

# Sex ratio variation in the cooperatively breeding alpine marmot *Marmota marmota*

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In cooperatively breeding vertebrate species, a clear theoretical prediction about the direction of sex ratio adjustment can be made: mothers should bias the sex ratio of their offspring towards the helping sex when helpers are absent. A consistent trend in the direction predicted by theory exists in cooperative birds, but theory is still poorly tested in cooperative mammals. Here, multivariate analyses are applied to a long-term data set to test this prediction in two ways in the alpine marmot: (1) across females in a population and (2) in individual females across multiple years. It was shown that in the alpine marmot offspring sex ratio was biased towards the helping sex (males) when helpers were absent, whereas helped mothers produced unbiased sex ratio. Unhelped mothers did not adjust the litter size but produced more sons and fewer daughters than helped mothers. These results support the theoretical prediction and explain well the male bias observed among juvenile alpine marmots at the population level. The occurrence of possible sex ratio manipulations in cooperatively breeding vertebrates is also discussed. *Key words*: cooperative breeders, generalized linear models, *Marmota marmota*, sex ratio variation. [*Behav Ecol* 15:997–1002 (2004)]

Whether parents adjust the sex of their offspring has long intrigued evolutionary biologists (Darwin, 1871; Fisher, 1930) and is still a disputed question in vertebrates (Hardy, 2002; Krackow, 2002). Trivers and Willard (1973) were the first to propose that females should bias offspring sex ratio towards the most profitable sex. Their seminal paper has stimulated many theoretical (Charnov, 1982; Frank, 1990) and empirical (e.g., Clutton-Brock et al., 1984; Hewison and Gaillard, 1999) tests. However, adaptive sex ratio variation is still poorly documented in vertebrates (e.g., Komdeur et al., 1997), and it is often argued that sex ratio variations in vertebrates show no consistent pattern (Brown and Silk, 2002; Cockburn et al., 2002; Williams, 1979), due to the lack of parental manipulation ability (Krackow, 2002). Furthermore, another major problem with testing sex ratio theory in vertebrates is that clear theoretical predictions about the direction of sex ratio adjustment can be made in very few cases, so it is extremely hard to unambiguously test for adaptive sex ratio adjustment (West and Sheldon, 2002; West et al., 2002).

Cooperatively breeding vertebrate species provide an important exception to this last problem because a clear theoretical prediction can be made (West and Sheldon, 2002). Specifically, offspring sex ratio should be biased towards the helping sex when helpers are absent (Gowaty and Lennartz, 1985; Pen and Weissing, 2000). Using a meta-analysis, West and Sheldon (2002) gave evidence that a consistent trend exists in cooperatively breeding birds in the direction predicted by theory. Indeed, the prediction was supported in all cooperative species included in the meta-analysis (*Picoides borealis*, Gowaty and Lennartz, 1985; *Dacelo novaeguineae*, Legge et al., 2001; *Phoeniculus purpureus*, Ligon and Ligon, 1990; *Acrocephalus sechellensis*, Komdeur et al., 1997) and more recently in *Manorina melanophrys* (Ewen et al., 2003). This suggests that chromosomal sex determination is not an absolute constraint on sex ratio variations (see also

West et al., 2000) that may possibly take place before ovulation (Komdeur et al., 2002).

However, the extent to which adaptive sex ratio variation occurs in cooperatively breeding mammals is currently unknown because the theoretical prediction has been tested only in one species: the African wild dog, *Lycan pictus* (Creel et al., 1998). Here, the prediction was again supported—females forming new packs lack helpers and produce an excess of the sex that helps more (males), whereas multiparous females breed in larger packs including helpers and produce female-biased litters (Creel et al., 1998). In this study, I investigate whether the secondary sex ratio of offspring (measured at weaning) is biased towards the helping sex when helpers are absent in another cooperatively breeding mammal: the alpine marmot *Marmota marmota*.

