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INVITED REVIEW

Sociality, individual fitness and population dynamics of yellow-bellied marmots

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Abstract

Social behaviour was proposed as a density-dependent intrinsic mechanism that could regulate an animal population by affecting reproduction and dispersal. Populations of the polygynous yellow-bellied marmot (*Marmota flaviventris*) fluctuate widely from year to year primarily driven by the number of weaned young. The temporal variation in projected population growth rate was driven mainly by changes in the age of first reproduction and fertility, which are affected by reproductive suppression. Dispersal is unrelated to population density, or the presence of the father; hence, neither of these limits population growth or acts as an intrinsic mechanism of population regulation; overall, intrinsic regulation seems unlikely. Sociality affects the likelihood of reproduction in that the annual probability of reproducing and the lifetime number of offspring are decreased by the number of older females and by the number of same-aged females present, but are increased by the number of younger adult females present. Recruitment of a yearling female is most likely when her mother is present; recruitment of philopatric females is much more important than immigration for increasing the number of adult female residents. Predation and overwinter mortality are the major factors limiting the number of resident adults. Social behaviour is not directed towards population regulation, but is best interpreted as functioning to maximize direct fitness.

Keywords: age structure, dispersal, matriline, population growth rate, reproductive suppression

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Introduction

It is generally recognized that vertebrate populations have the capacity to increase their numbers far beyond the numbers observed. Although populations fluctuate from year to year, they appear to be regulated around some mean density. Early models of population regulation emphasized extrinsic factors, such as weather, food, parasites and predators, and developed the concepts of density-dependent and density-independent regulation (see Krebs 1985, for review).

Subsequently, population biologists began to question whether extrinsic factors acted as the primary control agents and suggested that populations were self-limiting. Errington (1956) stated 'In analysis of the population dynamics of animals, we must not ignore the role of social intolerance as a limiting factor. Social intolerance may or may not be tied up with food supply or other of the more obvious needs of a population at a given time'. Experiments on Norway rats demonstrated the potential role of social behaviour to influence population growth. Two ways that social behaviour acted were: (i) the development of local groups that restricted the use of space to group members and (ii) social stability within the group favoured reproductive success (Calhoun 1952). Behavioural displays could serve as cues to population density in a self-regulating feedback system (Wynne-Edwards 1965). Dispersal could play a major role in intrinsic regulation by maintaining population density below carrying capacity (Lidicker 1962). Briefly, social behaviour could affect population numbers through its effects on dispersal, reproduction and recruitment.

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In a comprehensive review of population regulation in mammals, a model was developed that predicted that female territoriality, the threat of infanticide, and the presence of male relatives in the natal home range were the proximate mechanisms for intrinsic population regulation (Wolff 1997). This model predicts that young females exhibit reproductive suppression to avoid incest or to conserve reproductive effort when threatened by infanticide. Dispersal was viewed as having limited potential to regulate population density, and it was further suggested that intrinsic regulation was unlikely in polygynous species.

It is quite difficult to determine which factor or factors regulate population density in natural populations. For example, predation is rarely detected and social behaviour cannot be readily observed in most species of mammals. However, in diurnal, social mammals, it is possible to describe the role of sociality in population dynamics. In this work I, (i) present a graphical model for the role of social behaviour in regulating population numbers; (ii) present new data on population numbers from five well-studied sites; (iii) test the model of population regulation by using the new population numbers and previously published data and (iv) present an interpretation of the role of social behaviour in population limitation.

The model

Population growth occurs through recruitment (animals born in the site) and immigration. As population increases, social competition increases (Fig. 1); as a consequence of increased numbers, natality, recruitment and immigration decrease and dispersal increases. These processes cause the population and social competition to decrease. Subsequently, natality, recruitment and immigration increase, dispersal decreases and the population again increases. During the increase and decrease phases, nonregulatory mortality such as predation may reduce numbers, but social competition is the major factor that regulates animal numbers.

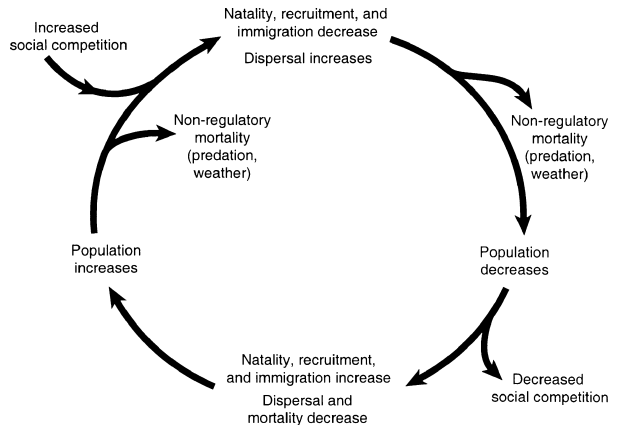

Fig. 1 A model for density-dependent intrinsic population regulation. Arrows indicate the direction of change. Arrows directed away from the cycle indicate mechanisms that counter the population change; arrows pointing towards the cycle enhance the direction of change.

