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Immigration of a pregnant female in an alpine marmot family group: behavioural and genetic data

Immigration d'une femelle gravide dans un groupe familial de marmottes alpines : données comportementales et génétiques

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RÉSUMÉ

Un cas d'acceptation d'une femelle gravide par le mâle dominant d'un groupe familial de marmottes alpines *(Marmota marmota)* (population de la Grande Sassière, Parc national de la Vanoise, Alpes françaises) a été confirmé par l'étude conjointe de l'analyse du polymorphisme de 6 séquences microsatellites et d'observations comportementales. Ces premiers résultats semblent indiquer que le système de reproduction de la marmotte alpine est plus complexe qu'on ne le croyait, que la polygynie n'est pas exclue et que des femelles adultes peuvent rejoindre des groupes voisins. Cette acceptation aurait été interprétée comme une paternité extra-couple si des données de terrain très complètes n'avaient été disponibles. ▲

Mots clés : Marmota marmota, *paternité, système de reproduction, poil, PCR, microsatellites.*

ABSTRACT

The acceptance of a pregnant female by the dominant male of a family group of alpine marmots (Marmota marmota) *(population of La Grande Sassière, Parc national de la Vanoise, French Alps) was revealed by the combined results from microsatellite polymorphism analysis and behavioural studies. These first results seem to indicate that the mating system of the alpine marmot is more complex than previously thought, that polygyny cannot be excluded, and that adult females can join neighbouring groups. This acceptance would have been interpreted as an extra-pair fertilization if complete field data had not been available.* ▲

Key words: *Marmota marmota,* paternity, mating system, hair, PCR, microsatellites.

VERSION ABRÉGÉE

La marmotte alpine est un rongeur sciuridé. Elle fait partie d'un genre monophylétique présentant une complexité dans la structure sociale qui en fait un modèle particulièrement intéressant pour l'étude de l'évolution de la socialité chez les mammifères. *Marmota marmota* semble monogame mais des cas de paternités extra-couples ont été suggérés. Il se pourrait donc que le système de reproduction de la marmotte alpine soit plus complexe que prévu et que la polygynie ne soit pas exclue. Nous présentons ici le cas de l'acceptation d'une femelle gravide par le mâle dominant d'un autre groupe.

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Au cours de la saison 1993, dans le Parc national de la Vanoise (Alpes françaises), les individus de 2 groupes familiaux de marmottes (groupes A et B) ont été capturés, ainsi que les mâles adultes des groupes voisins (C et D). Des prélèvements sanguins ont été effectués sur toutes les femelles adultes pour des mesures des taux d'hormones sexuelles (progestérone). Des poils ont été prélevés pour les analyses génétiques de filiation. Des observations comportementales sur les interactions sociales ont été réalisées de mai à août 1993. L'ADN a été extrait des cellules se trouvant à la base des poils. Six séquences microsatellites ont été utilisées pour les typages génétiques. L'amplification de l'ADN a été réalisée par une réaction de polymérisation en chaîne (PCR) en 2 étapes. Les produits PCR ont été utilisés pour le marquage radioactif.

Le groupe A se compose de 8 individus (2 mâles adultes, un dominant et un subordonné, 1 femelle adulte et 5 jeunes de 1 an). Le groupe B se compose de 1 mâle, de 2 femelles adultes (une dominante et une subordonnée) et de 3 jeunes de

1 an. Des interactions agonistiques entre ces 2 femelles ont été observées. La femelle subordonnée a été chassée de son groupe et a migré dans le groupe A. La femelle dominante du groupe A a disparu à ce moment-là. Les taux hormonaux des 3 femelles montrent qu'elles étaient toutes les 3 gravides. Début juillet, 4 jeunes sont sortis du terrier principal du groupe A. Les résultats génétiques montrent une incompatibilité allélique entre les 4 marmottons, les 2 mâles du groupe A et la femelle dominante de ce dernier. Par contre, ils montrent une compatibilité avec le mâle adulte du groupe B et la femelle subordonnée de ce groupe qui a migré en A.

