Behav Ecol Sociobiol (2006) 59: 597–605
DOI 10.1007/s00265-005-0086-8

ORIGINAL ARTICLE

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Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice

Received: 17 March 2005 / Revised: 22 August 2005 / Accepted: 1 September 2005 / Published online: 20 December 2005

Abstract Extra-pair paternity (EPP) can be influenced by both social setting and female mate choice. If evidence suggests that females try to obtain extra-pair copulations (EPCs) in order to gain genetic benefits when mated to a homozygous and/or to a related male, females may not be able to choose freely among extra-pair mates (EPMs) as the social mate may constrain female access to EPMs. In this study, we investigated, first, how EPP depended on social setting and specifically on the number of subordinate males in the family group in a highly social and monogamous mammal, the alpine marmot. Second, we investigated how EPP depended on female mate choice for genetic benefits measured as male mate-heterozygosity and within-pair relatedness. Our results reveal, first, that EPP depended on the social setting, increasing with the number of subordinate males. Second, EPPs were related to relatedness between mates. Third, EPMs were found to be more heterozygous than within-pair males. Thus, social setting may constrain female choice by limiting opportunities for EPC. However, after accounting for social confounding factors, female choice for genetic benefits may be a mechanism driving EPP in monogamous species.

Communicated by E. Korpimäki

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Keywords Constrained-female hypothesis · Heterozygosity · Mating system · Microsatellite · Relatedness · Inbreeding · Good genes

Introduction

The occurrence of extra-pair paternities (EPPs) among monogamous species is well documented (for a review, see Griffith et al. 2002) and has led to a distinction between social and genetic mating systems (Birkhead et al. 1987). However, the pattern and the evolutionary causes of EPP are still under investigation (Jennions and Petrie 2000; Zeh and Zeh 2001; Griffith et al. 2002), especially for mammalian species (Wolff and Macdonald 2004).

For EPP to occur, females should have opportunities for extra-pair copulations (EPCs). In highly social and monogamous species, social setting can greatly influence these opportunities. Indeed, the availability of extra-pair mates (EPMs) may depend on the ability of the dominant male to monopolize breeding (Gowaty 1996; Westneat and Stewart 2003). Dominant males may monopolize breeding by controlling their female partner through mate guarding and/or by driving away potential EPMs (Johnsen et al. 1998; Hoi Leitner et al. 1999). Since such potential EPMs are subordinate males, dominant males must expend more effort to monopolize breeding as the number of subordinates increases (Shellman Reeve and Reeve 2000). Thus, when the number of subordinates present in the social group increases, the dominant's control over within-group and extra-group males as well as mate guarding decrease. Consequently, females may get free access to EPMs, and EPP occurrence is expected to increase (Peters et al. 2001; Richardson and Burke 2001; Double and Cockburn 2003).

If the opportunity for EPC exists, females may seek EPC whenever two assumptions are fulfilled (Slagsvold and Dale 1994; Jennions and Petrie 2000). First, the choice of the social mate must have been constrained, leading to the necessity for the female to adjust the quality of its partner. Second, an EPM of sufficiently higher quality than the pair mate must be available. Field studies indicate that females then can actively seek EPC (Westneat and Stewart 2003 for a review), and there is considerable evidence that they do so for genetic benefits (e.g. Kempenaers et al. 1997; Richardson et al. 2001; Foerster et al. 2003). Three main genetic benefits have been proposed:

(a) Female preference for good genes. A female may seek EPC when mated to a male of poor quality, and EPMs should exhibit phenotypic characteristics signalling the possession of good genes.

(b) Female preference for genetic compatibility (Zeh and Zeh 1996, Brown 1997). Assuming that heterozygosity at key or at many loci correlates with survival (e.g. Coulson et al. 1998; Marshall and Spalton 2000; Slate et al. 2000b; Foerster et al. 2003) and with traits favoured in mate choice (Brown 1997; Ditchkoff et al. 2001; Hansson and Westerberg 2002), females may choose dissimilar EPMs to promote offspring heterozygosity (Brown 1997; Foerster et al. 2003). However, females may be unable to assess genetic similarity and may base their choice on average male heterozygosity, a feature that enhances the likelihood of producing competitive heterozygous offspring (Brown 1997).