The animal

The yellow-bellied marmot is a large, diurnal ground-dwelling sciurid that lives in montane and alpine areas of western North America (Frase & Hoffmann 1980). Populations in the Upper East River Valley, Colorado, where this research was conducted, occur on patches of rocky outcrops or talus associated with meadows interspersed with aspen and spruce-fir forests and often bordered with willows. Burrows are located under boulders, in rocks, under tree or shrub roots or under buildings (Svendsen 1974). The population sites extended over a range of 5 km.

Sociality evolved as a consequence of large-bodied marmots living in an environment with a short growing season. Marmots cope with a long, cold season without food by accumulating fat during the short growing season and hibernating. Because young cannot both prepare for hibernation and grow to maturity, they are retained in their natal area through at least their first hibernation (Armitage 2007); this retention leads to the formation of social groups. The basic social unit of the yellow-bellied marmot consists of mother:daughter:sister kin groups. The kin group may persist through time as a matriline. Typically a matriline consists of one to five adult females, yearlings (marmots in their second summer of life) and young. Several matrilines may occur on a large patch and are called colonies. Matrilines are territorial and exclude other females from the matrilineal home range (=territory) even if the excluded females are kin ($r \leq 0.25$). Thus, space-use overlap is high among matrilineal females but low among females of different matrilines (Armitage 1984). Small patches, designated satellites, generally have an adult female and yearlings or young. Adult males associate with and defend one or more matrilines and usually are unrelated to the adult females (Armitage 1998). An adult male may not live with a satellite female because a noncolonial male may include several satellite sites within his territory (Salsbury & Armitage 1994).

Methods

Each year since 1962, marmots were live-trapped,-weighed and reproductive status determined. Reproductive status of females was determined by nipple development (Armitage & Wynne-Edwards 2002). Virtually, all individuals at the study sites were trapped and marked each year. At the time of first capture, mar-

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mots received a uniquely numbered Monel metal tag in each ear for permanent identification. Each animal was marked with a nontoxic fur dye for identification during behavioural observations. Age was known for every animal first trapped as a young. Age of animals first trapped as yearlings or 2-year-olds was determined from body mass. Animals first trapped at age three or older could not be accurately aged, but were at least 3-years-old.

For this study, I tallied all of the residents in four age-sex categories (young, yearlings, adult females and adult males) at five sites (River/Bench, Marmot Meadow, Picnic, and North Picnic colonies and Boulder satellite) that were trapped every year from 1964 to 2002. Animals trapped in 1962 and 1963 were not included in the demographic analysis because not all sites were trapped and observed in these years. However, data from these years were used to verify age and sex of marmots in this data set. The numbers for each site were summed over all sites to determine the total number of residents at the five sites. Behavioural observations occurred at all colony sites but not at the satellite site Boulder. Observations occurred in the morning (07:00–10:00) and afternoon (16:00–20:00) when marmots are most active (Armitage *et al.* 1996) from June through August; total hours of observation approximated 6000.

For previously published demographic analyses, a postbreeding census partial life cycle model was used (Oli & Armitage 2004). Five demographic variables were parameterized: age of first reproduction, age of last reproduction, juvenile survival rate, adult survival rate and fertility rate. These variables were used to calculate the projected population growth rate. Both prospective (elasticity) and retrospective (life table response experiment, LTRE) analyses were performed to explore the functional dependence of projected population growth rate and to quantify temporal changes in growth rate to changes in the demographic variables. Further details of the analytic procedure are presented in Oli & Armitage (2004). The results from these studies and the new analyses reported here are used to evaluate the role of social behaviour in population dynamics.

