

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Cooperative breeding in marmots

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Whenever individuals live in stable social groups and not all individuals breed, group members may breed cooperatively. While well-documented in a variety of birds and mammals, there is some controversy over whether, and to what degree, sciurid rodents breed cooperatively. We identify cooperative breeding when: individuals delay dispersal beyond reproductive maturity, reproduction in mature individuals is suppressed, and when non-breeders provide alloparental care. In this paper we note that the 14 species of marmots (*Marmota* spp.), large ground-dwelling sciurid rodents found throughout the Northern Hemisphere, provide an excellent taxon in which to study the evolution of cooperative breeding. Marmot species fit none, some, or all of the attributes of cooperative breeding. Most interestingly, delayed dispersal and alloparental care may be de-coupled interspecifically, and possibly intraspecifically, making marmots an excellent taxon for additional study. Environmental harshness increases maturation time and is associated with dispersal delayed beyond reproductive maturity. The opportunity to gain direct fitness may be associated with gaining indirect fitness by alloparental behavior. In addition to its theoretical attraction, cooperative breeding has profound implications for conservation and management of species that breed cooperatively. To maximize marmot production, managers and breeders need to pay particular attention to social group structure to prevent the expression of reproductive suppression. If cooperative breeding results from an environmental constraint, habitat modifications may increase the percent of females that breed.

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Whenever individuals live in stable social groups and not all individuals breed, group members may breed cooperatively. Cooperative breeding profoundly influences a species' population biology by reducing the

number of breeding adults, increasing the reproductive rate of female breeders, and increasing juvenile survival. Cooperative breeding is well-documented in a variety of birds (Brown 1987, Stacey and Koenig 1990) and some

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mammals (Gittleman 1985, Solomon and French 1997). There is some confusion over its distribution in sciurid rodents. For instance Hoogland (1981, 1983) and Michener and Murie (1983) disagreed whether the evidence was sufficient to catalog black-tailed prairie dogs (*Cynomys ludovicianus*) as cooperative breeders. Belding's ground squirrels (*Spermophilus beldingi*) exhibit nepotistic behavior and Sherman (1980) suggested they bred cooperatively. A recent review in Solomon and Getz (1997) mis-cited J. Waterman (personal communication cited in Packer et al. 1992) and reported the Columbian ground squirrel (*Spermophilus columbianus*) to be a cooperative breeder. Alpine marmots (*Marmota marmota*) provide alloparental care (Arnold 1993a, b) and were thus suggested to be cooperative breeders (Jennions and Macdonald 1994). But, there is ongoing debate over the criteria used to identify cooperative breeding (Crespi and Yanega 1995, Sherman et al. 1995, Solomon and French 1997). Finally, the word "cooperative" may be a misnomer because it is generally recognized that although individuals may "cooperate" to maximize their inclusive fitness, there may be considerable reproductive conflict in a "cooperatively" breeding group (e.g., Reyer 1986, Brown 1987, Brown and Brown 1990, Koenig and Stacey 1990).

While Jennions and Macdonald (1994) require only costly alloparental care to identify a species as a cooperative breeder, we follow Solomon and French (1997) and note that cooperative breeding is present when three attributes occur. Combinations of these attributes lead to a continuum of cooperative breeding (sensu Sherman et al. 1995). First, individuals delay dispersal beyond reproductive maturity. Second, reproduction is suppressed in reproductively mature individuals. Third, non-breeding individuals provide some form of alloparental care. Theoretically, alloparental behavior could be directed to the offspring, or to the lactating mother (e.g., Moehlman and Hofer 1997). The first two attributes lead to reproductive skew (Keller and Reeve 1994, Sherman et al. 1995); the third attribute may be an evolved strategy to gain indirect fitness while forgoing immediate gains in direct fitness.

We acknowledge that this three-part definition of cooperative breeding is somewhat controversial. Some view gradation in cooperative breeding as best reflected by the type and nature of alloparental care directed towards juveniles (J. Murie pers. comm.). For instance, alarm calling would not be a specialized alloparental behavior whereas nursing the young of another individual would be a specialized alloparental behavior. Others suggest that adopting a three-part definition ignores some of the complexities seen in the better-studied avian cooperative breeders (W. Koenig pers. comm.). For instance, mate-sharing and joint nesting occur in some cooperatively breeding birds (Craig and Jamieson 1990, Koford et al. 1990): such complexities are lost in a simple three-part definition. Nevertheless, we adopt

the three-part definition for two reasons: the first two attributes establish the demographic situation required for the evolution of more complex alloparental behavior, and the three-part definition identifies traits that ultimately allow us to study the evolution of both reproductive skew and more complex alloparental behavior. We note that by emphasizing the importance of reproductive suppression, we focus on a fundamental question of cooperative breeding: explaining why all group members do not reproduce. Ultimately, we believe (following Keller and Reeve 1994 and Sherman et al. 1995) that reproductive skew will be a common metric that may allow us to better compare and therefore understand the evolution of sociality in diverse taxa, each with their own specialized social adaptations. Thus, while we acknowledge potential inadequacies of this definition, we nevertheless apply it to describe cooperative breeding in marmots and in other ground-dwelling sciurid rodents.