Les approches comportementales et génétiques ont permis de mettre en évidence un cas d'acceptation d'une femelle gravide et d'adoption de ses jeunes par le mâle dominant du groupe A. Ce résultat permet de discuter 3 points: (1) la possibilité qu'une femelle subordonnée mette bas dans un groupe qui n'est pas le sien à l'origine ; (2) la possibilité qu'un mâle adulte accepte des jeunes qui ne sont pas les siens ; (3) la possibilité que quelques mâles soient polygynes.

Il ressort de cette étude que la complémentarité entre les approches comportementales et génétiques est de première importance lorsque l'on travaille sur les systèmes de reproduction. Ce qui a été interprété comme une adoption en combinant le terrain et la génétique moléculaire aurait pu être interprété comme une paternité extra-couple si nous nous en étions tenus aux seules analyses génétiques. ▲

Sociality in mammals cannot be understood and analyzed without reference to the mating system [1-3]. Marmots are of considerable interest as diverse social and reproductive systems are represented in the genus *Marmota*. The least social of all marmots is *Marmota monax* in the New World [4-6]. *Marmota flaviventris* seems to be mainly arranged in one-harem colonies (unimale polygyny) [7-10]. The basic social structure of *Marmota olympus* and *M. caligata* consists of one adult male and one or more adult females (monogamous or bigamous) [4], depending on the harshness of environmental conditions [11]. All of the Eurasian species appear to be at least moderately social and many, like *Marmota marmota* and *Marmota camtschatica*, are highly social [4, 12, 13].

The alpine marmot (*Marmota marmota*) is a social rodent which inhabits the alpine and mountain-meadow zones of the Alps and western Carpathians. The family groups are composed of a dominant pair and their offspring of one or several years. *Marmota marmota* seems to be monogamous (field data) [12]. However, the main burrow harbors several sexually mature individuals (in addition to the dominant pair). Mating generally takes place in the burrow, so that in the field, it is very difficult to identify the father of each offspring. According to Arnold [13], the possibility of extra-pair paternity exists between a subordinate male and the dominant female. In the population of Berchtesgaden (Germany), Arnold [13] observed that some young were carrying genotypes incompatible with the territorial male of their family group using analysis of allozymes on 2 informative loci. However, in this population, Rassmann *et al.* [14] revealed a very low degree of polymorphism by multilocus DNA fingerprinting and a low genetic variability was also obtained by Preleuthner and Pinsker [15] in Austrian populations by electrophoretic analysis of allozyme variation. Therefore, a large-scale study of paternity analysis to confirm this result requires the use of more sensitive methods.

Microsatellites are short tandem repeats of mono-, di-, tri- or tetranucleotide sequence motifs, dispersed frequently and randomly throughout eukaryotic genomes and exhibiting high mutation rates. Therefore, microsatellites are useful for studying species that show low levels of variability with conventional markers such as allozymes or minisatellites and for populations that are inbred or have experienced severe geographic bottlenecks [16, 17].

Even with very polymorphic loci (and all the more so if related individuals can sire the same female), genetic studies can give ambiguous results. Parallel behavioural studies are of prime importance to understand genetic data. Following a previous work on the social organization of *Marmota marmota*, we investigated the precise mating system of this species. In this paper, we present a case of acceptance of a pregnant female by a neighbouring family group, as revealed by behavioural observations in the field, hormonal levels of the females, and confirmed by microsatellite polymorphism analysis. Our preliminary results raise questions about kin recognition and mating systems in *Marmota marmota*.

Materials and methods

Field procedures

The field study was conducted in the Réserve naturelle de la Grande Sassière, Parc national de la Vanoise (French Alps). The study site is at an elevation of 2,350 m.

Since 1990, 275 different marmots have been captured using live traps [18]. They were weighed, and sexed according to the anogenital distance [12]. Several marking devices were used. A numbered ear tag was attached to each ear. In addition, a piece of colored plastic was attached to one ear and the fur was dyed to ensure rapid identification of the individuals in the field. An electronic device (Transpondeur TROVAN) was injected under the neck skin. This provided a permanent individual identification, but reading by an adapted detector required marmots to be held by hand.

