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Social structure and facultative mating systems of hoary marmots (*Marmota caligata*)

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Abstract

Mate-choice theory predicts different optimal mating systems depending on resource availability and habitat stability. Regions with limited resources are thought to promote monogamy. We tested predictions of monogamy in a social rodent, the hoary marmot (*Marmota caligata*), at the northern climatic extreme of its distribution. Mating systems, social structure and genetic relationships were investigated within and among neighbouring colonies of marmots within a 4 km^2 valley near Kluane National Park, Yukon, Canada, using 21 microsatellite loci. While both monogamous and polygynous populations of hoary marmots have been observed in the southern reaches of this species' range; northern populations of this species are thought to be predominantly monogamous. Contrary to previous studies, we did not find northern hoary marmot social groups to be predominantly monogamous; rather, the mating system seemed to be facultative, varying between monogamy and polygyny within, as well as among, social groups. These findings reveal that the mating systems within colonies of this species are more flexible than previously thought, potentially reflecting local variation in resource availability.

Keywords: hoary marmot, *Marmota caligata*, mating system, microsatellites, parentage, social structure

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Introduction

Mating systems are influenced by variation in habitat productivity across a diverse range of taxa (e.g. Elle & Hare 2002; Bryja & Stopka 2005; Kudo & Kasagi 2005; Wong, Munday & Jones 2005; Rossmanith *et al*. 2006). In mammalian systems in particular, limited resource availability in harsh environments has been associated with a monogamous mating strategy (Kleiman 1977; Wittenberger & Tilson 1980; Smith & Ivins 1984; Clutton-Brock 1989). Presumably, monogamy occurs when resources are limited so that females avoid competition with other females for resources on the male's territory (Wittenberger & Tilson 1980), and males cannot monopolize more than one female during breeding (Emlen & Oring 1977). The genus *Marmota* provides an example of the variation that can exist in mating strategies among closely related species. Marmot mating systems are most often either monogamous or polygynous (Arnold 1990; Blumstein & Armitage 1998, 1999) with social behaviour varying within and among species (Armitage 2003). The degree of marmot sociality, and hence monogamy (Allainé 2000), has been hypothesized to increase with environmental harshness (higher altitudes and latitudes) where shorter growing seasons lead to delayed juvenile dispersal, longer protection and provision by parents, and to larger social groups (Barash 1974a; Arnold 1990; Armitage 1999; Allainé 2000). It has also been proposed that marmot species with a monogamous mating system gain advantages through suppressing reproduction in subordinates for the benefits of social thermoregulation (Allainé 2000); efficiencies that would likely be all the more important in harsher climes. In North America, highly social marmots (*Marmota caligata*, *M. vancouverensis* and *M. olympus*) are considered to be generally monogamous [although some populations are observed to have polygynous social groups (Armitage 2003)], whereas moderately social and solitary marmots (*M. flaviventris* and *M. monax*, respectively) display polygyny (Armitage & Johns 1982). Here, we explore the presumed monogamous mating system of *M. caligata* in the northern extremes of its distribution.

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Hoary marmots (*M. caligata*) are one of the largest members of the squirrel family (Sciuridae), weighing up to 8–10 kg and reaching a body length of 50 cm. The species inhabits areas with rocky talus slopes and alpine tundra vegetation throughout northwestern North America and is distributed from the Rocky Mountains (north from Montana and Idaho) to the Pacific coast of British Columbia and Alaska (Banfield 1974). Within the Yukon, its distribution is less continuous, spanning the mountainous territory from the Mackenzie mountains west to Alaska (Banfield 1974). Hoary marmots are gregarious, normally existing in family groups of a dominant male, adult females, yearlings, infants and socially subordinate males on the periphery of the dominant males' home-range (Barash 1974b, 1976, 1981). All members of the family group hibernate together (Holmes 1984). Dominant females are thought to be able to suppress the reproductive activity of other adult females within the colony (Wasser & Barash 1983; Barash 1989; Armitage 1999; Blumstein & Armitage 1999) and only have a litter every other year (Barash 1974b, 1989; Lee & Funderburg 1982). Hence, the mating system of the species is normally presumed to be monogamous (Holmes 1984), although polygyny has been observed in southern populations (Barash 1974b, 1989; Wasser & Barash 1983). Holmes (1984) suggested that the two factors explaining the variation in the mating strategies within this species were distance between hibernacula and forage availability. Both of these resources are thought to be in limiting quantities in northern regions of this species' distribution, and hence Holmes' (1984) reasoning as to why he exclusively observed a monogamous mating strategy in Alaska relative to observations of polygyny in some southern populations.