The alpine marmot is a large ground-dwelling squirrel living in mountain open meadows, preferentially exposed to south (Allainé et al., 1994). The basic social unit is a family group of 2–20 individuals composed of a territorial dominant breeding pair, mature subordinates of 2–4 years, yearlings, and juveniles (Perrin et al., 1993). Extra-pair paternity (EPP) occurs in 31% of litters and about 20% of juveniles are born to extra-pair fertilizations, so the alpine marmot is predominantly, but not strictly, genetically monogamous (Goossens et al., 1998). The occurrence of extra-group EPP (EPP due to males not belonging to the family group) seems independent of the presence of subordinate males in the family group (Goossens et al., 1998). After 30 days of gestation, dominant females give birth to 1–7 pups in late May. Juveniles stay into the natal burrow during lactation (40 days) and emerge in late June and early July. Males are slightly heavier than females both at birth (7%, corresponding to about 2.3 g; Allainé et al., 2000) and at weaning (males: 380 g, and females: 330g; Allainé et al., 1998), but not at adulthood (Farand, 2000). At the population level, the sex ratio at weaning is biased towards males (sr = 0.58, 95% CI = [0.51; 0.64]), and this bias is well explained by the helper repayment hypothesis (Allainé et al., 2000).

The alpine marmot is an excellent organism with which to test the predictions of sex ratio theory applied to cooperatively breeding species, because the underlying assumptions

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of theory have been shown to hold. Specifically, one sex (males) provides breeders with immediate fitness benefit by increasing offspring survival during hibernation while the other (females) provides breeders with immediate fitness cost by decreasing offspring survival during hibernation (Allainé and Theuriau, 2004). How males help is still unclear, but they probably warm juveniles by producing heat during arousals, while females probably compete for heat with juveniles at some critical stage (Allainé and Theuriau, 2004). Here, I test the theoretical prediction that litter sex ratio should be relatively more male biased when subordinate male helpers are absent (prediction 1). I use a long term data set to test this prediction in two ways: (1) across females in a population, utilizing variation between females in the occurrence or absence of helpers; and (2) in individual females across multiple years, to test whether secondary offspring sex ratios produced by individual females varied in response to the presence or absence of helpers. I also test alternative predictions: (1) The alpine marmot does not meet the criteria of the Trivers and Willard's (1973) hypothesis because the alpine marmot is a monogamous and polytocous species, so I predict that the sex ratio of offspring at weaning is independent of mothers' body condition (prediction 2). (2) Males are heavier than females at birth and at weaning. If this sexual dimorphism represents a differential energetic cost for mothers, females in poor body condition should bias their offspring sex ratio towards the cheaper sex (females) (prediction 3). (3) There is no general trend for one sex to disperse before the other (Frey-Roos, 1999; Magnolon, 1999) and no reason to suspect that the dominants compete more strongly for resources with one sex than with the other (Clark, 1978). Consequently, mothers are not expected to overproduce helpers only when resources are abundant, i.e., in good territories (Komdeur et al. 1997). So, I predict that the secondary sex ratio produced by mothers is independent of the interaction between the presence of helpers and territory quality (prediction 4). In the case that adaptive offspring sex ratio variation occurred, I examine how this happened. To do so, I investigate whether the litter size and the number of juvenile males and females were modified.

## 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 and high mountain weather. From 1990 to 2002, 607 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 10× and a 20–60× telescope allowed the determination of family composition in early spring and of reproductive events in 14 family groups from 1992 to 2002, representing a total of 127 group-years. I identified dominants and recorded the number of subordinate males and females, the number of yearling males and females, the date of emergence, and the size of litters.

### Statistical analyses

I used R 1.8.0 package (Ihaka and Gentleman, 1996) to build generalized linear mixed models (Penalised Quasi Likelihood, PQL, procedure for models with non-normal error structure). Mixed models allow consideration of both fixed

and random terms. Random terms entered into the model took into account repeated measures of different individuals within the same group. 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 whose elimination would be significant. The significance of fixed terms was assessed using Wald statistics ( $\chi^2$  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 non-significant terms are from the fitted model and each nonsignificant term is added separately. Interactions were never significant and not presented in tables.

### Sex ratio

The size and the date a litter emerged were recorded. Juveniles were then trapped as soon as possible (generally within 3 days after emergence) and sexed by examination of the ano-genital area. Sex ratio within litters was computed as the proportion of males.

