

Is there an optimal number of helpers in Alpine marmot family groups?

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The consequence of helping behavior on breeders fitness is still controversial. We used multivariate analyses to investigate for the effects of male and female subordinates on breeders' components of fitness in the Alpine marmot, *Marmota marmota*. We found that male and female subordinates, respectively, increased and decreased juvenile survival during winter. Thus, we give evidence that male subordinates should be considered as helpers, and that helpers provided breeders with immediate reproductive success gains, whereas subordinates females were costly. Helpers had no positive effects on female body condition, on persistence (future survival) of dominants, and on future reproduction (occurrence and size of a litter). Helpers thus did not provide breeders with delayed fitness benefits, and therefore, the load-lightening hypothesis was not supported. On the contrary, helpers had delayed fitness cost for dominant males and, consequently, for dominant females. Immediate benefits counterbalanced by delayed costs suggested an optimal number of helpers in the family group both from male and female perspectives. An optimality model well predicted the observed mean number of helpers in Alpine marmot family groups. Optimal numbers of helpers were slightly different for males and females, suggesting a potential conflict of interest between dominants. We finally discuss the possible mechanisms of helping that may explain the observed pattern in the Alpine marmot. *Key words*: cooperative breeding, load-lightening hypothesis, *Marmota marmota*, mixed models, optimality. [*Behav Ecol* 15:916–924 (2004)]

The evolution of cooperative breeding has stimulated theoretical and empirical work and remains an open field of research (Cockburn, 1998). The fitness consequences of cooperative breeding have been considered both for helpers (Clutton-Brock, 2002; Emlen, 1997) and for breeders (see Brown et al., 1982; Clutton-Brock et al., 2001; Crick, 1992; Russell et al., 2002).

Consequences of helping behavior on breeders reproduction and survival are still problematic in cooperative breeders because we have to disentangle the direct effect of helpers from the trivial consequences of group size and territory quality (Cockburn, 1998). Multivariate and experimental studies proved that helpers might provide breeders with immediate fitness benefits by increasing current reproductive success. This is documented both in birds (Brown et al., 1982; Emlen and Wrege, 1991; Heinsohn, 1992; Koenig and Mumme, 1987; Mumme, 1992; Woolfenden and Fitzpatrick, 1984) and in mammals (Clutton-Brock et al., 2001; Powell and Fried, 1992; Russell et al., 2002; Solomon, 1991). Helpers may increase annual reproductive success of breeders by feeding young, by reducing predation, or by warming juveniles during hibernation (for reviews in birds and mammals, respectively, see Solomon and French, 1997; Stacey and Koenig, 1990). However, in other cases helpers had no apparent effect on annual reproductive success of breeders (Bekoff and Wells, 1986; Ligon and Ligon, 1990; Magrath and Yezzerinac, 1997; but see Magrath, 2001; Woodroffe and Macdonald, 2000) but might provide breeders with some delayed benefits. Helping behavior may then lighten the workload of breeders (Crick, 1992) and, consequently, the parental investment of breeders (sensu Trivers, 1972), thus enhancing future survival and/or future reproduction of breeders (Khan and Walters, 2002).

Interestingly, the negative effect of helpers on breeders reproduction and survival is poorly documented. The presence of helpers may be costly for the breeders if the retention of helpers (that generally delay dispersal) corresponds to a prolonged period of parental investment (Fitzpatrick and Woolfenden, 1988) or if helpers compete with breeders for food in poor environmental conditions (Komdeur, 1996).

The aim of this article is to use multivariate analyses and modeling to analyze the effects of helpers on breeders reproductive success and survival in the Alpine marmot, *Marmota marmota*, a mammal species still not always considered to be cooperative. We investigated for (1) immediate effects (benefits or costs) of nonreproductive subordinates on breeders reproductive success. For that, we analyzed the simultaneous effects of male and female subordinates on juvenile survival during winter. This, combined with the effect of territory quality, will allow disentangling the direct effect of helpers from the consequence of group size and territory quality, (2) delayed effects (benefits or costs) of helpers on major components of breeders fitness. For that, we analyzed the effect of male subordinates on dominant body condition, on future survival (persistence as dominant the following year), and on future reproduction (occurrence and size of a litter the following year). (3) Last is the occurrence of an optimal number of helpers in Alpine marmot family groups. Because we found the expected positive effect of the number of male subordinates on juvenile survival (immediate fitness benefits; Allainé et al., 2000) and a negative effect of the number of male subordinates on the persistence of the dominant male (delayed cost for the dominant male), our results suggested an optimal number of helpers in the family group from the dominant males perspective. Therefore, we finally modeled the optimal number of male subordinates for dominant males and females, respectively, and compared estimates to the observed mean number of male subordinates in the family groups.