In this study, we investigate parentage, social structure and mating systems of a northern population of hoary marmots in the southwest Yukon Territory, Canada, using microsatellite loci. Marmots found within this location are representative of a population in as harsh an environment as has been studied to date, and thus elucidating the mating system of this population provides a robust test of hypotheses of social- and mating-system evolution. Our objectives were to (i) verify visual observations of parentage and reproductive dominance within the population using molecular markers; (ii) elucidate parental relationships that were not observed; and (iii) reveal the mating-system strategies within different social groups of this northern hoary marmot population. It is important to note that in order to clearly test hypotheses relating environmental variables to mating strategies, ambiguities in the interpretation of mating success must be avoided. Molecular investigations of social groups and underlying mating systems have proven invaluable in providing further insight into social and life-history evolution that have been difficult to determine from observation alone (Ross 2001). For instance, behavioural observations of copulation, dominance and other fitness correlates have often proven to be inadequate predictors of true parentage (Avise 1994; Hughes 1998). In turn, this has challenged long-held paradigms in behavioural ecology, such as the presumed monogamy of many avian species (Gibbs *et al*. 1990; Birkhead & Møller 1992, 1998; Petrie & Kempenaers 1998; Conrad *et al*. 2001; Richardson *et al*. 2001) and specific behavioural measures of reproductive success in polygynous ungulates (Coltman *et al*. 1999).

Materials and methods

Social-group observations

Marmots were studied near Kluane National Park in the Ruby Ranges of the southwest Yukon Territory, Canada (138°W 62°N; Fig. 1) in a 4-km^2 area at an elevation of 1650–1900 m. Here, the snow-free growing season is approximately 70 days with a mean July temperature of approximately 7 °C (Hik *et al*. 2001). The terrain is made up mostly of boulderfields (36%) and vascular plants (27%). The remainder consists of bare ground, mosses and lichens. In mid-August, the peak biomass of available forage ranges from 42 g/m^2 adjacent to boulderfields, to 71 g/m^2 further into the meadows and is dominated by *Dryas octopetala*, *Carex* spp. and *Salix reticulata* (Hik *et al*. 2001). The amount of available forage here is considerably less than the 117 g/m^2 determined by Holmes (1979) in south-central Alaska in what is the only other study of high-latitude hoary marmot populations.

Marmots were live-captured from 1999 to 2002 in wire cage traps (66 × 23 × 23 cm and 107 × 38 × 51 cm; Tomahawk Live Trap Co., Tomahawk, Wisconsin) and were marked with uniquely numbered metal eartags (Monel 1005–3, National Band and Tag Co., Newport, Kentucky). To facilitate identification without recapturing, each marmot was marked with a unique combination of one- or two-coloured wires attached to the eartag and a one- or two-character–letter/number combination dyed into the fur above the tail (Clairol Hydrience, #52 Black Pearl, Clairol Canada, Montreal, Quebec or Nyanzol-D American Color and Chemical Corp., Charlotte, NC). More details are provided by Karels *et al*. (2004).

Locations of trapped ($n = 643$ captures) and observed marmots ($n = 3729$ sightings) were recorded according to a north-orientated grid surveyed and marked with wooden stakes at 50-m intervals. Observations were recorded by all personnel conducting field work in the study area, including those that were not working directly on this study or this species.

Observation and trapping locations were pooled and analyzed using the overlap routine in program Ranges V (Kenward & Hodder 1996) to detect social groupings. Marmots with > 75% overlap in the 95% kernel estimate

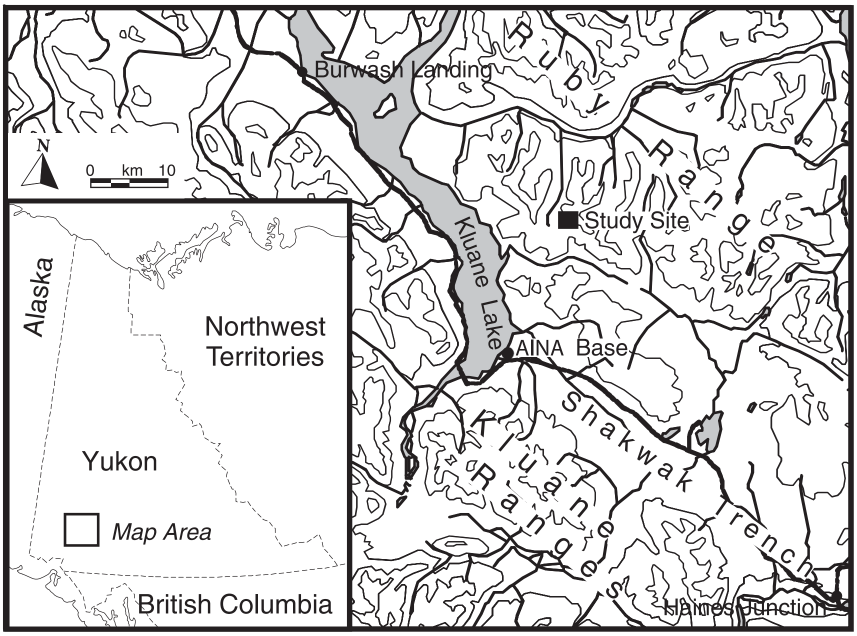

Fig. 1 Hoary marmots were studied in the Ruby Ranges of the southwest Yukon Territory, Canada (138°W, 62°N), approximately 30 km from the Arctic Institute of North America (AINA) research base. The study area was located at high elevation (1650–1900 m).