Results: new population analyses

Populations fluctuated widely from year to year (Fig. 2). The total number of residents increased significantly over time at the five sites:

$$\text{Total number} = -1655 + 0.869\,\text{year}, p = 0.009$$

However, this increase over time explained only a small proportion of the variation in numbers (R^2 – adj = 0.149). The number of young was directly related to the number of adult females:

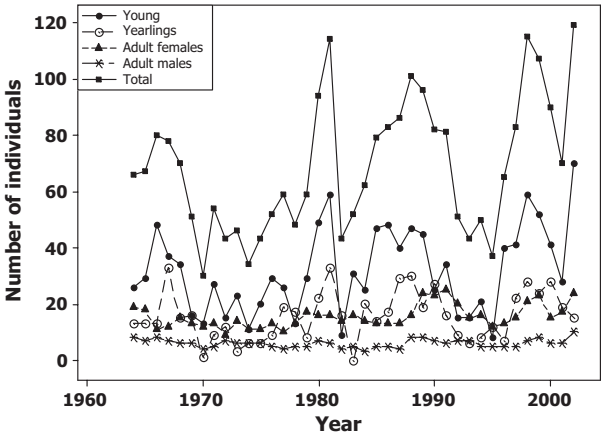

Fig. 2 Population numbers of young, yearling and adult yellow-bellied marmots at five sites (River/Bench, Marmot Meadow, Picnic, Boulder and North Picnic) from 1964 to 2002.

$$\text{Number of young} = 7.49 + 1.55\,\text{number of females}, p = 0.008.$$

It is not surprising that the presence of more adult females resulted in the weaning of more young. However, the result contradicts the predictions from the model; the number of young should decline as the number of adult females increases (Fig. 1). This pattern persists when birth rate is considered; birth rate was not significantly related to the number of adult females and <8% of the variation in birth rate was explained by the number of adult females. Moreover, only 15.0% of the variation in the number of young is related to the number of females, which suggests that other factors significantly affect the production of young. A regression analysis revealed that the number of young in a year predicted the number of yearlings in the subsequent year:

$$\text{Number of yearlings} = 0.26 + 0.503\,\text{number of young}, p = 0.000.$$

This relationship explains most of the variation in the number of yearlings (R^2 – adj = 0.649). The remaining variation can be explained by differential survival of young among the sites. On average, 49.3% of the young survive as yearlings. Survivorship (measured by capture–mark–recapture) varies among sites owing to predation, summer drought and prolonged snow cover (Armitage 1994, 2004a; Ozgul *et al.* 2006).

Although the number of adult males contributes significantly (p = 0.007) to the total population, the number is small (range 3–10, x = 6); thus, adult males contribute little to population dynamics. The fluctuation in the number of adult females is much greater than that of adult males (SD = 4.1 vs. 1.5) and the number of young fluctuates most widely (Fig. 2). From this description of

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population trends, one would expect that demographic factors affecting the production of young would most significantly influence population growth rate.

Results: previous published analyses

Temporal dynamics

The projected population growth rate (sensitivity analysis) exhibited temporal fluctuations in all colonies (Oli & Armitage 2004). Elasticity analyses indicated that juvenile survival would have the largest relative influence on projected population growth rate. Juvenile survival ranked first in 32 years of the 37-year study (Oli & Armitage 2004). Age of first reproduction ranked first in the other 5 years; none of the other demographic variables ranked first and rarely second. Elasticity of population growth rate to changes in age of first reproduction and juvenile survival was significantly higher in years of positive population growth than in years of negative population growth.

Life table response experiment comparisons revealed that the annual changes in population growth were negative in 17 years and positive in 19 years. The demographic variables varied substantially in their contributions to changes in population growth. In some years, one variable had a positive influence whereas other variables had a negative influence (Oli & Armitage 2004). Overall, age of first reproduction (27.8%) and fertility (38.9%) made the largest contribution to change in population growth whereas the contributions of adult survival were insubstantial. During population decline, age of first reproduction and fertility made the largest contribution to changes in population growth; in contrast, during increases, fertility and juvenile survival made the largest contributions and age of first reproduction was a close third.

Sociality

The effects of sociality are expressed at the level of the matriline and indicate that both cooperation and competition occur. Both net reproductive rate (NRR) and survival increase as matriline size increases to a peak of three adult females (suggesting cooperation) and both decline in matrilines of four and five (Armitage & Schwartz 2000). High values of NRR occurred in large matrilines when females of all ages reproduced, low values occurred when nearly all young females failed to wean a litter (suggesting competition) but some older females did so (Armitage 2007). A female is more likely to reproduce as her age increases and the presence of an older female significantly decreases the probability that a female of any younger age will reproduce (Nuckolls 2010). Although females in one matriline inhibit reproduction in an adjoining matriline (Armitage 1986), most reproductive suppression occurs within a matriline (Armitage 2003a). Similarly, reproductive suppression in alpine marmots occurs when sexually mature females living in the same territory as their mother do not breed (Lenti-Boero 1999).

