

Original Article

Mate change in a socially monogamous mammal: evidences support the “forced divorce” hypothesis

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Three main hypotheses have been proposed to explain mate switching in monogamous species: the “better option” hypothesis, the incompatibility hypothesis, and the “forced divorce” hypothesis. We tested the predictions of these hypotheses for the first time in a monogamous mammal using long-term data from a natural population of Alpine marmots (*Marmota marmota*). Generally, pair disruption resulted in one of the pair members staying on the territory and re-pairing with a younger incomer, whereas the other disappeared from the territory. Replaced individuals were rarely found as dominant in a territory but were often injured or found dead. Individuals gained no benefit from mate switching: new mates were neither heavier, larger, or more heterozygote nor more genetically compatible than previous mates. Moreover, no increase in reproductive success was observed after re-pairing. The relationship between reproductive failure and occurrence of mate change was mainly due to infanticide by the incomer. Our results support the “forced divorce” hypothesis in the Alpine marmot and suggest that mate switching has strong consequences on breeding success. We discuss the importance of taking into account the cases of forced divorce while studying mate switching process and its evolutionary consequences in monogamous species. *Key words*: mammals, mate choice, monogamy, reproductive strategies, sexual selection. [*Behav Ecol* 22:120–125 (2011)]

The partner an individual mates with is an important determinant of reproductive success. This is particularly true in species mating monogamously where individuals of each sex form exclusive pair bonds with a single partner for at least one reproductive event (Kleiman 1977). However, mate choice is a competitive process that takes place over a limited time (Luttbeg 2002), and individuals may often be paired to a suboptimal partner. Therefore, tactics may have evolved to modify initial mate choice and adjust mate acquisition in such systems. Two such tactics have been suggested: extrapair copulation and mate switching.

The evolutionary causes of mate switching (also called “divorce,” Rowley 1983) are still debated, and several hypotheses have been proposed to explain this phenomenon (reviewed in Choudhury 1995). On the one hand, mate switching has been proposed to be an adaptive tactic allowing an individual to adjust a nonoptimal mating (Coulson 1966). Mate switching can then be a way to modify initial mate choice and to re-pair with a more optimal partner. Therefore, mate switching should occur after reproductive failure and reproductive success is expected to increase after re-pairing. Two main adaptive hypotheses have been proposed. First, under the “better option” hypothesis, mate switching is beneficial only to the pair member initiating divorce and re-pairing with a higher quality mate (Ens et al. 1993). Second, under the incompatibility hypothesis, both members of a pair should disrupt the

pair bond in order to re-pair with a more compatible partner (Coulson 1966). In this case, both members should increase their reproductive success by re-pairing with a partner of higher compatibility. Incompatibility may refer either to genetic incompatibility or to behavioral incompatibility. Whatever the hypothesis, one (or both) pair member deserts or chases away its partner (Ens et al. 1996).

On the other hand, the “forced divorce” hypothesis proposes mate switching as a nonadaptive process resulting from the intrusion of a third individual who outcompetes one member of the couple (Taborsky and Taborsky 1999). In this case, mate change is determined by the outcome of intrasexual competition. Mate switching should therefore be independent of the previous reproductive success, and the reproductive success is not expected to increase after re-pairing. In this case, none of the members of a separated pair should benefit from partner change, and the new mate is not expected to be of better quality or better compatibility than the previous one.

Mate switching has been reported in different taxa, such as birds (Black 1996), reptiles (Bull 2000), primates (Palombit 1994), rodents (Svendsen 1989), fishes (van Breukelen and Draud 2005), and invertebrates (Beltran and Boissier 2008). However, empirical tests of mate switching hypotheses have been conducted mainly in birds (Choudhury 1995; Black 1996; Dubois and Cézilly 2002) but never in monogamous mammals. In this paper, we examined the pattern of mate switching in the Alpine marmot (*Marmota marmota*). The Alpine marmot is one of the rare socially monogamous mammals where pair members stay together (up to 8 consecutive years on our study site) or change from one reproductive season to the other and is then well suited to test for the

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hypotheses of mate switching. We tested predictions associated with both adaptive and nonadaptive hypotheses of mate change. For this purpose, we addressed the following questions: 1) What is the fate of pair members after mate switching? 2) Does reproductive success influence the occurrence of mate change? 3) Is the new partner different than the previous one? and 4) Does reproductive success increase after re-pairing?