(Worton 1989) of home range were assigned to the same social group. We then verified the social group assignments of individuals continuously during the duration of the study from observations of behaviour and social interactions between individuals. Observations of marmots sharing the same hibernaculum and non-agonistic interactions between individuals were used to verify our social-group assignments. Young of the year were assigned to the social group of their putative mother.

The dominant male of each social group was identified by morphological and behavioural characteristics. Large males (> 5 kg) with palpable testes, dark cheek patches and exhibiting territorial behaviour (i.e. scent marking by cheek rubbing of burrow openings and boulders) were considered to be the reproductive marmots in each social group. Only one marmot with all of these characteristics was found in each social group in a single year.

Based on visual observations, between nine and 11 social units were defined in each of the years of observation (Fig. 2). Samples were obtained from captures from within each group, including: group 1 ($N = 47$); group 2 ($N = 23$); group 3 ($N = 7$); group 4 ($N = 19$); group 5 ($N = 22$); group 6 ($N = 7$), a social group that appeared in the 2002 field season, formed by an adult male that dispersed from social group 5; group 7 ($N = 12$); groups 8, 9 and 10 that were difficult to distinguish prior to 2001 as observations were insufficient ($N = 45$); and group 11 ($N = 7$) that went extinct during the winter of 2001. Beyond the individuals found within the defined social units from visual observation, one male that was considered to be a floater between social groups and five samples from unknown social groups were also included in the analyses. Ear biopsies were obtained from 195 marmots, including 42 litters consisting of 135 young, between 1999 and 2002, which comprised approximately > 90% of the census population in the valley (T. Karels & D. Hik, unpublished).

Laboratory methods

DNA was extracted using a DNAeasy® Tissue Extraction kit (QIAGEN). Twenty-one polymorphic microsatellites were amplified using primers developed in Alpine marmots (*Marmota marmota*) (Goossens *et al*. 1998: SS-Bibl4, SS-Bibl18, SS-Bibl25 and SS-Bibl31; Hanslik & Kruckenhauser 2000: MS6, MS45, MS47 and MS53), the European ground squirrel (*Spermophilus citellus*) (Hanslik & Kruckenhauser 2000: ST10) and Columbian ground squirrels (Stevens *et al*. 1997: GS12, GS14, GS17, GS22 and GS25). Microsatellites were also developed from hoary marmots for this study (2g4, 3b1, 2h6a, 2h6b, 2h10, 2g2 and 2h15; see Kyle *et al*. 2004). Amplification conditions are given in Davis & Strobeck (1998). DNA fragments were visualized using an ABI Prism™ 377 DNA sequencer (PE Applied Biosystems Inc., Foster City, California). DNA fragments were analysed using the programs GeneScan™ analysis 2.02 and genotyper® 2.0 (PE Applied Biosystems Inc.).

Hardy–Weinberg equilibruim

Departures from Hardy–Weinberg equilibrium (HWE) were tested for each of the 21 loci using genepop 3.1d (Raymond & Rousset 1995) that uses a Markov Chain Method following the algorithm of Guo & Thompson (1992). genepop was also used to evaluate genotypic disequilibria among loci.

