

# Sociality, mating system and reproductive skew in marmots: evidence and hypotheses

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## Abstract

Marmot species exhibit a great diversity of social structure, mating systems and reproductive skew. In particular, among the social species (i.e. all except *Marmota monax*), the yellow-bellied marmot appears quite different from the others. The yellow-bellied marmot is primarily polygynous with an intermediate level of sociality and low reproductive skew among females. In contrast, all other social marmot species are mainly monogamous, highly social and with marked reproductive skew among females. To understand the evolution of this difference in reproductive skew, I examined four possible explanations identified from reproductive skew theory. From the literature, I then reviewed evidence to investigate if marmot species differ in: (1) the ability of dominants to control the reproduction of subordinates; (2) the degree of relatedness between group members; (3) the benefit for subordinates of remaining in the social group; and (4) the benefit for dominants of retaining subordinates. I found that the optimal skew hypothesis may apply for both sets of species. I suggest that yellow-bellied marmot females may benefit from retaining subordinate females and in return have to concede them reproduction. On the contrary, monogamous marmot species may gain by suppressing the reproduction of subordinate females to maximise the efficiency of social thermoregulation, even at the risk of departure of subordinate females from the family group. Finally, I discuss scenarios for the simultaneous evolution of sociality, monogamy and reproductive skew in marmots. © 2000 Elsevier Science B.V. All rights reserved.

*Keywords:* Reproductive skew; Sociality; Monogamy; Polygyny; Marmots

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## 1. Introduction

In mammals, social monogamy is rare (less than 3% of species, Kleiman, 1977), and mainly found among canids (Kleiman and Eisenberg, 1973), primates (Rutberg, 1983), rodents (Elwood,

1983) and small ungulates (Dunbar, 1984). The evolution of social monogamy in mammals has been widely debated (Kleiman, 1977; Wittenberger and Tilson, 1980; Van Schaik and Dunbar, 1990; Mock and Fujioka 1990), but may be caused by females being solitary and occupying exclusive ranges rather than by the need for paternal care (Komers and Brotherton, 1997). Female

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spacing may well explain social monogamy in small ungulates (e.g. Kirk's dik-dik *Madoqua kirkii*, Komers, 1996) and in small rodents that live in stable pairs. Note that strict genetic monogamy is generally found in these species (Kirk's dik-dik, Brotherton et al., 1997; California mouse *Peromyscus californicus*, Ribble, 1991; oldfield mouse *P. polionotus*, Foltz, 1981; horse-shoe bat *Rhinolophus sedulus*, Heller et al., 1993). However, there is a situation where female overdispersion cannot be invoked to explain social monogamy in mammals. Indeed, in some mammal species, the basic social unit is the family, where sexually mature individuals are associated with a dominant breeding pair (alpine marmot *Marmota marmota*, Perrin et al., 1993a; Ethiopian wolf *Canis simensis*, Sillero-Zubiri et al., 1996; dwarf mongoose *Helogale parvula*, Rood, 1980; Creel and Waser, 1991; African wild dog *Lycaon pictus*, Frame et al., 1979). Some of these sexually mature individuals do not reproduce, but help parents in rearing young. These species are generally considered as cooperative breeders (Solomon and French, 1997). Note that extra-pair paternity has been described for these species (alpine marmot, Arnold, 1990b; Goossens et al., 1998; Ethiopian wolf, Sillero-Zubiri et al., 1996; dwarf mongoose, Keane et al., 1994).

Whenever individuals live in stable social groups, opposing forces of competition and cooperation may lead to reproductive skew (Vehrencamp, 1983). The degree to which reproduction is skewed in social groups may have profound consequences on the mating system and on the social structure of species. Indeed, complete skew in reproduction leads to social monogamy whereas shared reproduction permits forms of social polygamy. In these types of social structures, understanding the evolution of social monogamy requires an understanding of the evolution of reproductive skew. Two theories have emerged to explain the evolution of reproductive skew in social groups. First, the "Optimal Skew Hypothesis" (OSH) suggests that in each group, a dominant individual is able to manipulate the reproduction of subordinates to maximise its own inclusive fitness (Vehrencamp,

1980, 1983). Subordinate individuals are expected to leave the social group if they can maximise their fitness by leaving. However, if group living confers an advantage on the dominant individuals, they are expected to concede just enough reproduction to subordinates to retain them in the group (the staying incentive, Reeve and Ratnieks, 1993). Alternatively, the "Limited Control Hypothesis" (LCH) suggests that dominant individuals have incomplete control of the reproduction of subordinates (Clutton-Brock, 1998). The respective share of reproduction for subordinates and dominants may be then determined by a "tug-of-war" within the social group and may depend on their relative fighting ability.