(c) Female preference for genetic diversity (Williams 1975). In an unpredictable environment, females may benefit from producing genetically different offspring.

Under the latter two hypotheses, we expect that females are more likely to seek EPC when mated to a homozygous and/or to a related male, two features that reduce the likelihood of producing competitive and diverse offspring (Brown 1997).

In this paper, we investigated how EPP depended on the social setting (i.e. number of subordinate males) and on female choice (i.e. male characteristics) in a highly social and monogamous mammal: the alpine marmot *Marmota marmota*. Alpine marmots live in family groups composed of a dominant pair, subordinates, yearlings and juveniles of the year, and all family members share a common home range and hibernate together (Arnold 1990b; Perrin et al. 1993; Allainé 2000). Only one litter is raised in the family group during a given year. The alpine marmot is particularly appropriate for our purpose because—although socially monogamous—EPP is known to occur (Arnold 1990a; Goossens et al. 1998a). Indeed, although dominant females monopolize reproduction (Goossens et al. 1998a) through physiological suppression of subordinate reproduction (Hacklander et al. 2003), dominant males are unable to monopolize breeding, and EPP occurs in about one third of litters (Goossens et al. 1998a). Finally, heterozygosity at the set of microsatellites studied positively correlates with juvenile survival, especially under harsh conditions (Da Silva et al., in press).

Here, we first re-examined the genetic mating system of the alpine marmot using 12 polymorphic microsatellite loci. Second, we investigated whether the number of subordinate males within the family groups was a determinant of EPP. Third, we analysed the pattern of EPM choice. Because no correlation was found between male characteristics and the probability of being cuckolded (Goossens et al. 1998a), we hypothesised that females did not seek EPC for good genes, and tested the predictions that (a) EPP should be more frequent when the within-pair male is homozygous and/or related to the female and (b) extra-pair fathers should be more heterozygous and/or less related to the female. Fourth, we investigated whether subordinate males—either related or not related to the dominants—sired extra-pair young.

Materials and methods

Study site and field methods

The study site was located at 2,350 m a.s.l. in La Grande Sassière Nature Reserve, Vanoise National Park (French Alps, 45°29′N, 6°59′E). It covered 40 ha of open meadows characterized by alpine vegetation.

From 1990 to 2002, alpine marmots were caught from the beginning of April to the end of July for a minimum of 45 days a year. Marmots were trapped using two-door, live-capture traps baited with dandelion *Taraxacum densleonis* and placed near the entrance of the main burrow of each group, allowing captured individuals to be assigned to family groups. Once caught, individuals were tranquillized with Zolétil 100 (0.1 ml kg^{-1}) and individually marked. All individuals received a numbered ear tag and a transponder (model ID100, Trovan, Germany) for permanent individual recognition. In addition, a piece of coloured plastic was attached to one ear and the fur was dyed for rapid identification in the field. For genetic parentage analysis, hair samples (before 1998) and skin biopsies made using a biopsy punch (after 1998) were collected on all trapped individuals.

The composition of 20 family groups was assessed from capture–recapture data and from intensive observations with 10×50 binoculars and 20×60 telescopes from a distance of 80–200 m, depending on the topography. On average, each group was observed 1 h/day for a minimum of 30 h/year. One-hour sessions were randomly distributed during periods of activity, from 8.00 a.m. to 12.00 a.m. and from 5.00 p.m. to 9.00 p.m. For each group, the number of yearlings, 2-year-olds and adult individuals of each sex and their social status were recorded. Individuals were classified as yearlings, 2-year-olds or adult individuals from their size. Finally, scent-marking behaviour (Bel et al. 1999) and aggressive interactions allowed us to identify dominant individuals. The date and the size of litters emerging from the natal burrow were carefully monitored from additional daily observations.