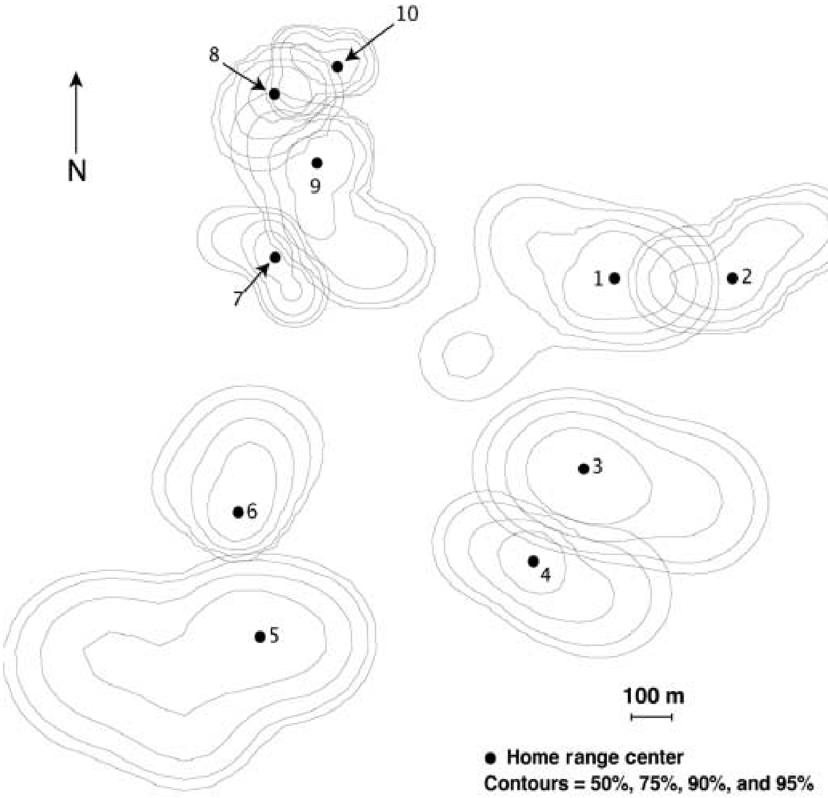

Fig. 2 Distribution and arrangement of ten hoary marmot social groups occurring in an alpine valley in southwest Yukon in 2002. Social group home range (50%, 75%, 90%, 95% contours represent lines of equal likelihood of location of the animal) was determined by adaptive kernel analysis of observed locations of all members of the social group. Social groupings of the marmots were initially identified by analysing the home-range distribution of individuals (individual data not shown). Marmots with > 75% overlap in home-range determined by 95% kernel analysis were categorized to the same social group. Based on visual observations, between nine and 11 social units were defined in each of the years of observation. Groups 8, 9 and 10 were difficult to distinguish visually prior to 2001, as observations were insufficient to discern if subsocial groups may have existed. Group 11 (not shown) went extinct during the winter of 2001.

Parentage

Visual parentage assignments were first verified by exclusion. Putative mothers that shared an allele at 21/21 loci were considered the true parent when the next-closest maternal match was excluded at two or more loci. Paternity was assigned if the next-closest father was excluded at two or more loci (taking the maternal genotype into account). The program CERVUS 2.0 (Marshall *et al*. 1998) was also used in cases where offspring had no putative parents match at 21/21 loci or when more than one individual could not be excluded as the parent using the aforementioned criteria. CERVUS 2.0 calculates the log likelihood ratio for each candidate parent and carries out simulations to estimate the critical difference in the log likelihood ratios of the candidate parents at 80% and 95% confidence levels. CERVUS was run with the following options for simulations: 10 000 cycles, 100 candidate parents, 0.75 candidate parents sampled, 0.98 of loci typed, 0.05 loci mistyped and 10 relatives with relatedness of 0.25 related to the known parents.

Results

Tests of disequilibria

After accounting for sample-wise error (Dunn–Sidak method; Sokal & Rohlf 1995), several loci were found not to be in HWE in some social groups including: group 1 (loci 2h6b, SS-Bibl4, SS-Bibl25, SS-Bibl31, MS6, MS47), group 2 (locus MS47) and pooled groups 8, 9 and 10 (locus SS-Bibl25). For group 1, MS6 and MS47 were found to deviate from HWE from an heterozygote excess whereas an heterozygote deficit lead to HWE deviations for locus SS-Bibl25 in group 1 and pooled groups 8, 9 and 10. Given that deviations from HWE did not occur in all groups for the same locus, all loci were retained for analyses. Genotypic disequilibrium was observed for several locus combinations in several social groups including: group 1 (GS14/2h15, 2h6b/GS17, SS-Bibl4/SS-Bibl31, 2h6b/MS6, SS-Bibl4/MS6, 2h6b/MS47, 2h15/MS47, SS-Bibl4/MS47), group 2 (2h6a/GS22) and pooled groups 8, 9 and 10 (GS25/GS14, GS14/SS-Bibl18, 2h15SS-Bibl18, GS12/SS-Bibl25, SS-Bibl4/MS47 and SS-Bibl31/MS47). As genotypic disequilibria were not found for these loci in several social groups, it is unlikely that they are physically linked and were therefore retained for further analyses. Despite all loci being retained for all analyses, based on parentage results from CERVUS 2.0, three microsatellite loci did have a relatively high frequency of null alleles: MS47, GS22 and SS-Bibl25, partially explaining the observed deficit of heterozygotes for some loci.

Parentage

Of the 42 litters studied over the 4-years period we were able to either corroborate or determine both maternity and paternity for 35 litters (83%) based on exclusion or CERVUS 2.0 parentage results with > 80% confidence (Table 1). There were seven cases of unresolved parentage: one unknown mother, four unknown fathers, and two cases where neither parent was resolved. Molecular findings were able to corroborate maternity in 34/36 (94.4%) litters where maternity had been assigned in the field. Only in two litters from group 7 in 1999 (our first year of study) did genetic and visual observations disagree (Table 1). In six litters where maternity was not assigned, genetic observations found a maternal match (Table 1). In 24/32 (75%) of litters where paternity was assigned by visual observations, the observations were corroborated by the molecular markers. We were also able to determine parentage for 10 litters that did not have associated visual observations (Table 1).

Social structure

The social structure of the groups within this study population were highly variable. Groups were primarily composed of between one and four reproductive females and one reproductive male, although two monogamous pairings were observed in group 2 when two male–female pairs were reproductive in 2001 (Table 1). Normally 0–3 nonreproductive adult male and female marmots were found within each social group, although up to 11 nonreproductive adult individuals of each sex were observed in group 1. The number of juveniles and young of the year was highly variable for the respective social groups.