Marmots provide an excellent taxon to discuss the evolution of reproductive skew. Indeed, marmot species offer a great diversity in social structure (Armitage, 1981; Michener, 1983), in mating system, in the degree of cooperation and reproductive suppression (Blumstein and Armitage, 1999) and, consequently in the degree of reproductive skew, particularly among females. Here, I examine possible explanations for the variability in the degree of reproductive skew among females of marmot species. From theoretical formalizations of the two alternative hypotheses (Ragsdale, 1999; Reeve et al., 1998), I identified four possible explanations for the evolution of contrasting levels of reproductive skew in female marmots. Then, from the literature, I give arguments supporting or refuting these four different explanations of the variability in the degree of reproductive skew among females of marmot species.

## 2. Social structure, mating system and reproductive skew

The recent review of Blumstein and Armitage (1999) gives the basis to compare information on marmot social structures, mating systems and levels of female reproductive skew (Table 1). The 14 marmot species are monophyletic, hibernators and can be roughly classified into three social and cooperative breeding categories.

### 2.1. Solitary species

The woodchuck *Marmota monax* is the only member of this group. Males and females live alone and typically hibernate singly. Pups disperse during their first year of life. Intrasexual cohesive interactions are rare or absent (Bronson, 1964). Intersexual interactions are limited to the breeding period when the home range of male woodchucks overlaps those of several females, and males are thought to copulate with all females whose home ranges are included within their own (Ferron and Ouellet, 1989). To my knowledge, no molecular data is available to confirm the degree of polygyny of this polygynous mating system and the extent of promiscuous or monogamous mating is still to be investigated.

### 2.2. Species with intermediate level of sociality

Only the yellow-bellied marmot *M. flaviventris* falls in this category. Yellow-bellied marmots live in enlarged family groups typically consisting of one dominant adult male and his harem. The

harem (mean size of 2.27 females) is a male reproductive unit composed of one or more female groups (mean number of 1.47; Armitage, 1986). Female groups are organised in matrilineal units that consist of closely related kin. Plural breeding regularly occurs within a male's harem. The yellow-bellied marmot is then socially polygynous but a large proportion (> 33%) of males are socially monogamous (Armitage, 1986). A polygynous mating system has been confirmed by molecular data (Schwartz and Armitage, 1980). Although generally more than a single matrilineal female breeds in a given year, two-year-old females living with adults reproduce less often than expected (Armitage, 1989), indicating that facultative reproductive suppression may occur among mature females (Armitage, 1998).

### 2.3. Species with complex level of sociality

Although additional information is still required for most Asian species (except *M. caudata*) and for *M. broweri*, it seems that socially complex species share some characteristics (Table 1): (i)

Table 1  
Mating system, degree of sociality and reproductive suppression in the 14 marmot species

Species	Mating system <sup>a</sup>	Sociality <sup>b</sup>	Reproductive suppression	Joint hibernation	References <sup>c</sup>
<i>M. monax</i>	P	1	–	–	1,2,3,4
<i>M. flaviventris</i>	P	2	–(+)	–(+)	5,6,7
<i>M. marmota</i>	M (Pa)	3	+	+	8,9,10,11
<i>M. caudata</i>	M (Pa)	3	+	+	12,7
<i>M. olympus</i>	M	3	+	+	13,7
<i>M. caligata</i>	M-B	3	+	+	14,15,27
<i>M. vancouverensis</i>	M (P)	3	+?	+	16,7,17
<i>M. browerii</i>	M?	3?	+	+	18,7
<i>M. bobac</i>	M (P)	3	+	+	19,20,7,28
<i>M. himalayana</i>	M?	3?	?	?	20
<i>M. menzbieri</i>	M	3	+?	+	21,22,20
<i>M. sibirica</i>	M	3	?	+	23,7
<i>M. baibacina</i>	M	3	+	+	24,20,7
<i>M. camtschatica</i>	M	3	+	+	25,26,7

<sup>a</sup> Mating system: P = polygyny; Pa = polyandry; M = monogamy; B = bigamy.