MATERIALS AND METHODS

Study species

The Alpine marmot is a highly social hibernating rodent living in family groups composed of a dominant breeding pair, subordinate adults of the 2 sexes, yearlings, and offspring of the year (Allainé 2000). Alpine marmots are territorial, and territories shared by all members of a family are defended essentially by the dominant breeding pair. Mating occurs immediately after the end of hibernation. Although dominant Alpine marmots monopolize reproduction (Arnold and Dittami 1997; Hacklander et al. 2003), subordinate males sometimes sire extrapair young (Goossens et al. 1998; Cohas et al. 2006). Dominant females give birth to 1 litter per year. After 40 days of lactation in the burrow, weaned pups emerge above ground from mid-June to mid-July and stay at least 2 years in their natal family group. Then, when sexually mature (at 2 years old), individuals can either disperse or delay dispersal and stay as subordinate in their family group.

Most individuals have to disperse to reach dominance (Magnolon 1999). Dispersers can reach dominance in another group than their natal family group by finding a breeding vacancy, by taking over a territory, or in rare cases by funding a new territory (3 successful creations of new territories between 1990 and 2007 on the study site). Takeovers by unrelated males or females are followed either by infanticide (Coulon et al. 1995) or by abortion or absorption of embryos sired by the previous mate before birth (Bruce effect) (Hacklander and Arnold 1999). If they do not manage to reach dominance before hibernation, dispersing marmots are at high risk of death (Stephens et al. 2002).

Data collection

Study site and sampling methods

Study site and trapping methods are described in details in Cohas et al. (2008). Briefly, the study was conducted in a wild population of Alpine marmots located in La Grande Sassièrè Natural Reserve (at 2350 m asl in the French Alps, lat 45°29'N, long 6°59'E) from 1990 to 2007.

Marmots were caught on 21 different territories. Once captured, animals were sexed, weighed, and measured; dominance status was assessed considering scrotum development for males and teat development for females; and hair samples were collected for genetic analysis. In addition, animals were individually marked with a transponder (model ID100; Trovan, Germany) and a numbered ear tag placed on the left or the right ear depending on the sex. A colored plastic piece was added to the ear tag of dominant individuals for distant recognition.

Family group compositions were assessed from capture–recapture data and from daily observations. For each family group, the number of adults, 2 years old, yearlings, and pups of each sex was assessed according to individual size and ear tag position and color. During observations, scent marking and aggressive behavior were also used to confirm dominance status (Bel et al. 1995).

Genetic analyses

Individuals were typed at 16 microsatellite loci, and neither departure from Hardy–Weinberg equilibrium for any of the

loci (all $P > 0.05$) nor gametic linkage disequilibrium among any of the loci (all $P > 0.05$) was evidenced. Details of the genotyping method are given in Cohas et al. (2008).

Data analyses

Does reproductive success influence the occurrence of mate change?

We modeled for each sex the occurrence of mate change as a function of 2 components of reproductive success: the number of offspring at emergence and the survival of the litter. Survival of the litter was calculated as the proportion of juveniles that survived from emergence to the end of their first hibernation. We used generalized mixed models (GLMM) with a logit link, a binomial variance, and with the pair as the random factor to account for repeated measures.

Is the new partner better than the previous one?

