-Bibl1 + SS-Bibl25 + SS-Bibl31, and SS-Bibl4 + SS-Bibl18 + SS-Bibl20). For each individual, amplification of the SS-Bibl loci was carried out in a 25-μl reaction (10 mM Tris-HCl (pH 9.0), 200 mM $(NH_4)2SO_4$, 50 μM each dNTP, 1.5 mM $MgCl_2$, 5 ng BSA, 0.1 U Amplitaq Gold DNA polymerase (Perkin Elmer), 0.5 μM (for FAM) or 0.75 μM (for TET) or 1 μM (for HEX) fluorescent primer, and the same concentration of the non-fluorescent primer). A PCR amplification of 50 cycles was carried out with initial denaturation at 95 °C for 10 min (95 °C for 15 s, 55 °C for 15 s, 72 °C for 30 s). PCR products were visualized on an agarose gel (SeaKem) to detect positive PCRs and to estimate the dilution factor for loading. All positive PCR products were separated in a 6% Long Range gel (FMC) at 2670 V for 2 h 30 min using an ABI PRISM 377 DNA sequencer (Perkin Elmer) with the marker GS350 Tamra. All gels were analyzed using Gene Scan Analysis 2.0. and Genotyper 1.1. software.

Data analysis

The genotype at each of the six loci was determined for each animal. Then, for each litter, the genotype of every young and its dam was used to implicate or eliminate the resident male as the sire. When the genotype of the resident male was compatible with those of juveniles born in the group, we assigned the paternity to the resident male. In this case, we calculated the probability that another male (related or not to the resident) was also compatible with the juveniles' genotypes. For that, we used the formula given in Paetkau and Strobeck (1997). This formula takes into account the mothers' genotypes and allele frequencies for the six loci. If the

Table 1 The six microsatellite loci used for parentage analysis in the Alpine marmot : primer sequences, number of alleles, and observed heterozygosity in our population

Locus	Primer Sequence (forward and reverse)	Number of alleles	Observed heterozygosity
SS-Bibl1	5′-CTGAAGCAGCCATCCAGTA-3′ 5′-TGGTGTTGCCATTGTTCT-3′	7	0.64 $\tau\beta o\delta\psi$
SS-Bibl4	5′-CCTAGGTTCAGTCTTCAACACA-3′ 5′-TGGTGTTGCCATTGTTCT-3′	6	0.52 $\tau\beta o\delta\psi$
SS-Bibl18	5′-ATGGTCATGGAAGGGAAG-3′ 5′-GGCATCTTCACAGTTGATCT-3′	6	0.66 $\tau\beta o\delta\psi$
SS-Bibl20	5′-ATTCTCTAGTCGTTAACAAGAATC-3′ 5′-CACCAGTGAAACTACATACAGTG-3′	5	0.73 $\tau\beta o\delta\psi$
SS-Bibl25	5′-CTCATGACTATGGCAGCC-3′ 5′-AGAACCTTGATTTAGCAGTAG-3′	5	0.41 $\tau\beta o\delta\psi$
SS-Bibl31	5′-TTACACCTTCTCTGGCTCC-3′ 5′-TCTGAGCGGATTGTCTTTAT-3′	4	0.60 $\tau\beta o\delta\psi2$

* F forward and R reverse

resident male was not the father, we examined the subordinate males for possible paternity. Using these methods, we established the pedigree of each family group for each year.

Results

We were able to extract enough DNA to type all 214 individuals sampled. The six microsatellite loci were polymorphic. The percentage of heterozygotes for the six loci varied from 41% (SS-Bibl25) to 73% (SS-Bibl20) (Table 1). Among the 12 family groups followed from 1992 to 1996, 34 litters emerged representing a total of 134 juveniles.

Patterns of parental exclusion

Except in one case (group E in 1995, see below), all of the juvenile genetic profiles were compatible with those of the putative mothers. Of the 134 juveniles typed, 26 (19.4%) had a genetic profile that did not match their putative father and 23 (17.2%) were incompatible with any of the males in their family group. A total of 108 juveniles were assigned to the resident males. The probability of a random male, related or not to the resident, being a potential father was 0.255 and 0.043, respectively. Thus, some males related to the resident (subordinates) could have cuckolded the resident without being identified. In all, 23 litters were entirely sired by the dominant male but in 8 litters, more than 50% of juveniles were a result of EPP.

