

Are extra-pair young better than within-pair young? A comparison of survival and dominance in alpine marmot

AURÉLIE COHAS, CHRISTOPHE BONENFANT, JEAN-MICHEL
GAILLARD and DOMINIQUE ALLAINÉ

Université de Lyon; Université Lyon 1; CNRS; UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43
boulevard du 11 novembre 1918, Villeurbanne F-69622, France

Summary

1. In socially monogamous species, females may seek extra-pair copulation to gain genetic benefits. In order to test this ‘genetic quality’ hypothesis, one must compare the performance of extra-pair young (EPY) and within-pair young (WPY). Such tests, however, are scarce and results published so far are inconclusive.

2. Here, we test the ‘genetic quality’ hypothesis using multistate capture–recapture models to compare age-specific survival and access to dominance between EPY and WPY in the alpine marmot *Marmota marmota*, a socially monogamous mammal showing extra-pair paternities.

3. When compared with WPY, survival of EPY was higher by 15%, 10% and 30%, for juveniles, yearlings and 2-year-old individuals, respectively. Survival at older ages did not differ.

4. Survival corresponded to true survival for yearlings and juveniles as dispersal does not occur before 2 years of age in marmots. For older individuals, survival estimates included a mixture of survival and dispersal. The 30% increase of the 2-year-old EPY survival might reflect delayed dispersal rather than high survival of EPY as compared with WPY.

5. WPY and EPY had the same probability (0.28) to access dominance at 2 years of age, but EPY were more successful at older ages than WPY (0.46 vs. 0.10).

6. Both survival and reproductive performance were higher in EPY than in WPY. The fitness advantages of adopting such a mixed mating tactic are thus likely to be high for marmot females. We suggest that obtaining genetic benefits is the main evolutionary force driving extra-pair paternity in alpine marmots.

Key-words: capture–mark–recapture, multiple paternity, multistate model, reproductive success, survival.

Journal of Animal Ecology (2007) **76**, 771–781
doi: 10.1111/j.1365-2656.2007.01253.x

Introduction

Extra-pair paternity (EPP) is a common reproductive tactic among socially monogamous species (Birkhead & Møller 1998). The benefits for males in adopting such a tactic are straightforward since by fertilizing extra-pair females, they increase their reproductive success by fathering additional offspring without

providing paternal care (Trivers 1972). The occurrence of this tactic in females is more puzzling as their reproductive success is not constrained by the number of sexual partners (Trivers 1972). Nevertheless, extra-pair copulation (EPC) is often actively elicited by females (Westneat, Sherman & Morton 1990; Westneat & Stewart 2003), suggesting that they also obtain fitness benefits. Although increasing the quantity of offspring is unlikely to drive EPP in female vertebrates (but see Sheldon 1994), increasing the offspring quality is an appealing alternative (Birkhead & Møller 1992; Zeh & Zeh 1996, 1997; Jennions & Petrie 2000; Tregenza & Wedell 2000; Griffith, Owens & Thuman 2002).

Several hypotheses have been proposed to account for an adaptive value of EPP through an increased

Correspondence: Aurélie Cohas, Université de Lyon; Université Lyon 1; CNRS; UMR 5558, Laboratoire de Biométrie et Biologie Évolutive, 43 boulevard du 11 novembre 1918, Villeurbanne F-69622, France. Fax: +33(0)472431388. E-mail: cohas@biomserv.univ-lyon1.fr

offspring quality. Females can increase the quality of their litter through direct benefits, such as nuptial gift, resource provisioning and/or defence of the offspring (Wolf 1975; Burke *et al.* 1989; Colwell & Oring 1989), or through increased genetic diversity (Williams 1975) that reduces the probability of reproductive failure in unpredictable environments (Watson 1991). Otherwise, females can only increase the genetic quality of extra-pair young (EPY) compared to within-pair young (WPY) (Griffith *et al.* 2002) through the acquisition of good genes (Hamilton 1990) or compatible genes (Zeh & Zeh 1996, 1997).

To assess these different hypotheses and the possible adaptive value of EPP, most previous studies have tested for: (1) the influence of male phenotypic (Dunn *et al.* 1994; Friedl & Klump 2002; Hansson & Westerberg 2002) and genetic (Blomqvist *et al.* 2002; Freeman-Callant *et al.* 2003; Eimes *et al.* 2005) characteristics on the occurrence of EPP; (2) phenotypic (Hasselquist, Bensch & Von Schantz. 1996; Forstmeier *et al.* 2002; Foerster *et al.* 2003) and genetic (Foerster *et al.* 2003) differences between within-pair males and extra-pair males; and (3) phenotypic (Strohbach *et al.* 1998; Whittingham & Dunn 2001; Schmoll *et al.* 2003) and genetic (Foerster *et al.* 2003) differences between WPY and EPY. However, owing to the difficulty of monitoring individuals throughout their lifetime, tests of the crucial prediction of different fitness between EPY and WPY are scarce (but see Schmoll *et al.* 2003), and have generally been limited to juvenile survival of birds (Kempnaers, Verheyen & Dhondt 1997; Krokene *et al.* 1998; Strohbach *et al.* 1998; Kempnaers *et al.* 1999; Lubjuhn *et al.* 1999; Whittingham & Dunn 2001; Charmantier *et al.* 2004; Kraaijeveld *et al.* 2004).

The socially monogamous alpine marmot is a suitable animal model to fill this gap. Up to 31% of marmot litters contain EPY, and 16% of juveniles are EPY (Goossens *et al.* 1998a; Cohas *et al.* 2006). To assess whether having EPY leads to fitness advantage, we tested the prediction of the 'genetic quality' hypothesis that EPY should perform better than WPY.

Materials and methods

THE SOCIAL ORGANIZATION OF ALPINE MARMOTS

Alpine marmots are territorial cooperative breeders with a highly skewed reproduction towards dominant individuals. The basic social unit is a family group of two to 20 individuals with a territorial dominant breeding pair, sexually mature subordinates of at least 2 years of age, yearlings and juveniles (Perrin, Allainé & Le Berre 1993). Reproduction is suppressed in both sexually mature subordinate females (Hacklander, Mostl & Arnold 2003) and most subordinate males (Arnold 1990; Goossens *et al.* 1996; Cohas *et al.* 2006). Subordinate males act as helpers during hibernation, which substantially increases the survival of litters

(Arnold 1993; Allainé *et al.* 2000; Allainé & Theuriau 2004). Subordinates rarely inherit dominance in their natal territory (only about 5% of males and 12% of females). Most subordinates (> 2 years old) disperse, become transient individuals and may ultimately reach dominance (breeding vacancy or displacement of a dominant individual). They may have EPC during this period.

STUDY SITE AND FIELD METHODS

The study site is located in La Grande Sassièrre Nature Reserve (French Alps, 45°29'N, 6°59'E). From 1990 to 2002, marmots were caught from early April to late July. Marmots were trapped using two-door, live-capture traps baited with dandelion *Taraxacum densleonis*. Traps were placed near the entrance of the main burrow of each group allowing the assignment of captured individuals to a given family group. Once trapped, individuals were tranquilized with Zolétil 100 and individually marked with a numbered ear tag and a transponder (TrovanTM, Germany). Individuals were sexed using anogenital distance, aged from their size up to 3 years of age, and their social status was recorded. Animals were classified according to four age classes: juveniles (from 0 to 1 year), yearlings (from 1 to 2 years), 2 year olds (from 2 to 3 years) and adults (older than 3 years). Virtually all juveniles were captured within 3 days following emergence (Allainé 2004).