Paternity analysis

Details of the DNA microsatellite characteristics and methods are given in Goossens et al. (1998a), Hanslik and Kruckenhauser (2000) and Da Silva et al. (2003) and are only briefly presented here. Two hundred and fifty-

Table 1 Characteristics of the 12 microsatellites used in the parentage analyses

Locus	SS-Bibl1		SS-Bibl4		SS-Bibl8		SS-Bibl20		SS-Bibl31		MS45		MS47		MS53		Ma001		Ma018		Ma066		Ma091		Across all loci Individuals typed for		
	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	Allele	Frequency	5 loci	8 loci	12 loci
	100	0.15	175	0.01	138	0.01	206	0.01	167	0.46	109	0.37	178	0.03	135	0.14	306	0.11	296	0.20	235	0.59	163	0.12			
	102	0.19	179	<0.01	142	<0.01	208	0.23	169	0.31	111	0.57	182	0.18	143	0.47	308	0.61	298	0.80	245	0.41	171	0.15			
	104	<0.01	187	<0.01	144	0.35	216	0.38	171	0.19	113	0.06	184	0.21	145	0.39	310	0.28					173	0.05			
	106	0.50	189	0.17	146	0.14	218	0.30	173	0.04			186	0.19									176	0.19			
	108	<0.01	191	0.69	148	0.37	220	0.09					188	0.36									178	0.37			
	112	0.12	193	<0.01	150	0.13							190	0.02									180	<0.01			
	114	0.04											192	<0.01									182	0.12			
Number of individuals typed	499		496		499		499		499		246		245		246		98		98		98		98		499	246	98
Average exclusion probability	0.447		0.272		0.457		0.457		0.385		0.249		0.536		0.319		0.273		0.134		0.184		0.577		0.926	0.979	0.995

Average exclusion probability refers to the probability of excluding a randomly chosen candidate parent from parentage of an arbitrary offspring, given the offspring and mother genotypes

three individuals were typed at five microsatellite loci: SS-Bibl1, SS-Bibl4, SS-Bibl18, SS-Bibl20, SS-Bibl31 (Klinkitch 1993); 148 individuals trapped more recently were typed for the original five, plus three additional microsatellite loci: MS45, MS47, MS53 (Hanslik and Kruckenhauser 2000); and the last 98 individuals trapped after 2000 were typed for the previous eight and four more loci: Ma001, Ma018, Ma066, Ma091 (Da Silva et al. 2003). The characteristics of the microsatellites (Table 1) were obtained for all typed individuals with CERVUS 2.0 (Marshall et al. 1998; Slate et al. 2000a). Tests of Hardy–Weinberg equilibrium and of linkage disequilibrium were performed using GENEPOP 3.3 (Raymond and Rousset 1995) on dominant adults to avoid bias due to family structure and on all cohorts pooled to ensure adequate sample size (N=69 for SS-Bibl8, SS-Bibl4, SS-Bibl31, SS-Bibl20 and SS-Bibl11; N=31 for MS45, MS47 and MS53; N=11 for Ma001, Ma018, Ma066 and Ma091). They neither departed from Hardy–Weinberg equilibrium (all ps>0.05) nor showed linkage disequilibrium (all ps>0.05).

Genotyping allowed us to confirm maternity by the dominant female in each case and then to test if the dominant male was the sire. If no allelic incompatibility was observed between the genotype of a young and that of the dominant male, the young was assigned to the dominant male and was considered a within-pair young (WPY). For 16 litters (representing 28 young), some of the young could also be assigned to a subordinate male. However, since all young of the litter can be assigned to the dominant male, we considered these young as WPY for the sake of parsimony. We excluded the dominant as the father, and we considered the young as extra-pair young (EPY) if at least one allelic incompatibility was recorded. The EPY genotype was then compared to the genotype of all sexually mature males of the population. We then distinguished two types of EPY. A within-group EPY had a genotype compatible with the genotype of a subordinate male in the group. An extra-group EPY had a genotype incompatible with those of all subordinate males of the family group. Consequently, the true father of an extra-group EPY may be identified or unknown. Litters composed only of WPY were recorded as within-pair litters, those composed only of EPY were extra-pair litters, and those containing both WPY and EPY were mixed litters.

Although many exclusions of paternity were based only on one difference between the genotype of the young considered and its potential father (Fig. 1), we can be confident in paternity assignments for several reasons. We were sure not to misclassify a young as within-pair when it was a true EPY because the average probability of excluding a male as the father given that the mother was known was high, varying from 0.926 when considering individuals typed at five loci to 0.995 for individuals typed at 12 loci (Table 1). We can also be confident that we did not misclassify a young as extra-pair when it was in fact a true WPY. Indeed, we can discard the possibility of genotype error, as genotyping individuals using DNA extracted from hair has been proven to give highly reliable