Mating system

The different types of matings encountered are presented in Table 2. We defined monogamy (Mo) as the case where the resident pair produced all the offspring born in their family group. We distinguished two types of EPP. Within-group EPP (WG-EPP) corresponded to the situation where a subordinate group male may have sired all or some of the juveniles born in his group. In

contrast, extra-group EPP (EG-EPP) corresponded to the situation where all or some juveniles in a group had alleles incompatible with those of the dominant and the subordinate males of the group. In these two latter situations, the dominant females copulated with more than one male and were polyandrous. We classified a mating as promiscuous (Pr) when all the juveniles born in a family group did not have the same father and the same mother. Polygyny (Po) corresponded to the situation where one male sired more than one litter in his group during a single year. We identified 22 cases (66.7%) of monogamy. Among the 11 cases (33.3%) where juveniles were the result of a non-monogamous mating, we found 8 cases (24.2%) of EG-EPP, 1 case (3.03%) of WG-EPP, 1 case (3.03%) of polygyny and 1 case (3.03%) of promiscuity. Promiscuity occurred in group E in 1995 when seven juveniles emerged. Genetic profiles indicated that four of them were compatible with the putative mother. The three remaining juveniles had a profile compatible with that of a subordinate female. Neither of these two litters was sired by only one male. This case of promiscuity raised the number of litters to 35. The case of polygyny was observed in group B in 1993 and has been described elsewhere (Goossens et al. 1996). The resident male of group B copulated with both the resident and a subordinate female. The subordinate female replaced the resident female of group A and gave birth in this group. The resident male of group A accepted her and her offspring. The only case of WG-EPP was observed in group B in 1994. Two males (2- and 3-year-olds) from group C arrived in group B in late 1993 when the resident male was no longer observed. In 1994, the older male became the resident and the younger one his subordinate. The subordinate may have sired three of the five juveniles born in group B in 1994. Multiple paternities involving the resident males were observed in eight of the nine litters where EPP occurred.

Extra-group fathers

We tried to identify the fathers responsible for the eight EG-EPPs among the resident and subordinate males of

Table 2 Group composition, mating type, and proportions of juveniles from extra-pair paternity in the 12 family groups studied (*Gr* family group; *Group composition* number of mature males and mature females in the family group: *Mdo* dominant male, *Fdo* dominant female, *Mad* or *Fad* adult male or female (more than 3 years), *M3* or *F3* 3-year-old male or female, *M2* or *F2* 2-year-old male or female, * dominant male or female changing; *M* mating type: *Mo* monogamy, *Imm* immigration (see text), *Po* polygyny (see text), *EG-EPC* extra-group extra-pair copulation, *WG-EPC* within-group extra-pair copulation, *Pr* promiscuity; *Nj* number of juveniles issuing from extra-pair paternity out of the total number of young by litter

Gr	1992 Male	1992 Female	1992 M	1992 Nj	1993 Male	1993 Female	1993 M	1993 Nj	1994 Male	1994 Female	1994 M	1994 Nj	1995 Male	1995 Female	1995 M	1995 Nj	1996 Male	1996 Female	1996 M	1996 Nj
A	Mdo	Fdo	EG-EPC	2/5	Mdo	Fdo*	Imm	4/4	Mdo*	Fdo	Imm	4/4	Mdo*	Fdo	Mo	0/5	Mdo	Fdo	Mo	0/4
B	1 M3 Mdo	Fdo	Mo	0/4	1 Mad Mdo	1 Fad Fdo	Po	0/6	2 M2 Mdo*	3 F2 Fdo	WG-EPC	3/5	1 M2 Mdo	Fdo	Mo	0/3	1 M3 Mdo	Fdo		
C	1 M2 Mdo	1 F2 Fdo	EG-EPC	3/4	Mdo	Fdo*	EG-EPC	3/4	1 M³ 1 M2 Mdo*	2 F2 Fdo	EG-EPC	3/4	1 M³ 1 M2 Mdo	1 F2 Fdo	Mo	0/2	1 M3	1 F2		
Ch. D	2M2 Mdo	1 F2 Fdo	EG-EPC	1/3	2 M³ 3 M2 Mdo*	1 F2 Fdo	Mo*	0/3	3 M2 Mdo Mdo	1 F3 1 F2 Fdo Fdo	Mo EG-EPC	0/2 1/4	Mdo Mdo	Fdo Fdo	Mo Mo	0/2 0/6	Mdo Mdo	Fdo Fdo	Mo	0/3
E	Mdo	Fdo 1 F2	Mo		Mdo	Fdo 1 F3	Mo	0/4	Mdo	Fdo 1 Fad	Mo	0/4	2 M2 Mdo*	2 F2 Fdo	Pr	4 + 3	1 M3 Mdo*	1 F2 Fdo	EG- EPC	4/4
F	Mdo	Fdo	Mo	0/3	Mdo*	Fdo	Mo*		Mdo	Fdo 1 Fad	Mo	0/5	Mdo	Fdo 1 F3	Mo	0/5	1 M3 Mdo	1 F2 Fdo	Mo	
F					Mdo*	Fdo	Mo	0/3	Mdo	Fdo 1 F2	Mo		Mdo	Fdo 1 F3	Mo		Mdo	Fdo	Mo	
G					Mdo* Mdo	Fdo Fdo	Mo EG-EPC	0/4 2/4	Mdo Mdo	Fdo Fdo	Mo EG-EPC	3/4	Mdo Mdo*	Fdo Fdo	Mo	0/5	Mdo Mdo	Fdo Fdo	Mo	0/3
I							EG-EPC	3/4			EG-EPC	3/4		1 F3							
J					1 Mad 1 M2 Mdo 1 Mad 1 M2	1 Fad 1 F3 Fdo 1 Fad 1 F2	Mo	0/5	1 Mad 1 M3 Mdo* 2 M2	1 Fad 1 F3 Fdo 1 Fad 2 F2	Mo	0/5	Mdo*	Fdo 1 Fad 1 F3	Mo	0/2	1 M2 Mdo*	3 F3 1 F2 Fdo	Mo*	0/2
O													Mdo 1 Mad 2 M2	Fdo 1 F2	Mo	0/2	Mdo*	Fdo	Mo	0/2
R													Mdo 1 Mad	Fdo 1 Fad	Mo	0/4	Mdo 1 Mad	Fdo 1 Fad	Mo	0/2