At the time of trapping, blood samples (4 ml) were collected in heparined tubes from the saphenal vein of each adult female. After centrifugation in the field (4,000 t/min during 10 min), the plasma was frozen for laboratory analysis. Hairs were also taken from each animal in order to carry out genetic analyses for filiation. They were stored in individual envelopes and kept dry in our laboratory at room temperature.

All of the family groups studied have been known since 1990 and their history has been traced each year [18, 19]. Marmots were observed with binoculars and an 11-30 X telescope from a distance of 80-200 m. Social interactions

were recorded between 8:00 to 12:00 and 17:00 to 21:00, GMT + 2h, during May, June, July and August 1993. Home ranges were calculated according to the convex polygon method [20] and using the technique described by Armitage [21].
All living members of the family groups A and B as well as all males from the neighbouring groups C and D were analyzed in this study.

Laboratory procedures

• *Progesterone titration.* Plasmatic progesterone levels have been determined by radioimmunoassay (RIA) for 24 females captured at different reproductive stages since 1991. In captive non pregnant females, plasmatic progesterone levels showed low variations (mean = 0.34 ng/ml; 95% confidence interval = [0.08-0.6]; extrem values observed = [0.1-0.6]; Saboureau, unpublished data and [22]). We then decided to consider that a female was pregnant when her progesterone level was above 1 ng/ml. These results are close to *Marmota monax* where unpregnant females had low progesterone levels (0.1 ng/ml) while the mean levels of pregnant females varied from 2.3 in early stages to 5.7 in late gestation [23]. Our method was calibrated with field observations: predictions on the reproductive status of females were compared with the occurrence of a litter in the family.
• *DNA extraction.* DNA was extracted from 3 hairs per individual by cutting a 1-cm portion from the root end of the hair and placing it in 400 µl of a 5% Chelex-100 (Bio-Rad) suspension [24]. The sample was incubated at 56°C for 5-6 h, and then in a boiling water bath for 8 min. Ten microlitres of the supernatant were added to the polymerase chain reaction (PCR) mix.
• *DNA amplification and genetic typing.* Six microsatellite loci were investigated in this experiment [25]. Three primers were designed per locus *(Table I)*. The DNA amplification was performed in a 2-step polymerase chain reaction. The first step used diluted external microsatellite primers to reduce the formation of primer-dimer artifacts [26]. During the second step, a nested primer was introduced. The first step was performed in a final volume of 25 µl (750 mM Tris-HCl (pH 9.0), 200 mM $(NH_4)_2SO_4$, 50 µM of each dNTP, 1.5 mM $MgCl_2$, 0.5 units of Red GoldStar DNA polymerase (Eurogentec), 0.01 µM of each external primer), 10 µl of DNA were added and a PCR amplification of 30 cycles (93°C for 10 s, 55°C for 30 s, 72°C for 1 min using a Perkin Elmer Gene Amp PCR System 9600) was carried out. Between the first and second steps, a volume of 25 µl (750 mM Tris-HCl (pH 9.0), 200 mM $(NH_4)_2SO_4$, 50 µM of each dNTP, 1.5 mM $MgCl_2$, 0.5 units of Red GoldStar DNA polymerase, 1 µM of external primer and 1 µM of the corresponding internal primer) was added to the same tube. This step consisted of 35 cycles of amplification (93°C for 10 s, 55°C for 30 s, 72°C for 1 min). The PCR products were purified on a low-melting agarose gel, and used as the template for the radioactive marking. An additional amplification was performed in a volume of 25 µl with 0.2 µl of the unlabelled external primer and 0.04 µl of end-labelled internal primer (gamma-33P). A PCR amplification of 1-3 cycles (93°C 10-20 s, 55°C 30 s, 72°C 1 min) was carried out. Amplification products were separated by electrophoresis on a 6% polyacrylamide gel for 2 h at 45 mA and this gel was exposed to autoradiography film for 12 h.

Data analysis

Homozygotes appear as single bands and heterozygotes as 2-banded patterns representing the co-dominant alleles. Of the 2 alleles present at a given locus in an individual, one is inherited from the father and the other from the mother. The paternity exclusions were performed by the method of presence-absence of alleles.