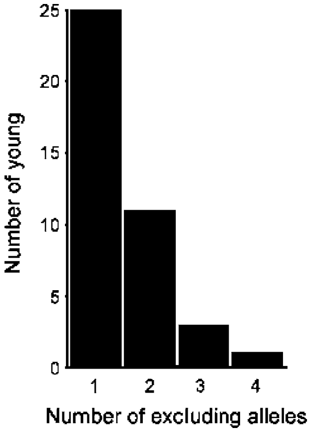

Fig. 1 Distribution of the number of EPY alleles that did not match the genotype of the putative father

and repeatable genetic profile for this species, with genotyping error due to null allele and false allele occurring at a rate below 0.002% (Goossens et al. 1998b). The absence of null alleles was further confirmed by the fact that none of the dominant females was excluded as the mother of its putative offspring (235 mother–offspring pairs). Finally, even if the occurrence of a novel allele may also result from mutation processes, the microsatellite loci average mutation rate, estimated to be 1.67×10^{-4} per generation in *M. marmota* (Rassmann et al. 1994), cannot explain the high number of EPY observed in our study (Table 2). Indeed, given the number of offspring typed and the number of loci for which they were typed, only 0.5 offspring would be expected to result from mutation.

Individual genetic diversity and pairwise relatedness

Since not all individuals were typed for the same number of loci, we used standardized individual heterozygosity (SH) measured as the proportion of heterozygous loci divided by mean heterozygosity of typed loci (Coltman et al. 1999). We used IDENTIX 1.0 software (Belkhir et al. 2002) to compute three estimators of relatedness: Queller and Goodnight's estimator (Rqg, Queller and Goodnight 1989), Lynch and Ritland's estimator (Rlr, Lynch and Ritland 1999) and Identity (I, Belkhir et al. 2002). We present only results with Queller and Goodnight's estimator because estimates of the three estimators were very close (Rqg vs I: $r=0.94$, Rqg vs Rlr: $r=0.89$ Rlr vs I: $r=0.81$) and the results found with the two other estimators were similar.

Table 2 Distribution of the different kinds of offspring among the different types of litters

Young from	WPY	EPY		Total
		WG-EPY	EG-EPY	
Within pair litter	161 (47)	–	–	161 (47)
Mixed litter	38 (18)	4 (2)	25 (16)	67 (18)
Extra pair litter	–	6 (2)	1 (1)	7 (3)
Total	199 (65)	10 (4)	26 (17)	235 (68)

Numbers of litters are given in brackets

WPY Within-pair young, *EPY* extra-pair young, *WG-EPY* within-group extra-pair young, *EG-EPY* extra-group extra-pair young

Characteristics of dominant pairs

We calculated and compared the relatedness of all possible pairs in the population (excluding two-year-old individuals because they rarely reproduced—one case out of 224 in 12 years) to the relatedness of the observed dominant pairs. The same individuals occurred in different pairs, and therefore, pairs could not be assumed to be independent. We therefore bootstrapped the males within years 2,000 times. We used the repetitions of a given male between years since turnover of individuals between years was high and possible pairs differed greatly between years. Bootstrapping males instead of males within years gave similar results. We then compared the mean relatedness of observed dominant pairs and of possible pairs obtained from each bootstrap sample.

We used linear mixed models to compare heterozygosity between dominant and potentially reproductive males (Pinheiro and Bates 2000). Heterozygosity was the response variable; year, type of individual (dominant or potentially reproductive) and their interaction were fixed terms; and the individual was the random factor since some individuals were present in several years. Heterozygosity was log-transformed to satisfy the assumption of homogeneity of variance.

Modelling extra-pair paternity

We investigated the effect of fixed terms on the occurrence of EPP. To account for repeated measures (17 pairs were present for 2–5 years in the dataset), we used generalized estimating equations (GEE) (Diggle et al. 2002). This procedure is likely to be more robust (as compared to generalized mixed models) because it makes broad hypotheses about data structure, and is particularly adapted to departures from normality and small sample sizes within clusters (Carlin et al. 2001). Thus, we used GEE (Liang and Zeger 1986; Zeger and Liang 1986) with the pair as the clustering factor. We chose an exchangeable correlation matrix specifying the same correlation between all observations of a same cluster (Horton and Lipsitz 1999). We used GEE with the same link and variance function as in a logistic regression (i.e. logit link and variance given by a binomial distribution) to examine the effects of the number of subordinate males in the family group, within-pair relatedness, male-mate standardized heterozygosity and their interactions on the occurrence of EPP. The significance of fixed terms was assessed using the robust *z* statistics of parameter estimates (Diggle et al. 2002).