neighboring groups. About 65% of neighboring groups were trapped. This allowed us to perform 63 tests of paternity exclusion. Only one neighboring male (resident of group G) was compatible with one juvenile of group D in 1994. Although not all of the potential neighboring males were considered, this suggests that resident or subordinate males were not likely to sire juveniles in a neighboring group.

Male reproductive success

We were unable to determine whether the resident males engaged in EPC, i.e., if they adopted a mixed strategy. We were able to identify whether a male was a victim of EPC. We can therefore calculate the percentage of juveniles the resident male sired among the juveniles born in his group. Some resident males were followed for more than 1 year, so we calculated the total percentage of juveniles they sired in their group. The distribution of these percentages (Fig. 1) appeared to be bimodal. Most of resident males (68%) sired all the juveniles born in their group. Some males were occasionally cuckolded and three males sired less than 50% of juveniles born in their group. Two males were systematically cuckolded. The occurrence of EG-EPC did not depend on the presence of subordinate males in the group ($\chi^2 = 0.85$, $df = 1$, $P = 0.36$). Thus, the presence of subordinate males does not seem to decrease the efficiency of mate guarding by the resident male (if it exists). The probability that a resident male was cuckolded in a given year did not depend on the fact that he was present (exact

Fisher test, $P = 0.32$), that he reproduced in the group ($P = 0.29$) or that he was cuckolded ($P = 0.3$) the previous year. But this probability was greater ($\chi^2 = 8.8$; $df = 2$, $P = 0.01$) for males in the valley (10/17) than on south-facing (2/11) and on north-facing (0/6) slopes.

Discussion

Examination of mammalian mating systems using a molecular genetic approach is becoming more common (e.g., Searle 1990; Packer et al. 1991; Ribble 1991; Boellstorff et al. 1994; Morin et al. 1994; Travis et al. 1996; Clapham and Palsbøll 1997). In monogamous mammals, exclusive mating has been confirmed by molecular data for the six species in which a search was undertaken (*R. sedulus*, Heller et al. 1993; *P. polionotus* Foltz 1981; *P. californicus*, Ribble 1991; *P. maniculatus*, Ribble and Millar 1996; *L. pictus*, Girman et al. 1997; *M. kirkii*, Brotherton et al. 1997). Our results indicate that the genetic mating system of the Alpine marmot is quite different from the expected monogamous social breeding system. Only two thirds of resident pairs were found to mate monogamously and EPPs were frequent. The potential for the occurence of EPC was high because resident males could have been cuckolded by their own subordinate males, by satellite males, and by males of neighboring family groups. In the Alpine marmot, Arnold (1990) found that only 5% of litters were not sired entirely by a resident male and 2% of juveniles resulted from EPP. Our estimates were larger (33.3%