<sup>b</sup> Sociality: 1 = asocial; 2 = intermediate sociality; 3 = high sociality.

<sup>c</sup> 1: Michener, 1983; 2: Meier, 1992; 3: Ferron and Ouellet, 1989; 4: Bronson, 1964; 5: Armitage, 1989; 6: Armitage, 1991; 7: Blumstein and Armitage, 1999; 8: Goossens et al., 1998; 9: Arnold, 1990a,b; 10: Perrin et al., 1993b; 11: Arnold, 1988; 12: Blumstein and Arnold 1998; 13: Barash, 1973; 14: Holmes, 1984; 15: Barash, 1974b; 16: Bryant, 1996; 17: Heard, 1977; 18: Raush and Bridgens, 1989; 19: Le Berre et al., 1994; 20: Bibikow, 1996; 21: Maschkin, 1982; 22: Maschkin and Baturin, 1993; 23: Zimina, 1978; 24: Mikhailyuta, 1991; 25: Mosolov and Tokarsky, 1994; 26: Kapitonov, 1978; 27: Wasser and Barash, 1983; 28: Rymalov, 1994

The basic social unit is the family group composed of a resident pair, subordinate adults, yearlings and juveniles of the year (*Marmota marmota*, Allainé et al., 1994; Perrin et al., 1993a; *M. caudata*, Blumstein and Arnold, 1998). In the hoary marmot (Holmes, 1984) and in the Olympic marmot (Barash, 1973) subordinate adults are restricted to one mature female. Subordinates are adults that postpone dispersal beyond sexual maturity (two year-olds), and often until they are three-, four- or even five-year-olds (Arnold, 1990a; Frey-Roos, 1999; Magnolon, 1999); (ii) singular breeding predominates (Table 1) and, consequently this group of species should be considered as socially monogamous (Armitage, 1996; Bibikow, 1996). Generally only the resident pair rears offspring (Arnold, 1990a; Goossens et al., 1998; Holmes, 1984), although plural breeding occasionally occurs in the grey marmot (Mikhailyuta, 1991), in the steppe marmot (Rymalov, 1994), and in the Vancouver marmot (Bryant, 1996). In the hoary marmot, two adult females may breed biennially and alternately (Barash, 1974a). This biennial rhythm of female reproduction is determined by environmental constraints rather than by competition between females for reproduction; (iii) when the dominant female skips reproduction (regularly the case in the Olympic marmot, Barash, 1973), female subordinates do not breed. This suggests reproductive suppression among subordinate females and leads to complete reproductive skew in these social groups (see Goossens et al., 1996 and Blumstein and Arnold, 1998 for examples of occasional failed reproductive suppression respectively in *M. marmota* and *M. caudata*). The mating system has been investigated only in the alpine marmot. Molecular analyses of paternity have been conducted for two long-term studied populations (one in Germany, Arnold, 1990a; one in France, Goossens et al., 1998). In the two cases, the dominant male sired all pups born in his group in most social groups (70% in France, 83% in Germany, Hackländer et al., 1999). In the remaining groups, the resident female mated polyandrously and multiple paternity occurred. In litters fathered by more than one male, the resident male always sired some juveniles. The juveniles not sired by

the resident male were fathered by subordinate males of the group (Arnold, 1990a) or by extra-group males (Goossens et al., 1998). This indicates that reproduction is not completely suppressed in subordinate males (Arnold and Dittami, 1997).

In this group of species, the alpine and the golden marmots are probably the most socially integrated during the active summer period, but detailed data are still lacking for the other species. Adult males are socially well integrated into the social group. They interact cohesively with the other members of the family and all individuals hibernate together in the same hibernaculum (Arnold, 1993a; Perrin et al., 1993b; Blumstein and Arnold, 1998). These two species present all attributes of cooperative breeding (Blumstein and Armitage, 1999).

