Male-biased sex ratio in litters of Alpine marmots supports the helper repayment hypothesis

Dominique Allainé,[a] **Francine Brondex,**[a] **Laurent Graziani,**[a] **Jacques Coulon,**[a] **and Irène Till-Bottraud**[b]

[a]UMR 5553–Biologie des Populations d'Altitude, Université Claude Bernard, Lyon 1. 43, Bd du 11 novembre 1918, F-69622 Villeurbanne Cedex, France, and [b]UMR 5553–Biologie des Populations d'Altitude, Université Joseph Fourier, BP 53, F-38041 Grenoble Cedex 9, France

In a French population of Alpine marmots (*Marmota marmota*), the sex ratio at weaning was biased in favor of males. This bias also seemed to exist at birth. Under Fisher's equal allocation principle, this means that daughters should be more costly to produce than sons. Because the Alpine marmot can be considered a cooperative breeding species, we investigated whether the differential cost between sons and daughters may be explained by the helper repayment hypothesis. The Alpine marmot uses social thermoregulation during hibernation, allowing juveniles to better survive over winter. In the study population, juvenile survival during winter increased with group size. More precisely, juvenile survival during winter increased with the number and with the proportion of subordinate males in the hibernating group, but juvenile survival did not depend on the number of subordinate females. As our results did not support alternative hypotheses to explain the observed bias in sex ratio among offspring at emergence, we conclude that the helper repayment hypothesis is the best candidate to explain the observed offspring sex ratio bias in Alpine marmots. By participating in social thermoregulation, subordinate males may repay part of the investment they received from their parents and thus become less costly to produce. We suggest that only subordinate males helped because they may gain direct fitness benefits, whereas subordinate females may only expect indirect fitness benefits from helping. Finally, the offspring sex ratio per individual parent was male biased, but mothers adjusted the size and the sex composition of their litters according to their phenotypic condition as expected from the Trivers-Willard hypothesis. *Key words:* Alpine marmots, cooperative breeding, helper repayment hypothesis, *Marmota marmota,* sex ratios. *[Behav Ecol 11:507–514 (2000)]*

A mong cooperatively breeding birds, the offspring sex ratio in the population is often biased toward the helping sex (Ligon and Ligon, 1990; Pruett-Jones and Lewis, 1990; Rabenold, 1990; Russell and Rowley, 1996). Under Fisher's (1930) equal allocation principle, a skewed sex ratio in the population might arise when one sex is more costly to produce than the other. Further, theoretical sex ratio modeling (Charnov, 1982; Frank, 1990) predicts a bias toward a sex if the fitness payoff through production of that sex exceeds the fitness payoff through production of the other sex. Consequently, the term ''cost'' should be used sensu Trivers (1972)—involving a decrease in direct fitness components.

The helper repayment hypothesis (Emlen et al., 1986; Gowaty and Lennartz, 1985; Lessels and Avery, 1987) has been proposed to explain such a differential cost between sons and daughters, and consequently sex ratio bias, in populations of cooperatively breeding birds. If offspring of one sex help parents in rearing young, they repay part of the cost of their production (helper repayment model; Emlen et al., 1986) and become less costly to produce. However, helping is costly and may affect the direct fitness of helpers (Solomon and French, 1997). As a consequence, the helping sex will enhance the parents' fitness only when the fitness gain through helpers exceeds the direct fitness loss of helpers (Koenig and Walters, 1999). It would then be valuable for the parents of each family to invest in the production of the helping sex, thus leading

to a biased sex ratio at the population level. On the other hand, mothers are expected to produce an excess of the more profitable sex according to their own phenotypic condition (Silk, 1983; Trivers and Willard, 1973). If mothers differ in their phenotypic condition within populations of cooperatively breeding species, the helping sex may not be systematically the more profitable sex for the mother. For example, Komdeur (1996) recently found that the most profitable sex was the helping sex only on high-quality territories in the Seychelles warbler (*Acrocephalus sechellensis*), a cooperatively breeding bird. He observed that sex ratios were biased toward the helping sex only in good territories. Thus, the pattern of sex ratio variation within populations of Seychelles warblers depended on both helper repayment and competition for local resources (Clark, 1978).

Sex ratio bias at the population level is poorly described in socially monogamous mammals that breed cooperatively. The adult sex ratio is male biased in the Ethiopian wolf (*Canis simensis:* Sillero-Zubiri et al., 1996), in mole rats (*Heterocephalus glaber:* Solomon and Getz, 1997; *Cryptomys hottentotus:* Genelly, 1965), and in the Mongolian gerbils (*Meriones unguiculatus:* Agren et al., 1989) but almost nothing is known about the offspring sex ratio (but see *Lycaon pictus:* Frame et al., 1979; Malcolm and Marten, 1982). The Alpine marmot is such a socially monogamous mammal that breeds cooperatively. The basic social unit is the family group, composed of a territorial resident pair, subordinates, yearlings, and juveniles of the year (Perrin et al., 1993). All family members share a same home range and hibernate together. According to Blumstein and Armitage (1999), cooperative breeding occurs in marmots when a species presents three attributes (see also Solomon and French, 1997): first, individuals delay dispersal beyond reproductive maturity; second, reproduction is

suppressed in reproductively mature individuals, and third, nonbreeding individuals provide costly alloparental care. Using this definition, the Alpine marmot can be considered a cooperatively breeding species. First, subordinates delay dispersal beyond reproductive maturity and stay in their family group until they are 2, 3, or 4 years old (Arnold, 1990a; Perrin et al., 1993). Second, the Alpine marmot is a ''despotic'' species (Vehrencamp, 1983) where physiologically induced reproductive suppression of subordinates is almost complete (but see Goossens et al., 1996, for examples of occasionally failed suppression). In males, the reproductive suppression is mainly directed toward subordinates unrelated to the resident male (Arnold and Dittami, 1997). However, although Alpine marmots are socially monogamous, extrapair paternity may be frequent and sometimes attributable to subordinates that were related to the resident male (Goossens et al., 1998). Third, in the course of hibernation, subordinates (and residents) warm juveniles during periodic arousals and allow them to save fat reserves (Arnold, 1988). In particular, subordinates groom and cover juveniles with hay. This form of alloparental care during hibernation may increase juvenile survival (Arnold, 1993), and consequently the parents' fitness, but is energetically costly for helpers (Arnold, 1990b). Social thermoregulation has only been described in the Alpine marmot, but joint hibernation is widespread among other social marmot species (Barash, 1973; Blumstein and Armitage, 1999; Holmes, 1984).