Fig. 1 Distribution of the reproductive success of the resident male (percentage of juveniles sired by the resident male in his group) in 12 family groups of Alpine marmots
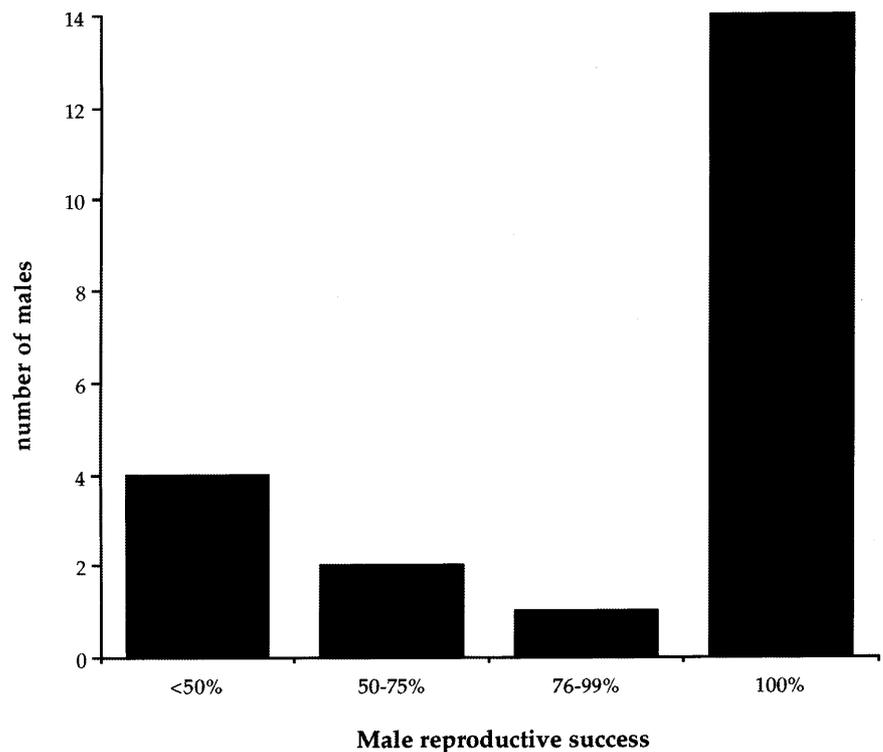
and 19.4%, respectively). Such contrasting results may be explained in two ways. First Arnold's (1990) analysis was based on only two informative loci. Here we used six informative microsatellite loci. Our approach was thus more powerful in detecting EPP. The probability that a random unrelated male or the sibling of the resident male had a genetic profile that would result in an inability to exclude the resident male was only 4.3% and 0.25%, respectively. Second, it is also possible that EPP in our population was more frequent than in the Berchtesgaden population. Indeed, the Berchtesgaden population followed by Arnold (1990) is located at low altitude and family groups were patchly distributed whereas marmots in our population were densely and continuously distributed. The close proximity of family groups may thus offer more opportunities for EPC.

Non-monogamous matings may result in a family group with subordinate females giving birth (as a result of polygynous or promiscuous matings) or in some cases juveniles not being sired by the resident male (as a result of EPC by subordinate group males or extra-group males) or both.

Subordinate females commonly fail in their attempts at reproduction (Zelenka 1965; Bibikow 1968). Mechanisms preventing subordinate females from raising a litter may act at different stages of the reproductive process. Subordinate females may fail to conceive, may reabsorb their embryos, or may lose their offspring as a result of infanticide by the resident females (Rood 1980; Hoogland 1995). Our results show that subordinate females raised 2 of the 35 litters studied. This may occur in particular situations. As previously described (Goossens et al. 1996), a subordinate female may raise a litter when she has the opportunity to do so outside her group. In our case, a resident male mated both with the resident female and with a subordinate. The pregnant subordinate female had the opportunity to give birth in a neighboring group where she was accepted and where she replaced the previous resident female (Goossens et al. 1996). This cryptic situation resulted in only one litter per group, and could only be revealed by the combination of field observations and molecular data. A subordinate female may also raise a litter in her natal group (see also Barash 1976) in particular circumstances. Changes in the resident pair may disturb dominance relationships within a group and may result in unusual mating such as promiscuity. In this situation, two females may give birth in the same family group (group E in 1995). Each of the litters was sired by more than one male. Contrary to some other mammal species (Rood 1980), the subordinate female successfully raised her offspring.