Alpine marmots are large ground-dwelling squirrels living in mountain open meadows. The basic social unit is a family

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group of two to 20 individuals, composed of a territorial dominant breeding pair, mature subordinates of 2–4 years, yearlings, and juveniles (Perrin et al., 1993). The mating system is predominantly but not strictly monogamy because dominant males are frequently cuckolded (Goossens et al., 1998). Although sexually mature, subordinate females are reproductively suppressed (Arnold, 1990; Goossens et al., 1996), whereas subordinate males sometimes sire extrapair young (Arnold, 1990; Goossens et al., 1998). Alpine marmots emerge from hibernation in late March or early April, and mate in late April. After 30 days of gestation, dominant females give birth to one to seven pups. Juveniles emerge from the natal burrow in late June and early July, after 40 days of lactation. Offspring stay in their natal group at least until 2 years old, when they reach sexual maturity. Subordinates of both sexes rarely get a dominant position in their natal territory and may disperse at 2 years old, but frequently delay dispersal until they are 3 or even 4 years old (Frey-Roos, 1999; Magnolon, 1999). Male subordinates are supposed to help parents in warming juveniles during hibernation (Arnold, 1990) because juvenile survival during winter increases with the presence of male subordinates in the hibernaculum (Allainé et al., 2000; Arnold, 1993). Thus, the Alpine marmot can be considered as a cooperatively breeding species (Allainé, 2000; Blumstein and Armitage, 1999) for three reasons: dispersal is delayed beyond sexual maturity, reproductive suppression of subordinates is almost complete, and, although in an unusual way, subordinate males may help dominants in rearing juveniles.

METHODS

Study site and data collection

The study site was located in the Natural Reserve of La Sassièrre (Parc National de la Vanoise, French Alps, 45°29' N, 6°59' E) at an elevation of 2350 m. The site is characterized by alpine vegetation (Gensac and Rothé, 1974) and high mountain weather (Farand et al., 2002).

From 1990–2001, 595 individuals from 23 family groups were permanently marked with a numbered ear tag and an electronic device (Trovan) put under the skin, allowing individual identification. Each trapped individual was sexed, weighed, and measured for several morphological traits. Intensive observation with binoculars $\times 10$ and a $\times 20$ –60 telescope allowed us to determine family composition in early spring. Takeovers, dispersal events, or individual disappearances thereafter were recorded. Thus, changes in the composition of family groups were known, and group composition was checked in September, allowing us to determine the number of subordinates of each sex during hibernation.

Statistical analyses

We used R 1.5.0 package (Ihaka and Gentleman, 1996) to build respectively linear (restricted maximum likelihood [REML] procedure for models with normal error structure) and generalized linear (penalized quasi likelihood [PQL] procedure for models with nonnormal error structure) mixed models. Mixed models allow considering both fixed and random terms. Random terms entered into the model took into account repeated measures of the same individuals (analyses on male and female dominants, see below) and of different individuals within the same litter (analysis of the juvenile survival during winter, see below). To fit the model, we used the same procedure as used by Russell et al. (2002). Discrete terms were always factorized. All exploratory fixed

terms were initially entered into the model and then dropped sequentially. The fitted model included only fixed terms for which elimination would be significant. The significance of fixed terms was assessed by using their Wald statistics (chi-square distribution for each term fitted last in the model). In the tables, statistics, and p values of significant terms ($p < .05$) are from the fitted model (all significant terms included), whereas statistics and p values of nonsignificant terms are from the fitted model and each nonsignificant term added separately. Information on interactions (depicted by asterisk) is presented only when significant. The tables present also the average effect and the standard error of each term of the fitted model.

Juvenile survival

Winter is critical for juvenile marmots, and the juvenile survival is an important component of breeders' current reproductive success. Juvenile survival was computed as the proportion of juveniles entering hibernation that emerged as yearling the following year. The number of yearlings still present in the family group the following year was estimated by counting them early in spring and from capture data. The number of yearlings is a reliable indicator of juvenile survival because dispersal did not occur among yearlings (Perrin et al., 1993). Moreover, yearlings were easily identifiable early in spring because they are smaller than are adults. All juveniles known to die during summer were discarded from the analysis of winter survival. In particular, takeovers by males were followed by the disappearance of all 25 juveniles in five family groups. We also discarded juveniles for which the fate during winter was uncertain. We were able to determine the composition of the hibernating group for 44 family groups. The analysis was then done on 161 juveniles from 44 litters.

We ran a generalized linear mixed model to investigate for the terms that affected the juvenile survival during winter. To take into account repeated sampling of different juveniles within the same litter, we used the litter as a random term in the analysis. The fixed exploratory terms considered were as follows: (1) the number of nonreproductive subordinates of both sexes. This will allow analyzing the immediate effects of nonreproductive subordinates on breeders' fitness. We built two different models. In the first model, we consider globally all the nonreproductive subordinates of both sexes. In the second model, we consider separately the two types of nonreproductive subordinates—sexually mature subordinates and yearlings—of both sexes. In both models also were considered (2) litter size, (3) territory exposure to sun as an indicator of territory quality (Allainé et al., 1998). Exposure to sun was factorized as south-facing versus north-facing and valley territories.