#### *Across females in a population analysis*

I ran a generalized linear mixed model with a binomial error to investigate for the terms that affected the sex ratio within litters. To take into account repeated sampling of different litters born to the same mother in a same territory, I used the mother nested to the territory as a random term in the analysis. The fixed exploratory terms considered were as follows. (1) The presence of helpers in the family group was used to test prediction 1. (2) The mothers' body condition was used to test predictions 2 and 3. The female body condition was measured by the residual of the regression of body weight on the date of capture. (3) The territory's exposure to sun was used to test prediction 4. Snow melt occurs earlier in south-facing slopes, so mothers have access to food early and gain body mass more rapidly than in other exposures to sun (Allainé et al., 1998). Consequently, juveniles emerge earlier, are heavier, and have a higher growth rate in south-facing slopes than in other exposures to sun (Allainé et al., 1998). So, exposure to sun was assumed to be a reliable indicator of territory quality. (4) Litter size was used as an exploratory term; if a differential mortality occurred into the natal burrow, biased sex ratio might be observed within small litters (prediction 5). (5) The presence of a litter the previous year was used to test two predictions; if a cost of reproduction occurred that resulted in the dominant female being in lower body condition, the sex ratio might be biased towards the cheaper sex from an energetic point of view (females) the following year (predictions 6 and 3). (6) Finally, the change of the resident male or dominant male is often associated with infanticide (Coulon et al., 1995). So, juveniles born the previous year might all disappear, and this might reduce the number of yearling males (potential helpers) in the group.

#### *In individual females across multiple year analysis*

I used the same procedure but the data set corresponded to the 10 females of the 29 that were followed several years and that bred sometimes with and sometimes without helpers. It was then possible to test specifically whether a given mother produced offspring sex ratios in the direction predicted by theory when in the presence or in absence of helpers. To test this, I used the mother as the random term and the presence of helpers in the family group as the fixed term in the analysis.

**Table 1**  
Generalized linear mixed model (binomial error) showing the effect of terms on sex ratio within litters

Model terms	Wald statistic ( $\chi^2$ )	df	<i>p</i>
Presence of helpers	8.74	1	.003
Mothers body condition	0.75	1	.39
Litter size	0.02	1	.89
Exposure of the territory to sun <sup>a</sup>	<0.01	1	.99
Presence of a litter the previous year	2.54	1	.11
Change of dominant male	0.36	1	.55

<sup>a</sup> Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

### Numbers of juveniles

#### *Across females in a population analysis*

In the absence of helpers, mothers may adjust the offspring sex ratio by modifying the litter size, by increasing the number of juvenile males, or by decreasing the number of juvenile females. I built three generalized linear mixed models with a Poisson error to investigate for the terms affecting litter size, number of juvenile males, and number of juvenile females, respectively. Again, to take into account repeated sampling of different litters born to the same mother in the same territory, I used the mothers nested to the territory as random terms in the analysis. The fixed exploratory terms considered were the same as for the analysis of the offspring sex ratio (see above). However, I checked the prediction that litter size increased with female body condition (Hackländer and Arnold, 1999; King and Allainé, 2002) using a one-tailed test.

#### *In individual females across multiple years analysis*

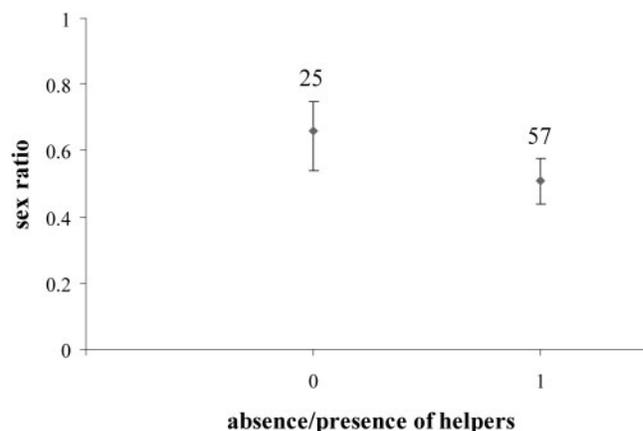
Finally, I also tested for whether a given mother ( $n = 10$ ) modified litter size, number of juvenile males, and number of juvenile females when in presence of helpers, using generalized linear mixed models with a Poisson error, the mother as the random term, and the presence of helpers in the family group as the fixed term.