Marmots as cooperative breeders

Although generally not recognized as cooperative breeders (e.g., Solomon and Getz 1997; but see Armitage 1986, Jennions and Macdonald 1994), the 14 species of marmots (*Marmota* spp.), large ground-dwelling sciurid rodents found throughout the Northern Hemisphere, provide an excellent taxon in which to study the evolution of cooperative breeding. In this paper, we review literature on marmot social behavior and note that species fit none, some, or all the attributes of cooperative breeding. Perhaps most interestingly, delaying dispersal and providing alloparental care may be de-coupled in marmots, which makes them an excellent taxon for additional study.

Marmots are hibernators whose active seasons range from 4 to 8 months each year during which time marmots must mate, raise young, and gain sufficient body mass to survive hibernation. Understanding social variety in marmots has long been the subject of study (Barash 1974a, 1989, Armitage 1991, Arnold 1993a, Bibikow 1996, Blumstein and Armitage 1998). Sociality in the genus *Marmota* spans the range of solitary living to what we now suggest is cooperative breeding.

To identify delayed dispersal, we reviewed the literature and noted the age at which marmots left their natal home range and compared that with the age at first reproduction. In the section on why delay dispersal, we derive a "maturity index" to further understand the evolution of delayed dispersal. Reproductive suppression was difficult to document. Suppression can occur through direct agonistic behavior or by pheromonal activity that delays sexual maturation or inhibits fertilization, implantation, or birth (Wasser and Barash 1983). All lead to the same result: failure to recruit

young. Thus, we identify reproductive suppression (or the possibility of reproductive suppression) when, in a given year, there is evidence that only a single female breeds or weans young in multi-female groups. Despite our broad definition of reproductive suppression, we acknowledge that animals could fail to reproduce for non-social reasons (e.g., food limitation). However, such reproductive failure could be the consequence of dominant females excluding subordinate females from food resources. We assume that alloparental behavior could conceivably occur in the summer or in the winter and discuss various possible "helpful" behaviors.

The largely solitary woodchuck (*Marmota monax*) exhibits what we now call "diffuse" harem polygyny (Armitage and Blumstein 1999). Females live alone and do not interact cohesively with other adult females (Bronson 1964, Meier 1992). Males defend home ranges that overlap one or more female home ranges but do not interact with females outside the breeding season. Pups mature quickly and disperse before their first hibernation. Individuals typically hibernate alone, and 20–43% of females breed as yearlings (Snyder 1962). Woodchucks express none of the attributes of cooperative breeding.

All other species live in obvious social groups. Available information demonstrates that group member's summer home ranges overlap (to variable extents), group members share summer burrows (to variable extents), and group members may hibernate together. Alloparental care may function by directly helping parents reduce their workload or by directly helping the young (e.g., Moehlman and Hofer 1997). Marmot group members may provide potential alloparental care in the summer or in the winter. In the summer, group members could conceivably maintain burrows, defend against conspecific intruders, look for and warn others of predators (all marmot species alarm call in response to predators – Blumstein and Armitage 1997), interact affiliatively with pups, and/or nurse pups. In the winter, group hibernation and coordinated thermoregulation may be especially helpful and may be required for young to survive in bad years (Arnold 1993a, b). Hibernating marmots undergo cycles of torpor and arousal throughout the winter. Adults may help thermoregulate juveniles by coordinating their arousal cycles and by maintaining euthermy for longer periods of time. The time period between the end of hibernation and the beginning of the growing season may be particularly stressful because animals are euthermic (i.e., they maintain an elevated body temperature of about 37°C), but must rely on their fat reserves for energy (Armitage and Blumstein 1999); mortality of juveniles and yearlings increases when prolonged snow cover occurs (Arnold 1993b). Adult thermoregulation may be especially important to increase the probability that smaller juveniles have sufficient resources to survive this period of energy stress for those species that must wait a long

time for the beginning of the growing season. Even without sophisticated thermoregulation, huddling may increase overwinter survival (Madison 1984) and alloparental thermoregulation may be important for other rodents (Solomon 1991). Below we illustrate how other social marmot species may meet some or all the attributes of cooperative breeders.

The more socially complex (Blumstein and Armitage 1997) yellow-bellied marmot (*M. flaviventris*) illustrates what we refer to as "concentrated" harem polygyny (Armitage and Blumstein 1999). Home ranges of related females overlap and an adult male's home range may overlap one or more of these "matrilines" (Armitage 1991). Pups do not reach adult body mass during their first year and dispersal is postponed to the yearling stage.

Pups hibernate with their litter mates and sometimes with their mother in the same burrow system their first winter (Lenihan and Van Vuren 1996), but most adults hibernate singly in separate burrow systems. Observations of captive juveniles housed together showed that all group members hibernated in a huddle (K. B. Armitage, D. T. Blumstein and B. C. Woods unpubl.). Here and elsewhere we infer group hibernation when marmots were reported to hibernate in the same burrow system. Excavated burrows may have more than one hibernation chamber (A. A. Bryant pers. comm.), but there are numerous reports of marmots in the same burrow system hibernating in the same chamber (Nekipelov 1978, Rausch and Bridgens 1989, Arnold 1990b, Mosolov and Tokarsky 1994, Tokarsky 1996, Vasilev and Solomonov 1996; A. A. Bryant pers. comm.). Hibernation in the same hibernaculum provides the opportunity for thermoregulatory benefits, whether these benefits occur needs to be better quantified in the laboratory and field. Group hibernation appears facultative in yellow-bellied marmots; in low-altitude populations, adults typically hibernate singly, while in high-altitude populations, matrilineal females hibernate socially (Johns and Armitage 1979).