In this study, we addressed offspring sex ratio bias at the population level, especially in relation to the helper repayment hypothesis in the Alpine marmot. We attempted to answer the following questions:

1. To what extent is the offspring sex ratio biased in our population of Alpine marmots?

2. Does the helper repayment hypothesis may account for such a bias? We first verified two prerequisites of the helper repayment hypothesis: (a) a significant effect of helping on parents' fitness (i.e., juvenile survival during winter should increase with the presence and/or the number of subordinates) and (b) helpers and juveniles should be related. We then investigated whether the offspring sex ratio was biased toward the helping sex. The prediction is that the sex produced in excess should be the helping sex and that juvenile survival during winter should increase with the number and/or the proportion of subordinates of this sex but should not depend on the number of subordinates of the other sex.

3. Do alternative hypotheses also account for such a bias? Four alternative hypotheses were tested. The offspring sex ratio in the population may be biased toward (a) the rarer sex in the population, (b) the smaller sex (i.e., the sex that induces the lowest direct metabolic cost for the mother; Clutton-Brock et al., 1981), (c) the sex that has lower survival during the period of maternal investment, or (d) the sex that disperses earlier (local resource competition; Clark, 1978).

4. Is the variability in offspring sex ratio among families correlated with the mother's phenotypic condition? We investigated the relationship between the sex ratio and mother's body mass, body condition, and territory quality. To test for a possible confounding influence of litter size with mother's condition on sex ratio variation (Williams, 1979), we investigated the correlation between mother's body mass and specific sequences of litter type (based on size and sex composition of the litters).

METHODS

The study site was located in the Natural Reserve of La Sassière (Parc National de la Vanoise, French Alps, 45°29′ N, 6°59′ E). The site is an open meadow covered with alpine vegetation (Gensac and Rothé, 1974) and characterized by high mountain climate. The population of Alpine marmots has been studied since 1990. Each year, Alpine marmots were caught using two-door, live-capture traps equipped with a central release. From 1990 to 1998, 479 individuals belonging to 23 family groups were individually marked. We used two kinds of markings: for permanent individual recognition, we used numbered ear tags combined with the injection of a TROVAN transponder under the skin; for visual recognition fur was dyed and a piece of colored plastic was fixed to the other ear. Mothers were trapped and weighed as soon as possible. We included only data on mothers weighed during their pregnancy in statistical analyses.

Litter size at emergence (range 2–7) and the date the young emerged from their natal burrows were recorded from daily observations of the family groups with binoculars and a 20–60× telescope. To determine sex ratio in litters at emergence, juveniles were trapped as soon as possible and usually within 3 days. Juveniles were then weighed and sexed using ano-genital distance (Zélenka, 1965). We computed sex ratio as the proportion of males. The analysis of sex ratio was performed only on litters for which the sex of all juveniles that emerged was known. In some cases, some juveniles disappeared just after they emerged due to infanticide or for an unknown reason. Litters for which we were unable to trap some juveniles were discarded. However, these litters were considered in the analysis of a systematic bias if they presented an excess of juveniles of one sex. For example, a litter of five juveniles where only four were trapped and sexed, among which we identified three males (or females) and one female (or male) was classified as a male-biased (or female-biased) litter. This conservative procedure did not bias the result because we observed the same trapability for juvenile males and females.

To evaluate the sex ratio at birth, we trapped pregnant females and maintained them in captivity. Pregnancy was diagnosed in the field by palpation and confirmed by X-rays 1 week before parturition. Females were then housed in cages divided into two compartments of the same size (90 × 70 × 50cm). The first compartment, the nest, was maintained in darkness except for a red light that allowed direct observation and recording with a highly sensitive camera. The second compartment was supplemented with food and water ad libitum and lit using the natural photoperiod. The two compartments were connected by a pipe (18 cm diameter and 60 cm length). Litter size and sex composition were determined at birth. Sex was determined from ano-genital distance and careful examination of the ano-genital region. Sex was confirmed when neonates were older. Neonates were weighed and marked with eosin. After weaning, we received an agreement to release mothers and their young on unoccupied territories, and they were regularly observed until the end of the active season.

We determined group composition in the field early in the spring, and every change during the season was recorded. We were able to determine the age of dispersal for most of subordinates. Although the exact age of individuals was often known, we used the following four categories: residents, subordinates, yearlings, and juveniles. Because south-facing slopes were preferred (Allainé et al., 1994) and the mothers' condition was best on these slopes (Allainé et al., 1998), the slope aspect was assumed to determine home-range quality. Home ranges were classified into three different aspects: south-facing, north-facing, and bottom of the valley. Juvenile survival during hibernation was calculated as the proportion of juveniles entering hibernation that emerged as yearlings the following year. Juvenile survival during their first year of life was

calculated as the proportion of juveniles emerging from their natal burrows that emerged as yearlings the following year.

To analyze the effect of ecological factors (years, aspect, and date of emergence) on sex ratio variation, we used generalized linear models with a logistic transformation of data. The effects of group size and number of subordinates of either sex on juvenile survival were investigated by logistic regression. Because some group sizes were poorly represented, we decided to pool groups into size categories to present meaningful mean observed values (and confidence intervals). Analyses were run using GLIM software (Francis et al., 1993), and the significance of factor effects were tested by likelihood ratio tests. We tested systematic bias at the family level by a binomial test with correction for continuity. Differences in the intensity of the bias between male-biased and female-biased litters were tested by a Wilcoxon matched-pairs test.