GENETIC AND PATERNITY ANALYSES

Genetic analyses

For genetic analyses, hairs were collected from 1992 to 1997, and tissue biopsies thereafter from all trapped individuals. From these samples, 253 individuals were typed at five microsatellite loci: SS-Bib11, SS-Bib14, SS-Bib118, SS-Bib120, SS-Bib131 (Klinkicht 1993), 148 individuals were typed for three additional loci: MS45, MS47, MS53 (Hanslik & Kruckenhauser 2000), and 96 individuals were typed for four more loci: Ma001, Ma018, Ma066, Ma091 (Da Silva *et al.* 2003). Details on microsatellite characteristics and methods can be found in Goossens *et al.* (1998a), Goossens, Waits & Taberlet (1998b), Hanslik & Kruckenhauser (2000), Da Silva *et al.* (2003) and Cohas *et al.* (2006).

Tests of Hardy–Weinberg equilibrium and of linkage disequilibrium were performed using GENEPOP v3.3 (Raymond & Rousset 1995) on dominant adults only to avoid bias due to family structure and on all cohorts gathered to ensure adequate sample size ($n = 69$ for SS-Bib11, SS-Bib14, SS-Bib118, SS-Bib120 and SS-Bib131, $n = 31$ for MS45, MS47 and MS53, $n = 11$ for Ma001, Ma018, Ma066 and Ma091). They revealed 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 $P > 0.05$).

Paternity analyses

Genotypes of each young and of the dominant pair were used to check maternity of the dominant female (always the case) and then, paternity of the dominant male. We defined a young as WPY if its genotype matched with the dominant male genotype and as EPY if it did not. Litters composed only of WPY were recorded as within-pair litters, those composed only of EPY were extra-pair litters, and those containing both WPY and EPY were recorded as mixed litters.

When paternity exclusions were based only on one difference between the genotype of the young considered and its potential father, the possibility of both false inclusion or exclusion of a young can be discarded (Goossens *et al.* 1998b; Cohas *et al.* 2006). A young identified as a WPY cannot be an EPY because the average probability of excluding a male as the father given that the mother was known was very high (from 0.926 for individuals typed at five loci to 0.995 for individuals typed at 12 loci). Likewise, a young identified as an EPY cannot be a WPY because genotyping errors due to null and false alleles occurred at a rate below 0.002% (Goossens *et al.* 1998b) and mutations were rare (average mutation rate of microsatellite loci of 1.67×10^{-4} per generation in *M. marmota*, (Rassmann, Arnold & Tautz 1994) so that only 0.5 offspring would be expected to come from mutation.

COMPARISON OF EPY AND WPY: ALL LITTERS

Here, we considered individuals captured between 1992 and 2002. All individuals of unknown paternity were discarded as were all individuals born in families without helpers since EPY did not occur (Cohas *et al.* 2006) and the presence of helpers increases significantly juvenile survival (Arnold 1993; Allainé *et al.* 2000; Allainé & Theuriau 2004). The final data set consisted of 220 individuals (506 encounters) of 66 litters from 18 different family groups. Forty-five individuals (119 encounters) were EPY born in 10 family groups and 175 individuals (387 encounters) were WPY born in 18 family groups. Ten young (22 encounters) were born in six extra-pair litters, 73 young (187 encounters) were born in 19 mixed litters and 137 young (297 encounters) were born from 41 within-pair litters.

We used multistate capture–recapture model (MS-CR, Lebreton & Pradel 2002) to investigate the pattern of both marmot survival and social state transition because recapture probability of individuals was much lower than 1 (recapture probability varying from 0.37 to 0.92, Farand, Allainé & Coulon 2002). By taking advantage of MS-CR, we accounted for the social state of an individual (*s* for subordinate vs. *D* for dominant), and estimated both the probability of survival for subordinate and dominant individuals and the probability that an individual changes from subordinate to dominant state. The data included thus recapture histories (e.g. 00111220220 for an individual marked as young

at occasion 3, recaptured as subordinate at occasions 4 and 5, recaptured as dominant at occasions 6, 7, 9 and 10, and not captured at occasions 1, 2, 8 and 11).

A MS-CR model corresponds to a transition matrix and associated vectors of survival and capture probabilities (Nichols 1992) as follows:

$$\begin{bmatrix} \Psi^{ss} & 1 - \Psi^{ss} \\ 1 - \Psi^{DD} & \Psi^{DD} \end{bmatrix}_t \begin{bmatrix} \Phi^s \\ \Phi^D \end{bmatrix}_t \begin{bmatrix} p^s \\ p^D \end{bmatrix}_t \quad \text{eqn 1}$$

where capture (p), apparent survival (Φ), and state transition conditional to survival (Ψ) probabilities are defined as: p_t^a , the probability that an individual in state a in year t is captured during that year, Φ_t^a , the probability that an individual in state a in year t survives and does not permanently emigrate from the study area between t and $t + 1$ and Ψ_t^{ab} , the probability that an individual in state a in year t is in state b in year $t + 1$, given that it survived and did not permanently emigrate from the study area between t and $t + 1$, where t begins at time of marking.

Marmots less than 3 years of age have never been identified as dominant (Farand *et al.* 2002; Stephens *et al.* 2002; Grimm *et al.* 2003) so that the transition between social states only concerned adult individuals (Fig. 1). Consequently, for individuals younger than 2 years, the model simplified to:

$$[\Phi]_t [p]_t \quad \text{eqn 2}$$

Dominant marmots never revert to subordinate status (Arnold 1993; Farand *et al.* 2002; Stephens *et al.* 2002; Grimm *et al.* 2003). Thus, for individuals older than 2 years, we fixed state transition probabilities from dominant to subordinate at zero ($\Psi^{Ds} = 1 - \Psi^{DD} = 0$). This procedure *de facto* constrained state transition probabilities from dominant to dominant to 1 ($\Psi^{DD} = 1$). Hence, we had only one state transition probability to estimate (i.e. the probability of staying subordinate Ψ^{ss}). Then, for individuals older than 2 years of age, the model can be written as:

$$\begin{bmatrix} \Psi^{ss} & 1 - \Psi^{ss} \\ 0 & 1 \end{bmatrix}_t \begin{bmatrix} \Phi^s \\ \Phi^D \end{bmatrix}_t \begin{bmatrix} p^s \\ p^D \end{bmatrix}_t \quad \text{eqn 3}$$

Data analyses were conducted on two data sets. Within-pair litters include females being paired to an optimal male resulting in WPY of high quality or females being paired to a suboptimal male but unable to engage in EPCs resulting in WPY of low quality. Consequently, the presence of WPY born to females being paired with an optimal male can confound any possible difference in survival and state transition between WPY and EPY. To account for such heterogeneity, we first tested for a difference in both survival and state transition probabilities between WPY born in within-pair and in mixed litters (data set 1). No difference between WPY born

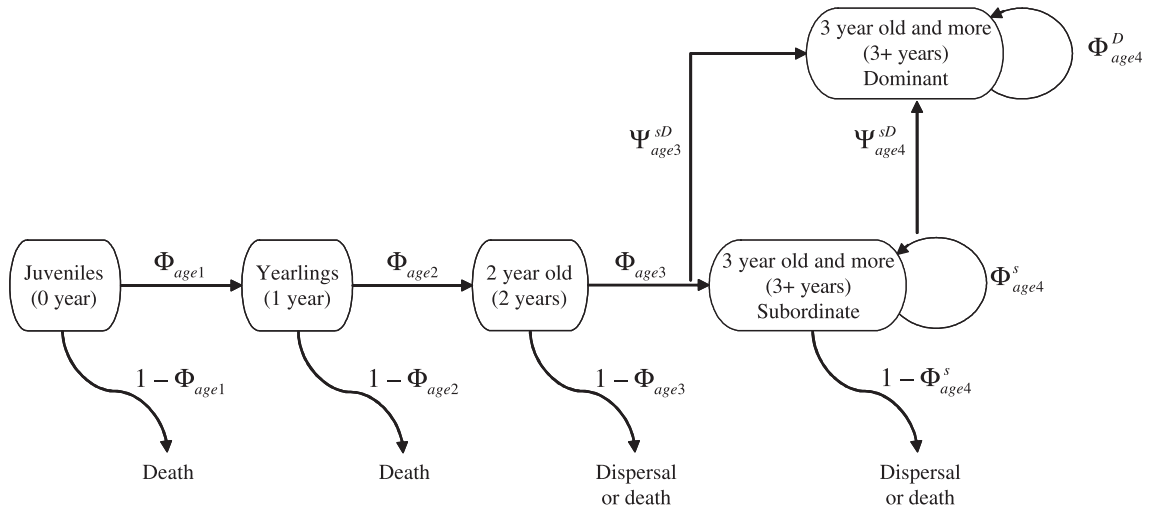


Fig. 1. Life cycle of alpine marmots. Four age classes are represented. Each arrow represents the transition from one age class to the next with its associated probability: Φ represents the survival probability and Ψ represents the state transition probability. For alpine marmots older than 2 years of age, Φ represents apparent survival thus $1 - \Phi$ encompasses both survival and dispersal and Ψ is conditional to Φ .