Younger females, 2- or 3-years-old, are most likely not to reproduce if an older female is also present in the matriline. Reproductive suppression is independent of the number of older adults present, which indicates a lack of density dependence. The primary effect of reproductive suppression is to increase the age of first reproduction (Armitage 2003a). The percentage of younger females that reproduce is lower when the older female is reproductive than when the older female is nonreproductive. Although reproduction of a 2-year-old is significantly less likely when her mother is present than when her mother is absent, the 2-year-old is more likely to reproduce if her mother is the older female than if the older adult is not her mother, e.g. a sister (Armitage 2003a). As a consequence of reproductive suppression, only about 20% of 2-year-olds reproduce when an older female is present in the matriline, but more than twice as many reproduce when an older female is absent.

Sociality affects reproduction in other ways. A female is more likely to wean a litter if a same-age kin is present and no older female is present. This effect does not occur if an older female is present. When neither same-age kin nor older females are present, a female is more likely to reproduce if younger adult kin are present (Armitage 2003a). These patterns also suggest cooperation, but the mechanisms underlying these relationships are unknown.

In addition to the probability of reproducing, sociality affects the total lifetime number of young produced. Lifetime number of young increases as the average number of younger adults present increases and decreases as the average number of older adults present increases, as the average number of same-aged adults present increases, and as relative matriline density increases (Nuckolls 2010). Larger than average matrilines occur when the matriline consists primarily of younger females (Armitage & Schwartz 2000; Armitage 2007).

Dispersal

Virtually all males disperse, mainly as yearlings but some as 2-year-olds (Armitage 1991; Schwartz *et al.* 1998). Dispersal by female yearlings is conditional and is not a function of matriline density, total number of adult female residents in a colony, body mass, the presence of her father or of agonistic behaviour (Armitage *et al.* 2011). A yearling female is unlikely to disperse if

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her mother is present and social behaviour is amicable with her mother, if she engages in play, and if space-use overlap is high with her mother, with the other matriline females and with other yearling females. A variable selection procedure revealed that the critical factor affecting the probability of dispersal was space-use overlap with the mother; none of the social behaviour variables or other space-use variables entered the model. Greater space-use-overlap with the mother promoted philopatry, i.e., recruitment.

Dispersal by female yearlings does not occur when adults are absent (Brody & Armitage 1985), thus some female yearlings remain philopatric even though the mothers are absent (Armitage *et al.* 2011). Furthermore, female yearlings may remain philopatric when mothers are absent if unoccupied space is available in the habitat patch. The movement to unoccupied space leads to the formation of a new matriline (Armitage 1984).

Discussion

Effects of sociality

Sociality affects demographic mechanisms of population growth and decline. Reproductive suppression is the major factor that determines the age of first reproduction, which strongly affects observed changes in projected population growth rate. Infanticide is a form of reproductive suppression which occurs in the social prairie dogs. Lactating black-tailed prairie dogs (*Cynomys ludovicianus*) kill the offspring of close kin (Hoogland 1985); this behaviour reduces fecundity (a population effect) and increases the fitness of the lactating female (an individual fitness effect) whose offspring populate the coterie. Sociality also affects fecundity; the age structure of a matriline and matriline size can either increase or decrease the number of offspring weaned depending on the distribution of older, younger and same-aged adult females in the matrilines. The way in which sociality affects the demographic mechanisms of population growth may depend, in part, on the life history characteristics of the species. When the population density of a Uinta ground squirrel (*Spermophilus armatus*) was reduced, age of maturity did not change and changes in fertility contributed most to projected population growth rate (Oli *et al.* 2001). The difference in the importance of age of maturity (age of first reproduction) between the social yellow-bellied marmot and the relatively asocial Uinta ground squirrel likely results from the ground squirrel typically reproducing at age 1 year; thus, the opportunity to increase the age of maturity appears to be limited and cannot be reduced in this annual breeder as it cannot reproduce in the first summer of its life.

Food supplementation of Columbian ground squirrel (*Spermophilus columbianus*) populations increased population density (Dobson & Oli 2001). Fertility rate and the age of maturity generally made the largest contributions to observed changes in population growth rate. The Columbian ground squirrel typically reproduces at age 2 years, but can reproduce at age one, i.e. in its second summer of life. Thus, like the yellow-bellied marmot, sociality can affect population growth by affecting the age of maturity.