To test Williams's (1979) hypothesis, we inferred three theoretical sequences of litter types with improving mothers' body mass. Based on the sexual dimorphism in size at emergence of juveniles (Allainé et al., 1998), the first sequence corresponded to the situation where the direct metabolic cost of producing a male was slightly greater than that of producing a female. However, the metabolic cost of producing a son may exceed that expected from sexual dimorphism in size. Thus, we constructed two other theoretical sequences. The second and third sequences corresponded to the cases where the direct metabolic cost of producing a male was slightly greater than that of 1.5 females and 2 females, respectively. The values of these relative metabolic costs were chosen both to introduce a significant change in the theoretical sequence and to keep a biological meaning. We then calculated Spearman's rank correlation between each of these sequences and the mothers' body mass. We paid special attention to the key nonsignificant effect (based on small sample size) of females' presence on juvenile survival when the presence of males is taken into account by assessing the power of the test we performed. As recommended by Steidl et al. (1997), we used information provided by confidence intervals rather than a posteriori power analyses. We calculated the effect (with its confidence interval) of adding three females in the hibernaculum (the maximum number observed) on the juvenile survival during winter. This effect was expressed in percent change when compared with the effect of no females. We calculated four percent-changes corresponding to the situations where one, two, three, or four males were present, respectively. We chose a 20% change (of the same order as that observed for males; see Figure 2A) as the threshold for a biologically significant effect. If the biologically significant effect (20% change) lies above the upper limit of the observed change, we reasonably conclude the null hypothesis to be true (at the level 5%; Steidl et al., 1997); if not, the test was inconclusive.

RESULTS

Sex ratio at emergence

From 1990 to 1997, we recorded the emergence of 73 litters in our study area. The exact litter size at emergence was known for 66 litters. The average litter size was 4.11 ± 0.14 (SE). Complete sex composition at emergence was determined for 53 litters, representing a total of 207 juveniles. The overall sex ratio was 0.578 and significantly departed from 0.5 (95% CI = 0.511–0.643). Although variability existed among years, the year effect was not significant ($\chi^2 = 2.39$, df = 7, $p = .93$). The sex ratio varied from 0.525 to 0.638 among years where more than five complete litters were recorded. Thus, the annual overall sex ratio was always>0.5 (binomial test, $n = 5$, $p = .03$). When we also integrated years with small da-

tasets (fewer than five complete litters), sex ratios varied over a larger range (from 0.5 to 0.75), but again were never <0.5. This indicates that the bias in favor of males at the population level was consistent from year to year (binomial test; $n = 7$, $p < .01$). The sex ratio (SR) did not vary ($\chi^2 = 0.12$, df = 2, $p = .94$) according to slope aspect (south-facing: SR = 0.594, $n = 17$; valley: SR = 0.568, $n = 26$; north-facing: SR = 0.583, $n = 10$). The sex ratio among litters did not vary with the date of emergence (logistic regression, $\chi^2 = 0.06$, df = 1, $p = .80$), but male-biased litters tended to emerge earlier (Man-Whitney U test, $U = 336.5$, $p = .07$). Finally, sex ratio decreased with litter size ($r = -.312$; $n = 53$; $p = .024$). A sex ratio of 1 was observed only in small litters (two, three, or four offspring).

To investigate for possible interactions between causal factors that might bias sex ratio, we performed a multiple logistic regression on the four main factors: year, slope aspect, date of emergence, and litter size. None of the factors had a significant effect, regardless of the order they were entered in the model (p values varied from 0.32 to 0.93). Also, none of the six possible interactions was significant (date of emergence $\times$ slope aspect: $\chi^2 = 0.64$, df = 2, $p = .72$; slope aspect $\times$ litter size: $\chi^2 = 5.52$, df = 6, $p = .48$; year $\times$ date of emergence: $\chi^2 = 9.99$, df = 5, $p = .08$; slope aspect $\times$ years: $\chi^2 = 9.53$, df = 9, $p = .39$; year $\times$ litter size: $\chi^2 = 6.72$, df = 10, $p = .75$; litter size $\times$ date of emergence: $\chi^2 = 5.87$, df = 3, $p = .12$).

Sex ratio at birth

We were able to trap seven pregnant females. Five of these gave birth to 24 young. The remaining two females were probably incorrectly diagnosed as pregnant; X-ray failed to confirm pregnancy previously diagnosed by palpation. However, it is also possible that undetected fetal reabsorptions (or miscarriages) occurred due to handling stress or some other cause. We occasionally observed that pregnant females (based on progesterone titration) failed to raise offspring to emergence (unpublished data). Three neonates (one of them was sexed) in one litter died and were cannibalized by their mother. Among the 22 neonates sexed, 13 were males, giving an overall sex ratio of 0.59. If we eliminate the litter in which the two neonates were unsexed, the sex ratio was again 0.59. Although our sample size is small, this result suggests that the bias in favor of males observed at emergence also exists at birth.

Test of the helper repayment hypothesis

The overall survival of juveniles during winter (s) was 0.813 (95% CI = 0.739–0.870) and did not depend on the litter size ($\chi^2 = 2.01$, df = 1, $p = .156$). The presence of subordinates significantly increased ($\chi2 = 5.74$, df = 1, $p = .016$) the juvenile winter survival (without subordinates, $s = 0.69$, CI = 0.537–0.811; with subordinates, $s = 0.869$, CI = 0.830–0.901). Juvenile winter survival was reduced ($\chi^2 = 4.22$, df = 1, $p = .04$) in groups smaller than the average ($s = 0.756$, CI = 0.649–0.839) compared to larger ones ($s = 0.893$, CI = 0.781–0.951). The juvenile winter survival increased with the number of nonjuveniles in the hibernating group ($\chi^2 = 4.06$, df = 1, $p = .043$; Figure 1).