in various types of litters was reported (see below). We then tested for a difference in survival and state transition probabilities between EPY and WPY by considering EPY and WPY born in both within-pair and mixed litters to increase the power of the analysis (data set 2).

Data analyses on each data set were performed following three steps (Lebreton *et al.* 1992). In the first step, we tested whether a global model compatible with our biological knowledge fitted our data with regard

to the ‘3i hypothesis’ (Burnham *et al.* 1987). This Goodness-Of-Fit (GOF) test was performed using U-CARE (Choquet *et al.* 2005). The second step was to select the most parsimonious model from our global model which did not include effects of litter type or offspring type. Following Burnham & Anderson (2000), we reduced the number of parameters of the global model by considering only a priori biological hypotheses based on our field experience and the literature (Arnold 1993; Farand *et al.* 2002; Stephens *et al.* 2002; Grimm *et al.* 2003; Allainé 2004). We thus considered age, time and sex effects and their interactions on all capture, survival and state transition probabilities. Consequently, the most general model was denoted $P_{age \times t \times sex}^s \Phi_{age \times t \times sex}^s \Psi_{age3-4 \times t \times sex}^{ss} P_{age \times t \times sex}^D \Phi_{age \times t \times sex}^D \Psi_{age3-4 \times t \times sex}^{sD}$ (Table 1). We did not include litter size because it did not influence juvenile survival in our population (Allainé *et al.* 2000) and did not differ according to the occurrence of EPP (mean litter size \pm SE = 3.22 ± 1.31 vs. 3.24 ± 1.32 , $t = 0.07$, d.f. = 66, $P = 0.95$, 41 and 25 litters without and with EPY, respectively). We used the Akaike’s Information Criterion (AIC) corrected for small sample size (AICc, Burnham, White & Anderson 1995) for model selection (Johnson & Omland 2004). The third step was to test for the effects of ‘litter type’ (data set 1) and ‘offspring type’ (data set 2), by comparing the most parsimonious global model with related models including the corresponding ‘type’ effect on survival and state transition probabilities. We used log-likelihood ratio tests (LRT) between nested models to assess the significance of these effects. LRT were two-tailed for ‘litter type’ but one-tailed for ‘offspring type’ because we expected EPY to have both higher survival and higher probability to become dominant than WPY. All models were fitted with the generalized logit link function, using M-SURGE 1.7.1

Table 1. Abbreviations used in models notations

Abbreviations	Meanings
p	capture probability
Φ	survival probability
$1 - \Phi$	mortality probability (encompass both mortality and dispersal probabilities for individuals older then 2 years of age)
Ψ	state transition conditional to survival probability
Subscript	
Age	age as a four modalities categorical variable
age1	age from 0 to 1 year
age2	age from 1 to 2 years
age3	age from 2 to 3 years
age4	age from 3 to 4 years
agex-y	age from age x to age y
agex,y	age x and age y
sex	sex
t	time
type_L	litter type (within-pair litter or mixed litter)
type	young type (WPY (within-pair young) or EPY (extra-pair young))
*	interactive effect
+	additive effect
Superscript	
S	subordinate status
D	dominant status

(Choquet *et al.* 2004). All estimates are given as mean \pm SE.

COMPARISON OF EPY AND WPY: MIXED LITTERS ONLY

We tested the effect of offspring type on survival using only offspring born in mixed litters. We only included those individuals captured as juveniles between 1992 and 1999 and as yearlings between 1992 and 2000 to limit the confounding effects of having capture probability less than 1 (Table 3). We thus used 29 EPY and 28 WPY born in 14 families in these tests.

To account for the family structure, we used Generalized Estimating Equation (GEE) (Diggle *et al.* 2002). This procedure is more robust than Generalized Linear Mixed Models because it makes broad hypotheses about data structure, and is well-suited to departure from normality and small sample sizes within clusters (Carlin *et al.* 2001). We chose an exchangeable correlation matrix specifying the same correlation between all observations of a same cluster (Horton & Lipsitz 1999). We used GEE with the logit link and variance given by a binomial distribution as in a logistic regression to examine the effects of the offspring type (EPY vs. WPY) on juvenile survival. The significance of fixed terms was assessed using the robust z -statistics of parameter estimates (Diggle *et al.* 2002). All statistical analyses were performed using R 2.3.1 software and the *gee* library (R Development Core Team 2003). Unless otherwise stated, all tests were one-tailed because we expected EPY to have higher survival than WPY. The level of significance was set to 0.05 and parameter estimates are given \pm SE.

Results

COMPARISON OF EPY AND WPY: ALL LITTERS

First step: goodness of fit tests

We first performed GOF tests of our model as a single state model (see Appendix S1, Supplementary material for details). The full time-dependent model (p_t, Φ_t) adequately fitted our two data sets (data set 1: $\chi^2 = 35.866$, d.f. = 28, $P = 0.146$; data set 2: $\chi^2 = 35.923$, d.f. = 28, $P = 0.144$). When performing a multistate GOF test (Pradel, Wintrebert & Gimenez 2003), we found qualitatively similar results with little evidence for a lack of fit when considering the overall GOF-test (fit to $p_t^s, \Phi_t^s, \Psi_t^{ss}, p_t^D, \Phi_t^D, \Psi_t^{sD}$; data set 1: $\chi^2 = 50.314$, d.f. = 35, $P = 0.045$; data set 2: $\chi^2 = 48.620$, d.f. = 37, $P = 0.096$). The low P -values of these latter tests stemmed from an age-effect on survival rate (Appendix S1, Supplementary material) and not longer occurred once the first capture had been removed (fit to $p_t^s, \Phi_t^s, \Psi_t^{ss}, p_t^D, \Phi_t^D, \Psi_t^{sD}$; data set 1: $\chi^2 = 20.224$, d.f. = 31, $P = 0.931$; data set 2: $\chi^2 = 22.789$, d.f. = 35, $P = 0.944$).

Second step: selection of the global model

For both data sets, the model of capture probability with the lowest AICc included differences among age classes and a dependence of adult capture probability on social status (Table 2a). The age- and state-dependent model competed well (AICc-weight 0.49 vs. 0.32 for data set 1 and 0.44 vs. 0.27 for data set 2, Table 2a) and was retained as the most parsimonious. We then modelled the survival probability. The model with the lowest AICc included effect of both age classes and status of adults (Table 2b). This model was at least twice better supported than the two next models and was retained as the best model (Table 2b). We finally modelled the transition from subordinate to dominant status. The model with the lowest AICc included the effects of age classes (three times better supported than the next model, Table 2c). In summary, the best model for both data sets (named *B*) included age- and state-dependent capture and survival probabilities, and age-dependent transition probabilities (Table 1).