Female body condition

Female body condition has been computed as body mass corrected for date of capture (the same procedure was adopted for male body condition). We considered, as far as possible, females in the same reproductive stage to avoid possible bias on female weight. The analysis considered 36 measures (female-year) of body condition from 20 dominant females. We used a linear mixed model to investigate which terms affected the dominant female body condition. To take into account repeated sampling of the same females, the individual female was used as a random term in the analysis. The fixed exploratory terms considered were as follows: (1) the number of helpers. According to the load-lightening hypothesis, the presence of helpers may allow dominants to reduce energy expenditure in warming juveniles and thus to save fat reserves. So, the presence of helpers may result in

dominant females being in better condition the following year. This allows testing the occurrence of delayed effects (energetic effects) of helpers on breeders. (2) The change of the resident male was also considered. King and Allainé (2002) previously found a correlation between the female condition and the persistence of the dominant male that may express the hibernating condition encountered by the family group. (3) Lastly, territory exposure to sun was considered. Because marmots showed habitat preferences (Allainé et al., 1994) and because these preferences affected female body mass (Allainé et al., 1998), we took into account the exposure to sun (i.e., territory quality) in our analysis.

Persistence of dominants

Survival of dominants during winter was difficult to assess because we cannot exclude the occurrence of a dominant eviction from his territory before our first visit (generally in late April or in early May) in some years. We rather used dominant persistence than dominant survival. The persistence did not correspond exactly to the survival of the dominant, but our field observations indicated that evicted individuals were often in poor body condition and had low chance to survive. Moreover, if exceptionally an evicted dominant was successful in recovering a dominant position in another group, the change of one dominant in a family group during spring was generally associated with the absence of reproduction in the current year (Hackländer and Arnold, 1999; King and Allainé, 2002). So, nonpersistence as dominant was assumed to reduce the fitness of the non-persistent dominant. The persistence of dominants from one year to the another was encoded by a one if the dominant was still dominant in the same family group the following summer and by a zero if not. The persistence of the dominant male was determined for 69 male-years concerning 36 different males. The persistence of the dominant female was determined for 72 female-years concerning 26 different females. We built two generalized linear mixed models to investigate which terms affected the persistence of dominant males and dominant females. We used the individual male and female as a random term to take into account repeated sampling on the same dominants (males and females, respectively). In both models, the fixed exploratory terms considered were as follows: (1) the number of helpers. A possible delayed effect of helpers on breeders fitness is an increase in survival (may be through reduced energetic costs of reproduction, see above). We then analyzed whether the presence of helpers affected the persistence of dominants. The data led us to consider linear and quadratic effects of helpers, especially on male persistence. Also considered were (2) the number of subordinate females and (3) the body condition of the dominant in poor condition a given year may have reduced persistence to the next year. (4) Lastly, we considered the presence of a litter the previous year. We tested whether the reproductive cost associated with the presence of a litter a given year affected future dominants persistence.

Future reproduction

We determined both the occurrence of a litter and the litter size in 36 groups-years concerning 20 dominant females. Litter size at emergence (range = 1–7) and the date the young emerged were recorded. Young were caught, weighed, and sexed generally within 3 days after emergence from the natal burrow (for more details on the method, see Allainé et al., 2000). We used generalized linear mixed models with binomial and Poisson errors to investigate which terms

Table 1

Generalized linear mixed model showing the effects of terms on juvenile survival during winter

Model terms	Wald statistic (χ^2)	df	<i>p</i>
No. of nonreproductive males ^a	5.12	1	.023
No. of nonreproductive females	0.36	1	.55
Litter size	0.36	3	.94
Exposure of the territory to sun ^b	2.09	1	.15

Minimal model	Average effect	SE
Constant	1.000	0.50
No. of nonreproductive males	0.532	0.235

^a Nonreproductive individuals correspond to mature subordinates and yearlings together.

^b Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

affected the occurrence of a litter and litter size, respectively. In both cases, we used the individual female as a random term to take into account repeated sampling on the same dominant females. In both cases, the fixed exploratory terms considered were as follows: (1) the number of helpers. Another possible delayed effect of helpers on breeders' fitness is an increase in future reproduction (may be through reduced energetic costs of reproduction and increased survival during hibernation, see above). We then investigated for whether the presence of helpers affected the probability of occurrence and/or the size of the litter the following year. (2) We also considered the dominant female body condition. The occurrence (Hackländer and Arnold, 1999) and the size (King and Allainé, 2002) of the litter depend on female body condition. (3) Lastly, we considered the change of the dominant male that also affects future reproduction (Hackländer and Arnold, 1999; King and Allainé, 2002) and (4) territory exposure to sun.