### 3. Factors affecting reproductive skew in marmots

From this short review of social structure and mating system in marmot species, it appears that although the composition of social groups are quite similar in the yellow-bellied marmot and in the group of monogamous marmot species, the mating system and the pattern of reproductive skew are very different. In the group of monogamous species, the reproduction of subordinate females is suppressed leading to social monogamy, while in the yellow-bellied marmot, subordinates (recruited daughters) reproduce, leading to social polygyny. The question arising then, is why low reproductive skew occurs among female yellow-bellied marmots while a complete skew is observed among the females of the monogamous species? To examine this question, I compared the yellow-bellied marmot with the best known monogamous species, the alpine marmot. I also used information on other monogamous species when available. From reproductive skew theory (Ragsdale, 1999; Reeve et al., 1998; Vehrencamp, 1983), I deduced that marmot species may differ in: (1) the ability of dominant females to control reproduction of subordinates; (2) the degree of relatedness between female group members; (3) the benefit for subordinates of re-

maintaining in the social group; (4) the benefit from maintaining group cohesion with subordinates. Then I examined whether these four possibilities may account for the difference in reproductive skew observed between the yellow-bellied and the alpine marmots.

### *3.1. The ability of dominant females to control reproduction of subordinates*

The two alternative hypotheses proposed to explain the evolution of reproductive skew (OSH and LCH) basically differ according to the ability of dominant females to control the reproduction of subordinate females. Then, I have first to compare the yellow-bellied marmot and the alpine marmot according to the ability of dominant females to control the reproduction of subordinate females.

The fighting ability of subordinate females and, consequently, their share of reproduction, may depend on their access to resources and on their efficiency in converting resources into an increase in their share of reproduction (Reeve et al., 1998). In matrilineal yellow-bellied marmots, all females share a common home range and may use the same burrows (Armitage, 1991). They forage in the same area (Carey, 1985) and consequently, they are not restricted in their access to resources. Body mass of two-year-old females is a little lower than older ones (Armitage et al., 1976), so, the relative competitive ability of two-year-old females can reasonably be considered a little lower than that of older females. Under these conditions, the LCH predicts an even distribution of reproduction among group members and could account for the observed pattern in the yellow-bellied marmot. From these observations, I cannot discard the possibility that yellow-bellied marmot females are unable to control the reproduction of their subordinates (LCH). No information is available on the ability of dominant females to physiologically suppress the reproduction of subordinate females.

The complete reproductive skew observed in the alpine marmot occurs either because dominant females are able to control the reproduction of subordinate females and do not have to con-

cede them reproduction, or because subordinate females are poorly efficient in increasing their share of reproduction. All group members share a common home range, forage in the same area, and use the same burrows (Perrin et al., 1993a). Consequently, the failure of reproduction among subordinates cannot be attributed to restricted access to resources within the territory. If the LCH applies in the alpine marmot, subordinate females should have very low fighting ability that can be due to a lower body mass (only among the two-year old subordinate females, Hackländer et al., 1999). Rather, some observations suggest that total control is more likely in the alpine marmot. First, subordinate females do not reproduce when the dominant female skips reproduction in a given year (Arnold, 1993b). Second, during the breeding period, dominant females often interact aggressively with subordinate ones (Magnolon, 1999) resulting in a high level of glucocorticoids in the blood of subordinate females (Hackländer and Arnold, 1999; Hackländer et al., 1998, 1999). This hormone is characteristic of a stressed state and may lead to abortion in subordinate females. Third, physiological suppression of reproduction is also known to occur in subordinate males and, especially, in those non-related to the dominant male (Arnold and Dittami, 1997). The same pattern may be true for the yellow-bellied marmot.

The difference in reproductive skew between yellow-bellied and alpine marmots may arise either because yellow-bellied females are unable to control the subordinate's reproduction or because they concede reproduction to their daughters, while alpine marmot females completely suppress the reproduction of their subordinate females.

### *3.2. The degree of relatedness between group members*

Both alternative hypotheses (OSH and LCH) predict an effect of genetic relatedness on the degree of reproductive skew in social groups. When the relatedness is symmetrical among members of the social group (i.e. associations where members are equally related to each other's offspring, Reeve and Keller, 1995) the OSH predicts that the reproductive skew should increase with

Table 2

Predicted effects of relatedness on reproductive skew by the Optimal Skew Hypothesis (OSH) and the Limited Control Hypothesis (LCH) when relatedness between group members is symmetrical and asymmetrical