Recapture probabilities were similar in both data sets (Table 3). They decreased with age, respectively, from 0.853 ± 0.045 for juveniles to 0.384 ± 0.154 for subordinates individuals older than 3 years for data set 1 and from 0.886 ± 0.036 to 0.380 ± 0.144 for data set 2 (Table 3) and markedly depended on social status (0.722 ± 0.084 vs. 0.384 ± 0.154 for dominants vs. subordinates and 0.751 ± 0.069 vs. 0.380 ± 0.144 for data set 1 and 2, Table 3). Survival corresponded to the true survival for juveniles and for yearlings because natal dispersal in marmots does not occur prior to 2 years of age, and also for dominant adults as breeding dispersal does not occur. Survival increased with age from 0.697 ± 0.045 for juveniles to 0.878 ± 0.060 for dominant adults for data set 1 and from 0.720 ± 0.038 to 0.857 ± 0.054 for data set 2. For subordinates, survival estimates was lowered, respectively, for data set 1 and for data set 2, to 0.462 ± 0.089 and 0.503 ± 0.080 for 2-year-old individuals, and to 0.627 ± 0.119 and 0.571 ± 0.101 for individuals of 3 years of age and older (Table 3). Finally, the overall transition probabilities from subordinate to dominant status were low, and decreased from 0.307 ± 0.082 for 2 years old to 0.091 ± 0.066 for older individuals for data set 1 and from 0.280 ± 0.068 to 0.153 ± 0.079 for data set 2 (Table 3).

Third step

We used model *B* as the starting point and investigated, using data set 1, the influence of being born in a within-pair litter or a mixed litter for WPY and, using data set 2, the influence of being EPY or WPY on survival and state transition (i.e. access to dominance) probability.

INFLUENCE OF THE TYPE OF LITTER FOR WPY

No models including the effects of the litter type had lower AICc than model *B* (Table 4). Model *B* received

Table 2. Model selection based on AICc for the five best capture models (a), survival models (b), and state transition models (c) nested in the most global model $p_{age+sex}^s \Phi_{age+sex}^s \Psi_{age3-4+sex}^{ss} p_{age+sex}^D \Phi_{age+sex}^D \Psi_{age3-4+sex}^{sD}$ where p, Φ, Ψ stand, respectively, for capture, survival and state transition probability. The subscripts age, sex and t stand, respectively, for age (categorical variable with 1, 2, 3 and 4 standing for juveniles, yearlings, 2 years of age and adults), sex and time

	k	Data set 1			Data set 2			
		Deviance	AIC _c	W _i	Deviance	AIC _c	W _i	
(a) Capture model								
B	$p_{age}^s p^D$	12	701.18	727.11	0.495	894.29	919.79	0.440
p2	$p_{age+sex}^s p_{sex}^D$	13	700.86	729.12	0.181	893.01	920.77	0.270
p3	p_{age}	11	704.35	727.97	0.322	898.62	921.89	0.154
p4	$p_{age+t}^s p_t^D$	21	690.46	738.50	0.002	876.91	923.58	0.066
p5	$p_{age+t+sex}^s p_{t+sex}^D$	22	690.22	740.88	0.005	876.10	925.24	0.029
(b) Survival model								
B	$\Phi_{age}^s \Phi^D$	12	701.18	727.11	0.779	894.29	919.79	0.529
Φ2	$\Phi_{age+sex}^s \Phi_{sex}^D$	14	701.14	731.77	0.076	891.37	921.42	0.234
Φ3	$\Phi_{age+sex}^s \Phi_{sex}^D$	13	700.77	730.48	0.145	893.89	921.65	0.209
Φ4	$\Phi_{age+sex}^s \Phi_t^D$	21	695.87	743.91	0.000	884.31	930.98	0.025
Φ5	$\Phi_{age+t+sex}^s \Phi_{t+sex}^D$	22	695.72	746.37	0.000	884.22	933.36	0.002
(c) State transition model								
B	$\Psi_{age3-4}^{ss} \Psi_{age3-4}^{sD}$	12	701.18	727.11	0.698	894.29	919.79	0.675
Ψ2	$\Psi_{age3-4+sex}^{ss} \Psi_{sex}^{sD}$	13	701.09	729.35	0.228	894.29	922.05	0.218
Ψ3	$\Psi_{age3-4+sex}^{ss} \Psi_{sex}^{sD}$	14	701.07	731.691	0.071	893.55	923.60	0.101
Ψ4	$\Psi_{age3-4+t}^{ss} \Psi_t^{sD}$	20	692.77	738.23	0.003	885.93	930.15	0.004
Ψ5	$\Psi_{age3-4+sex+t}^{ss} \Psi_{sex+t}^{sD}$	21	692.16	740.20	0.001	885.89	932.55	0.001

*Indicates interactive effects. The superscripts s and D stand for subordinate and dominant states. AICc, Akaike's Information Criterion corrected for small sample bias; k , number of estimated parameters.

Table 3. Estimates of capture, survival and state transition probabilities obtained for the most parsimonious model $p_{age}^s p^D, \Phi_{age}^s \Phi^D, \Psi_{age3-4}^{ss} \Psi_{age3-4}^{sD}$ where p, Φ, Ψ stand, respectively, for capture, survival and state transition probability. The subscript age refers to a categorical variable with 1, 2, 3 and 4 standing for juveniles, yearlings, 2 years of age and adults. Estimates are given \pm SE

Age	Data set 1 : WPY from within-pair and mixed litters			Data set 2 : WPY and EPY from within-pair and mixed litters		
	p	Φ	Ψ subordinate to dominant	p	Φ	Ψ subordinate to dominant
0	0.853 \pm 0.045	0.697 \pm 0.045	–	0.886 \pm 0.036	0.720 \pm 0.038	–
1	0.636 \pm 0.085	0.818 \pm 0.098	–	0.664 \pm 0.071	0.804 \pm 0.077	–
2	0.660 \pm 0.108	0.462 \pm 0.089	0.307 \pm 0.082	0.688 \pm 0.094	0.503 \pm 0.080	0.280 \pm 0.068
3+ subordinate	0.384 \pm 0.154	0.627 \pm 0.119	0.091 \pm 0.066	0.380 \pm 0.144	0.571 \pm 0.101	0.153 \pm 0.079
3+ dominant	0.722 \pm 0.084	0.878 \pm 0.060	–	0.751 \pm 0.069	0.857 \pm 0.054	–

The superscripts s and D stand for subordinate and dominant states.

at least twice (survival) and 1.4 (transition) as much support as any model including a litter type effect. Thus, WPY whether born in within-pair or in mixed litters had similar probability to survive and to access dominance.

INFLUENCE OF THE TYPE OF OFFSPRING

Two models that included the effects of offspring type had lower AICc than model B . These models received twice as much support as model B (Table 5a). One

included an additive effect of the type of offspring on yearling and juvenile survival, and the other, the model $B_{\Phi_{type}}$, also included offspring type effects on survival of 2 years old (Table 5a). Given the low AICc value, we retained $B_{\Phi_{type}}$ as the best model. Survival was higher for EPY than for WPY up to 3 years of age, and was equal thereafter. Survival probabilities for EPY and WPY were 0.803 \pm 0.053 vs. 0.698 \pm 0.041 for juveniles and 0.605 \pm 0.097 vs. 0.466 \pm 0.083 for 2 year olds (Fig. 2a). Analyses using GEE modelling confirmed these results (Appendix S2, Supplementary material).