The new and the previous partners were compared according to body mass, body size, individual heterozygosity, and genetic similarity using conditional logistic regressions for matched case-control study (Hosmer and Lemeshow 2000), with previous partner encoded as control and the new partner encoded as case. Body mass was corrected for the date of capture using general additive models (Hastie and Tibshirani 1990). Body size was estimated by the first axis of principal component analyses performed on 6 morphometric variables (ulna length, tibia length, body length, mandible length, pelvis width, and head width). Individual heterozygosity was measured as standardized heterozygosity (Coltman et al. 1999), and genetic similarity between members of a pair was measured as estimator of Queller and Goodnight (1989). We compared whether the new partner presented a higher dissimilarity to its mate than the corresponding previous partner and whether the new partner presented a similarity to its mate closer to 0.16 (the optimal similarity for this population of Alpine marmots; Cohas et al. 2008) than the corresponding previous partner.

The new and the previous partners were also compared according to age (known for more than 91% of individuals). Because new mates were always younger than old ones (phenomenon, known as “separation” of variables; Albert and Anderson 1984; that forbids the use of a generalized linear model with standard maximum likelihood estimation), we used a generalized linear model using a penalized likelihood approach to reduce the bias of maximum likelihood estimates (Firth 1993). For that, we used the age difference between cases (new partners) and controls (previous partners) for each stratum (re-paired individuals) as described by Hosmer and Lemeshow (2000).

Does reproductive success increase after re-pairing?

To test whether reproductive success increased after re-pairing, we compared the number of offspring at emergence and the proportion of juveniles that survived from emergence to the end of their first hibernation for a given individual during its last reproductive event with its previous partner and its first reproductive event with its new partner. We used a conditional logistic regression for matched case-control study (Hosmer and Lemeshow 2000), with previous partner encoded as control and the new partner encoded as case. The partners' sex was also taken into account.

All statistical analyses were performed using R 2.8.1 software (R Development Core Team 2008). The packages used were R function `glmer` in package “lme4” (Bates and Sarkar 2006) for the GLMM, R function `clogit` in package “Survival” (Therneau 2009) for the conditional logistic regressions, and R function `brglm` in package “brglm” (Kosmidis 2008) for the penalized likelihood approach. The significance of the effect of the tested variables was assessed using the z statistics of coefficient

estimates. All tests were 2-tailed, the level of significance was set to 0.05, and parameter estimates are given \pm s.e.

RESULTS

Mate change pattern

Mate switching occurred when 2 pair members in year t no longer formed a pair together in year $t + 1$. During the studied period, we counted 123 pairs and 50 pair disruptions corresponding to an annual mate change rate of 17.21%. Typically, pair disruption resulted in one pair member staying on the territory (the stayer) and reproducing with a new partner (the incomer), whereas the other disappeared from the territory (the replaced). As a whole, females changed of partner in 30 occasions, whereas males in 20.

Following these 50 pair disruptions, we identified 55 re-pairing. All the stayers, except one male ($n = 49$, 19 males and 30 females), re-paired on their territory with the incomer. The fate of the majority of the replaced was unknown ($n = 38$, 21 males and 17 females). The fate of 12 replaced was known: Two of them (1 male and 1 female) created a new territory with a new partner, 4 of them (3 males and 1 female) re-paired on an existing territory, and the 6 others (5 males and 1 female) were found dramatically injured or dead after a fight.

The exact timing of pair breaking was known in 15 cases, thanks to direct observation of fights resulting in eviction ($n = 2$), of death of the evicted individual and/or of infanticide ($n = 13$).

Most of incomers (30 of 55) were subordinate from other family groups in our study site. Six males and 12 females were subordinates in an adjacent territory, and 9 males and 3 females were subordinates in a more remote territory. Only 3 male and 1 female incomers were previously dominant in another territory and managed to reestablish dominance. Four males and 2 females inherited dominance in their natal territory. Finally, 16 individuals came from outside our study site and were captured for the first time as dominant.

Change of partner also led to perturbation in the social structure of the groups. The average number of subordinates in family groups of 5.41 before mate change dropped to 3.91 after the change (paired Student test: $t = 3.18$, $n = 44$, $P = 0.002$).