Nearly all yearling males and about half of the yearling females disperse as yearlings before their second hibernation. Age of first reproduction is two years; however, two-year-olds living with adults reproduce less often than expected whereas two-year-olds living singly or with other two-year-olds reproduce as frequently as expected. Older matrilineal females also may be reproductively suppressed (Armitage 1986, 1989, 1998). Ultimately, more than a single matrilineal female breeds. Breeding females may share burrows and nurse related non-offspring (Armitage and Gurri-Glass 1994).

Yellow-bellied marmots possess some of the attributes of cooperative breeders: females may delay dispersal past reproductive maturity (5 of 25 radio-telemetered dispersers did so – Van Vuren 1990), female reproduction can be suppressed, and there may be alloparental care such as communal nursing (Armitage

and Gurri-Glass 1994). Interestingly, none of these behaviors is obligate and yellow-bellied marmots may be a prime example of facultative cooperative breeding. More data are required to better understand fitness payoffs of foregoing breeding.

Olympic marmots (*M. olympus* – Barash 1973) and southern populations of hoary marmots (*M. caligata* – Barash 1974b) are more socially complex and also illustrate “concentrated” harem polygyny (Armitage and Blumstein 1999). During the active season, a single adult male’s home range overlaps the home ranges of one or a few adult females. Groups may have an additional “satellite male” that possibly could breed. In contrast to yellow-bellied marmots, males are more “socially integrated” with females: the sexes interact amicably and hibernate socially. Females’ active season home ranges overlap but each typically uses a different main sleeping burrow (D.T. Blumstein unpubl.).

Female Olympic marmots (Barash 1973) and both monogamous (Holmes 1984) and bigamous (Barash 1974b) hoary marmots breed biennially. Biennial breeding may be environmentally determined. Females of at least eight other marmot species skip reproduction for one or more years after reproducing; reproductive females cannot always fatten sufficiently in order to reproduce in subsequent years (Armitage and Blumstein 1999). Occasionally, a second non-parous female is present in an Olympic marmot family, which suggests possible reproductive inhibition. In the southern, bigamous hoary marmots, females may skip an additional year when both females would be expected to breed. When both females bred, the subordinate female produced about half as many young and one-fifth as many yearlings as the dominant female; this pattern was called partial reproductive suppression (Wasser and Barash 1983).

In both species, all group members hibernate together and juveniles postpone dispersal for at least two years. These species may have all of the attributes of cooperative breeders: delayed dispersal, reproductive suppression in at least some females, and the opportunity for summer and potentially winter alloparental care.

While the overall group structure is similar, some species (e.g., alpine – *M. marmota* – Arnold 1993a, and golden – *M. caudata aurea* – Blumstein and Arnold 1998) are more socially integrated during the summer active season than previously discussed species. These two species may exhibit all three attributes and may be classified as cooperative breeders. In these species, home ranges of all group members completely overlap during the summer and all individuals hibernate together in one hibernaculum (Arnold 1993a, Blumstein and Arnold 1998). Only a single adult female breeds in each social group sug-

gesting reproductive suppression of subdominant females. In alpine marmot groups, where the dominant, territorial female reproduces every second year, subordinate females do not breed during the skipped year (Arnold 1993a). Reproductive suppression may not be complete: in one case two adult females weaned young in one golden marmot social group (Blumstein and Arnold 1998), and subordinate female alpine marmots may start litters but never produce any surviving young (Arnold 1990a). Both species appear to be primarily monogamous. Recent evidence suggests that dominant adult male alpine marmots may suppress reproduction in subdominant males (Arnold and Dittami 1997). When male reproductive suppression fails, young males may mate with the breeding female (often their mother) suggesting that for alpine marmots, monogamy may merge into polyandry (Arnold et al. 1994). Golden marmot social groups with more than a single pair of adults tend to be male-biased suggesting the opportunity for polyandrous matings (Blumstein and Arnold 1998). Dispersal typically is postponed to age 3 or older. Overwinter thermoregulatory alloparental behavior is documented in alpine marmots (Arnold 1993a) and may occur in golden marmots (Blumstein and Arnold 1998). Briefly, older alpine marmots actively warm related pups (but not unrelated pups) in the hibernaculum which increases pup overwinter survival. Providing alloparental care relieves parents and increases their overwinter survival as well. Providing alloparental care thus increases helpers’ indirect fitness in two ways. Because males tend to remain in their natal group longer than females, and because males may not be totally reproductively suppressed (Arnold and Dittami 1997), alloparental behavior may be a strategy to ultimately gain direct fitness (see Reyer 1986) by siring their own young. Regardless, dispersal delayed past reproductive maturity, coupled with reproductive suppression in one or both sexes, and summer and winter alloparental care meet all the attributes of cooperative breeding.

The remaining marmots for which data are available are reported to hibernate socially (Table 1), exhibit delayed-dispersal (Table 1), and either exhibit singular breeding (*M. broweri* – Rausch and Bridgens 1989) or there are suggestions of reproductive suppression (Table 1 and Armitage 1996). However, singular breeding and reproductive suppression are neither universal, nor obligate. Bibikow (1996) reported that two-year-old gray marmots (*M. baibacina*) typically did not breed in their natal social group but did breed when colonizing recently vacated areas (e.g., following population reduction work), and high alpine populations of gray marmots sometimes have plural breeding (Mikhilyuta 1991). Causes and consequences of plural breeding need to be better studied.