Table I
Primer sequences and repeat type for the 6 microsatellite loci used. We designed 6 new sets of 3 primers using sequences provided by D. Tautz [24]

Locus	Primer	Sequence 5'-3'	Repeat type
SS-Bibl1	SS-Bibl1F	CTGAAGCAGCCATCCATCCAGTA	(CA)19
	SS-Bibl1RI	AGCATGCCCATGTAAGGT	
	SS-Bibl1R	ATGGTTCTCCACCACTAGC	
SS-Bibl4	SS-Bibl4F	CCTAGGTTCAGTCTTCAACACA	(CA)20
	SS-Bibl4RI	CGGTGGTGTCTTAATTTGTT	
	SS-Bibl4R	TGGTGTTGCCATTGTTCT	
SS-Bibl18	SS-Bibl18F	ATGGTCATGGAAGGGAAG	(CA)20
	SS-Bibl18FI	TCAAATGACCCAATCACC	
	SS-Bibl18R	GGCATCTTCACAGTTGATCT	
SS-Bibl20	SS-Bibl20F	ATTCTCTAGTCGTTAACAAGAATC	(GA)21
	SS-Bibl20RI	GGCTGTTCAAATATGGGTAG	
	SS-Bibl20R	CACCAGTGAAACTACATACAGTG	
SS-Bibl25	SS-Bibl25F	CTCATGACTATGGCAGCC	(CA)16
	SS-Bibl25FI	CTGGCTATGAGTGGGAAAC	
	SS-Bibl25R	AGAACCTTGATTTAGCAGTAG	
SS-Bibl31	SS-Bibl31F	TTACACCTTCTCTGGCTCC	(CA)21
	SS-Bibl31RI	CCCTGACACTTTGGTTCTC	
	SS-Bibl31R	TCTGAGCGGATTGTCTTTAT	

F: forward; R: reverse; I: internal

Results

Field data

The territories of groups A and B were adjacent and their areas overlapped by about 10% [18]. Members of these groups were all trapped in early May 1993. At this time group A was composed of 8 marmots: an adult male (MdA), a 3-year-old male (MsA), an adult female (FdA) and 5 yearlings. Group B was composed of an adult male (MdB), an adult female (FdB), a 3-year-old female (FsB) and 3 yearlings. MdA is the father of FsB. During May, daily antagonistic interactions were observed between FdB and FsB. The adult female FdB was always the initiator of aggressions and chased and pursued FsB. In early June, FsB migrated to group A where she was recaptured in July and where she seemed to have integrate. At that time, the previous resident female FdA of group A was no longer seen and we do not know if she died or was evicted by FsB.

Matings occurring in late April and May corresponding to the gestation period (33 days [27]), births generally occurred from late May to early June. Young marmots stay in their natal burrow for about 40 days during which time they are lactated by the mother.

Six young emerged from the burrow in group B on 12 July and 4 in group A on 10 July. Because FsB moved from group B to group A at the time of birth, the question arose of the parental origin of the group A offspring. Were they littered by the resident female (FdA) before she disappeared or, more probably were they issued from FsB after she had immigrated from group B?

This question is resolved by the results of analyses of sexual hormone levels. In the field, the difference in plasmatic progesterone levels was highly significant between pregnant and non pregnant females (mean = 4.69 ± 1.42 ng/ml and 0.63 ± 0.03 ng/ml respectively, t-test: $df = 22$, $p < 0.0001$). FdA, FdB and FsB had progesterone levels equal to 10.65, 5.78 and 1.91 ng/ml respectively. All of these values are above 1 ng/ml so we concluded that all of these females were pregnant in May 1993. If young born in group A were issued from FsB, as we supposed, FsB was accepted by the resident male of A and he also adopted her new borns.

The question then arises of who sired FsB offspring: the dominant male of group B or one of the males of group A?