RESULTS

Juvenile survival

From 1990–2001, 343 juveniles emerged from 90 litters. The mean litter size (3.81 ± 0.12 , SE) is slightly smaller than that reported by Allainé et al. (2000; mean = 4.11 ± 0.14). We determined the winter survival of 198 juveniles from 53 litters. The overall winter survival of juveniles was 0.78 (95% confidence interval [CI]: 0.72–0.84). The juvenile survival during winter did not differ ($\chi^2 = 0.799$; df = 1, $p = .371$) between sexes (male survival = 0.75, CI: 0.67–0.83, $n = 116$; female survival = 0.817, CI: 0.73–0.90, $n = 82$).

The juvenile survival during winter was primarily affected by the number of nonreproductive males (mature subordinates and yearlings considered together) but was independent of the number of nonreproductive females, of litter size, and of territory exposure to sun (Table 1). Juvenile survival increased with the number of nonreproductive males but not linearly (Figure 1), indicating that additional males did not provide additive effects on juvenile survival during winter. When considering mature subordinates (i.e., 2 year old or more) and yearlings separately, the juvenile survival increased with the number of male subordinates and tended to decrease with number of female subordinates (Table 2). The positive effect of subordinate males on juvenile survival partly compensated

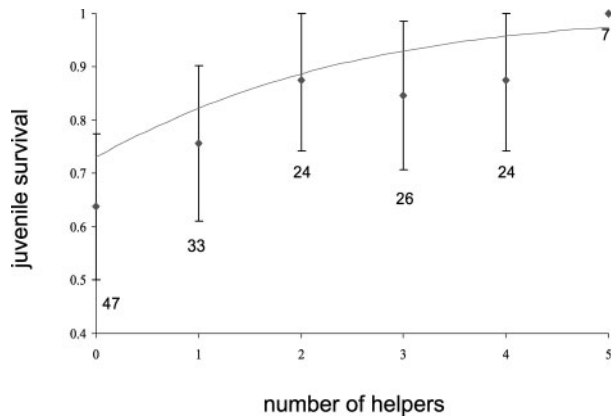


Figure 1
Survival of juvenile Alpine marmots during winter as a function of the number of helpers in the hibernating group. Solid line indicates curve predicted by the logistic regression; squares, mean observed values with 95% confidence intervals. Numbers indicate sample size.

for the negative effect of subordinate females. Indeed, the higher the number of male subordinates the lower the negative effect of female subordinates (Figure 2). Both male and female yearlings had nonsignificant positive effects on juvenile survival during winter (Table 2). The opposed effect of yearling and subordinate females explains the absence of effect of the number of nonreproductive females (mature subordinates and yearlings considered together) (Table 1).

Future reproduction

A litter was produced by 64% of the dominant females. This percentage is in agreement with those reported by Hackländer and Arnold (1999, 64%) and King and Allainé (2002, 71%). The probability that a litter emerged the current year depended on a change of the dominant male, on female body condition in spring, on territory exposure to sun, and on the interaction between male change and female body condition (Table 3). The occurrence of a litter was low (close to zero) whatever the female body condition when the dominant male changed, but was higher and increased with the female body condition when the dominant male did not change. Finally, females reproduced less often in south-facing slopes than in other exposures to sun. The probability that a litter emerged the current year depended neither on the number of helpers nor on the presence of a litter the previous year (Table 3).

The litter size a given year increased with female body condition and tended to be lower when dominant male changed (Table 4). The litter size depended neither on the number of helpers in the family group nor on exposure to sun or on the presence of a litter the previous year (Table 4).

Body condition

The female body condition affected the occurrence and the size of a litter but depended neither on the number of helpers in the family group nor on successful reproduction the previous year (Table 5). Thus, we failed to reveal a cost of reproduction. The female body condition did not depend on the persistence of his mate as dominant (Table 5).

Persistence of dominants

The persistence of the dominant female increased with its body condition the previous year (Table 6), but was

Table 2
Generalized linear mixed model showing the effects of terms on juvenile survival during winter

Model terms	Wald statistic (χ^2)	df	<i>p</i>
No. of mature subordinate males	4.24	1	.039
No. of mature subordinate females	2.81	1	.09
No. of yearling males	2.20	1	.14
No. of yearling females	1.29	1	.26
Litter size	0.47	3	.93
Exposure of the territory to sun ^a	2.32	1	.13

Minimal model	Average effect	SE
Constant	1.676	0.476
No. of mature subordinate males	1.245	0.604
No. of mature subordinate females	-0.972	0.579

Mature subordinates and yearlings were considered separately.

^a Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

independent of the occurrence of a litter the previous year, of the number of helpers (linear or quadratic), and of the number of females in the hibernating group (Table 6). The persistence of the dominant male depended on a quadratic effect of the number of helpers (Table 7), indicating that dominant male persistence increased and then decreased as the number of helpers increased (Figure 3). Clearly, a number of helpers greater than one represented a fitness cost for the dominant male when considering its persistence as dominant. The persistence of the dominant male depended neither on its body condition, nor on the number of subordinate females and tended to decrease when successful reproduction occurred the previous year (Table 7).