Table 1. Degree of cooperative breeding in marmots and other selected sciurid rodents.

	DELAYED DISPERSAL?	SUMMER SOCIALLY INTEGRATED?	WINTER ALLOPARENTAL CARE?	REPRODUCTIVE SUPPRESSION?
Degree of cooperative breeding in marmots				
<i>M. montax</i>	NO (1)*	NO only females and pups until dispersal (1)	NO (2)	YES?† (3)
<i>M. flaviventris</i>	NO as yearlings YES (rare) females may delay (4)	YES some space use overlap within matriline (4)	NO in lower elevations (4) YES? in higher elevations (5)	YES (6)
<i>M. baibacina</i>	YES? (7)	NO "seasonally re-group" (7) do not maintain summer groups (8)	YES? group hibernate (9)	YES females (6, 10) multiple females may breed
<i>M. caligata</i>	YES (11, 12)	YES some space use overlap (13)	YES? group hibernate (11)	YES (11, 12)
<i>M. olympus</i>	YES (14)	YES some space use overlap (13)	YES? group hibernate (14)	YES females alternate years (14)
<i>M. camtschatica</i>	YES? (15)	YES mostly to fully socially integrated (16)	YES? group hibernate (15)	YES one breeding female (16)
<i>M. bobac</i>	YES (17, 18)	YES fully integrated but this varies geographically (19)	YES? group hibernate (37)	YES only one female gives birth each year (18)
<i>M. caudata aurea</i>	YES disperse > 2-yr olds (20)	YES fully integrated (20)	YES? group hibernate (20)	YES females (20)
<i>M. marmota</i>	YES (21)	YES (13, 21)	YES? group hibernate (21)	YES females (21) YES males (22)
Species that require further study for rough classification				
<i>M. broweri</i>			YES? group hibernate in single nest (23)	YES (23)
<i>M. himalayana</i>				
<i>M. menzbieri</i>	YES? (24)	YES integrated (24)	YES? group hibernate (38)	
<i>M. sibirica</i>	YES (25)	YES separate a bit during the summer (26)	YES? group hibernate (9)	
<i>M. vancouverensis</i>	YES (27)		YES? group hibernate (28)	YES? monogamy to polygyny under "special" conditions (27)

Table 1. (Continued)

	DELAYED DISPERSAL?	SUMMER SOCIALLY INTEGRATED?	WINTER ALLOPARENTAL CARE?	REPRODUCTIVE SUPPRESSION?
Degree of cooperative breeding in other ground-dwelling squirrels for which body-mass data was available				
<i>S. hieldingi</i>	NO (29, 30)	NO females and pups until dispersal (29, 30)	NO (31)	NO (32)
<i>S. parryii</i>	NO (29, 30)	NO females and pups until dispersal (29, 30)	NO (31)	NO (32)
<i>S. armatus</i>	NO (39, 40)	NO (41)	NO (40, 41)	YES? Greater proportion of yearling females bred following population reduction (40)
<i>S. tereticaudus</i>	NO (43, 44)	NO (44)	NO (44)	YES? Poor reproductive success associated with wounding and stress in high-density populations (43) Poorer reproduction by yearlings than expected by weight (44)
<i>S. richardsonii</i>	NO (29, 30)	NO, females and pups until dispersal (29, 30)	NO (31)	NO (32)
<i>S. saturatus</i>	NO (29, 30)	NO, females and pups until dispersal (29, 30)	NO (31)	NO (32)
<i>S. townsendii</i>	NO (29, 30)	NO, females and pups until dispersal (29, 30)	NO (31)	NO (32)
<i>S. columbianus</i>	YES (29, 30)	YES (29, 30)	NO (33)	YES? (32)
<i>C. ludovicianus</i>	YES (34)	YES (34)	(YES?) do not hibernate but nest communally (34)	YES (34)
<i>C. gunnisoni</i>	YES (35, 36)	YES (35, 36)	YES? (35)	YES (35, 36)
<i>C. leucurus</i>	NO (45)	YES (34, 46)	NO (34, 45)	NO (47)

* Numbers in parentheses refer to the following references: 1, Meier 1992; 2, Ferron 1996; 3, Snyder 1962; 4, Armitage 1991; 5, Johns and Armitage 1979; 6, Armitage 1996; 7, Berendyaev and Kul'kova 1965; 8, Bibikov and Berendyaev 1978; 9, Zhmina 1978; 10, Mikhilyuta 1991; 11, Holmes 1984; 12, Barash 1974b; 13, D. T. Blumstein unpubl.; 14, Barash 1973; 15, Mosolov and Tokarsky 1994; 16, Kapitonov 1978; 17, Ismagilov 1956; 18, LeBerre et al. 1994; 19, Shubin et al. 1978; 20, Blumstein and Arnold 1998; 21, Arnold 1993b; 22, Arnold and Dittami 1997; 23, Rausch and Bridgens 1989; 24, Maschkin 1982; 25, Sunzov 1981; 26, Letov 1978; 27, Bryant 1996; 28, Bryant 1990; 29, Armitage 1981; 30, Michener 1983; 31, Arnold 1993a; 32, Armitage 1986; 33, Elliott and Flinders 1991; 34, Hoogland 1995; 35, Rayor 1985; 36, Rayor 1988; 37, Bibikov 1996; 38, Bibikov 1996; 39, Knopf and Balph 1977; 40, Slade and Balph 1974; 41, Balph and Stokes 1963; 42, Neal 1965; 43, Dunford 1977a; 44, Dunford 1977b; 45, Clark 1977; 46, Tileston and Lechleitner 1966; 47, Bakko and Brown 1967.