More precisely, juvenile winter survival increased with the number of nonjuvenile males (i.e., including yearlings; $\chi^2 = 10.07$, df = 1, $p < .002$) and with the number of subordinate males ($\chi^2 = 5.01$, df = 1, $p = .025$; Figure 2A). Thus, juvenile winter survival was on average 0.717 (CI = 0.60–0.83) when only the resident male was present during hibernation and was up to 1 with at least four subordinate males in the hibernating group (Figure 2A). Juvenile winter survival also in-
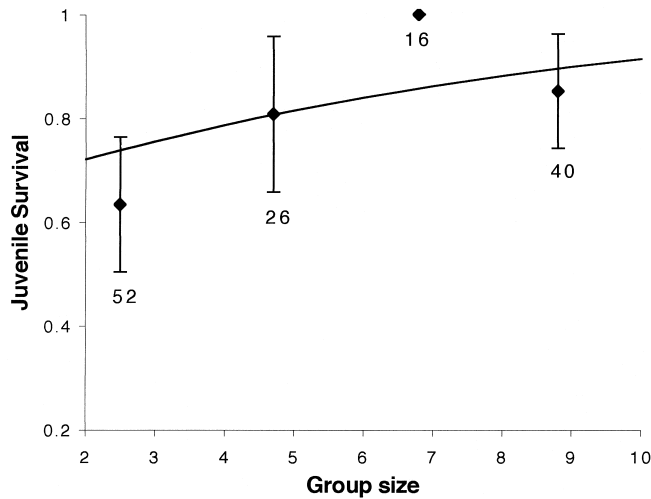
Figure 1
Survival of juvenile Alpine marmots during winter as a function of the hibernating group size. Group size is the number of nonjuvenile individuals in the hibernaculum. Solid line: curve predicted by logistic regression; squares: mean observed values with 95% confidence intervals. Numbers indicate sample sizes.

creased with the proportion of nonjuvenile males ($\chi^2 = 7.36$, df = 1, $p = .007$) and with the proportion of subordinate males ($\chi^2 = 7.39$, df = 1, $p = .006$). We examined the relationships between juvenile survival and the number of subordinate males separately in south-facing slopes (high-habitat quality) and in other aspects (lower habitat quality) to correct for a possible confounding effect of habitat quality on juvenile survival during winter. The effect of the number of subordinate males on juvenile survival was similar ($\chi^2 = 0.26$, df = 1, $p = .61$) in the two environmental conditions.

Juvenile survival depended neither on the number of nonjuvenile females ($\chi^2 = 0.79$, df = 1, $p = .37$) nor on the number of subordinate females in the hibernating group ($\chi^2 = 0.26$, df = 1, $p = .61$; Figure 2B). Because the effect of the presence of female subordinates may be confounded with the presence of subordinate males, we investigated for the effect of the presence of subordinate females on juvenile survival in hibernating groups when the effect of subordinate males was taken into account. Again, juvenile survival during winter did not depend on the number of subordinate females (multiple logistic regression, test on the significance of the slope for female subordinates effect: $p = .28$). Using the upper limit of the 95% confidence interval of the logistic regression slope, the effect of adding three subordinate females (the maximum observed) led to an increase of 29%, 14%, 6%, and 2% in juvenile survival when the numbers of adult males in the group were, respectively, one, two, three, and four. Thus, we can accept the null hypothesis (no female effect) when two, three, or four males were present in the hibernaculum. When only the dominant male was present (without subordinate males), the test was inconclusive, and we cannot rule out the possibility that adding three subordinate females may have increased the juvenile survival during winter (biological significance was 20% change, see Methods).

We had information on relatedness between hibernating group members in 29 cases. In six cases, there were neither subordinates nor yearlings in the hibernating group. In all the 23 remaining cases, subordinates and/or yearlings were at least half-sibs of the juveniles. Thus, in all these 23 cases, the resident male and/or the resident female were the parents of subordinates and yearlings hibernating with the juveniles. In 10 cases, subordinates and/or yearlings and juveniles were
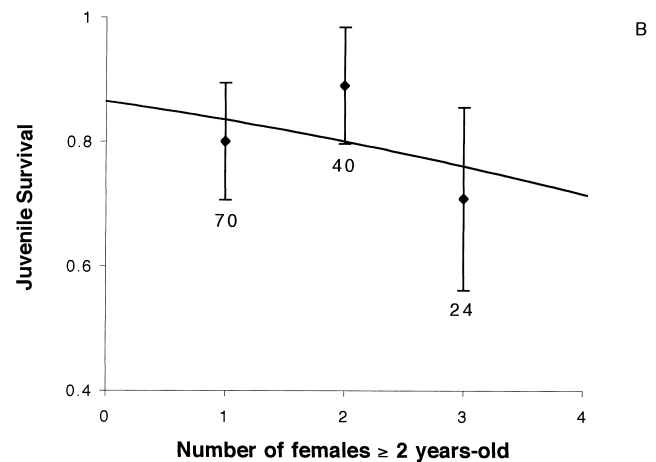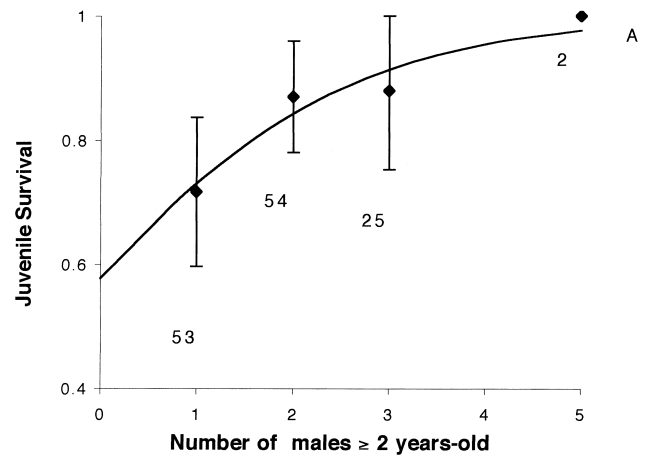

Figure 2
Survival of juvenile Alpine marmots during winter as a function of the number of (A) subordinate males and (B) females in the hibernating group. Solid line: curve predicted by logistic regression; squares: mean observed values with 95% confidence intervals. Numbers indicate sample sizes.

full-sibs. In eight cases, subordinates and/or yearlings and juveniles were half-sibs. In the five remaining cases, subordinates and/or yearlings and juveniles were at least half-sibs. This latter situation corresponds to the case where we know that at least one resident (the male or the female) was a parent of both subordinates and/or yearlings and juveniles. Winter survival rates of juveniles hibernating with full-sibs (0.865 ± 0.056 SE) and half-sibs (0.848 ± 0.062) subordinates and/or yearlings did not significantly differ ($\chi^2 = 0.04$, df = 1, $p = .84$). If we suppose that the subordinates (and/or yearlings) considered at least half-sibs were in fact full-sibs, the survival rate of juveniles increases to 0.912 ± 0.037. Even in this case, the difference between the survival values (0.912 versus 0.848) was not significant ($\chi^2 = 0.81$, df = 1, $p = .37$). Thus, we conclude that winter survival of juveniles is the same when juveniles hibernated with either full-sibs or with half-sibs subordinates and/or yearlings.