Mating system

The mating system was clearly resolved in 33/42 litters: 14 litters were from monogamous pairings of dominant animals whereas 19 litters were from a polygynous system. Included in this total was a case of two monogamous pairings in social group 2 in 2001 where a subordinate male and female were reproductively successful. In nine of the litters from groups 7, 8, 9 and 10, social structure was not clearly defined; as such, we did not attempt to assign a mating system to these groups.

In the social groups that were clearly resolved, the mating system was not static. For example, in group 5 in 1999 there was a monogamous pair but in two subsequent years (2000 and 2002) polygyny was found to be the mating system. In group 2 in 2001, there was evidence of two monogamous mating pairs; however, only one monogamous pair was observed in 2000 and polygyny in 2002. Only monogamy was observed in group 11 (1999 only), group 3 (1999 and 2002) and group 4 (2000, 2001 and 2002). Polygyny was observed in group 1 for all four years of the study.

Table 1 Characteristics within each social group documented by both visual and molecular means. Marmots of unknown age were assigned a minimum age category based on statistical classification of ages using body measurements described in Karels *et al*. (2004). Table contains columns with the number of: observed individuals within the social group (N), which may differ from the number of animals captured from each social group; observed juveniles in each group (Juv); 1- and 2-year-old individuals (1 year and 2 years, respectively); nonreproductive males and females that are > 3 years of age (NRF (3 +) and NRM (3 +), respectively). Under the subheading of each group for each respective year, the number of litters and the number of juveniles sampled from each litter is listed. These rows also contain the parents of each litter, their respective minimum estimated ages (Female parent (min. age) and Male parent (min. age), respectively), and whether or not the molecular findings agreed with visual observations of reproductive success (Agreement (F/M))

Social group/year	*N*	Juv	1 year	2 year	NRF (3 +)	NRM (3 +)	Female parent (min. age)	Male parent (min. age)	Agreement (F/M)	Mating system
Group 1 1999	23	16	1	0	1	1				Polygyny
Litter 1		6					K (4)	60 (4)	y/y	
Litter 2		3					SA (4)	60 (4)	y/y	
Litter 3		1					L (4)	60 (4)	y/y	
Litter 4		2					O (4)	60 (4)	y/y	
Group 1 2000	22	6	12	1	2	0				Polygyny
Litter 1		2					O (5)	60 (5)	y/y	
Litter 2		3					T (5)	60 (5)	y/y	
Group 1 2001	36	16	3	12	0	1				Polygyny
Litter 1		3					O (6)	60 (6)	y/y	
Litter 2		4					SA (6)	60 (6)	y/y	
Litter 3		5					K (6)	60 (6)	y/y	
Litter 4		3					T (6)	60 (6)	y/y	
Group 1 2002	29	8	6	1	5	6				Polygyny
Litter 1		3					O (7)	60 (7)	y/y	
Litter 2		5					T (7)	60 (7)	y/y	
Group 2 2000	12	2	0	5	3	0				Monogamy
		2					unr	18 (4)	?/y	

Table 1 *Continued*

Social group/year	*N*	Juv	1 year	2 year	NRF (3 +)	NRM (3 +)	Female parent (min. age)	Male parent (min. age)	Agreement (F/M)	Mating system
Group 2 2001	17	6	2	0	5	0				Monogamy
		3					21 (4)	18 (5)	y/y	
		3					J (6)	13 (3)	y/n	
Group 2 2002	16	5	4	1	3	0				Polygyny
		3					20 (4)	18 (6)	y/y	
		2					22 (4)	18 (6)	y/y	
Group 3 1999	5	3	0	0	0	0				Monogamy
		3					P (4)	VG (4)	y/y	
Group 3 2002	9	5	0	0	1	1				Monogamy
		5					P (7)	VG (7)	y/y	
Group 4 2000	11	4	0	1	3	1				Monogamy
		4					U (5)	24 (4)	y/y	
Group 4 2001	9	2	2	0	3	0				Monogamy
		2					U (6)	24 (5)	y/y	
Group 4 2002	11	5	2	2	0	0				Monogamy
		5					U (7)	24 (6)	y/y	
Group 5 1999	10	1	0	1	2	4				Monogamy
		1					L2 (3)	50 (4)	y/*	
Group 5 2000	12	5	1	0	1	2				Polygyny
		3					L2 (4)	50 (5)	y/*	
		2					41 (4)	50 (5)	y/y	
Group 5 2002	15	9	1	1	1	0				Polygyny
		5					? (7)	C (5)	y/*	
		4					41 (6)	C (5)	y/*	
Group 6 2002	16	12	0	0	0	0				Polygyny
Litter 1		3					80 (3)	X (5)	y/y	
Litter 2 (NS)		—					—	—		
Litter 3 (NS)		—					—	—		
Group 7 1999	10	7	0	0	0	0				
		5					unr	unr	n/n	
		2					62 (5)	xx8 (4)	n/n	
Group 7 2001	12	3	0	7	0	0				Monogamy
		3			0	1	67 (6)	35 (5)	y/y	
Groups 8–10 1999	—	—	—	—	—	—				
		4					31 (3)	83 (—)	*/*	
		3					74 (—)	83 (—)	*/*	
		3					unr	unr	?/?	
Groups 8–10 2000	—	—	—	—	—	—				
		5					31 (4)	dy2 (—)	y/*	
		3					74 (—)	unr	*/?	
Group 8– 2002	6	3	0	0	1	0				Monogamy
		1					71 (5)	84 (4)	y/n	
Group 9– 2002	19	11	0	1	2	1				
		3					46 (3)	unr	y/n	
		3					74 (—)	unr	*/?	
Group 10– 2001	14	3	2	4	1	2				Monogamy
Litter 1		3					85 (4)	unr	y/n	
Group 10– 2002	15	3	3	2	3	2				Monogamy
Litter 1		2					56 (4)	2 (3)	y/n	
Group 11 1999	6	4	0	0	0	0				Monogamy
Litter 1		4					I (4)	D (4)	y/n	