Optimal number of helpers

A high number of helpers was beneficial for current reproduction (increased juvenile survival) and costly for future reproduction (reduced persistence of the dominant male that in turn affected reproduction of the dominant female). Our results then clearly indicated that an optimal number of helpers should exist both for dominant males and females. We then built optimality models to find the optimal number of helpers that maximizes the fitness of dominant males and females respectively.

The fitness of dominant male, $w(h)$, and female, $f(h)$, having h helpers has been calculated respectively as follows:

$$w(h) = \sum_{i=0}^{\infty} p(h)^i * r * c * s(h) \quad (1)$$

$$f(h) = \sum_{i=0}^{\infty} r^i * p(h) * c * s(h) \quad (2)$$

where $p(h)$ is the probability of staying dominant the following year when h helpers are present, and r is the female persistence that is independent of h (see above). The probability of producing a litter a given year directly depends on the persistence of both dominants (King and Allainé 2002); c is the product of the mean litter size by the juvenile survival during summer (assumed to be independent of h , see above for litter size), $s(h)$ is the juvenile survival during winter

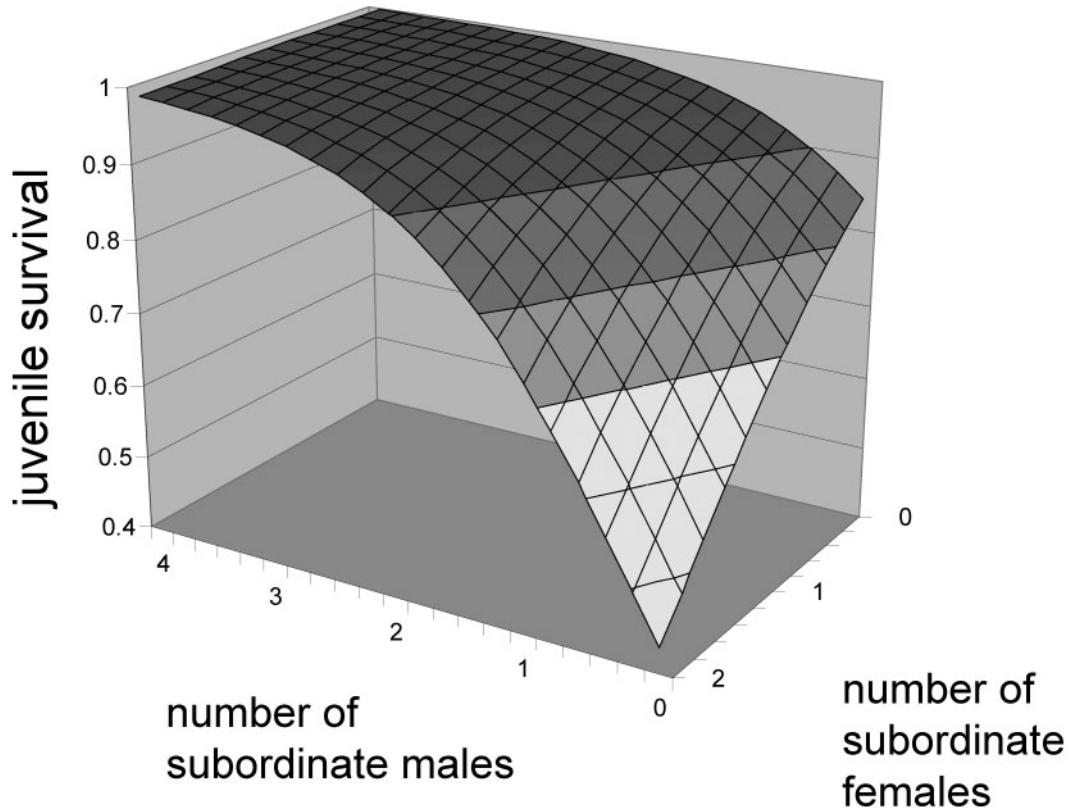


Figure 2
Survival(s) of juvenile Alpine marmots during winter as a function of the number of male and female subordinates in the hibernating group. Legend of colors: blue, $s > 0.9$ (number of observations in this area: $n = 54$); red, $0.8 < s < 0.9$ ($n = 76$); green, $0.7 < s < 0.8$ ($n = 14$); and yellow, $0.4 < s < 0.7$ ($n = 17$).

when h helpers hibernated with the juveniles, and i is the number of years. $W(h)$ and $f(h)$ can be rewritten as

$$w(h) = \frac{r^* c^* s(h)}{1 - p(h)} \tag{3}$$

$$f(h) = \frac{p(h) * c^* s(h)}{1 - r} \tag{4}$$

$s(h)$ is drawn from the modeling of the juvenile survival as a function of the number of helpers (“juvenile survival”):

$$\text{logit } s(h) = 1.00 + 0.53.h \tag{5}$$

$$\text{and } s(h) = \frac{e^{1+0.53.h}}{1 + e^{1+0.53.h}} \tag{6}$$

$p(h)$ is drawn from the modeling of the male persistence as a quadratic function of the number of helpers (“persistence of dominants”):

$$\text{logit } p(h) = 0.986 + 0.8434h - 0.2827h^2 \tag{7}$$

$$\text{and } p(h) = \frac{e^{0.986+0.8434.h-0.2827.h^2}}{1 + e^{0.986+0.8434.h-0.2827.h^2}} \tag{8}$$