Tests of alternative hypotheses

The male-biased sex ratio observed among offspring at emergence in our population was consistent in other age classes

Table 1

Sex ratio (SR = proportion of males) for different age classes in the population

Age classes	SR	n	p
Yearlings	0.567	210	.0225
Two year olds	0.578	135	.0424
Three year olds	0.451	51	.7125
Adults	0.556	214	.0436

n is sample size; p is the p value when testing if the sex ratio of a given age class is still male biased (one-tailed binomial test).

except among 3-year-old subordinates (Table 1). This was probably the consequence of the great dispersal rate of 2-year-old males (see below).

We weighed neonates born to the captive females. Mean weight at birth was 32.86 ± 1.22 g (mean $\pm$ SE; $n = 22$), and neonate males were 7% heavier than neonate females (nested ANOVA: sex effect: $F = 7.57$, df $= 1,21$, $p = .014$). This sexual dimorphism was also previously observed at emergence (mean juvenile body mass was 0.380 ± 0.016 kg for males and 0.329 ± 0.013 kg for females; ANOVA: $F_{5,72} = 6.03$, $p < .02$) in this population (Allainé et al., 1998).

We had data on survival between the emergence from the natal burrow and the emergence from the first hibernation for 125 juveniles (75 males and 50 females). A total of 57 (76%) males and 36 (72%) females survived to yearling age. The difference was not significant ($\chi^2 = 0.25$, df $= 1$, $p = .62$).

Finally, we were able to determine the exact age of dispersal for 70 subordinates (37 males and 33 females). Only 3 (8.1%) males and 6 (18.2%) females inherited the home range of their parents and became philopatric. Most subordinates (84.3%) dispersed when 2 or 3 years old. A total of 21 (56.7%) males and 12 (36.4%) females dispersed when 2 years old. Thus males tended to disperse earlier than females ($\chi^2 = 2.91$, df $= 1$, $p = .08$).

Sex ratio variation among families

A male bias was observed in 31 litters, whereas a female bias was noted in only 15 litters. In nine litters, the number of males equaled that of females. The number of male-biased litters was significantly greater than expected under a binomial distribution (binomial test with correction for continuity, $Z = 2.21$, $p = .027$). Moreover, the magnitude of the bias was greater among male-biased litters than among female-biased litters (Wilcoxon matched-pairs test, $Z = 2.55$, $p = .011$). This indicates that the bias was low in litters with an excess of females but higher in litters with an excess of males.

The distribution of observed sex ratio (Figure 3) presents a peak around 0.6. A sex ratio of 0 was never observed, but sex ratios of 1 were frequent. The variability in sex ratio was not related to a mother's body mass ($r = .06$, $n = 34$, $p = .75$). Moreover, mothers heavier than the average did not skew the sex ratio of their offspring at emergence differently from mothers with lighter than average body mass (Mann-Whitney U test, $U = 130$, $n = 34$, $p = .62$). The mother's condition was also measured as the residual of the regression between body mass and body length (structural size; Dobson, 1992). Again, the variability in sex ratio was not related to a mother's body condition ($r = .04$, $n = 34$, $p = .82$). For mothers in good and poor conditions, overall sex ratios were 0.581 and 0.597, respectively. However, litter size was positively correlated with a mother's body mass ($r = .34$, $n = 44$; $p = .026$). Therefore, mothers may adjust the combination of litter size
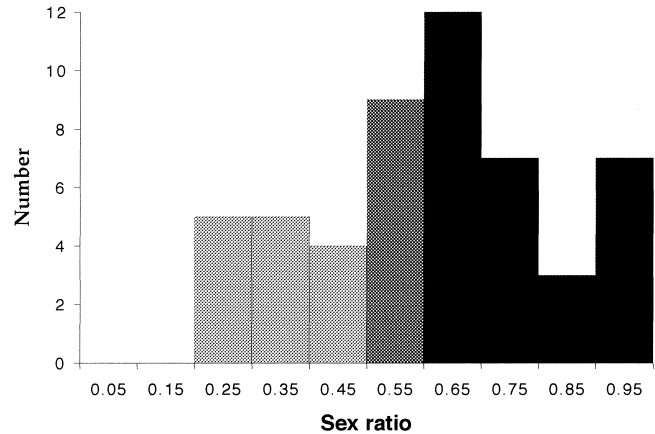

Figure 3
Distribution of weaning sex ratios observed in our population of Alpine marmots. Black bars indicate litters with an excess of males. Light gray bars indicate litters with an excess of females. The medium gray bar in the middle of the graph indicates litters with balanced sex ratio.

and (primary and/or secondary) sex ratio of their offspring according to their phenotypic condition (Williams, 1979). The mothers' body mass was positively correlated (Spearman's rank correlation) with all three theoretical sequences of litter type. The best correlation was found when the direct metabolic cost of producing males was greater than that of two females (cost is 1 female: $r = .703$, $p = .007$; cost is 1.5 females: $r = .78$, $p = .003$; cost is 2 females: $r = 0.80$, $p = .0027$; Figure 4).