## RESULTS

From 1992 to 2002, the family composition and the occurrence of a litter were recorded for a total of 127 group-years. A litter occurred in 84 of these 127 group-years (66%). This percentage is in agreement with those reported by Hackländer and Arnold (1999) and by King and Allainé (2002). I discarded from the analysis two litters for which no juveniles were sexed because they all disappeared before capture. The analysis was then performed on 82 litters: for 63 litters, all juveniles that emerged were sexed, and for 19 additional litters some juveniles disappeared or were not trapped. Assuming that mortality (and/or capture probability) was not sex-biased (Farand et al., 2002), the sex ratio in these 19 litters should be representative of the secondary sex ratio at weaning. Consequently, these 19 litters were included in the dataset. However, I also performed the complete analysis without these 19 litters. The conclusions were strictly the same, so I only present the results of the analysis on the 82 litters in the following.

### Sex ratio

The sex ratio within litters varied from 0 to 1. Among the 82 group-years where a litter emerged, helpers were absent in



**Figure 1**

Sex ratio within litters of alpine marmots when helpers were absent (0) or present (1). The sex ratio is the proportion of males. The bars indicate the 95% confidence interval; the numbers indicate numbers of litters considered.

25 (30.5%) cases and present in 57 (69.5%) cases. The mean number of helpers present was 2.41.

#### *Across females in a population*

The sex ratio within litters was only affected by the presence of helpers (Table 1). As predicted, mothers produced a greater proportion of sons (sex ratio = 0.66; 95% confidence interval = [0.52; 0.75],  $n = 25$  litters for a total of 82 juveniles) when helpers were absent. When helpers were present, mothers produced litters with an unbiased sex ratio (sex ratio = 0.49,  $n = 57$  litters for a total of 220 juveniles; Figure 1). None of the other factors considered—mothers' body condition, territory exposure to sun, presence of a litter the previous year, litter size, change of the dominant male—affected the sex ratio within litters (Table 1). In particular, the offspring sex ratio did not depend on the interaction between the presence of helpers and the territory exposure to sun (Wald statistic:  $\chi^2 = 0.77$ ,  $df = 1$ ,  $p = .38$ ). So, in the alpine marmot, the production of helpers when they were absent was not affected by territory quality.

#### *In individual females across multiple years*

Ten mothers remained several years (2 to 8 years) in their territory and faced both social environments: the presence and the absence of helpers. As predicted, females produced offspring at a sex ratio according to their social environment (Wald statistic:  $\chi^2 = 9.56$ ,  $df = 1$ ,  $p = .002$ ). A given mother produced a greater proportion of helpers when they were absent in the family group (sex ratio = 0.65; 95% confidence interval = [0.54; 0.74]) than when they were present (sex ratio = 0.46; 95% confidence interval = [0.36; 0.56]).

### Numbers of juveniles

#### *Across females in a population*

The mean litter size was  $3.7 \pm 0.14$  (SE,  $n = 63$  complete litters). The litter size was only affected by the mothers' body condition (Table 2). Specifically, litter size increased with mothers' body condition as previously reported (Hackländer and Arnold, 1999; King and Allainé, 2002). None of the other factors considered—territory exposure to sun, presence of a litter the previous year, change of the dominant male—affected the litter size (Table 2). In particular, mothers did not adjust the litter size when helpers were absent (Table 2). So, in the absence of helpers, mothers biased the offspring sex ratio

**Table 2**  
Generalized linear mixed model (Poisson error) showing the effect of terms on litter size

Model terms	Wald statistic ( $\chi^2$ )	df	<i>p</i>
Mothers body condition	2.54	1	.055 <sup>b</sup>
Presence of helpers	0.37	1	.54
Exposure of the territory to sun <sup>a</sup>	0.01	1	.92
Presence of a litter the previous year	0.37	1	.54
Change of dominant male	0.02	1	.89

<sup>a</sup> Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

<sup>b</sup> One-tailed test, see text.

towards males without changing the litter size. Consequently, I expected mothers to produce more sons and fewer daughters when helpers were absent. As expected, the number of sons and daughters produced within litters increased and decreased, respectively, when helpers were absent (Table 3). None of the other factors considered—territory exposure to sun, presence of a litter the previous year, change of the dominant male—affected the number of juveniles of each sex, except for the trivial effect of litter size (Table 3).