Does previous reproductive success influence partner change probability?

The effect of the number of young at emergence on mate change probability was not linear but quadratic ($\beta_{\text{number of young}} = -1.72 \pm 0.32$, $z = -5.36$, $n = 138$, $P < 0.001$, $\beta_{\text{number of young}}^2 = 0.25 \pm 0.06$, $z = 4.32$, $P < 0.001$; Figure 1a), and this effect was independent of the sex ($\beta = 0.25 \pm 0.46$, $z = 0.54$, $n = 138$, $P = 0.59$). Mate change probability was high when no young were observed at emergence, then decreased until 3 young emerged, and finally increased with the number of young at emergence.

The probability of mate change depended on previous offspring survival ($\beta = -3.86 \pm 1.25$, $z = -3.10$, $n = 35$, $P = 0.002$; Figure 1b), and the effect was independent of the sex ($\beta = 1.06 \pm 1.14$, $z = 0.93$, $n = 35$, $P = 0.35$). However, the probability of mate change no longer depended on previous offspring survival when infanticide events were removed ($\beta = -2.17 \pm 2.16$, $z = -1.01$, $n = 17$, $P = 0.31$), and this for both sexes (females: $\beta = -1.74 \pm 2.41$, $z = -0.72$, $n = 7$, $P = 0.47$; males: $\beta = -2.34 \pm 2.19$, $z = -1.07$, $n = 10$, $P = 0.28$).

Is the new partner better than the previous one?

The new partner and corresponding previous partner of stayers did not differ in any of the variables considered except

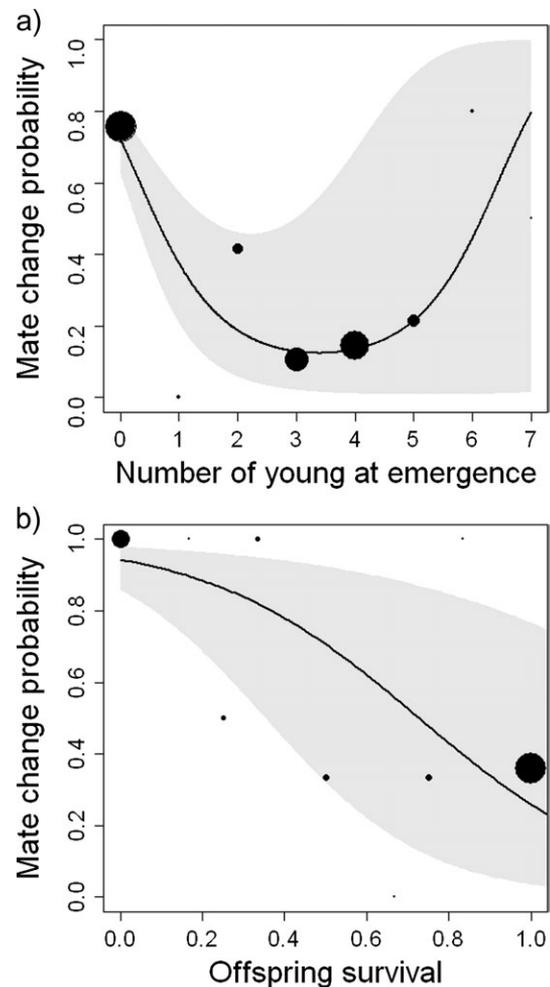


Figure 1

Mate change probability as a function of the number of young at emergence (a) and of the survival of the young from emergence to the end of their first hibernation (b). The dots represent the observed data, the size of the dots being proportional to the sample size. The line represents the fitted model. The gray surface represents the standard error around the fitted model.

in age and body mass (details shown in Table 1). The incomer was always younger than the replaced and tended to be heavier. This pattern did not depend on the sex of the stayer (over all variables tested: $0.26 < \chi^2 < 1.32$, degrees of freedom = 1, $0.25 < P < 0.56$).