Although juvenile survival of yellow-bellied marmots had the greatest effect in elasticity (prospective) analyses, it was of much less importance in LTRE (retrospective) analyses. Its major effect was its contribution to population decline (Oli & Armitage 2004). There is no evidence that juvenile survival is affected by sociality, but is strongly affected by environmental factors, especially those associated with the length of winter (Ozgul *et al.* 2006). For example, the decline in population in 1982 (Fig. 2) was associated with late snow cover and low rainfall in June (Schwartz & Armitage 2003). Also, survival is low in late litters as there is insufficient time for young to accumulate fat for hibernation (Armitage *et al.* 1976). By contrast, sociality affects survival of juvenile alpine marmots (*Marmota marmota*). The presence of nonreproductive adults in the marmot family increases juvenile survival because the adults warm the juveniles, thus reducing juvenile metabolism and conserving their fat resources (Arnold 1988).

Although the density of marmots is affected primarily by the number of young weaned, the density of adult residents is determined mainly by the number of adult females. The decline in the number of adult females occurs by predation and overwinter mortality (Armitage 1996; Schwartz & Armitage 2003) and the increase in the number of adult females occurs primarily by recruitment within matrilines (Armitage 1973, 1984, 1996). Of 168 females added to the population, 47 (27.9%) were immigrants and 121 (72.0%) were recruits. No immigrant successfully achieved residency in an established matriline; immigration was successful only when unoccupied space was available (because of over-winter mortality) in a habitat patch (Armitage 2003b). As predicted from the population model (Fig. 1), immigration was more frequent when the density of adult females was below the mean number of females for a site. However, there was no difference in the rate of recruitment when the density of females was above or below the mean, i.e. recruitment was density independent, and recruitment was as likely as immigration when densities were below the mean (Armitage 2003b). Recruitment and/or immigration occurred in half of the colony-years (a colony-year is one colony in 1 year).

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Population regulation

Social behaviour can affect population dynamics by infanticide, by delaying maturity, by limiting the size of the breeding population and by initiating dispersal (Krebs *et al.* 2007). In general, the impact of rodent social behaviour on population regulation remains problematical. We can ask the question: how are yellow-bellied marmot populations regulated? This question is best answered by examining the role of the basic social unit. A major factor that limits population growth occurs at the level of the matriline where adult females compete to determine whose offspring will be added to the population. Evidence indicates that this marmot population is not food-limited (Kilgore & Armitage 1978; Frase & Armitage 1989; Woods & Armitage 2003). Because of the short growing season, marmot populations do not reach a density that is limited by food. Time appears to be the critical factor that limits population growth (Andrewartha & Birch 1954). Mortality factors, such as weather, reduce marmot numbers in a density-independent manner. Predation is one major cause of mortality, and most disappearances of marmots during the summer were attributed to predators (Van Vuren 2001). Although a particular predation event can markedly reduce a local population (Armitage 2004a), the large majority of residents survive until hibernation and there is no evidence that relates predation to population density.

Available evidence indicates that density-dependent dispersal is fairly common in mammals, but some studies indicate no effect of population density (Matthysen 2005). In yellow-bellied marmots, dispersal did not vary with population density, which is in contrast to the population model (Fig. 1). Dispersal is related to the fitness strategies of individuals and highly dependent on mother:daughter relationships (Armitage *et al.* 2011).

Social competition, as expressed in reproductive suppression, was also independent of population density as it is not influenced by the number of older adults present. Nonregulatory mortality (Fig. 1) does not vary with population density, but depends on the presence of predators. For example, in some years, badgers are not seen and there is no evidence of badger predation. In other years, a red fox (*Vulpes vulpes*) may reside in a colony and heavily predate colony young. The small effect of the number of adult females on the number of young indicates that natality does not vary with population density. Rates of social behaviour are independent of population density (Armitage 1975) and are strongly related to kinship (Armitage & Johns 1982). Thus, available evidence does not support population regulation by a density-dependent feedback model driven by social behaviour; the model (Fig. 1) is rejected.

Marmot populations appear to be limited by environmental factors such as drought and prolonged snow cover (Armitage 1994). Snow cover persists longer in the spring at the up-valley sites (e.g. Picnic, North Picnic) than at the down-valley sites (e.g. River/Bench). Prolonged snow cover was associated with a significantly lower proportion of females weaning litters and smaller litter size (Van Vuren & Armitage 1991). At a higher elevation site, where snow cover typically lasted 30 days longer than in the East River Valley, no female was known to reproduce in consecutive years (Johns & Armitage 1979) and prolonged snow cover was associated with a total failure of reproduction and 100% mortality of the previous year's young (Woods *et al.* 2009). Possibly both typical and extreme weather patterns limit the marmot population to levels below carrying capacity. This hypothesis is supported by the recent finding that earlier snow melting resulted in earlier emergence from hibernation and increased survival, especially of adults, which produced a major increase in population numbers between 2000 and 2008 (Ozgul *et al.* 2010). The importance of prolonged snow cover in limiting marmot populations was dramatically demonstrated in the winter of 2010–2011 when heavy, late snow cover into mid June resulted in the mortality of 50% of the adults and 80% of the young (D.T. Blumstein personal communication). When snow cover is too thin during winter, the probability of survival by alpine marmots decreases (Allaine *et al.* 2008).