#### *In individual females across multiple years*

A given mother produced the same number of juveniles (Wald statistic:  $\chi^2 = 0.06$ ,  $df = 1$ ,  $p = .80$ ) when helpers were absent (mean litter size = 3.56; 95% confidence interval = [3.03; 4.18]) or present (mean litter size = 3.66; 95% confidence interval = [3.15; 4.24]). Mothers adjusted the sex ratio of their offspring by producing more sons (Wald statistic:  $\chi^2 = 4.87$ ,  $df = 1$ ,  $p = .027$ ) and fewer daughters (Wald statistic:  $\chi^2 = 5.05$ ,  $df = 1$ ,  $p = .025$ ) when helpers were absent (mean number of sons = 2.23; 95% confidence interval = [1.7; 2.9]; mean number of daughters = 1.20; 95% confidence interval = [0.9; 1.6]) than when they were present (mean number of sons = 1.62; 95% confidence interval = [1.2; 2.1]; mean number of daughters = 1.83; 95% confidence interval = [1.5; 2.3]).

## DISCUSSION

In cooperative breeders, a clear theoretical prediction about sex ratio adjustment can be made: mothers should bias the sex ratio of their offspring towards the helping sex when helpers are absent (Gowaty and Lennartz, 1985; Pen and Weissing, 2000; West and Sheldon, 2002). I tested this theoretical prediction against alternatives in a cooperative mammal, the alpine marmot. On the whole, the secondary sex ratio within litters was biased towards males (helpers) when helpers were absent in family groups. Moreover, the results clearly indicate that a given mother produced offspring sex ratios according the social situation she faced; mothers produced an excess of sons when helpers were absent but switched to the production of litters with unbiased sex ratio when helpers were present. These results strongly support the theoretical prediction and suggest the occurrence of adaptive sex ratio variation in the alpine marmot. My results are in agreement with those found in the African wild dog (Creel et al., 1998). It is therefore possible that the consistent trend found in cooperatively breeding birds (West and Sheldon, 2002) also exists in cooperative mammals.

Alternative hypotheses were not supported by the results. First, the alpine marmot is a monogamous species without sexual dimorphism in size among adults. So, there is no

**Table 3**  
Generalized linear mixed model (Poisson error) showing the effect of terms on number of juvenile males and on number of juvenile females (in italics)

Model terms	Wald statistic ( $\chi^2$ )	df	<i>p</i>
Litter size	32.20	1	<.0001
	<i>16.73</i>		<i>&lt;.001</i>
Presence of helpers	4.58	1	.032
	<i>5.32</i>		<i>.021</i>
Exposure of the territory to sun <sup>a</sup>	0.20	1	.65
	<i>0.65</i>		<i>.42</i>
Presence of a litter the previous year	1.15	1	.28
	<i>1.19</i>		<i>.28</i>
Change of dominant male	0.33	1	.57
	<i>0.31</i>		<i>.58</i>

<sup>a</sup> Exposure to sun is factorized as south-facing versus north-facing slopes and valley.

reason to expect a greater fitness return from males than from females. Moreover, I have no evidence that the mother's body condition affects differentially the fitness of sons and daughters. Therefore, the assumptions of the Trivers and Willard's (1973) hypothesis are not met in the alpine marmot. As expected, my results indicate that sex ratio variation in the alpine marmot is independent of mothers' body condition. Second, the sexual dimorphism at birth and at weaning suggests that males may be more energetically costly to produce than females. Mothers in poor condition may thus produce an excess of the cheaper sex (females). My results do not support this hypothesis because mothers in poor body condition produce small litters (see also Hackländer and Arnold, 1999; King and Allainé, 2002) that were not female-biased. Third, contrary to what is found in some cooperative bird species (Komdeur et al., 1997), the local resource competition may not hold in the alpine marmot, probably because both sexes disperse at approximately the same age (Frey-Roos, 1999; Magnolon, 1999). Helpers do not stay longer in the natal territory and, thus, do not compete more than subordinate females with dominants for resources. Consequently, helpers are not overproduced only when territories are of high quality (south-facing exposure). The environmental factors that determine the profitability of each sex may simply rely on the presence/absence of helpers, and thus they may be highly predictable (Charnov, 1982). I suggest that unhelped mothers bias the sex ratio of their offspring to have a number of helpers close to the optimal one (Allainé and Theuriau, 2004). Given a mean juvenile survival of 0.62 (Farand et al., 2002), producing an average of 2.23 males when helpers are absent provides mothers with 1.4 yearling males on average, which is close to the estimated optimal number of helpers in alpine marmot family groups (1.64; Allainé and Theuriau, 2004). Mothers with helpers produced balanced sex ratio, as already observed in some cooperatively breeding birds (e.g., Ewen et al., 2003; Gowaty and Lennartz, 1985; Legge et al., 2001). In the alpine marmot, helped mothers might not overproduce females for two main reasons. First, helped mothers still have interest in producing some males because most helpers present in a given year will disperse the following year. Indeed, given a mean survival rate of 0.71 (Farand et al., 2002) and a dispersal rate of 0.5 (Magnolon, 1999) for helpers, the number of helpers still present the following year, among the 2.4 present on average, is expected to be around 0.9. Producing an average 1.62 males when helpers are present provides mothers the following year