Table II
Paternity exclusion and allelic variation of individuals from family group A and of adult males from the neighbouring groups. The alleles in bold are incompatible with the alleles of adult males from the group A

Reference	Sex	Status in the group	Locus SS-Bibl1	Locus SS-Bibl4	Locus SS-Bibl18	Locus SS-Bibl20	Locus SS-Bibl25	Locus SS-Bibl31
Group A								
MdA	Male	Adult	C/C	F/F	K/K	N/O	Q/R	U/V
MsA	Male	Subadult	C/C	F/G	H/K	L/N	Q/Q	U/U
FdA	Female	Adult	C/C	F/G	J/K	M/O	R/R	U/V
FsB	Female	Adult	B/C	F/G	I/K	N/O	P/R	U/U
S8031	Female	Yearling	C/C	F/F	K/K	N/O	Q/R	U/V
S8035	Female	Yearling	C/C	F/F	K/K	N/O	Q/R	T/U
T7643	Female	Yearling	C/C	F/G	J/K	M/N	P/R	T/V
T7928	Male	Yearling	C/C	F/F	J/K	M/N	Q/R	U/V
T7932	Male	Yearling	C/C	F/F	J/K	N/O	Q/R	U/V
T7245	Female	Offspring	B/C	F/G	I/K	**M**/O	Q/R	U/V
T7268	Female	Offspring	C/**E**	F/F	**I/I**	N/O	Q/R	U/V
T7249	Male	Offspring	C/C	F/G	I/K	**M**/O	P/R	U/V
T7213	Male	Offspring	B/C	F/F	**I/I**	N/O	P/R	U/V
Group B								
MdB	Male	Adult	C/E	F/F	I/J	M/N	P/Q	T/V
FdB	Female	Adult	C/C	F/G	H/K	L/O	P/Q	T/U
S8084	Female	Yearling	C/E	F/F	H/I	L/M	P/Q	T/U
S8086	Female	Yearling	C/E	F/G	H/I	M/O	P/Q	T/U
S8028	Male	Yearling	C/E	F/G	H/I	M/O	P/P	T/V
T7397	Female	Offspring	C/E	F/G	H/I	N/O	P/Q	U/V
T7243	Female	Offspring	C/C	F/F	H/I	L/N	P/Q	T/U
T7262	Female	Offspring	C/E	F/G	H/I	N/O	P/Q	T/T
T7238	Male	Offspring	C/E	F/G	H/I	L/N	P/Q	T/V
T7260	Male	Offspring	C/E	F/F	H/I	L/M	P/Q	T/T
T7242	Male	Offspring	C/C	F/F	I/K	L/M	P/P	T/T
Group C								
Z6347	Male	Adult	C/C	F/F	H/K	N/N	P/P	T/T
Z6332	Male	Adult	C/C	F/F	H/K	N/N	P/P	T/T
T7983	Male	Adult	C/E	F/F	H/K	M/N	Q/Q	S/T
Group D								
S8051	Male	Adult	B/D	F/F	I/J	M/N	Q/Q	V/V
T7935	Male	Adult	A/C	F/F	I/J	M/N	Q/Q	U/V

Genetic data

The results are summarized in *Table II* for the 6 microsatellite loci. With one locus (SS-Bibl18) we can exclude the resident adult female (FdA) as the mother of all the offspring. With 3 loci (SS-Bibl1, SS-Bibl18 and SS-Bibl20) we can exclude the dominant and the subordinate males (MdA and MsA) as the fathers of all young born in group A in 1993. For the locus SS-Bibl1 *(Fig. 1)*, one offspring (T7268) carries the E allele which is an extra-group allele. However, this allele is present in the adult male of group B and in an adult male of group C. This later is excluded by the locus SS-Bibl18. For the locus SS-Bibl18, 2 young (T7268 and T7213) carry the I allele, an allele incompatible with both males of group A. For the locus SS-Bibl20, 2 other young (T7245 and T7249) also carry an allele (M) incompatible with those males. However, all genotypes are compatible with the maternity of the adult female FsB, coming from group B in June 1993, and all genotypes of the young are compatible with the adult male of group B (MdB) for all loci.