Comparison between pair and extra-pair mates

We were able to identify nine EPMs. This allowed us to investigate whether subordinate males sired EPY and to test whether cuckolded males were more homozygous and/or more related to their females than EPMs. For this, we considered all cases where at least one EPY had been identified and both parents and EPM were known. As the sample was very small (N=9), we used non-parametric Wilcoxon paired and binomial tests.

All statistical analyses were performed using R 1.8.1 software and the gee library (R Development Core Team 2003). Unless otherwise stated, all tests were two-tailed, the level of significance was set to 0.05, and parameter estimates are given ±SE.

Results

Genetic paternity analysis

Thirty-six (15.9±2.3%) of the 235 offspring were extra-pair, and 21 (30.9±5.6%) litters contained at least one EPY (Table 2). The mean number of EPY in these litters was 1.71±1.31, with 47.6±10.9%, 33.3±10.3% and 19.1±8.6% of the litters containing one, two and three EPY respectively. The number of EPY per litter was not randomly distributed (i.e. did not follow a Poisson distribution) either among all litters (Kolmogorov–Smirnov test: χ^2=9.56, df =3, p=0.02) or among litters containing at least one EPY (Kolmogorov–Smirnov test: χ^2=51.86, df=2, p<0.001).

No litters were fathered by more than two males. Among the 21 litters containing EPY, 18 (85.7±7.6%) were fathered by two males, one of which was always the dominant male (Table 2). The three (14.3±7.6%) remaining litters were exclusively fathered by an extra-pair male. Nevertheless, the three totally cuckolded dominant males sired young in other years.

Characteristics of dominant pairs

The mean genetic relatedness between partners within dominant pairs (0.214, CI 95% [0.212; 0.216]) was significantly higher than between possible partners in all possible pairs (0.009, CI 95% [0.008; 0.010]), the difference in relatedness between dominant pairs and possible pairs obtained from bootstraps being 0.205 (CI 95% [0.203;0.207]). The mean heterozygosity of dominant males (1.29±0.37) did not differ (χ^2=422.56, df=414, p=0.35) from the heterozygosity of other reproductive males in the population (1.06±0.35).

Modelling extra-pair paternity

Table 3 Generalized estimation equation models showing the effects of terms on the occurrence of EPP

Variable	Coefficient	Standard error of coefficient	p value
Number of subordinate males	0.534	0.260	0.039[a]
Male heterozygosity	−1.345	1.079	0.213
Relatedness of pair	1.841	2.705	0.496
(Relatedness of pair)^2	7.175	2.316	0.002[a]

All first-order interactions were omitted because they were not significant

[a] Significant values at the 0.05 level

Only families in which both parents and all offspring were known and typed were considered. Thus, the dataset included 322 individuals (87 adults and 235 offspring born to 68 litters, Table 2). The occurrence of EPP increased with the number of subordinate males in the family group; no EPP occurred when subordinate males were absent from the group, while nearly all males were cuckolded when more than four subordinate males were present. The occurrence of EPP depended on a quadratic effect of relatedness with the sexual partner. Consequently, EPP were frequent when relatedness was either very high or very low and reached a minimum when relatedness equalled to zero (Table 3, Fig. 2). The occurrence of EPP did not depend on male heterozygosity (Table 3).

Who sired EPY?

No male from a neighbouring group, regardless of social status, was identified as an EPM. Of the nine identified EPMs, six were subordinate group-members and three were transient individuals. Subordinate EPMs were not related to the dominant female or the dominant male, except in one case in which the brother of the dominant