In agreement with Wolff's (1997) model, dispersal does not regulate yellow-bellied marmot populations. Inbreeding, which is possible in about 10% of matings, is not avoided (Armitage 2004b). It is also unlikely that young females suppress their own reproduction to avoid possible infanticide, especially given the strong selection for early age of first reproduction and that delaying the age of first reproduction did not improve survival or increase the number of successful reproductive events or offspring production (Oli & Armitage 2003). Although some life history patterns are interpretable in terms of population regulation, the patterns are more consistent with the population limitation hypothesis (Murray 1999). This hypothesis predicts that over a wide range of population density, changes in population parameters are independent of density, but density may affect population dynamics below or above this range. Hence, the number of females explains little of the variation in the number of young. There may be some density effect at high numbers of adult females, e.g. the number of young declined when the number of females was high in 1998 and 1999 (Fig. 2). It is unclear what sets the carrying capacity. For example, a burrow

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area may house three adult females in some years but only one in other years with no apparent difference in food abundance. Space seems to be critical; females may require sufficient space where their young can forage safely from conspecific aggression and where daughters can be recruited without the need to enlarge the matrilineal territory. It is likely that the ultimate factors that set the carrying capacity are burrow sites and food. However, predation, weather events and social competition in most years and at most sites limit the population below carrying capacity.

I conclude that social behaviour affects population dynamics primarily through delaying maturity, reducing fecundity and limiting the size of the breeding population. These factors also affect fitness. I suggest that a more consistent relationship occurs between reproductive and behavioural events and individual fitness strategies. In this context, population dynamics is viewed as a consequence of individual attempts to maximize direct fitness.

Individual fitness

A female can maximize her fitness by producing reproductive daughters. Because the mortality rate of dispersers is higher than that of recruits (Van Vuren & Armitage 1994), the probability that a female will produce a reproductive daughter is greater by recruiting the daughter into her matriline. Recruitment of daughters establishes potential competition between mother and daughter over who reproduces and recruits daughters. The mother should enhance her direct fitness by weaning more daughters and suppressing reproduction by her daughter. Thus, the mother will incorporate additional individuals with whom she is related by $r = 0.5$ rather than accepting granddaughters with whom she is related by $r = 0.25$. However, the mother to maximize her fitness must have grandoffspring; thus eventually her daughters should reproduce. The highly successful females do produce granddaughters (Armitage 2002) and the key factor is recruiting a daughter (Nuckolls 2010).

Young adult females (below the population mean age of adults) produce significantly more daughters than sons and recruit more daughters than expected. Older females (above the mean age) wean about twice as many males as females ($p < 0.001$) and recruit fewer daughters than expected (Armitage 1987). Is weaning more males a successful reproductive strategy? This question is difficult to answer because virtually all resident, territorial males are of unknown origin and nearly all male dispersers travel beyond our study area. An adult male sires an average of 12.7 young during his lifetime compared to an average of 7.1 for successful females (Armitage 2004b). However, only about 16% of 1-year-old males live to age three (Schwartz *et al.* 1998) and only about 6% of the successful males account for the difference in average reproductive success between males and females. Thus, only about 1% of yearling males become highly successful (Armitage 2010). It seems unlikely that producing more sons than daughters is a successful reproductive strategy in general, but producing more sons may increase fitness when the probability of recruiting a daughter is near zero.

But why do daughters choose to remain in their natal area and encounter reproductive suppression? They do not remain philopatric to gain indirect fitness benefits as these do not compensate for the loss of direct fitness (Oli & Armitage 2008). The alternative is to disperse and attempt to become a resident in another habitat patch. The probability of successful dispersal into a colony is low; only six of 32 dispersing yearlings trapped at a colony site became residents; none were successful immigrants if philopatric yearlings were present (Armitage 2003b).