DISCUSSION

Male-biased sex ratio

In monomorphic monogamous species, the two sexes are supposed to be equally costly to produce, and a balanced sex ratio is then expected at the population level (Fisher, 1930). Exceptions have been described in birds (Bednarz and Hayden, 1991), and particularly in cooperative breeders (Gowaty and
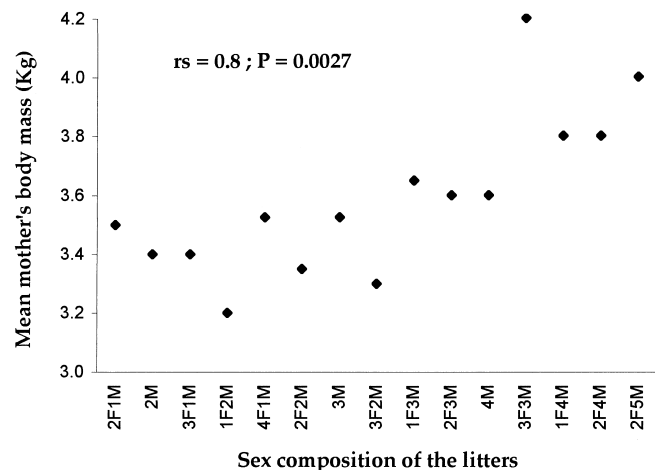

Figure 4
Mean mothers' body mass as a function of the theoretical sequence of litter type (size and sex composition) obtained when considering that the direct metabolic cost of producing males (M) was greater than that of two females (F). Spearman rank correlation (r_s) between the two series is shown.

Table 2

Tests of alternative hypotheses proposed to explain the male-biased sex ratio at the population level in litters of alpine marmots

Hypotheses	Predictions	Conclusion from our data
No difference in cost (sensu Trivers, 1972)		
Evolutionary equilibrium	More of the rarer sex	Not supported
Differences in cost (sensu Trivers, 1972)		
Metabolic cost	Males smaller than males	Not supported
Survival cost	Males less viable	Not supported
Local resource competition	Males disperse earlier	Supported[a]
Helper repayment	Only males help	Supported[b]

[a] Not supported by Arnold's (1990) data: males disperse later.

[b] Also supported by Arnold's (1993) data.

Lennartz, 1985, Ligon and Ligon, 1990), but almost nothing is known on offspring sex ratio bias in populations of monogamous mammals that breed cooperatively.

In the Alpine marmot, we found a male-biased sex ratio at weaning and at birth. The bias reported here is consistent with observations from another Alpine marmot population in Germany (SR = 0.58; $n = 476$; $p < .001$, in Blumstein and Arnold, 1998), suggesting that a male-biased sex ratio among juveniles may be a general trait of the Alpine marmot. More generally, a male-biased sex ratio could be the rule among socially monogamous marmots. Indeed, although not significant ($n = 63$; $p > .05$), Blumstein and Arnold (1998) reported for the golden marmot (*M. caudata*), a weaning sex ratio of 0.57, similar to that observed in the Alpine marmot. A male-biased trend, although not yet quantified, seems also to exist in litters of *M. sibirica* (Batbold J, personal communication). Such a male bias was not observed in a polygynous marmot species (*M. flaviventris*: Armitage, 1987).

How can we explain such a bias?

Under Fisher's (1930) arguments, we have to deduce from our results that either the population is not at an evolutionary equilibrium and currently producing more of the rarer sex or that the production of daughters may entail a greater cost (sensu Trivers, 1972) for mothers than the production of sons. The sex ratio was male biased in our population in all age classes (except among 3 years old, see Results). Therefore, the production of an excess of males is not the consequence of a frequency-dependent process (Table 2) to produce the rarer sex in the population (Fisher, 1930). Thus, females should be more costly (sensu Trivers, 1972) to produce than males in the Alpine marmot. Several hypotheses have been proposed to explain a differential cost between sons and daughters (Clutton-Brock and Iason, 1986) and consequently a biased sex ratio at the population level (Table 2). First, the two sexes may differ in the relative direct metabolic cost incurred by the mother during gestation and lactation (Hewison and Gaillard, 1996). If sexual dimorphism exists at birth and/or at weaning, the larger sex may be energetically more costly to produce than the smaller one (Clutton-Brock et al., 1981). If this energetic cost represents a fitness cost for the mother, the offspring sex ratio should be biased toward the smaller sex. Juvenile male Alpine marmots are heavier at birth than juvenile females, and the difference in body mass between the two sexes is even greater at weaning (Allainé et al., 1998). The sexual dimorphism at birth and at weaning thus cannot explain the male bias observed in our population.

Second, the offspring sex ratio should be biased toward the less viable sex. We found no between-sex difference in survival during the first year of life, or even in the survival pattern with age (Farand and Allainé, unpublished data). This is in accordance with the persistence of the male bias among adults and was expected for monomorphic monogamous species. The "less viable sex" hypothesis can be discarded.

Finally, the local resource competition hypothesis (Clark, 1978) predicts that the population sex ratio should be biased toward the dispersing sex. Indeed, members of the sex that delay dispersal compete with each other and with the residents for limited resources and incur a fitness cost. In the Alpine marmot, subordinates delay dispersal beyond reproductive maturity, and such a delay corresponds to a prolonged maternal investment (Armitage, 1981). According to the local resource competition hypothesis, female Alpine marmots may be more costly to produce than males if they disperse later. This hypothesis cannot be definitely discarded because we found that males tended to disperse earlier than females ($p = .08$, see Results). However, this hypothesis was not consistent with observations in the population studied by Arnold (1990a), in which females dispersed first, while a male-biased sex ratio was also observed.

Male repayment

Because the Alpine marmot is a cooperatively breeding species (Blumstein and Armitage, 1999; Jennions and Mcdonald, 1994), the offspring sex ratio bias may be better explained by the helper repayment hypothesis (Emlen et al., 1986; Gowaty and Lennartz, 1985). In our population, juvenile survival increased with the number of subordinate males in the hibernaculum, but not with the number of subordinate females or with territory quality (no confounding effect of territory quality; Cockburn, 1998). This suggests that only males helped or that males were more efficient in warming juveniles during hibernation. Subordinate male Alpine marmots shared with residents the cost of social hibernation (load-lightening hypothesis; Crick, 1992), and, consequently, the presence of subordinate males also increased the winter survival of residents (Arnold, 1990b). Subordinate males may thus repay part of the investment they received from their parents by participating in social thermoregulation. Because survival pattern did not differ between sexes and males tended to disperse earlier, we suppose that helpers incurred no or low direct fitness loss through helping. Even if this direct fitness loss exists, the sex ratio bias observed in favor of the helping sex suggests that the fitness payoff to parents of helping exceeds the direct fitness loss entailed by the helping sex (Koenig and Walters, 1999). Members of the helping sex are thus less costly to produce, justifying their production in excess (Table 2).