Key: (NS), litter not sampled; unr, unresolved, parent of litter not sampled; y, agreement between visually observed parent and molecular findings; n, disagreement between visually observed parent and molecular findings; ?, parent not observed visually, nor by molecular means; *, parent not visually observed, but molecular findings found a putative parent among the sampled individuals.

Discussion

Previous studies have suggested that hoary marmots are monogamous in their northern distribution (Holmes 1984), whereas polygynous populations have been reported in southern regions of this species' distribution (Barash 1974b, 1989; Wasser & Barash 1983). The observed monogamy in northern regions was thought to be a consequence of resource limitations such as the distribution of hibernacula in northern regions and also low primary productivity as reflected in the plant above-ground biomass (Holmes 1984). In contrast to previous studies, we observed two main mating strategies in this study: monogamy in 14/34 litters and polygyny in 19/34 litters. These findings suggest that the mating strategy in this species is facultative and these observations lead us to refute the hypothesis that harsh environments (as related to higher altitudes and latitudes, shorter growing seasons and less vegetation biomass) result in a predominantly monogamous mating system in this social rodent. In our study, the smaller social groups were most likely to consist of a monogamous pair whereas in the larger groups, polygyny predominated. It is unclear if mating systems were linked to habitat quality, male fitness or temporally variable resources. Regardless, the mating strategies employed by various social groups may have an important influence on survival and fitness given the potential benefits of larger groups in social thermoregulation during hibernation (Arnold 1990; Grimm *et al*. 2003; although see Blumstein & Arnold 1998; Armitage & Woods 2003).

Visual and molecular identification of parent–offspring relationships

Genetic observations largely corroborated visual observations of parent–offspring relationships within the hoary marmot social groups in this study. However, several relationships were uncovered using microsatellite markers that were not recorded in the field, including the reproductive success of a subordinate male and the reproductive success of a male that was initially not considered to be dominant. These cryptic interrelationships are of importance to the understanding of the various mating strategies employed by hoary marmots and the selective forces acting on the species as a whole.

There was 94.4% agreement for maternal–offspring relationships and 75.0% agreement for paternal–offspring relationships. Most of the litters where parentage could not be resolved were from groups 7, 8, 9 and 10. These groups were not easily classified into social units from visual observations, given the large number of individuals and the lack of geographical separation between the groups. Group 7 is only separated physically from groups 8, 9 and 10 by a small creek and individuals frequently moved back and forth between all of these groups. Our inability to resolve these relationships suggests that the parents were not sampled. It is unlikely that the unresolved paternal relationships were from males from adjacent social groups or populations outside the study area, given the lack of movement between groups during breeding that occurs before spring emergence for many groups (T. Karels, unpublished).

There were some disagreements between the molecular and visual observations, most of which could be attributed to our lack of information on individuals and social groups in the first year of our study. In group 11 in 1999, visual observations suggested that two males and one female made up the social group, but that neither male sired the litter. A large male that was not initially assigned to any social group but resided near this visually defined social unit, was found to be the father in this instance. Upon reflection of the observational data, other evidence did suggest that this individual was the dominant male including its large size relative to the other males and its peripheral association with this social group. In two litters from group 7 in 1999, genetic observations disagreed with visual maternal assignments (Table 1). It was assumed that the dominant pair for group 7 in 2001 was also dominant in 1999, but this was not the case. In the pooled subgroups 8, 9 and 10, three male individuals were thought to be dominant, but we found no evidence to suggest that one of the individuals was reproductively successful, and the other two males were not the fathers of the litters they were assumed to have sired from visual observations (Table 1). The only other disagreement between visual and molecular observations was in social group 2. The dominant male from 2000 to 2002 was cuckolded by another male for one of the two litters in that year. This male marmot overlapped groups 1 and 2 and acted more like a floater between the two.