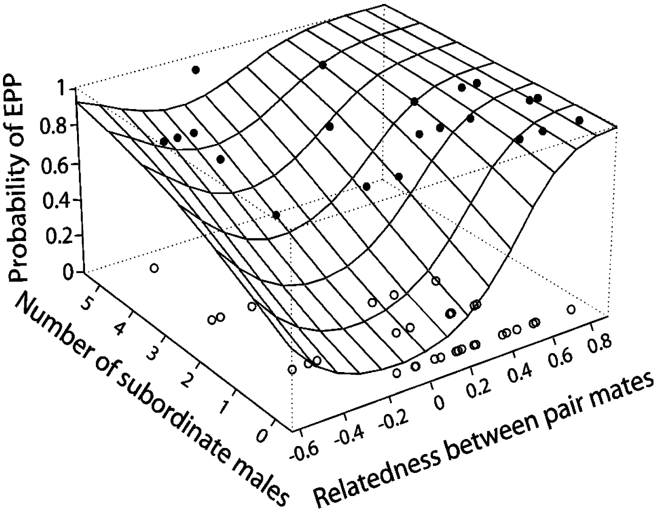

Fig. 2 Occurrence of EPP as a function of the number of adult subordinate males in the family group and relatedness between the pair mates. The *black circles* represent observed data greater than predicted values; the *open circles* represent observed data lower than predicted values and the *surface* represents the fitted model

male sired several offspring. Among the 36 EPY from complete families, 10 (27.8±7.5%) were born to within-group EPMs and 26 (72.2±7.5%) were inferred to be born to extra-group EPMs. Four (19.0±8.6%) of the 21 litters containing at least one EPY were fathered by a within-group subordinate male, and 17 (81.0±8.6%) were fathered by a transient individual (Table 2).

Comparison between pair and extra-pair mates

The nine EPMs we identified were not less closely related to the female than the within-pair males (EPM median=−0.19 vs within-pair mate [WPM] median=0.04, z=0.24, N=9, p=0.81; binomial test: $n_{\text{successes}}$=3, N=9, p=0.51), nor were they more likely to be optimally related to the female (with a relatedness close to 0) than the pair-male (absolute value of the difference between the pair and 0: EPM median=0.27 vs WPM median=0.41, z=0.24, N=9, p=0.81; binomial test: $n_{\text{successes}}$=4, N=9, p=1). However, EPMs were more heterozygous than WPMs (EPM median=1.35 vs WPM median=0.67, z=2.55, N=9, p=0.01; binomial test: $n_{\text{successes}}$= 9, N=9, p=0.004).

Discussion

Genetic mating system

Our results are consistent with Goossens et al. (1998a) and confirm that the genetic mating system of the alpine marmot clearly departs from that expected in a monogamous social system. Although monogamy predominates, polyandry is not rare and EPP often occurs (30.9±5.6% of litters contained EPY, and 15.9±2.3% of young were EPY).

Social setting and EPP

Among monogamous mammals, social setting and particularly the presence of subordinate males may determine the rate of EPP. Indeed, EPP is rare among species living in solitary pairs (*Peromyscus californicus*, Ribble 1991; *Rhinolophus sedulus*, Heller et al. 1993; *Madoqua kirkii*, Brotherton et al. 1997; *Hypogeomys antimena*, Sommer and Tichy 1999; for a counter-example, *Proteles cristatus*, Richardson 1987) but frequent among species living in extended families (*Peromyscus polionatus*, Foltz 1981; *Canis simensis*, Sillero-Zubiri et al. 1996; *Lycaon pictus*, Girman et al. 1997; *Cheirogaleus medius*, Fietz et al. 2000).

Our results confirm that social setting influences EPP in the alpine marmot. Specifically, in our study, EPP rarely occurred when few subordinate males were present. However, as the number of subordinates increased, EPP occurrence increased (see also Arnold et al. 1994). Dominant males may reduce EPP occurrence by preventing female access to EPMs (Peters et al. 2001; Richardson et al. 2001; Double and Cockburn 2003). Preventing access to EPMs can be achieved through both direct control of potential EPMs (i.e. its own subordinates, dominant or subordinate males of neighbouring groups, and transient individuals, Slagsvold and Dale 1994) and mate guarding (Johnsen et al. 1998; Hoi Leitner et al. 1999; Shellman Reeve and Reeve 2000).