We can find the optimal numbers of helpers h^* from the conditions:

$$\begin{aligned} [dw/dh]_{h=h^*} &= 0 \quad \text{and} \quad [d^2w/dh^2]_{h=h^*} < 0 \\ [df/dh]_{h=h^*} &= 0 \quad \text{and} \quad [d^2f/dh^2]_{h=h^*} < 0 \end{aligned}$$

We used Mathematica 3.0. software to solve for the values h^* that maximize $w(h)$ and $f(h)$, respectively. The optimal

number of helpers for males was $h^* = 1.642$, whereas $h^* = 2.065$ for females. Both these predicted values were compatible with the observed mean number of helpers in our family groups ($h = 1.743$, 95% CI = [1.403; 2.083]) that was intermediate between the two optima.

Table 3
Generalized linear mixed model showing the effects of terms on the occurrence of a litter a given year

Model terms	Wald statistic (χ^2)	df	p
Change of the resident male (Cmal)	26.99	1	.0003
Female body condition (Fbc)	33.39	1	.0001
No. of helpers ^a	0.20	1	.65
Exposure of the territory to sun ^b	14.27	1	.0014
Occurrence of a litter the previous year	1.86	1	.17
Cmal × Fbc	9.99	1	.009

Minimal model	Average effect	SE
Constant	2.419	0.949
Cmal (change < persistence)	-6.922	1.332
Female body condition	12.06	2.087
Exposure to sun (south < north)	4.91	1.29
Cmal × Fbc	-14.76	4.76

^a Helpers are nonreproductive males.

^b Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

Table 4
Generalized linear mixed model (Poisson error) showing the effects of terms on the litter size a given year

Model terms	Wald statistic (χ^2)	df	<i>p</i>
Change of the resident male (Cmal)	3.33	1	.068
Female body condition	4.5	1	.034
No. of helpers ^a	0.32	1	.57
Exposure of the territory to sun ^b	2.44	1	.12
Occurrence of a litter the previous year	0.0001	1	.99

Minimal model	Average effect	SE
Constant	1.867	0.468
Cmal (change < persistence)	-0.712	0.39
Female body condition	0.772	0.363

^a Helpers are nonreproductive males.

^b Exposure to sun is factorised as south-facing versus north-facing slopes and valley.

DISCUSSION

Fitness consequences of helping behavior for breeders

Our results provide evidence that effects of helpers on breeders reproductive success (juvenile survival) are not a consequence of group size or territory quality effects because male and female subordinates have antagonistic effects; the positive effect of subordinate males partly compensated for the negative effect of subordinate females. Thus, we can consider with confidence the occurrence of helping behavior in the Alpine marmot.

Helpers (subordinate males) provide dominants with immediate fitness benefits by increasing the juvenile survival during winter (Allainé et al., 2000). Thus, the presence of helpers increased the current reproductive success as previously observed in other mammal species (Clutton-Brock et al., 2001; Powell and Fried, 1992; Russell et al., 2002; Solomon, 1991). However, the shape of the relationship between juvenile survival and number of helpers during winter indicated that the positive effects of additional helpers were not additive but decreased as the number of helpers increased.

Helpers do not provide dominants with delayed fitness benefits in the Alpine marmot. According to the load-

Table 5
Linear mixed model showing the effects of terms on female body condition

Model terms	Wald statistic (χ^2)	df	<i>p</i>
Change of the resident male	0.197	1	.66
No. of helpers ^a	0.398	1	.53
Exposure of the territory to sun ^b	0.607	1	.43
Occurrence of a litter the previous year	0.384	1	.54

Minimal model	Average effect	SE
Constant	-0.06	0.076

^a Helpers are nonreproductive males.

^b Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

Table 6
Generalized linear mixed model (binomial error) showing the effects of terms on the persistence of dominant females

Model terms	Wald statistic (χ^2)	df	<i>p</i>
Female body condition	5.63	1	.017
No. of helpers (linear effect) ^a	0.88	1	.35
No. of helpers (quadratic effect)	0.75	1	.39
No. of nonreproductive females	0.74	1	.39
Occurrence of a litter the previous year	0.38	1	.54

Minimal model	Average effect	SE
Constant	2.014	0.558
Female body condition	2.800	1.082

^a Helpers are nonreproductive males.