	OSH	LCH
Symmetrical	skew increases with relatedness	skew decreases (or not affected) with relatedness
Asymmetrical	complete skew or skew increases with relatedness <sup>a</sup>	complete skew whatever the relatedness

<sup>a</sup> Optimal skew possible when the social group size is larger than 2 or when a mate change occurs between successive breedings.

increasing relatedness between group members while the LCH predicts the opposite (or no effect of relatedness) (Reeve et al., 1998). When the relatedness is asymmetrical among group members (i.e. associations where members are unequally related to each other's offspring) the LCH predicts a complete skew while reproductive concession may occur with the OSH when the social group size is larger than two or when a mate change occurs between successive breedings (Table 2). I therefore examined whether the difference in reproductive skew between yellow-bellied and alpine marmots may be accounted for by differences in relatedness between group members.

In the yellow-bellied marmot, the relatedness between matrilineal females is 0.5 on average (Armitage, 1991). Indeed, matrilines are generally composed of mother–daughter associations and takeover by a unrelated female does not occur (Armitage, 1987a). In this case, the participants (mothers and daughters) are unequally related to each other's offspring (asymmetrical relatedness) and only the optimal skew hypothesis predicts reproductive concession when female group size is larger than two (Reeve et al., 1998). The staying incentive then will increase as the strength of ecological constraints decreases. Whatever the group size, the LCH predicts that the evolutionary stable effort by the subordinate is zero because its genetic benefit completely overlaps with that of the parent. When relatedness is considered, the reproductive sharing observed in the

yellow-bellied marmot thus is not in accordance with the LCH.

In the alpine marmot, the average relatedness between dominant and subordinate females is 0.33 (Goossens, 1998). Replacement of a dominant female by an unrelated one may explain the lower value of relatedness within alpine marmot families than within matrilines of yellow-bellied marmots. In this case, the optimal skew predicted by the OSH depends both on relatedness between group members and on the strength of ecological constraints. Given the low relatedness between females in the family, a complete reproductive skew is expected only if the ecological constraints are very strong (Reeve et al., 1998).

From these observations on relatedness and reproductive skew, I conclude that dominant females are able to suppress the subordinate's reproduction in the two marmot species, but only female yellow-bellied marmots concede reproduction to their daughters. The question arising now is why reproductive concession occurs in the yellow-bellied marmot but not in the alpine marmot?

### 3.3. The benefit for subordinates of remaining in the social group

The subordinate may gain in remaining in the social group even without receiving any direct reproduction when its expected reproductive success through independent reproduction is lower than its expected reproductive success through staying with the dominant (Ragsdale, 1999). If it is not the case, the dominant should concede reproduction (staying incentive) to retain its subordinate in the group. However, the subordinate will disperse when the staying incentive is higher than the maximum reproduction the dominant is willing to concede to the subordinate (Fig. 1). The expected reproductive success of the subordinate through independent reproduction is supposed to depend on the strength of ecological constraints measured by the probability that subordinates disperse successfully (Vehrencamp, 1983). The expected fitness gain through staying with the dominant depends on the probability of inheriting resources (territory) and on indirect fitness benefit (Ragsdale, 1999; Reeve et al., 1998). I therefore