Table 4. Test of the effect of litter type on survival probabilities (a) and on state transition probabilities (b) with the most global model considered being $p_{age}^s p_{age}^D, \Phi_{age \times type_L}^s \Phi_{type_L}^D, \Psi_{age3-4 \times type_L}^{ss} \Psi_{age3-4 \times type_L}^{sD}$ where p, Φ, Ψ stand, respectively, for capture, survival and state transition probability. The subscripts *age* and *type_L* stand, respectively, for age (categorical variable with 1, 2, 3 and 4 standing for juveniles, yearlings, 2 years of age and adults), and type of litter. The superscripts *s* and *D* stand for subordinate and dominant states. Model selection was based on AICc and LRT

		Deviance	<i>k</i>	AIC _c	W _i	LRT
(a) Survival model						
B	$\Phi_{age}^s \Phi^D$	701.18	12	727.11	0.225	
Φ_{type_L1}	$\Phi_{[age1-2+type_L]+age3+age4}^s \Phi^D$	700.36	13	728.62	0.105	B vs. $\Phi_{type_L1} \chi^2 = 0.82$ d.f. = 1 <i>P</i> = 0.36
Φ_{type_L2}	$\Phi_{[age1+type]+age2+age3+age4}^s \Phi^D$	700.60	13	728.86	0.094	B vs. $\Phi_{type_L2} \chi^2 = 0.58$ d.f. = 1 <i>P</i> = 0.45
Φ_{type_L3}	$\Phi_{age1+[age2+type]+age3+age4}^s \Phi^D$	700.82	13	729.08	0.084	B vs. $\Phi_{type_L3} \chi^2 = 0.36$ d.f. = 1 <i>P</i> = 0.55
Φ_{type_L4}	$\Phi_{age1+[age2+age3+age4+type]}^s \Phi^D$	700.86	13	729.12	0.082	B vs. $\Phi_{type_L4} \chi^2 = 0.52$ d.f. = 1 <i>P</i> = 0.47
(b) State transition model						
B	$\Psi_{age3-4}^{ss} \Psi_{age3-4}^{sD}$	701.18	12	727.11	0.361	
Ψ_{type_L1}	$\Psi_{age3+[age4+type_L]}^{ss} \Psi_{age3+[age4+type_L]}^{sD}$	699.50	13	727.76	0.260	B vs. $\Psi_{type_L1} \chi^2 = 1.68$ d.f. = 1 <i>P</i> = 0.19
Ψ_{type_L2}	$\Psi_{[age3+type_L]+age4}^{ss} \Psi_{[age3+type_L]+age4}^{sD}$	700.55	13	728.81	0.154	B vs. $\Psi_{type_L2} \chi^2 = 0.63$ d.f. = 1 <i>P</i> = 0.43
Ψ_{type_L3}	$\Psi_{age3-4+type_L}^{ss} \Psi_{age3-4+type_L}^{sD}$	701.12	13	729.38	0.116	B vs. $\Psi_{type_L3} \chi^2 = 0.06$ d.f. = 1 <i>P</i> = 0.81
Ψ_{type_L4}	$\Psi_{age3-4+type_L}^{ss} \Psi_{age3-4+type_L}^{sD}$	698.88	14	729.50	0.109	B vs. $\Psi_{type_L4} \chi^2 = 2.30$ d.f. = 2 <i>P</i> = 0.32

AICc, Akaike's Information Criterion corrected for small sample bias; *k*, number of estimated parameters; LRT, two-tailed log-likelihood ratio tests.

Table 5. Test of the effect of offspring type on survival probabilities (a) and on state transition probabilities (b) with the most global model considered being $p_{age}^s p_{age}^D, \Phi_{age \times type}^s \Phi_{type}^D, \Psi_{age3-4 \times type}^{ss} \Psi_{age3-4 \times type}^{sD}$ where p, Φ, Ψ stand, respectively, for capture, survival and state transition probability. The subscripts *age* and *type* stand, respectively, for age (categorical variable with 1, 2, 3 and 4 standing for juveniles, yearlings, 2 years of age and adults) and type of offspring. The superscripts *s* and *D* stand for subordinate and dominant states. Model selection was based on AICc and LRT

		Deviance	<i>k</i>	AIC _c	W _i	LRT
(a) Survival model						
$B_{\Phi_{type}}$	$\Phi_{[age1-3+type]+age4}^s \Phi^D$	890.78	13	918.55	0.236	B vs. $B_{\Phi_{type}} \chi^2 = 3.51$ d.f. = 1 <i>P</i> = 0.03
Φ_{type1}	$\Phi_{[age1-2+type]+age3+age4}^s \Phi^D$	891.05	13	918.82	0.206	B vs. $\Phi_{type1} \chi^2 = 3.23$ d.f. = 1 <i>P</i> = 0.04
B	$\Phi_{age}^s \Phi^D$	894.29	12	919.79	0.126	
Φ_{type2}	$\Phi_{age1+age2+age3+age4+type}^s \Phi^D$	892.89	13	920.65	0.082	B vs. $\Phi_{type2} \chi^2 = 1.40$ d.f. = 1 <i>P</i> = 0.12
Φ_{type3}	$\Phi_{[age1-2]+type+age3+age4}^s \Phi^D$	890.70	14	920.75	0.078	B vs. $\Phi_{type3} \chi^2 = 3.58$ d.f. = 2 <i>P</i> = 0.09
(b) State transition model						
$B_{\Phi\Psi_{type}}$	$\Psi_{age3+[age4+type]}^{ss} \Psi_{age3+[age4+type]}^{sD}$	888.34	14	918.43	0.323	$B_{\Phi_{type}}$ vs. $B_{\Phi\Psi_{type}} \chi^2 = 2.44$ d.f. = 1 <i>P</i> = 0.06
$B_{\Phi_{type}}$	$\Psi_{age3-4}^{ss} \Psi_{age3-4}^{sD}$	890.78	13	918.55	0.236	
Ψ_{type2}	$\Psi_{age3-4+type}^{ss} \Psi_{age3-4+type}^{sD}$	887.65	15	920.00	0.147	$B_{\Phi_{type}}$ vs. $\Psi_{type2} \chi^2 = 3.13$ d.f. = 2 <i>P</i> = 0.11
Ψ_{type3}	$\Psi_{[age3+type]+age4}^{ss} \Psi_{[age3+type]+age4}^{sD}$	890.25	14	920.30	0.127	$B_{\Phi_{type}}$ vs. $\Psi_{type3} \chi^2 = 0.53$ d.f. = 1 <i>P</i> = 0.24
Ψ_{type4}	$\Psi_{age3-4+type}^{ss} \Psi_{age3-4+type}^{sD}$	890.76	14	920.81	0.098	$B_{\Phi_{type}}$ vs. $\Psi_{type4} \chi^2 = 0.02$ d.f. = 1 <i>P</i> = 0.45

AICc, Akaike's Information Criterion corrected for small sample bias; *k*, number of estimated parameters; LRT, One tailed log-likelihood ratio tests.

Estimates of survival for older individuals, whether subordinates or dominants, were the same as those obtained for the best global model *B* (Table 5a).

Only one model, $B_{\Phi\Psi_{type}}$ including the effect of the type of offspring on the transition from subordinate to dominant status was slightly better supported than the model $B_{\Phi_{type}}$ (Table 5b). This model included age-dependent effects and an additive effect of the offspring type on the probability to become dominant for

individuals older than 2 years. EPY had a four times higher probability to access to dominant status than WPY (0.459 ± 0.296 vs. 0.098 ± 0.070 , Fig. 2b) as adults.