The philopatric yearling becomes an adult recruit when 2-years-old, but the mean age of known-age immigrants is 2.8 years. In effect, the immigrant is unlikely to reproduce until 3-years-old (Armitage 2003b) and only 20 of 77 immigrants (all sites over 40 years) reproduced in their first year of residency (Armitage & Schwartz 2000). Thus, only 26% of immigrants reproduce by age 3 which is considerably less than the 39.6% of philopatric females. Of those females that reproduced at least once, the mean age of first reproduction for the five sites in this report was 3.01 ($N = 86$) for recruits and 3.7 ($N = 18$) for immigrants. However, the age of some immigrants was unknown. If they are assigned the minimal possible age (3 or 4), the mean age of first reproduction decreases to 3.48, which is considerably larger than that of recruits. For the five sites, 24.1% of the immigrants and 71% of the philopatric females reproduced by age 3. When the higher rate of mortality of dispersers is included in this scenario, dispersers have a much lower potential reproductive success than residents. In conclusion, philopatric yearling females are choosing the best option for maximizing reproductive success. Not only are they more likely to reproduce and to reproduce at a younger age, they also increase their inclusive fitness from the benefits of sociality, including indirect fitness benefits (Armitage & Schwartz 2000; Oli & Armitage 2008).

Although the effects of group size on fitness in mammals needs much further study (Silk 2007), the adaptive value of mammalian social systems, including the yellow-bellied marmot social system, is that sociality is directed towards maximizing inclusive fitness, especially the component of direct fitness (Clutton-Brock

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2009). Thus, social systems, including those based on kinship, are characterized by both cooperative and competitive behaviours. It is not necessary to invoke kin selection to account for the structure and function of these social systems. If altruism cannot be demonstrated, social behaviour can be explained by individual selection (Gadagkar 2011).

Conclusion

Both intrinsic and extrinsic mechanisms affect population dynamics of yellow-bellied marmots. Sociality and behaviour processes associated with population dynamics are best understood as ways to maximize fitness and that have population consequences. None of the behaviours, e.g. reproductive suppression, dispersal, are directed towards regulating population density but affect population dynamics such that population numbers may increase or decrease as a consequence of the interplay of cooperation and competition.

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References

Allaine D, Cohas A, Bonenfane C (2008) Demographic effects of climate fluctuations on an alpine marmot (*Marmota marmota*) population. *Sixth International Marmot Conference*, **Abstracts**, 12–13.

Andrewartha HG, Birch LC (1954) The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Armitage KB (1973) Population changes and social behavior following colonization by the yellow-bellied marmot. *Journal of Mammalogy*, **54**, 842–854.

Armitage KB (1975) Social behavior and population dynamics of marmots. *Oikos*, **26**, 341–354.

Armitage KB (1984) Recruitment in yellow-bellied marmot populations: kinship, philopatry, and individual variability. In: *The Biology of Ground-Dwelling Squirrels* (eds Murie JO, Michener GR), pp. 377–403. University of Nebraska Press, Lincoln, Nebraska.

Armitage KB (1986) Marmot polygyny revisited: determinants of male and female reproductive strategies. In: *Ecological Aspects of Social Evolution* (eds Rubenstein DS, Wrangham RW), pp. 303–331. Princeton University Press, Princeton, New Jersey.

Armitage KB (1987) Do female yellow-bellied marmots adjust the sex ratios of their offspring? *American Naturalist*, **129**, 501–519.

Armitage KB (1991) Social and population dynamics of yellow-bellied marmots: results form long-term research. *Annual Review of Ecology and Systematics*, **22**, 379–407.

Armitage KB (1994) Unusual mortality in a yellow-bellied marmot population. In: *Actual Problems of Marmots Investigation* (ed. Rumiantsev V), pp. 5–13. ABF Publishing House, Moscow.

Armitage KB (1996) Social dynamics, kinship, and population dynamics of marmots. In: *Biodiveristy in Marmots* (eds Le Berre M, Ramousse R, Le Guelte L), pp. 113–128. International Network on Marmots, Lyon.

Armitage KB (1998) Reproductive strategies of yellow-bellied marmots: energy conservation and differences between the sexes. *Journal of Mammalogy*, **79**, 385–393.

Armitage KB (2002) Social dynamics of yellow-bellied marmots: strategies for evolutionary success. In: *Holarctic Marmots as a Factor of Biodiversity* (eds Armitage KB, Rumiantsev VYu), pp. 9–16. ABF Publishing House, Moscow.

Armitage KB (2003a) Reproductive competition in female yellow-bellied marmots. In: *Adaptive Strategies and Diversity in Marmots* (eds Ramousse R, Allainé D, Le Berre M), pp. 133–142. International Network on Marmots, Lyon.

Armitage KB (2003b) Dynamics of immigration into yellow-bellied marmot colonies. *Oecologia Montana*, **12**, 21–24.

Armitage KB (2004a) Badger predation on yellow-bellied marmots. *American Midland Naturalist*, **151**, 378–387.