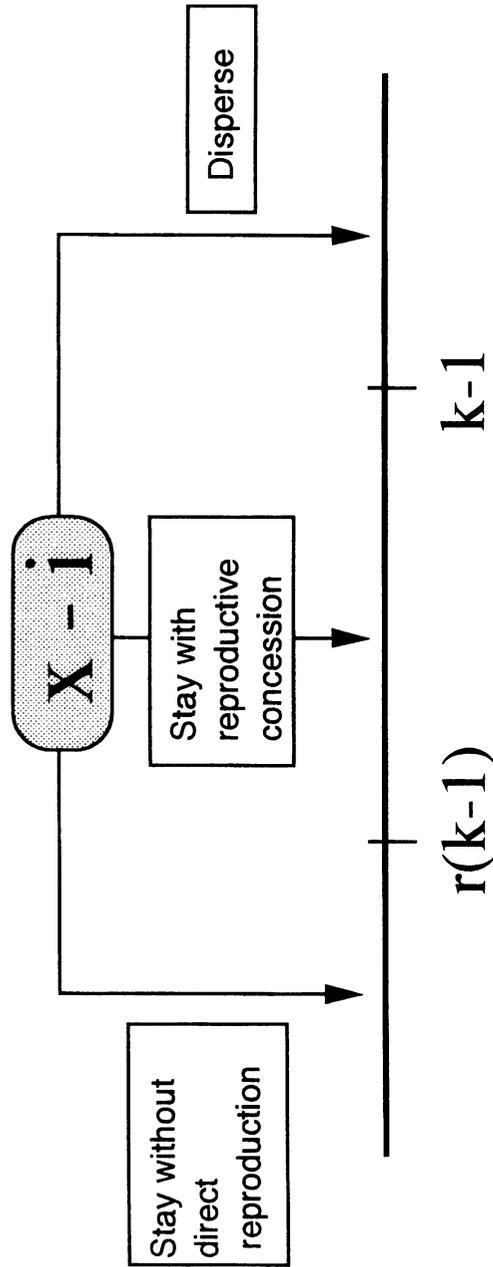


Fig. 1. Predicted decision of the subordinate female according to the expected fitness gain through direct and indirect reproductive success.  $x$  = expected direct reproductive success through independent reproduction;  $i$  = expected direct reproductive success through inheritance of resources;  $r$  = relatedness between group members;  $k$  = the overall direct reproduction of the social group relative to reproductive output for a lone dominant (standardised to be 1).

reviewed evidence on the probability of successful dispersal and of resources inheritance by subordinates of the two species.

In the yellow-bellied marmot, about 50% of yearling females are successful at remaining in their natal territory but the probability of getting a dominant position is poorly known. Survival of dispersing subordinates was only 16% less than survival of philopatric ones (Van Vuren and Armitage, 1994). Dispersers hibernated singly, but did not suffer a greater mortality (12%) than residents (10%, Van Vuren, 1990). These results suggest that the probability of successful dispersal may be high in the yellow-bellied marmot.

In the alpine marmot, natal dispersal roughly follows the same pattern in two populations: Berchtesgaden, Germany (Arnold, 1993b; Frey-Roos, 1999) and Vanoise, France (Magnolon, 1999). The percentages of philopatric females (those inheriting the natal territory) were 15% ( $n = 40$ ) and 18.3% ( $n = 86$ ) respectively in the Vanoise and in the Berchtesgaden populations. Thus, the probability of inheriting the natal territory is low in the alpine marmot and about 80–85% of females have to disperse. On average, 17.5 (Vanoise) and 21.5% (Berchtesgaden) of females established in directly neighboring territories. Among dispersers, about 50% were estimated to successfully obtain a territory (Arnold, 1993b). Among dispersers unable to establish themselves as territory owner in the year of dispersal, 96% were not retrapped later (Arnold, 1990a). This suggests a very high mortality rate in the floating population.

From these data, it is difficult to decide whether the two species differ in the probability of successful dispersal and in the probability of inheriting resources. However, an inter-individual variability in the probability of inheriting the natal territory and an inter-population variability in the strength of ecological constraints may exist in both species. Therefore, in both species we might observe the coexistence of social groups where subordinate females: (i) disperse; (ii) stay with direct reproduction; and (iii) stay without any direct reproduction. This is the case in the yellow-bellied marmot, even if the frequency of social groups belonging to the second category predomi-

nate (Armitage, 1989, 1991). In the alpine marmot, three populations of different density and elevation were studied for more than seven years but social polygyny was almost never reported (Goossens et al., 1996). This lack of variability in reproductive skew within and among populations of alpine marmots suggests that the benefit of subordinates for remaining in the social group may not be the principal selective force for the evolution of subordinate reproductive suppression in this species and possibly in other marmot species of the monogamous group. Indeed, among population variability in the mating system has only been reported for the hoary marmot (Holmes, 1984). In high latitude populations, only one female reproduced per family group. In low latitude populations, where climatic conditions were less harsh and food and hibernacula more abundant, a high proportion of bigamous social groups was observed (Holmes, 1984). Social polygyny was rarely observed in the golden marmot (Blumstein and Arnold, 1998).