COMPARISON OF EPY AND WPY: MIXED LITTERS ONLY

When considering mixed litters only, 24 of the 28 EPY (0.857 ± 0.066) and 21 of the 29 WPY (0.724 ± 0.083)

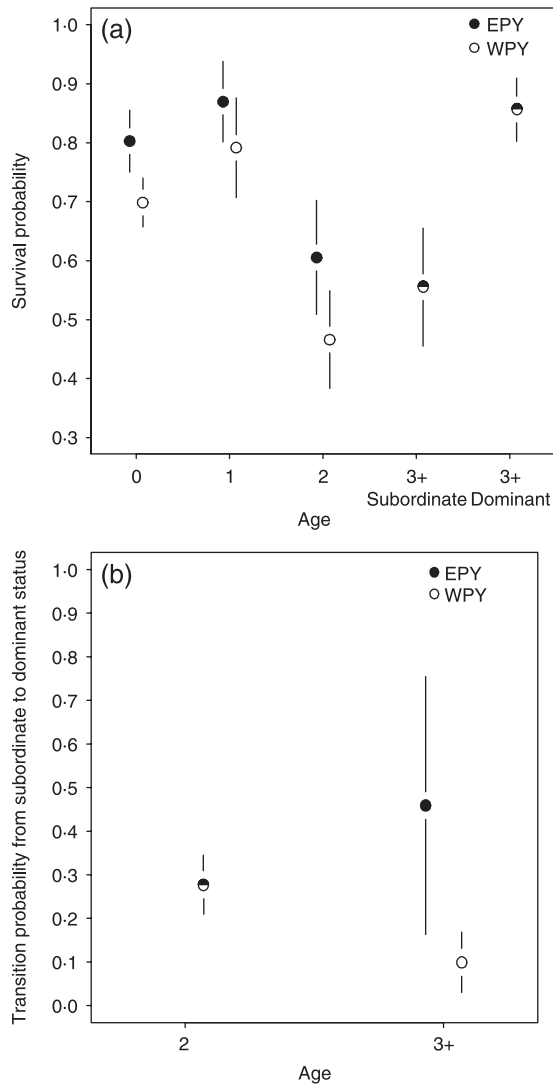


Fig. 2. Estimates of survival probability (a) and of transition probability from subordinate to dominant status (b) showing the effect of young type obtained for model $p_{age}^s, p_{age}^D, \Phi_{[age1-3+type]+age4}^s, \Phi^s, \Psi_{age3+[age4+type]}^{ss}, \Psi_{age3+[age4+type]}^{sD}$, where p, Φ, Ψ stand, respectively, for capture, survival and state transition probability. The subscripts *age* and *type* stand for age (categorical variable with 1, 2, 3 and 4 standing for juveniles, yearlings, 2 years of age and adults) and type of offspring. The superscripts *s* and *D* stand for subordinate and dominant states. Estimates are given \pm SE.

survived until their first year. Survival estimates were thus similar to those obtained from the selected MS-CR model. Juvenile survival did not significantly differ between EPY and WPY (Fisher test, $n = 28, 29, P = 0.33$). The comparison of the EPY and WPY taking into account a family effect again revealed a similar difference of juvenile survival between EPY and WPY (0.812 vs. 0.736) although not significant ($\beta = -0.442 \pm 0.453, z = -0.977, P = 0.164$). The power of these analyses was low. For the Fisher test, the probability of finding a significant result, given the sample size used, was 0.161 (255 individuals of each type of young would have been necessary to show a significant effect of the magnitude we had).

Discussion

The comparison between EPY and WPY performance provides a crucial test of the ‘genetic quality’ hypothesis. Our results on alpine marmots show that EPY outperformed WPY as predicted by this hypothesis. Specifically, EPY better survived during the critical period between birth and sexual maturity, but this difference did no longer occur once adult. EPY also became dominant more often than WPY. Fitness benefits for mothers are likely to be important. Indeed, EPY outperformed WPY in both components of offspring fitness, survival and dominance access, the latter being a good proxy of reproductive performance as, in alpine marmots, 85% and 100% of young are born to dominant males and to dominant females, respectively (Cohas *et al.* 2006).

The nine studies (Kempnaers *et al.* 1997, 1999; Krokene *et al.* 1998; Strohbach *et al.* 1998; Lubjuhn *et al.* 1999; Whittingham & Dunn 2001; Schmoll *et al.* 2003; Charmantier *et al.* 2004; Kraaijeveld *et al.* 2004) we found on the relative performance of EPY and WPY all focused on birds and provided inconclusive results. In only two studies on *Parus caeruleus*, a higher performance was reported for EPY involving a higher fledging survival (four populations, Kempnaers *et al.* 1997; Charmantier *et al.* 2004), and a higher local recruitment (one population, Charmantier *et al.* 2004). The difference in fledging survival was 31% in one population (Kempnaers *et al.* 1997), but only 6% in the other (Charmantier *et al.* 2004). Both methodological and biological reasons might explain the different pattern observed in birds and alpine marmot. First, in most studies, sample sizes were quite small [e.g. only 11 broods in Krokene *et al.*’s (1998) study], so that the statistical power to detect small effects [e.g. a 6% difference in fledging survival of Charmantier *et al.*’s (2004) study] was low. Moreover, a capture or resighting rate less than 1 has not been accounted for in previous studies, possibly leading to biased estimates of age-specific survival (Nichols 1992). Likewise, a possible effect of EPP on survival is easier to detect during a critical period of the life cycle. When survival from birth to fledging is as high as 90% (Strohbach *et al.* 1998; Whittingham & Dunn 2001; Schmoll *et al.* 2003), any advantage for EPY is almost impossible to detect. We accounted for these pitfalls in the present study by comparing performance between EPY and WPY based on a large sample size and by using capture–recapture methods. Our analyses allowed to get unbiased estimates of survival when capture rates are less than 1 (Nichols 1992). Moreover, survival of marmots before sexual maturity is low (Farand *et al.* 2002) and this period can be considered as critical (Stephens *et al.* 2002; Grimm *et al.* 2003; *Marmota flaviventris*, Oli & Armitage 2004).

Second, none of the bird species where EPY and WPY performance were compared are cooperative breeders. Compatible genes as inbreeding avoidance are more likely than good genes to drive EPP in marmots.

Indeed, the mean genetic similarity between social partners is higher, in our population, than between random pairs (Cohas *et al.* 2006) and dominant males do not physiologically suppress the reproductive function of their sons (Arnold & Dittami 1997). Dominant females in alpine marmot family groups are thus related to sexually mature males and EPCs may be a way to avoid inbreeding as previously suggested by a higher probability for males genetically similar to their social females to be cuckolded (Cohas *et al.* 2006). Inbreeding avoidance may be a likely and potentially strong evolutionary force driving EPP in alpine marmot, and has been invoked for cooperatively breeding species, both in mammals (*Canis simensis*, Sillero-Zubiri, Gottelli & Macdonald 1996) and in birds (*Malurus splendens*, Brooker *et al.* 1990). Such a feature is less likely to occur in most monogamous pairs of birds.

The differences in offspring performance we report here are unlikely to be due to other factors than genetic ones. Although we did not strictly compare cross-fostered young, environmental as well as maternal effects are unlikely to have produced the observed results because (1) EPP occurrence was independent on year or territory quality in alpine marmots litters (A. Cohas, unpublished data); (2) the occurrence of EPP does not depend on the number of helpers (both male yearlings and sexually mature male subordinates) present in a family group (A. Cohas, unpublished data), which is a variable affecting juvenile survival (Arnold 1993; Allainé *et al.* 2000; Allainé & Theuriau 2004), but on the number of sexually mature male subordinates present in a family group; (3) the number of helpers had only been shown to affect juvenile survival (Arnold 1993; Allainé *et al.* 2000; Allainé & Theuriau 2004), whereas we reported EPY to have a higher survival than WPY beyond their first year and to have higher access to dominance; (4) most females raised EPY and WPY born in both mixed and within-pair litters; and (5) WPY from mixed litters did not survive better nor had better access to dominance than WPY from within-pair litters. Although unlikely, a differential maternal investment in EPY and WPY (as reported in two bird species; Gil *et al.* 1999; Cunningham & Russell 2001) cannot be discarded.