In alpine marmots, the dominant male exerts some control of subordinates' reproduction by suppressing their reproductive functions through aggressive behaviour (Arnold and Dittami 1997). We can therefore tentatively conclude that as the number of competitors within a family increases, dominant males have to expend more effort to monopolize breeding (Shellman Reeve and Reeve 2000) and that consequently, the probability that a subordinate reproduces increases. However, subordinate males rarely sired EPY in this study—only 5.9±2.8% of litters and 4.3±1.3% of young were fathered by a subordinate male of the cuckolded dominant (see also Arnold 1990a, Arnold et al. 1994, Goossens et al. 1998a)—and EPP was mainly due to extra-group males. We therefore suggest that as the number of subordinate males increased, dominant males expended more time and energy keeping control over subordinates and consequently lost control over males from outside the family and/or became unable to guard their mate (mate guarding being costly, Komdeur 2001; Matsubara 2003; Plaistow et al. 2003). This hypothesis is all the more plausible because subordinate males only seldom participate in the defence of the territory in alpine marmots (Arnold and Dittami 1997). Males from outside the family may therefore not encounter any greater difficulty entering a territory as the number of subordinate males increases.

Dominants and subordinates of neighbouring groups were never identified as EPMs, confirming the control of subordinates by dominants. Because we trapped virtually all the dominants of the study site, we can reasonably conclude that dominant males do not engage in EPC. Dominant males likely face a trade-off between ensuring paternity and territory defence within their own family and seeking EPCs. It seems that seeking EPC and being dominant are mutually exclusive strategies. Transient individuals therefore appear to be the best candidates to sire EPY, as suggested by Arnold et al. (1994). In agreement with this hypothesis, transients sired 11.6±2% of young in no less than 25±5.2% of litters.

In the alpine marmot, the presence of subordinate males during hibernation increases survival of both offspring (Arnold 1990b; Allainé et al. 2000; Grimm et al. 2003; Allainé and Theuriau 2004) and dominants through social thermoregulation (Arnold 1990b). The presence of subordinate males thus increases the fitness of the dominant male (usually the father of the offspring). Because subordinate males only warm related offspring (Arnold 1993), Arnold and Dittami (1997) concluded that subordinates related to the dominant male should preferentially benefit from staying incentive (reproduction through EPC, Emlen 1982). Surprisingly, among the few subordinate males that sired EPY within their family group, only one was related to the dominant male, the others being unrelated to either the dominant male and/or the dominant female. Three hypotheses may explain this pattern. First, subordinate dispersal entails high costs (Arnold 1993; Frey-Roos 1998) that are enhanced by the high density of our study population. Even if dominants have an interest in keeping subordinate males within the group, the strength of ecological constraints may allow reproductive concession to be null for all subordinates (Verhencamp 1983). Second, if dominant males have a complete control of reproduction (optimal skew models), reproduction of related subordinates should be more heavily suppressed than for unrelated males (Kokko and Johnstone 1999; Reeve and Emlen 2000). Third, reproductive concessions made by dominant males may contradict female mate choice, leading to the absence of reproduction of the dominant female with subordinate males.

Nevertheless, participation of subordinate males to EPP may have been underestimated. Indeed, when the dominant male and a subordinate male could both be assigned as the father of a young, we assigned preferentially the young to the dominant male in our paternity analysis. Consequently, we may have slightly underestimated both the level of EPP and the participation of subordinates, especially those highly related to the dominant male and thus sharing many alleles with him (brothers and sons).

Female mate choice and EPP

Thus, when social setting allows EPCs, females may engage in such copulations whenever two assumptions are fulfilled. First, the choice of the social mate must have been constrained, leading to the necessity for the female to adjust the quality of its partner through EPP (Slagsvold and Dale 1994; Jennions and Petrie 2000). Second, an EPM of sufficiently higher quality than the pair mate must be available (Shellman Reeve and Reeve 2000).

In the alpine marmot, female choice is likely to be constrained. Indeed, as in other territorial species where social status determines access to reproduction (e.g. Calf et al. 2003), female alpine marmots compete over territories rather than mates and mate with any male reaching dominance, even at the cost of their reproduction (infanticide as Bruce effect being common in alpine marmots; Coulon et al. 1995; Hacklander and Arnold 1999). Because subordinates become dominant in their natal territories or in the immediate neighbourhood in 22 and 53% of territories, respectively, (Frey-Roos 1998), relatedness between pair mates and heterozygosity of pair males may result more from dispersal pattern and determinism of dominance than from female choice. Thus, engaging in EPC could be a way for female alpine marmots to adjust the quality of the sexual partner.