#### *3.4. The benefit for the dominant of retaining subordinates*

The basic assumption of the optimal skew hypothesis is that dominants gain benefit from maintaining group living (Vehrencamp, 1983). This implies that the fitness benefits from retaining subordinates in the group exceed the fitness costs associated with retaining and conceding reproduction to subordinate females. If it is not the case, dominants should systematically suppress the subordinate's reproduction even at the risk of the subordinate's departure from the family group. The difference in reproductive skew between yellow-bellied and alpine marmots may thus be accounted for by differences in the benefit gained from retaining subordinates in the family group. I therefore reviewed evidence on the benefits and costs of retaining subordinate females in these two species.

Dominant females may benefit from maintaining group living through cooperation. In the yellow-bellied marmot, cooperation seems not to be efficient either in deterring predators nor during hibernation. Indeed, marmots emit alarm calls

when deterring a predator (Blumstein and Arnold, 1995; Blumstein et al., 1997), and increased vigilance in groups with subordinates could reduce the mortality of juveniles, which are the most exposed to predation (Maschkin, 1982). However, in the yellow-bellied marmot, the mortality of juveniles to predation was the same among colonial and non-colonial females (Lenihan and Van Vuren, 1996a). Cooperation during winter does not occur in the yellow-bellied marmot because of the absence of joint hibernation (Johns and Armitage, 1979). Indeed, most adults hibernate singly and joint hibernation is rare and occurs only in high-altitude populations (Johns and Armitage, 1979). Pups hibernate generally only with their litter mates and rarely with their mother (Lenihan and Van Vuren, 1996b). However, cooperation may be advantageous for dominant females in competition with conspecifics. Indeed, subordinates cooperate in the defence of the home range against conspecifics (Armitage and Johns, 1982) thus preventing home range takeover by a non-related female (Armitage, 1988). Moreover, a large matriline may acquire the best burrow sites and foraging areas by excluding smaller matriline (Frase and Armitage, 1984). Also, large matriline may suppress reproduction of females from other matriline, thus reducing competition with other matriline for local resources (Armitage, 1986).

Costs of reproductive concession in the yellow-bellied marmot are associated with competition between females and/or between their offspring for limited resources resulting in a decrease in direct reproductive success when subordinates are present (Downhower and Armitage, 1971). Females of the same matriline share a common home range and thus compete for resources. If resources of the matriline home range are very poor, the dominant female may gain by suppressing the reproduction of subordinate females. This may explain why about 47% of females disperse (Armitage, 1991), why the reproduction of two-year-old females living with adults is less than expected (Armitage, 1989), and why females likely to recruit daughters produce female-biased litters (Armitage, 1987b).

In the alpine marmot, cooperation is not efficient in deterring predators or in competition with

conspecifics. Indeed, alpine marmots also give alarm calls when deterring a predator (Lenti Boero, 1992), but most juvenile mortality occurred within groups with subordinates (Arnold, 1990b). Territories are relatively stable in space over years (Perrin et al., 1993b) and the responsibility for defence of the family territory rests mainly with the resident pair. Although subordinates participate in the defence of the territory against conspecifics, they seem unable to prevent takeover by a male (Coulon et al., 1995). However, alpine marmot females may benefit from maintaining group living because subordinates help in rearing young. In particular, social thermoregulation has been described in this species (Arnold, 1988, 1990b). During periods of arousal, adults, but also subordinates and yearlings, actively warm related pups (Arnold, 1993a). This alloparental care behaviour during hibernation may increase juvenile survival, and consequently parents' fitness, but is energetically costly for subordinates and yearlings (Arnold, 1990b). This alloparental care may also reduce the workload of residents and may thus enhance their future reproduction. More generally, joint hibernation is widespread among the group of monogamous marmot species (Blumstein and Arnold, 1998).

Reproductive concession may be costly for the breeding success of the dominant female. To maximise the efficiency of social thermoregulation, it is likely that the number of juveniles to be warmed should be small (Hackländer et al., 1999). Moreover, male subordinates may be more efficient than female subordinates in helping during hibernation (Arnold, 1993a), because juvenile survival during winter increases with the number of males but not with the number of females in the hibernaculum (Allainé et al., in press). Thus, to maximise the efficiency of social thermoregulation, I hypothesise that female alpine marmots would gain by retaining subordinate males and by suppressing the reproduction of subordinate females, even at the risk of their departure (because they are not so useful in warming juveniles).

I therefore suggest that the cost of conceding reproduction to female subordinates may be generally high among monogamous marmot species, but not in the yellow-bellied marmot. Thus, the

benefit from maintaining group living, and more precisely in retaining subordinate females, may be different for these two types of marmot species.