† Question mark implies possibility inferred from reported data. Further studies are required to work out the details of question marked criteria which may or may not be supported given additional data.

‡ Juveniles hibernating only with parents and littermate siblings have increased overwinter survival. Juvenile overwinter survival decreases with total group size. However, uncertainty over genetic relationships between group members prevented the key test of alloparental care: do juveniles hibernating with known non-littermate siblings survive at higher frequencies?

Why delay dispersal?

Typically, the evolution of cooperative breeding is studied by focusing on factors that might delay dispersal and then focusing on factors that might influence providing alloparental care. For many species, it is very difficult to tease apart factors that select for delayed dispersal from factors that select for alloparental care (Brown 1987).

Because marmots are large and typically have a short active season, dispersal may be postponed until after the first hibernation to provide favorable conditions for maturation. We derived a maturity index (MI, sensu Barash 1989):

$$MI_i = EM_i/EM_a,$$

where EM_i = the emergence mass of yearlings or two-year olds, and EM_a = the emergence mass of adults (Table 2). We used emergence mass to minimize the effects of seasonal fattening for hibernation and to provide an estimate of somatic growth for juveniles and yearlings. Note that we use yearling emergence mass to calculate juvenile MI and two-year-old emergence mass to calculate yearling MI. We interpret MIs comparatively and assume that the smallest MI at which any species can disperse illustrates the lower limit of dispersal in the genus. Large species with relatively short growing seasons would be expected to require more years to mature than smaller species or species with longer growing seasons. We assume that an interaction between body size and length of the active season accounts for the different numbers of years it takes a given species to reach the minimum dispersal MI. Similarly, we assume that the smallest MI at which any species can reproduce illustrates the threshold for reproductive maturity. Thus, we define delayed dispersal as dispersal postponed beyond the threshold for reproductive maturity. Again, we compare the time at which a given species reaches the lower-critical MI limit for breeding and when it disperses from its natal social group.

Dispersal seems possible when $MI \geq 0.5$. Only the woodchuck (*M. monax*) achieves a $MI \geq 0.5$ in its first year (Table 2) and disperses before its first hibernation (Snyder et al. 1961). The MI of juvenile yellow-bellied marmots (*M. flaviventris*, K. B. Armitage unpubl.) is ≤ 0.40 and dispersal occurs after the first hibernation. The MI of juvenile *M. marmota*, *M. vancouverensis*, *M. sibirica*, *M. olympus*, *M. caligata*, *M. bobac*, and *M. caudata aurea* range from about 0.26 to 0.41 in their first year, and all disperse at age two or older (mass data from Barash 1973, 1989, Zimina 1978, Arnold 1993a, b, Heard 1977, A. A. Bryant pers. comm., D. T. Blumstein and W. Arnold unpubl.).

Reproduction seems possible the year after a MI of about 0.65 is achieved. For instance, juvenile *M. monax* with a MI of 0.67 reproduce as yearlings. The MI at the end of the second growing season of yearling female *M. flaviventris* and *M. marmota* is 0.76 and 0.79 respectively, and both species can breed as two-year-olds, although most breed later. The MI for yearling female *M. caudata aurea*, *M. caligata*, and *M. olympus* varies from 0.66 to 0.77 but they do not breed as two-year-olds. The MI of female *M. caudata aurea* reaches 0.88 at age two, but no known-age three-year-old ever reproduced. Although the MI of yearling *M. vancouverensis* is 0.86, no known-age two-year-old female has bred. *M. vancouverensis* can breed at age 3, but the average age of first reproduction is 4.3 yr (Bryant 1996). If MI values of 0.5 and 0.65 are considered thresholds for dispersal and breeding respectively, then *M. vancouverensis*, *M. caudata aurea*, and potentially *M. marmota* delay dispersal and breeding or both beyond reproductive maturity. Available data from other species (*M. baibacina*, *M. bobac*, *M. caudata caudata*, *M. caligata*, *M. flaviventris*, *M. broweri*) indicate that dispersal and reproduction are delayed beyond maturity, and (when reported) only a single adult female group member breeds (Rausch and Bridgens 1989, Armitage 1996, Bibikow 1996). While environmental resource limitation may explain slow growth, singular breeding and delayed reproduction are consistent with widespread reproductive suppression of younger ani-

Table 2. Maturity index (MI) and age of first reproduction for nine species of marmots. All values recorded to the nearest whole number. Unless noted, references for body mass data used to calculate MI are reported in Armitage and Blumstein (1999).

	Juvenile	Yearling	Two-year-old	Age of first reproduction
<i>M. monax</i>	0.67	0.87		1 ¹
<i>M. flaviventris</i>	0.39	0.76	1.0	2 ²
<i>M. caligata</i>	0.37	0.71		3 ³
<i>M. olympus</i>	0.42	0.77		3 ⁴
<i>M. bobac</i>	0.41			3 ⁵
<i>M. caudata aurea</i>	0.37	0.66	0.88	> 3 ⁶
<i>M. marmota</i>	0.39	0.79		2 ⁷
<i>M. sibirica</i>	0.26			2 ⁵
<i>M. vancouverensis</i>	0.38	0.86	1.0	3 ⁸

References: 1, Snyder 1962; 2, Armitage 1991; 3, Barash 1974b; 4, Barash 1973; 5, Zimina 1978; 6, Blumstein and Arnold 1998, unpubl.; 7, Arnold 1990a; 8, Bryant 1996.

mals by older animals; a pattern clearly evident in the wild and in captivity. When the territorial pair of wild *M. marmota* breeds, adult subordinates are suppressed to various extents (Arnold 1993b, Arnold and Dittami 1997). In a captive colony of *M. broweri* containing multiple adults of both sexes, only the two original adults bred in six consecutive years (Rausch and Bridgens 1989).