Although some experimental work would be required to strengthen our results that female alpine marmots benefit from the production of EPY by increasing their genetic quality, other evidence (Cohas *et al.* 2006; Cohas, Yoccoz & Allainé 2007; this study) supports that EPY perform better than WPY: (1) the frequency of EPP increased with the genetic similarity within the pair; (2) the nine identified extra-pair males were all more heterozygous than the corresponding within-pair males; (3) extra-pair males were preferentially transient individuals originated from distant family groups likely to be less genetically similar to the female than the pair male; (4) EPY were less genetically similar to their mother than their half siblings WPY (Cohas *et al.* 2007); (5) heterozygous juveniles better

survived over their first year than homozygous ones (Da Silva *et al.* 2006); and (6) EPY better survived and had access to dominance more often than WPY.

In summary, EPY perform better than WPY in alpine marmots, supporting the 'genetic quality' hypothesis in a mammalian species. Female alpine marmots are thus likely to engage in EPC in order to obtain genetic benefits. The benefits females get by adopting such a mixed tactic are potentially high. Future long-term studies are required to assess the fitness of offspring, and ultimately the fitness pay-offs of females adopting a mixed reproductive tactic.

Acknowledgements

We thank all students involved in the trapping of alpine marmots at La Sassièrè and Benoit Goossens for the typing of marmots. We warmly thank Jean-Dominique Lebreton and Remi Choquet for helpful advices on capture–recapture methodology and John Lesku for editing the English. Thanks are also extended to authorities of the Vanoise National Park for allowing us to work in the Grande Sassièrè Nature Reserve. Lastly, we thank two anonymous referees for helpful comments of a previous draft of this work. Financial support was received from CNRS (France) and the Région Rhône-Alpes (XI plan Etat-Région). The experiments conducted comply with current French laws.

References

- Allainé, D. (2004) Sex ratio variation in the cooperatively breeding alpine marmot *Marmota marmota*. *Behavioral Ecology*, **15**, 997–1002.
- Allainé, D. & Theuriau, F. (2004) Is there an optimal number of helpers in alpine marmot family groups? *Behavioral Ecology*, **15**, 916–924.
- Allainé, D., Brondex, F., Graziani, L., Coulon, J. & Till Bottraud, I. (2000) Male-biased sex ratio in litters of alpine marmots supports the helper repayment hypothesis. *Behavioral Ecology*, **11**, 507–514.
- Arnold, W. (1990) The evolution of marmot sociality. II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology*, **27**, 239–246.
- Arnold, W. (1993) Social evolution in marmots and the adaptive value of joint hibernation. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, **86**, 79–93.
- Arnold, W. & Dittami, J. (1997) Reproductive suppression in male alpine marmots. *Animal Behaviour*, **53**, 53–66.
- Birkhead, T.R. & Møller, A.P. (1992) *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Academic Press, London.
- Birkhead, T.R. & Møller, A.P. (1998) *Sperm Competition and Sexual Selection*. Academic Press, London.
- Blomqvist, D., Andersson, M., Kupper, C., Cuthill, I., Kis, J., Lanctot, R., Sandercock, B., Szekely, T., Wallander, J. & Kempenaers, B. (2002) Genetic similarity between mates and extra-pair parentage in three species of shorebirds. *Nature*, **419**, 613–615.
- Brooker, M.G., Rowley, I., Adams, M. & Baverstock, P.R. (1990) Promiscuity: an inbreeding avoidance mechanism in a socially monogamous species? *Behavioral Ecology and Sociobiology*, **26**, 191–199.

- Burke, T., Davies, N., Bruford, N. & Hatchwell, B. (1989) Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature*, **338**, 249–251.
- Burnham, K. & Anderson, D. (2000) *Model Selection and Inference*. Springer, Berlin.
- Burnham, K., Anderson, D., White, G., Brownie, C. & Pollock, K. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society Monograph 5.
- Burnham, K.P., White, G.C. & Anderson, D.R. (1995) Model selection strategy in the analysis of capture–recapture data. *Biometrics*, **51**, 888–898.
- Carlin, J.B., Wolfe, R., Brown, C.H. & Gelman, A. (2001) A case study on the choice, interpretation and checking of multilevel models for longitudinal binary outcomes. *Biostatistics*, **2**, 397–416.
- Charmantier, A., Blondel, J., Perret, P. & Lambrechts, M. (2004) Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? *Journal of Avian Biology*, **35**, 524–532.
- Choquet, R., Reboulet, A., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2004) M-SURGE: new software specifically designed for multistate capture–recapture models. *Animal Biodiversity and Conservation*, **27**, 207–215.
- Choquet, R., Reboulet, A.M., Lebreton, J.-D., Gimenez, O. & Pradel, R. (2005) *U-CARE 2:2 User's Manual*. CEFE, Montpellier, France.
- Cohas, A., Yoccoz, N., Da Silva, A., Goossens, B. & Allainé, D. (2006) Extra-pair paternity in the monogamous alpine marmot (*Marmota marmota*): the roles of social setting and female mate choice. *Behavioral Ecology and Sociobiology*, **59**, 597–605.
- Cohas, A., Yoccoz, N.G. & Allainé, D. (2007) Extra-pair paternity in alpine marmots, *Marmota marmota*: genetic quality and genetic diversity effects. *Behavioral Ecology and Sociobiology*, **61**, 1081–1092.
- Colwell, M. & Oring, L. (1989) Extra-pair paternity in the spotted sandpiper: a female mate acquisition tactic. *Animal Behaviour*, **38**, 675–684.
- Cunningham, E. & Russell, A. (2001) Differential allocation and 'good genes' – Comment from Cunningham and Russell. *Trends in Ecology and Evolution*, **16**, 21.
- Da Silva, A., Luikart, G., Allainé, D., Gautier, P., Taberlet, P. & Pompanon, F. (2003) Isolation and characterization of microsatellites in European alpine marmots (*Marmota marmota*). *Molecular Ecology Notes*, **3**, 189–190.
- Da Silva, A., Luikart, G., Yoccoz, N., Cohas, A. & Allainé, D. (2006) Genetic diversity–fitness correlation revealed by microsatellite analyses in European alpine marmots (*Marmota marmota*). *Conservation Genetics*, **3**, 371–382.
- Diggle, P.J., Heagerty, P.J., Liang, K.Y. & Zeger, S.L. (2002) *Analysis of Longitudinal Data*. Oxford University Press, Oxford.
- Dunn, P., Robertson, R., Michaud-Freeman, D. & Boag, P. (1994) Extra-pair paternity in tree swallows: why do females mate with more than one male? *Behavioral Ecology and Sociobiology*, **35**, 273–281.
- Eimes, J., Parker, P., Brown, J. & Brown, E. (2005) Extrapair fertilization and genetic similarity of social mates in the Mexican jay. *Behavioral Ecology*, **16**, 456–460.
- Farand, E., Allainé, D. & Coulon, J. (2002) Variation in survival rates for the alpine marmot (*Marmota marmota*): effects of sex, age, year, and climatic factors. *Canadian Journal of Zoology*, **80**, 342–349.
- Forstmeier, W., Kempenaers, B., Meyer, A. & Leisler, B. (2002) A novel song parameter correlates with extra-pair paternity and reflects male longevity. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **269**, 1479–1485.
- Foerster, K., Delhey, K., Johnsen, A., Lifjeld, J. & Kempenaers, B. (2003) Females increase offspring heterozygosity and fitness through extra-pair matings. *Nature*, **425**, 714–717.
- Freeman-Callant, C., Meguerdichian, M., Wheelwright, N. & Sollecito, S. (2003) Social pairing and female mating fidelity predicted by restriction fragment length polymorphism similarity at the major histocompatibility complex in songbird. *Molecular Ecology*, **12**, 3077–3083.
- Friedl, T. & Klump, G. (2002) Extrapair paternity in the red bishop (*Euplectes orix*): Is there evidence for the good-genes hypothesis? *Behaviour*, **139**, 777–800.
- Gil, D., Graves, J., Hazon, N. & Wells, A. (1999) Male attractiveness and differential testosterone investment in zebra finch eggs. *Science*, **286**, 126–128.
- Goossens, B., Coulon, J., Allainé, D., Graziani, L. & Bel, M.-C. (1996) Immigration of a pregnant female in an Alpine Marmot family group: behavioural and genetic data. *Comptes Rendus de l'Académie des Sciences Paris*, **319**, 241–246.
- Goossens, B., Graziani, L., Waits, L.P., Farand, E., Magnolon, S., Coulon, J., Bel, M.-C., Taberlet, P. & Allainé, D. (1998a) Extra-pair paternity in the monogamous Alpine marmot revealed by nuclear DNA microsatellite analysis. *Behavioral Ecology and Sociobiology*, **43**, 281–288.
- Goossens, B., Waits, L.P. & Taberlet, P. (1998b) Plucked hair samples as a source of DNA: reliability of dinucleotide microsatellite genotyping. *Molecular Ecology*, **7**, 1237–1241.
- Griffith, S., Owens, I. & Thuman, K. (2002) Extra pair paternity in birds: a review of interspecific variation and adaptive function. *Molecular Ecology*, **11**, 2195–2212.
- Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T. & Arnold, W. (2003) Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. *Oikos*, **102**, 124–136.
- Hacklander, K., Mostl, E. & Arnold, W. (2003) Reproductive suppression in female Alpine marmots, *Marmota marmota*. *Animal Behaviour*, **65**, 1133–1140.
- Hamilton, W. (1990) Mate choice near and far. *American Zoologist*, **30**, 341–352.
- Hanslik, S. & Kruckenhauser, L. (2000) Microsatellite loci for two European sciurid species (*Marmota marmota*, *Spermophilus citellus*). *Molecular Ecology*, **9**, 2163–2165.
- Hansson, B. & Westerberg, L. (2002) On the correlation between heterozygosity and fitness in natural populations. *Molecular Ecology*, **11**, 2467–2474.
- Hasselquist, D., Bensch, S. & von Schantz, T. (1996) Correlation between male song repertoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature*, **381**, 229–232.
- Horton, N.J. & Lipsitz, S.R. (1999) Review of software to fit generalized estimating equation regression models. *American Statistician*, **53**, 160–169.
- Jennions, M. & Petrie, M. (2000) Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 21–64.
- Johnson, J.B. & Omland, K.S. (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution*, **19**, 101–108.
- Kempenaers, B., Verheyen, G. & Dhondt, A. (1997) Extrapair paternity in the blue tit (*Parus caeruleus*): Female choice, male characteristics, and offspring quality. *Behavioral Ecology*, **8**, 481–492.
- Kempenaers, B., Congdon, B., Boag, P. & Robertson, R. (1999) Extrapair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis? *Behavioral Ecology*, **10**, 304–311.
- Klinkicht, M. (1993) Untersuchungen zum Paarungssystem des Alpenmurmeltiers, *Marmota M. marmota* mittels DNA fingerprinting. PhD Thesis, University of Munich, Germany.
- Kraaijeveld, K., Carew, P., Billing, T., Adcock, G. & Mulder, R. (2004) Extra-pair paternity does not result in differential sexual selection in the mutually ornamented black swan (*Cygnus atratus*). *Molecular Ecology*, **13**, 1625–1633.