#### 4. Discussion

All but one marmot species live in social groups. Among these social species, most appear to be primarily socially monogamous. In such monogamous marmot species, the reproduction of subordinate females is suppressed, and consequently, the reproduction is completely skewed in favour of the resident female. Only the yellow-bellied marmot is regularly polygynous, and reproduction among matriline females is more evenly distributed than among females of monogamous marmot species. Analysing the pattern of reproductive skew was therefore necessary to understand why the yellow-bellied marmot is polygynous while the other social marmot species are primarily monogamous.

From this review, I conclude that dominant females of both species are able to control the reproduction of their subordinate females and the observed skew should be predicted by the classical optimal skew models (Ragsdale, 1999; Reeve et al., 1998). In the yellow-bellied marmot, dominant females may benefit predominantly by maintaining females in their matriline. Given the pattern of relatedness (asymmetrical) between group members and the strength of ecological constraints (probably weak), dominant females should concede direct reproduction to their subordinates.

On the contrary, in the alpine marmot, dominant females may primarily benefit by suppressing the reproduction of their subordinate females, probably to maximise the efficiency of the social thermoregulation (by reducing the number of juveniles to be warmed). For subordinate females, the decision to disperse or to stay in the family group without direct reproduction may depend on a balance between residual reproductive values (Arnold, 1993b) associated to staying (affected by the probability of inheriting territory) and to leaving (affected by density and the body condition of the subordinate). On the other hand, dominants

may gain in having subordinate males in the family group because they are efficient in social thermoregulation. This may explain why males are produced in excess (Allainé et al., in press) and why resident males mainly suppress the reproduction of their unrelated subordinate males (Arnold and Dittami, 1997).

Precise estimates of some parameters (strength of ecological constraints, probability of inheriting resources) are still lacking for both species to test if observed reproductive skew among females correctly fitted the Optimal Skew models.

It is remarkable that social monogamy has evolved concurrently with the evolution of high sociality among marmot species. Indeed, all highly social marmot species exhibit (social and primarily genetical) monogamous mating systems. Previously, the degree of sociality has been associated both with the delay in the age of dispersal and with the harshness of the environment and the length of the active growing season (Armitage, 1981; Barash, 1974b; Blumstein and Armitage, 1998). However, delayed dispersal only implies the formation of social groups but has no bearing on the degree of sociality and on the mating system (Armitage, 1981). The question then is: why high sociality is associated with social monogamy in harsh environments? Two non exclusive scenarios may account for this pattern.

In the first scenario, the adaptation of marmots to harsh environments has required first the evolution of reproductive suppression of subordinate females to avoid competition between mothers and/or between offspring for limited resources. The absence of reproduction among subordinate females has offered then the opportunity for the occurrence of an efficient social thermoregulation during hibernation. The evolution of social thermoregulation has, in turn, required joint hibernation and consequently the delay of dispersal and the development of a high level of sociality among these marmot species.

In the second scenario, the adaptation of marmots to harsh environments has required first the evolution of social thermoregulation. It is likely that in harsh environments with a short active season, juvenile marmots may not have time to accumulate enough fat to survive hibernation.

Juvenile survival may thus critically depend on social thermoregulation (Allainé et al., 1998; Allainé et al., in press, Arnold, 1993a). The need for social thermoregulation has, in turn, required joint hibernation, delayed dispersal — and consequently high sociality — and has enforced reproductive suppression of subordinate females.

Whatever the scenario, sociality may have evolved in two steps among marmot species. Marmots diverged from an ancestral ground squirrel about six million years ago (Giboulet et al., 1997) and the first modern species of marmot is assimilable to *Marmota monax* (Hoffmann and Nadler, 1968; Kurten and Anderson, 1980). This first marmot species was therefore possibly solitary. Group living, later resulting from expansion into harsh environments (higher latitude or elevation), may have led to the yellow-bellied marmot form. Adaptation to harsher conditions during the Pleistocene may have enforced populations living in high latitude or elevation to develop social thermoregulation during hibernation. This, in turn, has led to the evolution of marmot species with high sociality and complete reproductive skew (social monogamy), and may have occurred independently in Eurasian and in North-American species (Kruckenhauser et al., 1999).

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