Other ground-dwelling sciurids have similar patterns. Those yearling female black-tailed prairie dogs (*Cynomys ludovicianus*) that reach a MI of about 0.84 breed; however about 90% of the yearling females have a MI of about 0.63 and do not breed. Most females do not disperse whereas yearling males, with an average MI of about 0.65 during the breeding season, disperse (Hoogland 1995). While the decrease in per capita reproduction with an increase in coterie size could result from resource limitation, it also could result from reproductive suppression. Given the prevalence of infanticide in black-tailed prairie dogs (Hoogland 1995), reproductive suppression seems a likely mechanism. Similarly, juvenile *C. gunnisoni* reach a MI of 0.84–0.90, but delay dispersal until after their first hibernation or later. Some yearling females reproduce (Rayor 1985). Because about 50% of the adult females produce litters any year, reproductive suppression may occur (Rayor 1985, 1988). By contrast, juvenile *C. leucurus* reach a MI of 0.72 and disperse as young and reproduce as yearlings (Tileston and Lechleitner 1966, Clark 1977). Juvenile *Spermophilus armatus*, *S. parryii*, *S. richardsonii*, *S. saturatus*, *S. tereticaudus*, and *S. townsendii* have a MI of about 0.76 or larger; all disperse as juveniles and reproduce as yearlings (Armitage 1981, Michener 1983, Arnold 1993a). Typically, more than 90% of the adult females breed; only in *S. armatus* and *S. tereticaudus* is there a suggestion of reproductive suppression (Table 1 and Armitage 1986). By contrast, juvenile female *S. columbianus* develop an average MI of 0.6 but disperse as yearlings, therefore, dispersal is delayed. Yearling *S. columbianus* typically do not breed (Murie et al. 1980). However, in one population (Festa-Bianchet 1981) some yearling females had a MI of 0.9 and reproduced, while yearlings in the same population whose MI averaged 0.76 did not breed nor did any of nine yearlings in another study area whose MI averaged 0.65. Reproductive suppression may occur occasionally as only 65–84% of the adult females reproduce (Armitage 1986).

The postponement of dispersal until after the first hibernation occurs in all species whose MI is <0.5 after the first summer of growth. The larger body size of marmots, coupled with a long winter requires that somatic growth of young be supplanted by fattening to provide energy for hibernation. Thus, environmental harshness influences the number of growing seasons required to mature.

Mortality factors probably influence dispersal decisions in those species who delay dispersal for one or more years after reaching the maturity threshold (MI = 0.65). For instance, dispersing yellow-bellied marmots suffer higher predation than philopatric marmots (Van Vuren and Armitage 1994). The increased mortality risk of dispersers, coupled with variation in breeder tenure, which in turn influences how long a subordinate individual must wait before breeding, may influence dispersal decisions in other taxa (e.g., Koenig et al. 1992, Lucas et al. 1997) and in marmots (Armitage 1992, 1996, Arnold 1992). Additionally, the probability of successful immigration into a breeding population (assuming the individual avoids predation) should also influence dispersal decisions. In *M. flaviventris*, immigration rarely occurs in an established population and is most likely to occur when space becomes available due to mortality of previous residents (Armitage 1991). Specific models (sensu Koenig et al. 1992) need to be developed to examine the relative importance to marmots of these and other factors suggested to delay dispersal in other taxa.

Is singular breeding the result of marmots avoiding inbreeding with close kin?

We believe that singular breeding is the result of reproductive competition and does not come about by marmots actively avoiding mating with close kin. We acknowledge that the question needs further study because the degree and type of singular breeding is a key question in the evolution of cooperative breeding (Emlen 1997). We may see singular breeding because individuals actively avoid inbreeding (e.g., Koenig and Pitelka 1979), because there is reproductive competition between dominant breeders and subordinates that leads to singular breeding (e.g., Emlen and Wrege 1992), or because it is the result of the outcome of both these processes (e.g., Koenig et al. 1998). Several lines of evidence suggest that singular breeding in marmots does not come about by actively avoiding breeding with close kin.

Adult male alpine marmots who have not dispersed from their natal group occasionally may join their father in mating with their mother (Arnold et al. 1994, Arnold and Dittami 1997). Arnold and Dittami (1997) noted that dominant males actively suppressed reproduction in other group males but did so in a way that reflected the relative cost of suppression. As their sons matured, the net cost of suppressing them was greater than the net cost for suppressing unrelated adult males. Thus, older sons may have been permitted to reproduce (see also Emlen 1997). These observations are consistent with the reproductive competition interpretation.