Contrary to our prediction, EPP did not increase linearly with social mate heterozygosity or with relatedness between pair mates. Rather, our results suggest that female alpine marmots may engage in EPC to choose an EPM with an intermediate level of genetic similarity, allowing her to produce young having an optimal inbreeding/outbreeding level. Similar findings have been reported for pied flycatchers, *Ficedula hypoleuca* (Rätti et al. 1995). Thus, females avoid the adverse effects of inbreeding (Ralls et al. 1986, Blouin and Blouin 1988), but also avoid excessive outbreeding to keep locally adapted combinations of genes (Price and Waser 1979, Shields 1983). Evidence of inbreeding avoidance are numerous in alpine marmots. In our study population, testosterone levels of subordinate males decreased with dominant female relatedness but not with dominant male relatedness (Magnolon 1999), a pattern related to inbreeding avoidance also found in *Microtus ochrogaster* (Carter et al. 1986) and *Peromyscus leucopus* (Wolff 1992). Further, dispersion rates of subordinate females increased when they were related to the dominant male (Magnolon 1999). Finally, only one case involving a mother–son pair has been observed in 12 years of study, implying that incestuous mating is avoided.

The fact that females may engage in EPC to avoid inbreeding reconciles the expectation of Arnold and Dittami (1997), i.e. that sons of the dominant male are the best EPM candidates because their reproductive functions are not suppressed, with our results showing that the few subordinate males that sired EPY were not the sons of the dominant male. Indeed, whether dominant males conceded reproduction to their sons or not, dominant females may avoid mating with sons of the dominant male if they are relatives. Since subordinate males of a family group have a high probability of being the sons of the dominant female, due to the low turnover of females (mean residency 5.48± 3.41 years, unpublished data), avoidance of mating with close relatives could greatly reduce the probability of subordinate males to be involved in EPP. Female choice for inbreeding avoidance may thus be an alternative explanation for the low percentage of subordinates and the high percentage of transient individuals that sired EPY, reconciling the observed pattern with the observation of Arnold and Dittami (1997) that reproductive inhibition by the dominant male is mainly directed towards non-sons.

Even if few subordinate males not related to the dominant female and a majority of transient individuals probably originating from distant populations sired EPY, the relatedness of EPM to the female was no closer to the optimal level than the relatedness of WPM. However EPMs were significantly more heterozygous than WPMs. It is possible that the comparison was done with a small sample, not representative of the social status of EPMs. Indeed, in this sample, 66.7 and 33.3% of individuals were subordinates and transient individuals, respectively, compared to 1.9 and 98.1% among all EPMs. Clearly, more data are needed to compare both the heterozygosity of EPMs and WPMs and the relatedness of EPMs and WPMs to the dominant female.

In conclusion, EPP did not occur (a) when the availability of a high-quality EPM was constrained either directly by mate control or indirectly by dominant male control of males of higher quality (i.e. in groups with few subordinate males and when the female was already paired to an optimally related male) and (b) when the necessity for EPP did not exist (i.e. when the female was already paired to an optimally related male). Therefore, female choice may interact with dominant male control of reproduction to drive EPP. We suggest that the social setting, particularly the number of subordinate males within alpine marmot family groups, contrains opportunities for EPC not by limiting the control of subordinates but by reducing the ability of the dominant male to control his mate and extra-group males. Further, we suggest that seeking EPC may be a mean by which female marmots can adjust the quality of their sexual partner and that female alpine marmots likely search for genetic benefits. However, to fully accept this genetic quality hypothesis and to further assess the relative importance of relatedness and heterozygosity in female mate choice, a comparison of EPMs vs WPMs, which accounts for potential confounding social factors, is required. Finally, following the advice of Westneat and Stewart (2003), we advocate intensive behavioural field observations to determine the extent to which males can control female sexual activities and the extent to which females solicit EPC.

Acknowledgements We thank all students involved in the trapping of alpine marmots at La Sassière. We would also like to thank Joanna Setchell and Joss Milner for editing the English. We are grateful to Dan Blumstein and David Westneat for their constructive comments on earlier version of the manuscript. Thanks are finally extended to authorities of the Vanoise National Park for granting us permission to work in La Grande Sassière Nature Reserve. Financial support was received from CNRS (France) and the Région Rhônes-Alpes (XI plan Etat-Région). The experiments conducted comply with current French laws.

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