- Krokene, C., Rigstad, K., Dale, M. & Lifjeld, J. (1998) The function of extra-pair paternity in blue tits and great tits: Good genes or fertility insurance? *Behavioral Ecology*, **9**, 649–656.
- Lebreton, J.-D. & Pradel, R. (2002) Multistate recapture models: modelling incomplete individual histories. *Journal of Applied Statistics*, **29**, 359–369.
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lubjuhn, T., Strohbach, S., Brun, J., Gerken, T. & Epplen, J. (1999) Extra-pair paternity in great tits (*Parus major*) – a long term study. *Behaviour*, **136**, 1157–1172.
- Nichols, J.D. (1992) Capture–recapture models: using marked animals to study population dynamics. *Bioscience*, **42**, 94–102.
- Oli, M. & Armitage, K. (2004) Yellow-bellied marmot population dynamics: demographic mechanisms of growth and decline. *Ecology*, **85**, 2466–2455.
- Perrin, C., Allainé, D. & Le Berre, M. (1993) Socio-spatial organization and activity distribution of the alpine marmot *Marmota marmota*: preliminary results. *Ethology*, **93**, 21–30.
- Pradel, R., Wintrebert, C. & Gimenez, O. (2003) A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture–recapture model. *Biometrics*, **59**, 43–53.
- R Development Core Team (2003) *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rassmann, K., Arnold, W. & Tautz, D. (1994) Low genetic variability in a natural alpine marmot population (*Marmota marmota*, Sciuridae) revealed by DNA fingerprinting. *Molecular Ecology*, **3**, 347–353.
- Raymond, M. & Rousset, R. (1995) GENEPOP Version 1.2: Population genetics software for exact tests and ecumenicism. *Journal of Heredity*, **86**, 248–249.
- Schmoll, T., Dietrich, V., Winkel, W., Epplen, J. & Lubjuhn, T. (2003) Long-term fitness consequences of female extra-pair matings in a socially monogamous passerine. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **270**, 259–264.
- Sheldon, B. (1994) Male phenotype, fertility, and the pursuit of extra-pair copulations by female birds. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **257**, 25–30.
- Sillero-Zubiri, C., Gottelli, D. & Macdonald, D.W. (1996) Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). *Behavioral Ecology and Sociobiology*, **38**, 331–340.
- Stephens, P., Frey-Roos, F., Arnold, W. & Sutherland, W. (2002) Model complexity and population predictions. The alpine marmot as a case study. *Journal of Animal Ecology*, **71**, 343–361.
- Strohbach, S., Curio, E., Bathen, A., Epplen, J. & Lubjuhn, T. (1998) Extrapair paternity in the great tit (*Parus major*): a test of the 'good genes' hypothesis. *Behavioral Ecology*, **9**, 388–396.
- Tregenza, T. & Wedell, N. (2000) Genetic compatibility, mate choice and patterns of parentage: Invited review. *Molecular Ecology*, **9**, 1013–1027.
- Trivers, R. (1972) Parental investment and sexual selection. *Sexual Selection and the Descent of Man* (ed. B. Campbell), pp. 136–179. Aldine-Atherton, Chicago, IL.
- Watson, P.J. (1991) Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). *Animal Behavior*, **41**, 343–360.
- Westneat, D. & Stewart, I. (2003) Extra-pair paternity in birds: causes, correlates and conflict. *Annual Review of Ecology and Systematics*, **34**, 365–396.
- Westneat, D., Sherman, P. & Morton, M. (1990) The ecology and evolution of extra-pair copulations in birds. *Current Ornithology*, **7**, 331–369.
- Whittingham, L. & Dunn, P. (2001) Survival of extra-pair and within-pair young in tree swallows. *Behavioral Ecology*, **12**, 496–500.
- Williams, G. (1975) *Sex and Evolution*. Princeton University Press, Princeton, NJ.
- Wolf, L. (1975) 'Prostitution' behaviour in a tropical hummingbird. *Condor*, **77**, 140–144.
- Zeh, J. & Zeh, D. (1996) The evolution of polyandry. I. Intra-genomic conflict and genetic incompatibility. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **263**, 1711–1717.
- Zeh, J. & Zeh, D. (1997) The evolution of polyandry II: Post-copulatory defences against genetic compatibility. *Proceedings of the Royal Society of London Series B. Biological Sciences*, **264**, 69–75.

Received 20 October 2006; accepted 30 March 2007

Supplementary material

The following supplementary material is available for this article online.

Appendix S1. GOF test details.

Appendix S2. Generalized estimating equation models of survival details

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1365-2656.2007.01253.x>

Please note: Blackwell Publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.