A degree of inbreeding may be tolerated in marmots and other cooperative breeders (e.g., Craig and Jamieson 1990, Honeycutt et al. 1991). Many marmot species experienced a periglacial expansion during the Pleistocene (Zimina and Gerasimov 1973, Bibikow 1996). Following the retreat of the Pleistocene glaciers, species ranges were restricted to the mountains, populations became isolated, and some species went through population bottlenecks that today can be inferred by relatively low genetic variability (Preleuthner and Pinsker 1993, Rassmann et al. 1994, Kruckenhauser et al. 1996). For some species, a history of some inbreeding may have made them more tolerant to periodic inbreeding today (e.g., Shields 1993), high costs of inbreeding avoidance may select for some degree of inbreeding tolerance (Waser et al. 1986), or population sizes naturally fluctuated in such a way that resulted in periods of time where relatives were more or less likely to mate (Rowely et al. 1993).

Many cooperative breeders live in patchy habitats which presumably are subjected to metapopulation dynamics. If so, a history of fluctuating population sizes and recolonizations may have removed some deleterious genes and generated some tolerance to periodic inbreeding. In this case, the fact that close kin (e.g., offspring-parents) do not mate, may emerge from demographic situations where parents and mature offspring are not in the same social group at the same time, or from direct reproductive competition leading to reproductive suppression between parents and their same-sex offspring (Pusey and Wolf 1996).

In yellow-bellied marmots, males disperse as yearlings before they breed. However, there is no evidence that females who are recruited into the social group avoid mating with their fathers or vice versa. Typically, male breeder tenure is less than three years; by the time a daughter matures, her father is not likely to be present (Armitage 1974). However, in about 1.2% of matings, a father was the only male present during the short breeding season and was assumed to have been the only male that could mate with one of his daughters (K. B. Armitage unpubl.). A previous allozyme study found that young were unquestionably fathered by the resident male (Schwartz and Armitage 1980). While parents and the offspring of some cooperatively breeding birds are never observed to mate (Ligon and Ligon 1990), some degree of inbreeding is seen in other cooperative breeding birds (Rowely et al. 1993, Koenig et al. 1998) and mammals (Hoogland 1995, Keane et al. 1996).

In the most social marmot species, it is extremely rare for more than one female in each social group to wean a litter. Embryo reabsorption is common in marmots (Bibikow 1996), and we predict that detailed studies will reveal that it is the subordinate females who are most likely to reabsorb their embryos. Sometimes more than one female in a social group lactates, but it is

extremely rare that more than one female weans young (Arnold 1990a, Mikhilyuta 1991, Blumstein and Arnold 1998). These observations are consistent with subordinate females mating but later being reproductively suppressed by dominant females.

Thus, there is evidence of reproductive suppression in both males and females. Unlike some birds, where incest-avoidance taboos "suppress" reproduction among family members, reproductive competition between potential breeders may be the norm in the most social marmots and is seen in some other cooperative breeding mammals (e.g., Creel and Waser 1997, French 1997). At a higher level, a cost of social complexity is a reduction in the proportion of breeding adult females (Blumstein and Armitage 1998). Presumably, there are benefits to individuals that outweigh these costs. One benefit is increased survival; beyond age 1, survivorship is greater in the more socially integrated species – *M. olympus*, *M. vancouverensis*, *M. caudata aurea* – than in *M. flaviventris* (Blumstein et al. 1999).

Why help?

We believe that environmental harshness is an important factor driving the evolution of helping behavior. Environmental harshness can be viewed three ways. First, harsh environments are those with short growing seasons. Short growing seasons mean that animals must quickly gain mass and store fat for the long winter. Second, food availability influences the ability to grow. In environments with limited food resources, the rate of somatic growth may be limited and maturation may be delayed. Third, the temperature in the hibernaculum influences the cost of thermoregulating during the winter. Colder burrows require animals to spend more energy during hibernation.

More generally, sociality in marmots seems to be environmentally forced, much as it is in cooperatively breeding birds (e.g., Brown 1987, Koenig and Mumme 1987, Koenig et al. 1992). As sciurid rodent social complexity increases, the per-capita reproductive rate decreases, as does the percent of females that breed (Blumstein and Armitage 1998). Any benefit from sociality must overcome these fundamental life-history costs.

Group-living marmots probably receive predator dilution benefits from grouping (Hamilton 1971). Once grouped there is evidence that social complexity drives the evolution of complex alarm communication (Blumstein and Armitage 1997). Thus grouped marmots presumably receive additional antipredator benefits from grouping. And, ectoparasites, in at least one marmot species, are not an obvious cost of sociality (Arnold and Lichtenstein 1993). Nevertheless, we and others (e.g., Barash 1989, Arnold 1990a, b) suspect that envi-

ronmental constraints are the main cause of sociality in marmots because of their impact on maturation and dispersal.

Marmots living in harsh environments delay dispersal and delayed dispersal results in the formation of extended family groups. Overwinter mortality, particularly for juveniles, is often a significant cause of marmot mortality (Armitage and Downhower 1974, Arnold 1993b, Blumstein and Arnold 1998). Group members should therefore hibernate together for two reasons (Arnold 1993a, b). First, suitable hibernacula may themselves be limited so animals may benefit by hibernating in the same suitable burrow. Second, huddling is energetically advantageous to all participants because the relative amount of surface area exposed to the cold burrow environment is reduced (e.g., *M. camtschatica* – Vasilev 1992). Huddling would be particularly advantageous in habitats with long and cold winters. Once group hibernation and social thermoregulation are present, all pre-requisites for the evolution of parental and alloparental care during the winter exist.