Social structure

The basic marmot social unit described by Barash (1974a) was also observed in this study population — a reproductive male, yearlings, young of the year, several adult females and nonreproductive adult males on the periphery of the social group. Social groups at our site were composed of between one and four reproductive females and one reproductive male; although, as mentioned, one case of serial monogamy was observed in group 2 (Table 1). Normally 0–3 nonreproductive, yet sexually mature, male and female individuals of three years of age or more were found within the social group, although up to 11 nonreproductive adults of each sex were observed in group 1. Most nonreproductive adults consisted of offspring from within the group. The number of juveniles and young of the year was highly variable for the respective social groups.

With the exception of the groups 7, 8, 9 and 10, where several different males were reproductively successful, male reproductive dominance appeared to be relatively stable. For instance, male individuals VG, 24, 18 and 60 were clearly the only reproductive males observed for their respective social groups for the duration of the study (Table 1). Only in social group 5 was succession clearly observed. In this case, individual C, a 4-year-old male thought to be from a social group peripheral to the study area, took over reproduction from individual 50 in 2001 when that marmot had disappeared after the summer of 2000.

In contrast to male dominance, female dominance was much more difficult to assign as several females were reproductive in the polygynous groups. According to Wasser & Barash (1983), in bigamous families of hoary marmots, when two females breed in the same year, the subordinate individual produces about 1/2 as many young and 1/5 as many yearlings as the dominant female. Furthermore, these authors state that no hoary marmot females have been observed to breed in successive years and in bigamous families, the females alternate in reproduction; that is, only one female reproduces in any given year. Polygynous social groups in our study did not clearly follow the behaviour observed by Wasser & Barash (1983), as we observed several cases of females reproducing concurrently with other females in the same social group and several cases of females sequentially reproducing over several years.

Female marmots are suspected to be able to suppress reproduction in female subordinates (Wasser & Barash 1983; Barash 1989; Armitage 1999; Blumstein & Armitage 1999; Hackländer *et al*. 2003). For instance, only dominant Alpine marmot (*Marmota marmota*) females from social groups with a stable social structure produce weaned young (Arnold 1990; Perrin *et al*. 1993), hence the primary mating strategy was presumed to be monogamous (although see Arnold 1990; Goossens *et al*. 1998). Two main mechanisms keep subordinates from reproducing in *M. marmota*; reabsorbing embryos from stress induced by the dominant female and infanticide by the dominant female (Arnold & Dittami 1997; Hackländer *et al*. 2003). In southern hoary marmot populations, 43% of females were observed to be reproductively successful by Barash (1989). Similarly, we found in our study that 45% of females were reproductively successful (average over 4 years, range from 32 to 71%, Table 1). It is unclear if the ratio of reproductively successful adult females to adult females is a matter of limited resources or of some level of reproductive suppression in hoary marmots, as dominant females are thought to be able to suppress the reproductive activity of other adult females within the colony (Wasser & Barash 1983; Barash 1989; Armitage 1999; Blumstein & Armitage 1999). The number of reproductive females ranged from one to four for the various social groups in this study. This may suggest that the female social hierarchy was not stable for several of the social groups, leading to unclear female dominance and, hence, polygyny. The lack of female hierarchy may in turn be due to the harsh environmental conditions in this region that has an important influence on the over-wintering survival of marmots (Barash 1989; Armitage & Blumstein 2002), although age structure has also been associated with social hierarchy in terms of reproductive suppression (Armitage & Schwartz 2000).

Mating systems

In the social groups that were clearly resolved, the mating system was not always static within the group. For example, in group 5 in 1999, there was a monogamous pair, but in two subsequent years that were sampled (2000 and 2002), polygyny was found to be the mating system. In group 2 in 2001, there was evidence of serial monogamy; however, monogamy was observed in 2000 and polygyny in 2002. Hoary marmots may be more similar in their mating strategies to other closely related North American marmot species, *M. flaviventris* and *M. olympus*, and less similar to the European Alpine marmot, *M. marmota*, than previously thought. Similar to findings for two other North American marmot species, hoary marmot social groups can consist of polygynous social groups (Barash 1975). For example, in *M. flaviventris* populations, larger habitat patches may be occupied by more than one polygynous group (Downhower & Armitage 1971; Armitage 1991). Furthermore, the facultative nature of the mating systems observed in this study of *M. caligata* was also observed by Salsbury & Armitage (1994) where the mating system of *M. flaviventris* males was observed to be both monogamous and polygynous in subsequent years.