Subordinate group males may cuckold the resident male although they are not expected to reproduce (see Girman et al. 1997). Our results show that subordinate male Alpine marmots are not likely to sire offspring in their group (see also Arnold 1990). Two mechanisms may prevent subordinate males from being successful in their attempts at reproduction. First, the resident male

may preclude access to the resident female either by guarding his mate (Barash 1981) or by inducing physiological suppression of reproduction in subordinates (Arnold and Dittami 1997). Although the resident male attempts to inhibit the reproductive ability of other group males, this inhibition seems to be mainly directed towards non-son subordinate males (Arnold and Dittami 1997). Second, inbreeding avoidance may prevent resident female/subordinate male copulations. In the only case of WG-EPP, the subordinate male which sired some offspring was not related to the resident female but was the brother of the resident male. Thus, these two mechanisms may be complementary in preventing subordinate males from siring offspring in the Alpine marmot.

Extra-group males may also cuckold the resident male. This has been largely documented in birds where percentages of EPP can be significant (Burke et al. 1989; Payne and Payne 1989; Brooker et al. 1990; Morton et al. 1990; Dunn and Cockburn 1996). In the Alpine marmot, the resident male may be cuckolded by neighboring resident males and subordinate males and/or by satellite males. Except for one case, we failed to find extra-group fathers among neighboring resident and subordinate males. More data are required to identify males undertaking EPC but it was clearly apparent that subordinate males did not gain reproductive success through EPC. At this time, we have no evidence that resident males engaged in a mixed reproductive strategy. Satellite males probably try to reproduce by seeking EPC. Whether satellite males adopted an alternative strategy or made the best of a bad situation is still to be investigated.

Why is EG-EPC so high in this population of Alpine marmots ? Several explanations may be proposed. First, the resident males do not control the reproductive functions of extra-group males. Second, resident males may be unsuccessful in guarding their mate from EPC. Our results showed that EG-EPC did not occur preferentially when subordinate males were numerous. Thus the guarding efficiency (if it exists) did not depend on the number of subordinate males in a group. Third, mate guarding may be unsuccessful because the resident female actively solicited EPC and escaped from the resident male. Female solicitation of EPC has been reported in birds (Smith 1988; Heg et al. 1993) and is also well documented among ground squirrels (Belding's ground squirrel, Hanken and Sherman 1981; California ground squirrel, Boellstorff et al. 1994; Columbian ground squirrel, Murie 1995; Gunnison's prairie dog, Travis et al. 1996). Benefits for resident female Alpine marmots engaging in EPC may be of three types. First, resident females may solicit EPC to avoid infanticide. Male takeover of a family group is generally followed by the killing of juveniles by the incoming male (Perrin et al. 1994; Coulon et al. 1995). Females may copulate with males most likely to perpetrate infanticide, i.e., satellite males searching for a territory. All male takeovers that we observed were

followed by the disappearance of juveniles and so it seems that we can discard this hypothesis. Second, females may copulate with extra-group males to increase the genetic diversity of offspring which may enhance female fitness when, for example, selection constraints are unpredictable (Maynard-Smith 1978). This hypothesis predicts that most litters should be multiply sired (Westneat et al. 1990). About 70% of the studied litters were not the result of multiple paternity, thus our results do not support the genetic-diversity hypothesis. Third, the good-gene hypothesis predicts that females may copulate with a male whose genetic quality is superior to that of their partner. By doing so, they can improve offspring viability (Hamilton and Zuk 1982) and/or offspring mating success (Weatherhead and Robertson 1979). Another prediction is that females paired with high-quality males should not engage in EPC whereas females paired with low-quality males should do so. This may result in some litters revealing no EPP and some with a high proportion of EPP. This is consistent with our observations (Table 2). Two attributes of this hypothesis are first, that good-quality males may coexist with poor-quality males which are regularly cuckolded and second, that females should be selective in their choice of copulating partners. Our data on the percentages of potential offspring effectively sired by resident males indicate that some males followed for more than 1 year were never victims of EPP whereas others were systematically cuckolded (Fig. 1). These differences in male reproductive success suggest a disparity in male quality, but we were unable to relate this difference in male quality to their body weight. Other phenotypic indicators of male quality need to be investigated. The occurrence of EPP varied among habitats, and we suspect that males were of better quality on the south-facing slopes, which appeared to be more attractive (Allainé et al. 1994, 1998). Indeed, the two males systematically cuckolded were in the valley and male turnover was low on the south-facing slopes (2 replacements of males out of 11). The low frequency of EPP observed on the north-facing slopes is more probably related to the low density of family groups in this less attractive habitat.

We conclude that genetic benefits are the most likely reason for resident females engaging in EPC (see also Lifjeld et al. 1993; Kempenaers et al. 1992). The extent to which females solicit and control the copulation in the Alpine marmot needs to be investigated.

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