lightening hypothesis (Crick, 1992), the presence of helpers may allow parents to reduce their energy expenditure in raising young. This in turn, may allow them to be in better condition and, consequently, to better survive and/or to have higher probability of reproduction the following year. Such delayed effects of helpers were reported both in mammals (effects on maternal condition and future reproduction; Russell et al., 2003) and in birds (effects on breeders survival; Khan and Walters, 2002). In the Alpine marmot, we confirmed that the condition of the dominant female affected its future survival (persistence as dominant) and its future reproduction (both the occurrence of a litter, Hackländer and Arnold, 1999; and the litter size, King and Allainé, 2002) in a given year. We confirmed that the persistence of dominants affected future reproduction. However, we found no positive effect of helpers on body condition of the dominant female and, consequently, on the persistence of dominants and on future reproduction. Thus, our results do not support the load-lightening hypothesis in the Alpine marmot. We propose that parents in the Alpine marmot do not lighten their workload when helpers are present. Rather, helping behavior adds to parental investment, thus increasing current reproductive success. Moreover, dominant males suffered a delayed cost through reduced persistence when the number of helpers exceeded a threshold close to one. We propose that

Table 7
Generalized linear mixed model (binomial error) showing the effects of terms on the persistence of dominant males

Model terms	Wald statistic (χ^2)	df	<i>p</i>
No. of helpers (linear effect) ^a	2.68	1	.10
No. of helpers (quadratic effect)	3.90	1	.048
Female body condition	0.52	1	.47
No. of nonreproductive females	1.11	1	.29
Occurrence of a litter the previous year	2.83	1	.092

Minimal model	Average effect	SE
Constant	0.986	0.49
No. of helpers (linear effect)	0.843	0.64
No. of helpers (quadratic effect)	-0.284	0.15

^a Helpers are nonreproductive males.

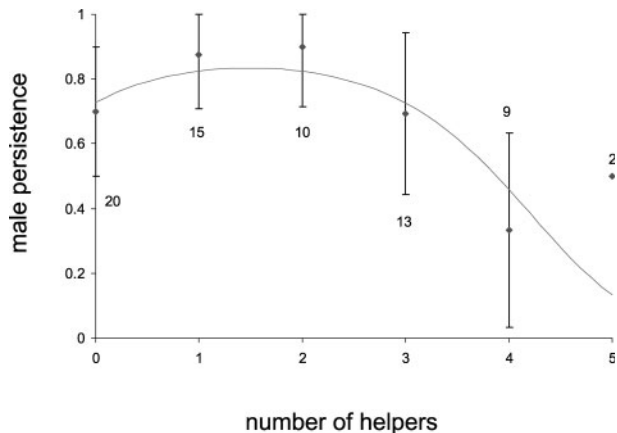


Figure 3
Probability of male persistence as dominant from one year to another as a function of the number of helpers in the hibernating group. Solid line indicates curve predicted by the logistic regression; squares, mean observed values with 95% confidence intervals. Numbers indicate sample size.

a too high number of helpers may be disadvantageous for the dominant male in Alpine marmots probably because of the competition with subordinates for reproduction. Such a negative effect of a high number of helpers was rarely reported. Komdeur (1996) found in the Seychelles warbler that a too high number of helpers might be costly for the parents because of the competition for food in poor territories.

Optimal number of helpers

The problem of the occurrence of an optimal number of helpers has still received poor consideration in mammals. In

the Alpine marmot, we found that a high number of helpers enhanced the juvenile survival during winter but decreased the persistence of the dominant male. Helpers are then beneficial for current reproduction but costly for future reproduction of the dominant male. Because persistence of the dominant male affected the occurrence and the size of a litter in a given year, dominant females suffered an indirect delayed effect from the presence of helpers. This indicated that an optimal number of helpers should exist both from dominant male and female perspectives. The optimal number of helpers was slightly lower for males (lower than two) than for females (about two), suggesting a potential conflict of interest between dominants. Although the model of optimality we used was simple, the estimated optimal number of helpers for males and females, respectively, well corresponded to the observed mean number of helpers within family groups. However, all family groups did not conform strictly to these optima (the range of number of helpers = 0–4), and experimental work is needed to better understand mechanisms controlling for the number of helpers within groups.

Mechanisms of helping behavior in the Alpine marmot

Many hypotheses have been proposed to explain the evolution of helping behavior (for a review, see Cockburn, 1998). In the Alpine marmot, understanding the evolution of helping behavior requires to consider first how males help. Helping behavior may consist in warming juveniles by grooming and covering them with hay and/or by producing heat during periodic arousals (Arnold, 1990). If the production of heat is the main form of helping behavior, then two plausible scenarios are possible (Figure 4). In the first scenario, helping behavior may be an unselected passive process (Jamieson, 1991). Helping via heat production may simply be the consequence of a need for periodic arousals.