Why do only males help?

Subordinate males may be more efficient in warming juveniles if, because of their body composition or other physiological reasons, they produce more heat than subordinate females. The greater the number of subordinate males, the greater heat production. However, subordinate males warm (by grooming and covering with hay; Arnold, 1990b) only closely related juveniles (Arnold, 1993). This indicates that helping from subordinate males is mainly an active process rather than a passive one. Because subordinates were always genetically related to juveniles in our hibernating groups, both sexes could gain indirect fitness benefit from helping by enhancing the production of nondescendant kin (Emlen, 1995) and/or by lightening the workload of parents (see Cockburn, 1998, for a review). However, helping during hibernation is energetically costly (Arnold, 1990b), and a subordinate is expected to help only if the fitness payoff from helping exceeds the fitness cost. Helping is probably too costly for subordinate females but not for subordinate males. One possible explanation for this difference is that females' future reproductive potential depends more critically on fat reserve than is true for males. Another possibility is that males, but not females, may gain direct fitness benefits from staying and are thus incited to help. Indeed, females sometimes mated polyandrously, and extrapair paternity was frequent in our population (more than 30% of litters, Goossens et al., 1998), so subordinate males may sire some juveniles in their family group (Arnold, 1990a). Male subordinates may gain fertilizations because the resident male either failed to suppress their reproduction (limited control hypothesis; Clutton-Brock, 1998) or allowed them (especially related males; Arnold and Dittami, 1997) to reproduce, inciting them to help (concession theory; Vehrencamp, 1983). In contrast, subordinate females were not allowed to breed (Arnold, 1990a; Goossens et al., 1996), probably because the presence of an additional litter in the family group may result in too high of an increase in the competition for resources (food and hibernacula) and in the cost of social thermoregulation.

Sex ratio variation among families

Parents are expected to skew the sex ratio of their offspring to maximize their own fitness (Trivers and Willard, 1973). In particular, when fitness returns from sons and daughters are different, mothers should bias the sex ratio of their offspring in favor of the most profitable sex according to their own phenotypic condition (Silk, 1983; Trivers and Willard, 1973). Variations in mothers' phenotypic condition may thus lead to variations in offspring sex ratio among litters, even in cooperative breeding species (see Komdeur, 1996; Komdeur et al., 1997, for a recent example in birds). There was no direct relationship between sex ratio variations and the mothers' physical condition or the mothers' environmental condition (aspect of the territory; Allainé et al., 1994). However, Alpine marmot mothers adjusted both the size and the sex composition of their litters according to their phenotypic condition (Williams, 1979). The observed sequence of litter types with improving mothers' condition, following that expected when sons are energetically more costly than daughters, supports the Trivers-Willard prediction in species with large litters (Williams, 1979). Some litter types were never observed, especially those consisting of only females. Possibly, when adjusting their reproductive effort, mothers prefer to produce smaller litters with at least some sons than larger ones with only daughters. In this way, mothers produced more systematically an excess of the helping sex, thus leading to the observed sex ratio bias at the population level. Thus, our results are consistent both with the helper repayment hypothesis (at the population level), and with the Trivers-Willard Hypothesis (at the individual level).

Conclusions

Our study offers the first convincing evidence of an offspring sex ratio bias in populations of a monogamous mammal that breeds cooperatively. Helping behaviors in birds mainly consist of territory defense and nourishment of juveniles. Here we showed that warming juveniles during hibernation is a form of helping behavior in the Alpine marmot that leads to a biased sex ratio at the population level. The helper repayment hypothesis is the more appropriate hypothesis to account for our observation of an offspring sex ratio bias at the population level.

REFERENCES

Agren G, Zhou Q, Zhong W, 1989. Ecology and social behaviour of Mongolian gerbils, Meriones unguiculatus, at Xilinhot, Inner Mongolia, China. Anim Behav 37:11–27.
Allainé D, Graziani L, Coulon J, 1998. Postweaning mass gain in juvenile alpine marmots Marmota marmota. Oecologia 113:370–376.
Allainé D, Rodrigue I, Le Berre M, Ramousse R, 1994. Habitat preferences of Alpine marmots Marmota marmota. Can J Zool 72:2193–2198.
Armitage KB, 1981. Sociality as a life-history tactic of ground squirrels. Oecologia 48:36–49.
Armitage KB, 1987. Do female yellow-bellied marmots adjust the sex ratios of their offspring? Am Nat 129:501–519.
Arnold W, 1988. Social thermoregulation during hibernation. J Comp Physiol B 158:151–156.
Arnold W, 1990a. The evolution of marmot sociality: I. Why disperse late? Behav Ecol Sociobiol 27:229–237.
Arnold W, 1990b. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behav Ecol Sociobiol 27: 239–246.
Arnold W, 1993. Energetics of social hibernation. In: Life in the cold: ecological, physiological, and molecular mechanisms (Carey C, Florant GL, Wunder BA, Horwitz B, eds). Boulder, Colorado: Westview Press; 65–80.
Arnold W, Dittami J, 1997. Reproductive suppression in male alpine marmots. Anim Behav 53:53–66.
Barash DP, 1973. The social biology of the Olympic marmot. Anim Behav Monogr 6:173–245.
Bednarz JC, Hayden TJ, 1991. Skewed brood sex ratio and sex-biased hatching sequence in Harris' hawks. Am Nat 137:116–132.
Blumstein DT, Armitage KB, 1999. Cooperative breeding in marmots. Oikos 84:369–382.
Blumstein DT, Arnold W, 1998. Ecology and social behavior of golden marmots (Marmota caudata aurea). J Mammal 79:873–886.
Charnov E, 1982. The theory of sex allocation. Princeton, New Jersey: Princeton University Press.
Clark AB, 1978. Sex ratio and local resource competition in a prosimian primate. Science 201:163–164.
Clutton-Brock TH, 1998. Reproductive skew, concessions and limited control. Trends Ecol Evol 13:288–292.
Clutton-Brock TH, Albon SD, Guinness FE. 1981. Parental investment in male and female offspring in polygynous mammals. Nature 289: 487–489.
Clutton-Brock TH, Iason GR, 1986. Sex ratio variation in mammals. Q Rev Biol 61:333–374.