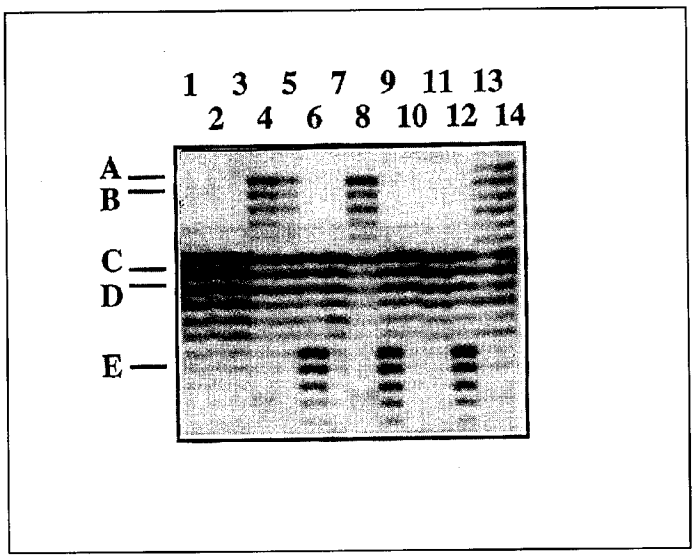

Figure 1. ***PCR products for locus SS-Bibl1 from a family group (A) of La Grande Sassière and from neighbouring group adult males on a denaturing polyacrylamide gel.*** *Lanes 1, 2 correspond to adult males MdA and MsA, lanes 3 and 4 correspond to adult females FdA and FsB, lanes 5, 6, 7, 8 correspond to offspring. Lane 9 corresponds to adult male of group B, lanes 10, 11, 12 correspond to adult males of group C and lanes 13, 14 correspond to adult males of group D. A, B, C, D and E are the allele names from groups A, B, C and D. Allele E is a paternal extra-group allele in group A.*

Discussion

The combination of genetic and behavioural approaches allowed us to solve a problem of parental uncertainty in a family group of alpine marmots. A litter emerged in a group (A) where the resident female (FdA, pregnant) was replaced by a pregnant subordinate female of a neighbouring group (B) at the time of birth. Field observations indicated that aggressiveness of FdB (the resident female of group B) towards her subordinate (FsB) provoked her dispersal. The dispersing FsB was observed again in the neighbouring group A in early June. At this time, FdA suddenly disappeared. Field observations alone did not allow the identification of the parents of the young that emerged in group A. Genotype analysis led us to exclude the dominant pair present in group A during the gestation period (FdA, MdA) as the parents of young that emerged in early July in this group. However, the genotypes of these young were compatible with the genotype of the subordinate female of the neighbouring group B (FsB) and with the genotype of the dominant male of group B (MdB). The combination of genetic and behavioural data then allowed us to conclude firstly that FsB replace FdA before the birth of the young and that she was the mother of young in group A; secondly FsB was fertilized by MdB. As a consequence, MdB had offspring from 2 females (FdB and FsB) and MdA sired no young this year.

Three comments can be drawn from these results: (1) Arnold [13] noted that only the dominant female gives birth and raises her offspring. Here we show that pregnant subordinate alpine marmots may disperse and raise their offspring in an other group; (2) MdA accepted FsB and her young. Previously, Coulon *et al.* [28] have shown that, in the alpine marmot, a male that takes over a family group kills the young born in the group before his arrival. In our case, the male accepted young he did not sire. Several hypotheses may explain this: (i) MdA may have recognized FsB and her young as kin; (ii) MdA was familiar with FsB before the birth of the young; (iii) MdA may have been unable to recognize the young as not his own. More data is needed to choose between these possible explanations; (3) some resident males may occasionally be polygynous, but our data is not sufficient to conclude monogamy to be the male mating system in this species.

Sociality and mating system of the Alpine marmot has to be carefully reexamined. A behavioural approach alone does not allow us to answer some questions (*e.g.* the identity of the mother of the young that emerged in group A) and genetic analyses alone may be misleading (there is extra-pair copulation between the male of group B and the female of group A). The complementation of behavioural and genetic approaches is powerful, enabling us to determine the consequences of interactions and movement of individuals on the social system of this species. ▼

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