with one yearling male on average and with 1.9 helpers (still close to 1.64). Second, subordinate females reduce juvenile survival during hibernation (Allainé and Theuriau, 2004) and thus represent an immediate fitness cost for mothers. This cost may counter-balance the frequency-dependent advantage of producing the rarer sex (Fisher, 1930).

Sex ratio variation appears to be inconsistent among most of the higher vertebrates (Brown, 2001; Hardy, 1997; Koenig et al., 2001). Moreover, adaptive sex ratio manipulation by mothers has been questioned (Hardy, 2002; Krackow, 1997), especially because the existence of proximal control mechanisms is doubtful (Krackow, 2002). Therefore, deviations from evenness have been interpreted as evolutionarily neutral variations of a binomial trait (Krackow, 2002). However, cooperatively breeding vertebrates may provide an exception to the neutral view on sex ratio variations. As previously noticed, a clear theoretical prediction can be made about the direction of sex ratio adjustment. This prediction is largely supported in cooperatively breeding higher vertebrates (Creel et al., 1998; Ewen et al., 2003; Gowaty and Lennartz, 1985; Legge et al., 2001; Ligon and Ligon, 1990; this study). Assuming that these studies are representative of cooperatively breeding species and not a biased sample (Palmer, 2000), these results strongly support the existence of a consistent trend in the direction predicted by theory (West and Sheldon, 2002). Although the control mechanism is still largely unknown, such a control may occur, at least in cooperative birds (Komdeur et al., 2002). Nevertheless, the proximal mechanism of sex ratio control, if it exists, still needs to be identified to prove facultative sex ratio manipulation in the alpine marmot. This proximal mechanism probably does not rely on sex-specific mortality during lactation for several reasons. First, data from captive pregnant females suggest that the sex ratio may be biased towards males at birth (sex ratio at birth = 0.59,  $n = 22$ ; Allainé et al., 2000). Second, secondary sex ratio was independent of litter size, so male-bias sex ratios were not observed predominantly within small litters. Finally, a given mother did not change the litter size, but rather the composition of the litter, when helpers were absent. Hence, the bias may occur before conception through sperm selection or during gestation via developmental asynchrony (Krackow, 1995) mediated by hormonal levels (James, 1989) or sex-specific fetal mortality, as previously reported in other rodents (Gosling, 1986). However, I currently have no data in favor of any of these mechanisms.

Studies showing facultative sex ratio adjustment often failed to reveal a clear consistent bias at the population level, even in cooperatively breeding species (Komdeur et al., 1997; Ligon and Ligon, 1990; but see Clarke et al. [2002] in birds and Creel et al. [1998] and Malcolm and Marten [1982], revisited by Koenig and Walters [1999], in mammals). This lack of concordance is understandable when admitting that it should not be expected systematically even in cooperative breeders. Indeed, the sex ratio at the population level is difficult to predict if a mixture of selective forces is acting or for many other reasons (Frank, 1990; Koenig and Walters, 1999; Pen and Weissing, 2000). For example, female Seychelles warblers without help benefit from producing helpers only in high quality territories (Komdeur et al., 1997). In this case, local resource competition (Clark, 1978) counters local resource enhancement (Emlen et al., 1986) and leads to parity at the population level (from Komdeur et al., 1997). On the contrary, the results presented here indicate that in the alpine marmot, whatever the territory quality, mothers without helpers have interest in producing helpers, whereas helped mothers produce balanced sex ratios. This pattern thus provides a comprehensive frame for the male-biased sex ratio found at the population level (Allainé et al., 2000).

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