Cockburn A, 1998. Evolution of helping behavior in cooperatively breeding birds. Annu Rev Ecol Syst 29:141–177.

Crick HQP, 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. Ibis 134:56–61.

Dobson FS, 1992. Body mass, structural size, and life history patterns of the Columbian ground squirrel. Am Nat 140: 109–125.

Emlen ST, 1995. An evolutionary theory of the family. Proc Natl Acad Sci USA 92:8092–8099.

Emlen ST, Emlen JM, Levin SA, 1986. Sex ratio selection in species with helpers at the nest. Am Nat 127:1–8.

Fisher RA, 1930. The genetical theory of natural selection. Oxford: Oxford University Press.

Frame LH, Malcolm JR, Frame GW, van Lawick H, 1979. Social organization of African wild dogs (*Lycaon pictus*) on the Serengeti plains, Tanzania, 1967–1978. Z Tierpsychol 50:225–249.

Francis B, Green M, Payne C, 1993. The GLIM system, release 4 manual. Oxford: Clarendon Press.

Frank SA, 1990. Sex allocation theory for birds and mammals. Annu Rev Ecol Syst 21:13–55.

Genelly RE, 1965. Ecology of the common mole-rat (*Cryptomys hottentotus*) in Rhodesia. J Mammal 46:647–665.

Gensac P, Rothé B, 1974. Carte de la végétation de la réserve de la Grande Sassière. Trav Sci Parc Nat Vanoise 5:77–104.

Goossens B, Coulon J, Allainé D, Graziani L, Bel MC, Taberlet P, 1996. Immigration of a pregnant female in an alpine marmot family group: behavioural and genetic data. CR Acad Sci Paris 319:241–246.

Goossens B, Graziani L, Waits L, Farand E, Magnolon S, Coulon J, Bel MC, Taberlet P, Allainé D, 1998. Extra-pair paternity in the monogamous alpine marmot revealed by nuclear DNA microsatellite analysis. Behav Ecol Sociobiol 43:281–288.

Gowaty PA, Lennartz MR, 1985. Sex ratios of nestling and fledgling red-cockaded woodpeckers (*Picoides borealis*) favor males. Am Nat 126:347–353.

Hewison AJM, Gaillard JM, 1996. Birth sex ratios and local resource competition in roe deer, *Capreolus capreolus*. Behav Ecol 7:461–464.

Holmes WG, 1984. The ecological basis of monogamy in Alaskan hoary marmots. In: The biology of ground-dwelling squirrels (Murie JO, Michener GR, eds). Lincoln: University of Nebraska Press; 250–274.

Jennions MD, Macdonald DW, 1994. Cooperative breeding in mammals. Trends Ecol Evol 9:89–93.

Koenig WD, Walters JR, 1999. Sex-ratio selection in species with helpers at the nest: the repayment model revisited. Am Nat 153:124–130.

Komdeur J, 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. Proc R Soc Lond B 263:661–666.

Komdeur J, Daan S, Tinbergen J, Materman C, 1997. Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. Nature 385:522–525.

Lessels CM, Avery MI, 1987. Sex ratio selection in species with helpers at the nest: some extensions of the repayment model. Am Nat 129: 610–620.

Ligon JD, Ligon SH, 1990. Female-biased sex ratio at hatching in the green woodhoopoe. Auk 107:765–771.

Malcolm JR, Marten K, 1982. Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). Behav Ecol Sociobiol 10:1–13.

Perrin C, Allainé D, Le Berre M, 1993. Socio-spatial organization and activity distribution of *M. marmota*: preliminary results. Ethology 93:21–30.

Pruett-Jones SG, Lewis MG, 1990. Sex ratio and habitat limitations promote delayed dispersal in superb fairy-wrens. Nature 348:541–542.

Rabenold KN, 1990. Campylorhynchus wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savanna. In: Cooperative breeding in birds: long term studies of ecology and behaviour (Stacey PB, Koenig WD, eds). Cambridge: Cambridge University Press; 159–196.

Russell E, Rowley I, 1996. Partnerships in promiscuous splendid fairy-wrens. In: Partnerships in birds. The study of monogamy (Black JM, ed). Oxford: Oxford University Press; 162–173.

Sillero-Zubiri C, Gottelli D, Macdonald DW, 1996. Male philopatry, extra-pack copulations and inbreeding avoidance in Ethiopian wolves (*Canis simensis*). Behav Ecol Sociobiol 38:331–340.

Silk JB, 1983. Local resource competition and facultative adjustment of sex ratio in relation to competitive abilities. Am Nat 121: 56–66.

Solomon NG, French JA, 1997. The study of mammalian cooperative breeding. In: Cooperative breeding in mammals (Solomon NG, French JA, eds). Cambridge: Cambridge University Press; 1–10.

Solomon NG, Getz LL, 1997. Examination of alternative hypotheses for cooperative breeding in rodents. In: Cooperative breeding in mammals (Solomon NG, French JA, eds). Cambridge: Cambridge University Press; 199–230.

Steidl RJ, Hayes JP, Schauber E, 1997. Statistical power analysis in wildlife research. J Wildl Manage 61:270–279.

Trivers RL, 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man, 1871–1971 (Campbell B, ed). Chicago: Aldine; 137–179.

Trivers RL, Willard DE, 1973. Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–91.

Vehrencamp SL, 1983. A model for the evolution of despotic versus egalitarian societies. Anim Behav 31:667–682.

Williams GC, 1979. The question of adaptive sex ratio in outcrossed vertebrates. Proc R Soc Lond B 205:567–580.

Zélenka G, 1965. Observation sur l'écologie de la marmotte des Alpes. Terre Vie 112:238–256.