The new partner and corresponding previous partner of replaced individuals who managed to re-pair did not differ in any of the variables considered (Table 1). The sample size was unfortunately too small to compare new and old partners according to body weight and body size (Table 1).

Does reproductive success increase after re-pairing?

For stayers ($n = 49$), the number of young emerged was higher with the new partner than with the previous partner ($\beta = 0.24 \pm 0.10$, $z = 2.40$, $n = 96$, $P = 0.002$). However the difference in the number of offspring emerged was no longer significant when cases where incomers may have arrived before young emergence, and therefore when infanticide were likely, were discarded ($\beta = -0.14 \pm 0.21$, $z = -0.66$, $n = 61$, $P = 0.51$). The same patterns were observed whatever the sex of the stayer (Likelihood Ratio Test for model with sex vs. model without

Table 1
Results of conditional logistic regressions showing differences between previous and new partners of re-paired individuals

Variables tested	β	Standard error	z	P	N
Individuals re-paired on the same territory (stayers)					
Age	-1.73	0.74	-2.35	0.02	31
Body mass	0.0026	0.0016	1.65	0.09	42
Size index	0.06	0.17	0.36	0.72	66
Standardized heterozygosity	0.37	1.09	0.34	0.73	95
Genetic similarity					
Higher	0.74	0.88	0.85	0.40	95
Optimal	-0.05	1.42	-0.03	0.97	95
Individuals re-paired on a different territory					
Age	-0.87	0.68	-1.28	0.20	9
Standardized heterozygosity	-3.36	3.81	0.82	0.38	12
Genetic similarity					
Higher	0.09	2.51	0.03	0.96	12
Optimal	-14.8	11.60	-1.27	0.20	12

sex: $\chi_1^2 = 1.14$, $P = 0.29$, without cases where incomers may have arrived before young emergence: $\chi_1^2 = 2.63$, $P = 0.10$).

Offspring survival tended to be higher after re-pairing ($\beta = 2.90 \pm 1.68$, $z = 1.72$, $n = 39$, $P = 0.08$). However, this tendency was not observed anymore when the cases of infanticide were removed ($\beta = 0.84 \pm 1.65$, $z = 0.51$, $n = 18$, $P = 0.61$).

The difference in offspring survival between young produced with the previous and the new partner of replaced individuals that re-paired could not be tested because no young was observed neither on their previous territory nor on their new territory in 5 cases of 6.

DISCUSSION

What hypothesis of mate change holds in the Alpine marmot?

Under adaptive hypotheses of mate switching, one or both pair members are expected to desert their partner, or chase it away, to re-pair with a better quality or a more compatible mate. Several lines of evidence do not support such hypotheses in the Alpine marmot. First, it is unlikely that replaced individuals have deserted their mates. Indeed, dominant Alpine marmots are territorial and sedentary and if they may have some opportunities to evaluate partners in the surrounding territories, they have no opportunity to evaluate potential partners far from it. We would therefore expect to find them as new dominants in neighboring territories. Contrary to this expectation, dominants never change of territory. Only 6% of them were found thereafter as dominant in a neighboring territory. Second, it seems also unlikely that stayers chased away their partner. Indeed, aggressive behaviors toward social partners were scarce and essentially took place at pair formation. However, more behavioral observations are needed to clarify the role of the stayer in pair disruption. Third, our study reveals no benefits neither in terms of partner's quality or compatibility nor in terms of reproductive success from mate switching and this in none of the re-paired individuals (re-paired on its territory or on a new one).

The only result that seems in favor of adaptive mate switching is that a low reproductive success (no young at emergence and no survival of young) was associated with a high occurrence of mate change suggesting reproductive failure initiated mate change (Choudhury 1995). Such a conclusion is often reported in bird studies, and meta-analysis of Dubois and

Cézilly (2002) revealed an overall significant pattern of higher mate change rate in unsuccessful breeding pairs. However, Jeschke et al. (2007) recently suggested that adaptive mate switching could probably be less common than previously thought due to a misinterpretation of correlation between breeding failure and mate change probability. Because take-over in the Alpine marmot results in infanticides (Coulon et al. 1995) and Bruce effect (Hacklander and Arnold 1999), reproductive failure is likely a consequence of mate change rather than a cause in this species.