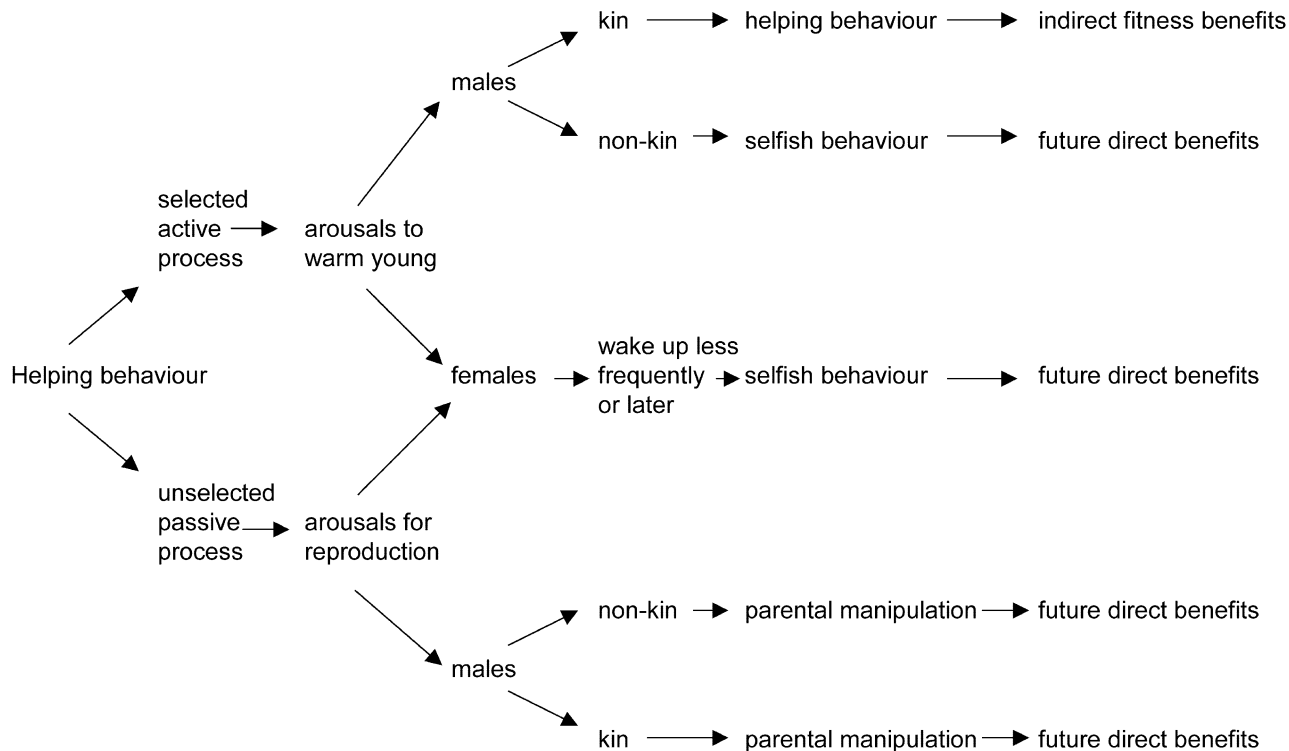


Figure 4
Two possible mechanisms of helping explaining the observed pattern in the Alpine marmot (see text).

This possibility does not explain why social thermoregulation (i.e., helping) is costly only for subordinate males related to juveniles (Arnold, 1990). An alternative hypothesis is that helping results from the need to end hibernation early. Indeed, a careful examination of the Figure 1 in Arnold (1988) seems to indicate that adult males end hibernation earlier than do females. We hypothesize that adult males may need to wake up early to activate their reproductive function. The difference between the subordinates related and not related to the dominant male may be understood if the reproductive suppression in nonrelated subordinates (Arnold and Dittami, 1997) operates during hibernation. In the second scenario, helping behavior is a selected active process (Figure 4). Males may wake up specifically to produce heat to warm related juveniles. This scenario well explains why subordinates not related to juveniles do not help, but we have to check that they wake up less frequently than do subordinate males related to juveniles.

Behavior of the nonhelping sex

Studies of cooperatively breeding species rarely focused on fitness consequences of the behavior of the nonhelping sex. Our results provide evidence that members of the nonhelping sex (subordinate females) in the Alpine marmot negatively affected the juvenile survival during winter and thus represent a reproductive cost for dominants. This negative effect of subordinate females suggests that they probably compete with juveniles for heat. Two questions arise from this result. The first question is how do females compete with juveniles for heat? Arousal episodes during hibernation occur in both sexes (Arnold, 1993), indicating that subordinate females wake up and then produce heat during the course of hibernation. But it is possible that females wake up less frequently than do males and benefit from the heat produced (Figure 4). Another possibility is that subordinate females compete with juveniles at some critical stages. For example, males end hibernation early (Arnold, 1988), and females may gain heat at the end of hibernation when fat reserves are low and crucial for survival (Figure 4). The second question is why do females compete with juveniles for heat? Female reproduction probably depends on condition (Hackländer and Arnold, 1999). However, wake up is energetically costly and results in mass loss (Arnold, 1990). Then, subordinate females may be faced to a classical tradeoff of resource allocation: to invest in the current litter (indirect fitness benefits) to the detriment of saving fat reserve for the future reproduction or future dispersal (direct fitness benefits). Subordinate females seem to adopt a selfish strategy favoring their future direct reproduction over the current indirect fitness.

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