Woodchucks of all ages typically hibernate alone and lose a large absolute amount of body mass. Solitary hibernation seems tolerable because woodchucks have a long active season and therefore hibernation is relatively short. Interestingly, little is known about the behavior or ecology of woodchucks living in northern Canada or Alaska, which presumably must hibernate longer and in a colder environment than the more southern populations where woodchucks have been studied. However, woodchucks in Québec lose a greater percentage of their body mass during hibernation than woodchucks in Pennsylvania (Snyder et al. 1961, Ferron 1996).

Adult yellow-bellied marmots typically hibernate alone in the winter. In the field, single young can survive their first winter (K. B. Armitage unpubl.), but young often hibernate with others (Johns and Armitage 1979, Lenihan and Van Vuren 1996). In the laboratory, juveniles hibernated in the same cage huddled and exhibited coordinated bouts of arousal (K. B. Armitage, D. T. Blumstein and B. C. Woods unpubl.). Thus, alloparental thermoregulation may not be required in yellow-bellied marmots at 2900 m where this species has been intensively studied. However, at 3400 m where the climate is harsher, social hibernation among adults is more common (Johns and Armitage 1979).

Obligate group hibernators tend to live in areas with less above-ground standing crop than non-obligate hibernators (Table 1 in Armitage and Blumstein 1999) and/or in areas with longer winters (Bibikow 1996). Above-ground standing crop must be viewed cautiously. We know that some marmots forage selectively (e.g., Armitage 1979, Blumstein and Foggin 1997). We also know that overall food availability

ignores food composition – plant fatty acids may be particularly important for fat deposition (Florant et al. 1993). Nevertheless, perhaps in response to limited food and long winters, individuals hibernate together. Even with group hibernation, adults hibernating in groups lose a greater proportion of body mass overwinter (\bar{X} = 38%) than solitary yellow-bellied marmots (\bar{X} = 29%), and/or southern populations of woodchucks (\bar{X} = 29%; data and further discussion in Armitage and Blumstein 1999). Once individuals hibernate together, older animals may provide thermoregulatory alloparental care. Like alloparental care in other taxa, social thermoregulation seems to be a facultative strategy by which helpers gain indirect fitness by increasing their juvenile relatives survival. Alpine marmots help warm their juvenile relatives, while unrelated alpine marmots do not help (Arnold 1993a). Additionally, by remaining in the group and gaining indirect fitness, young males may also increase their chance of ultimately gaining direct fitness by breeding with the dominant female (Arnold and Dittami 1997).

Applied issues

In addition to the theoretical importance of documenting and studying the proximate and ultimate basis of cooperative breeding, understanding the distribution of cooperative breeding is important for wildlife conservation and management (Komdeur et al. 1995, Komdeur and Deerenberg 1997). Two marmot species are listed in the IUCN Red Data Book and at least five more of the 14 species are threatened (Anon. 1996). In Eurasia, hundreds of thousands of marmots are hunted annually (both legally and illegally) for food, fur, and fat (Bibikow 1996). As both conservation strategies and production strategies, marmots are bred in captivity and wild populations are managed (Bibikow 1996). In all of these cases, it is desirable to maximize marmot production.

We have two suggestions to maximize production. If sociality is environmentally forced, then it may be possible to increase available habitat. Such a manipulation might lead to animals dispersing and breeding as they mature rather than delaying dispersal and reproducing long after maturity. In fact, population reduction of gray marmots (*M. baibacina*) is followed by the movement of young animals into the vacated area and an eight-fold increase in reproduction by two-year-old females (Pole 1992). Our review suggests that reproductive suppression may be common in most species. Thus, to maximize production, managers must avoid situations that enable marmots to reproductively suppress each other. We suggest that in cases where production is to be maximized in cap-

tivity, it may be profitable to remove marmots from their natal groups as yearlings. In more natural conditions, alloparental behavior by older relatives may be crucial for juvenile overwinter survival (Arnold 1993a). In those cases, it might be more prudent to remove two-year-olds from their natal group. Thus, juveniles may gain the thermoregulatory benefits from hibernating with older relatives, and older animals will not delay their first reproduction long after reproductive maturity. Removed animals may be used to form captive breeding groups or may be translocated to new locations.

The future

Marmots provide an excellent taxon in which to study factors that influence dispersal, reproductive suppression, and alloparental care. Species vary in the time to natal dispersal which influences the opportunity for alloparental care and therefore cooperative breeding. Species with delayed dispersal exhibit facultative reproductive suppression. Nonbreeding relatives of the most social marmots may facultatively provide critical thermoregulatory alloparental care. Clearly, much more work is required to clarify the details of cooperative breeding in marmots. Arnold's (1990a, b, 1993a, b) pioneering work on factors that influence social thermoregulation can be used as a model for future studies to examine the degree to which other species provide thermoregulatory alloparental care.

There is no published well-supported phylogeny that includes all sciurids or even all marmots (Blumstein and Armitage 1997). Once developed, the evolution of the attributes of cooperative breeding can be studied with current phylogenetic techniques (Harvey and Pagel 1991). Such analyses may clarify questions such as, does alloparental care (or a specific type of alloparental care) evolve after delayed dispersal? Even without a well-supported phylogeny, marmots provide an outstanding opportunity to study the evolution of cooperative breeding in a group of species that have different attributes of cooperative breeding, and that may be facultative cooperative breeders. Explaining facultative cooperation may help us understand the ecological constraints that led to differences among species. We eagerly look forward to more studies clarifying the details of cooperative breeding in marmots and other ground-dwelling sciurids.

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