Genetic parentage analysis has shown that for both, hoary marmots and *M. marmota*, monogamy is less frequent than previously described in other studies (Barash 1976; Holmes 1984; Arnold 1990; Perrin *et al*. 1993). In molecular investigations of *M. marmota* populations, both within-group and external-group parentage of nondominant individuals was observed (Arnold 1990; Goossens *et al*. 1998). Goossens *et al*. (1998) found evidence of monogamy (66.7%; 11 cases), extra-group, extra-pair paternity (24.2%; 8 cases), polygyny (3.03%; 1 case), within-group, extra-pair paternity (3.03%; 1 case) and promiscuity (3.03%; 1 case). Within our study of hoary marmots, we also found fewer than expected monogamous pairings and evidence of within-group, extra-pair paternity, but there was no evidence of extra-group copulation nor polyandry. These differences may be partially accounted for by the varying social settings (see Cohas *et al*. 2006) and habitats occupied by marmots in the respective studies. In Goossens *et al*. (1998), males were cuckolded by subordinate males, satellite males, and by neighbouring males. There seemed to be a relationship between extra-pair paternity and different habitat types in *M. marmota*, with the suspicion that better quality males occupy better quality habitat and are also less likely to be cuckolded (Goossens *et al*. 1998). South-facing slopes seemed to be preferred by *M. marmota* (Macchi *et al*. 1992; Allainé *et al*. 1994) and extra-pair cuckoldry was less frequent with less male turnover in these regions (Goossens *et al*. 1998). Further study will be required to verify if associations between habitat quality and mating system occur in hoary marmots, similar to that observed for *M. marmota*.

Recruitment of parents from within social group

For all litters where parent–offspring relationships could be assigned, there was a near-complete restriction of mate selection to within the social group. Extra-group parentage was not observed in this species in accordance with the aggressive behaviour of dominant males and females defending their territory against dispersing individuals (Holmes 1984). This is reinforced by the fact that there is little opportunity for extra-pair paternity in most groups, as hoary marmots in the Yukon rarely come above ground in the spring until well after breeding occurs, thus limiting the ability of external marmots to gain reproductive opportunities (T. Karels, unpublished), especially when the ground is snow-covered at this time of year (Armitage 2003). This finding is similar to that of *M. flaviventris*, where a molecular investigation found no evidence of 'cheating' between social groups (Schwartz & Armitage 1980), but contrasts with findings for *M. marmota* where Goossens *et al*. (1998) found 17.2% of juveniles were sired by males outside the social group. Nine *M. caligata* individuals were observed moving among social groups between years; seven males and two females. Of these, three male individuals were reproductively successful upon dispersal, as observed for individual C in our study who moved from a social group peripheral to the study area to become the dominant male in the 'West' group in 2002. These observations suggest that there was always a surplus of males in the population ready to take over vacancies.

Hoary marmot behaviour in this population seems similar to that observed for *M. flaviventris* by Schwartz & Armitage (1980) in their allozyme study. They found a low exchange rate between social groups with only 40/790 marmots moving between groups and only 15 that were thought to result in gene flow. Schwartz & Armitage (1980) also found that *M. flaviventris* had a preferential recruitment of female juveniles from their natal colony, similar to that observed for hoary marmots in this study. Yet another similarity exists in that immigrants were rarely from known satellite animals, but most often from outside the study area, for both *M. flaviventris* and hoary marmots. However, unlike the observations of *M. flaviventris* by Schwartz & Armitage (1980) where there was a near-total dispersal of male offspring from their natal colony, less male dispersal was observed in this study for hoary marmots.

Dispersal events to create new social units

In contrast to observations in previous studies, dispersal did not always occur in 2-year-old individuals as previously described (Holmes 1984; Armitage 1999; Blumstein & Armitage 1999), but in several instances, both male and female 3-year-old individuals had not yet dispersed from the social group (e.g. group 1 in 2002; Table 1). Increasing latitude and altitude is correlated with delayed dispersal of young and larger social groups (Arnold 1990), although much information also suggests that social organization strongly influences time of dispersal as well (Armitage 1999). When dispersal did occur, however, it sometimes resulted in reproductive success. In 2002, a 5-year-old male from social group 5, two 3-year-old females from group 7, and one female from an unknown source formed a new group. In this instance, one of the 3-year-old females mated with the 5-year-old male.

We have demonstrated that hoary marmots in the northern climatic extremes of their geographical distribution are not strictly monogamous, but that polygynous social groups are also observed in northern regions similar to observations of southern hoary marmot populations (Barash 1974b, 1989; Wasser & Barash 1983). Interestingly, both monogamous and polygynous social groups can exist within the same population of this species, revealing that social and mating structure in this species largely parallel one another. We are uncertain at this point which mating system provides the best fitness advantages for this species in its northern environment, and further demographic research should provide insight into this problem. Males would likely gain greater fitness in polygynous groups; however, to determine fitness advantages for females, further research would need to compare how offspring survive in monogamous vs. polygynous groups.

Molecular investigations can provide important insight in understanding mating systems that often elude us by observation alone. In our study, the rarity of extra-pair copulation was a surprise and distinguished the mating system of hoary marmots (*M. caligata*) from that of Alpine marmots (*M. marmota*). Furthermore, molecular investigations of additional populations of hoary marmots and other marmot species would clarify the interrelationships between social and mating structure with environmental variables such as latitude, elevation and resource availability.

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