Alternatively, our results fit the predictions associated to the forced divorce hypothesis. Besides, these results offer some direct support for forced mate switching. In all witnessed mate changes, fights resulting in takeovers and death of the dominant were observed, suggesting that forced eviction by an intruder is frequent in Alpine marmots (see also Hacklander and Arnold 1999). Moreover, incomers were younger than the replaced individuals and previously identified as subordinate elsewhere, suggesting that they are dispersing individuals in search of dominants to challenge.

An alternative nonadaptive hypothesis would imply an obligate mate switching resulting from the death of the partner. Although death during summer is unlikely in Alpine marmots (summer survival probability of 0.99; Stephens et al. 2002), case of death during hibernation (or just after emergence) due to bad condition may occur (Farand et al. 2002). However, in more than 60% of mate switching, changes occurred at the end of spring or summer. This observation also indicates the predominance of takeovers in mate change process in the Alpine marmot.

Although it is usually admitted that mate change in case of forced divorce has no net benefit or cost to the stayer (see Figure 19.1 in Ens et al. 1996), our results show that it may not be the case in Alpine marmots. Indeed, mate change always implying the loss of one reproductive attempt is likely costly in this species (King and Allainé 2002).

Do incomers choose their mate?

Because the eviction of a dominant is risky, we may expect that incomers use some cues to choose the individuals they will challenge. First, they can select dominants in poor body condition, but incomers were neither heavier (only a trend was observed) nor larger than replaced individuals. Second, incomers might use information on the social settings and challenged individuals with several helpers. Indeed, in Alpine marmots, male dominants' persistence decreases as the number of helpers increases (Allainé and Theuriau 2004). Finally, incomers may challenge preferentially a dominant on a good territory or having a high-quality partner using the reproductive success as a cue. This may explain the unexpected high probability of mate change when the number of emerged young was important. However, given the large confidence interval, more data are needed to validate this potential mechanism.

Conclusions

Our results do not support adaptive hypotheses of mate switching and are rather in favor of nonadaptive hypotheses. In particular, forced mate switching may potentially be the main cause of mate change in the Alpine marmot. Bird studies supporting the forced divorce hypothesis are rare (Jeschke et al. 2007). One reason may be that observations and data collection often occurred only once either in breeding or in feeding period (Kokko et al. 2004; Moody et al. 2005; Valcu and Kempenaers 2008) and does not allow a total knowledge of breeding failure and territory takeover. Another reason may

be that the majority of studies in birds have been done on migratory species with a short life expectancy where opportunities of mate change for adaptive reasons through desertion or preemption are frequent (Dhondt and Adriaensen 1994).

On the contrary, in year-round territorial monogamous species, both members of a pair gain from long-term familiarity with territory (Gill and Stutchbury 2006). If the benefits of possessing a territory exceed the costs of being paired with a low-quality or an incompatible partner, individuals are expected to be faithful at least to their territory and consequently to their mate (Freed 1987; Morton et al. 2000). This should occur particularly when opportunities to move among territories are few because of saturated space and/or long-life expectancy of residents (Heg et al. 2003; Fedy and Stutchbury 2004). The Alpine marmot fits this prediction. Deserting a territory is probably very costly for a dominant, particularly in our saturated population, and would result in risks to be injured or killed during a fight or to hibernate alone. Therefore, in Alpine marmots, extrapair paternity, by bringing indirect benefits to females (Cohas et al. 2007), appears as the only tactic to adjust mate choice.

We thus predict that adaptive hypotheses of mate switching should be poorly supported in year-round territorial and long-lived monogamous species and that, as suggested by Møller (1992), extrapair paternity would be the only opportunity to modify a suboptimal mate choice.

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