Armitage KB (2004b) Lifetime reproductive success of territorial male yellow-bellied marmots. *Oecologia Montana*, **13**, 28–34.

Armitage KB (2007) Evolution of sociality in marmots: it begins with hibernation. In: *Rodent Societies: An Ecological & Evolutionary Perspective* (eds Wolff JO, Sherman PW), pp. 356–367. University of Chicago Press, Chicago, Illinois.

Armitage KB (2010) Individual fitness, social behavior, and population dynamics of yellow-bellied marmots. In: *The Ecology of Place* (eds Billick I, Price MV), pp. 134–154. University of Chicago Press, Chicago, Illinois.

Armitage KB, Johns DW (1982) Kinship, reproductive strategies and social dynamics of yellow-bellied marmots. *Behavioral Ecology and Sociobiology*, **11**, 55–63.

Armitage KB, Schwartz OA (2000) Social enhancement of fitness in yellow-bellied marmots. *Proceedings of the National Academy of Sciences USA*, **97**, 12149–12152.

Armitage KB, Wynne-Edwards KE (2002) Progesterone concentrations in wild-caught yellow-bellied marmots. In: *Holarctic Marmots as a Factor of Biodiversity* (eds Armitage KB, Rumiantsev VYu), pp. 41–47. ABF Publishing House, Moscow.

Armitage KB, Downhower JF, Svendsen GE (1976) Seasonal changes in weights of marmots. *American Midland Naturalist*, **96**, 36–51.

Armitage KB, Salsbury CM, Barthelmess EL, Gray RC, Kovach A (1996) Population time budget for the yellow-bellied marmot. *Ethology Ecology & Evolution*, **8**, 67–95.

Armitage KB, Van Vuren DH, Ozgul A, Oli MK (2011) Proximate causes of natal dispersal in female yellow-bellied marmots *Marmota flaviventris*. *Ecology*, **92**, 218–227.

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Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *Journal Comparative Physiology B*, **158**, 151–156.

Brody AK, Armitage KB (1985) The effects of adult removal on dispersal of yearling yellow-bellied marmots. *Canadian Journal of Zoology*, **63**, 2560–2564.

Calhoun JB (1952) The social aspects of population dynamics. *Journal of Mammalogy*, **33**, 139–159.

Clutton-Brock T (2009) Structure and function in mammalian societies. *Philosophical Transactions of The Royal Society B*, **364**, 3229–3242.

Dobson FS, Oli MK (2001) The demographic basis of population regulation in Columbian ground squirrels. *American Naturalist*, **158**, 236–247.

Errington PL (1956) Factors limiting higher vertebrate populations. *Science*, **124**, 304–307.

Frase BA, Armitage KB (1989) Yellow-bellied marmots are generalist herbivores. *Ethology Ecology & Evolution*, **1**, 353–366.

Frase BA, Hoffmann RS (1980) *Marmota flaviventris*. *Mammalian Species*, **135**, 1–8.

Gadagkar R (2011) Altruistic wasps? *Science*, **333**, 833–834.

Hoogland JL (1985) Infanticide in prairie dogs: lactating females kill offspring of close kin. *Science*, **230**, 1037–1040.

Johns DW, Armitage KB (1979) Behavioral ecology of alpine yellow-bellied marmots. *Behavioral Ecology and Sociobiology*, **5**, 133–157.

Kilgore Jr DL, Armitage KB (1978) Energetics of yellow-bellied marmot populations. *Ecology*, **59**, 78–88.

Krebs CJ (1985) *Ecology*, 3rd edn. Harper & Row, New York.

Krebs CJ, Lambin X, Wolff JO (2007) Social behavior and self-regulation in murid rodents. In: *Rodent Societies: An Ecological and Evolutionary Perspective* (eds Wolff JO, Sherman PW), pp. 173–181. University of Chicago Press, Chicago, Illinois.

Lenti-Boero D (1999) Population dynamics, mating system and philopatry in a high altitude colony of alpine marmots (*Marmota marmota* L.). *Ethology Ecology & Evolution*, **11**, 105–122.

Lidicker Jr WZ (1962) Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. *The American Naturalist*, **96**, 29–33.

Matthysen E (2005) Density-dependent dispersal in birds and mammals. *Ecography*, **28**, 403–416.

Murray BG (1999) Can the population regulation controversy be buried and forgotten? *Oikos*, **84**, 148–152.

Nuckolls K (2010) *Determinants of annual and lifetime reproductive success in female yellow-bellied marmots: a cross-generational study*. PhD dissertation, University of Kansas, Lawrence, Kansas.

Oli MK, Armitage KB (2003) Sociality and individual fitness in yellow-bellied marmots: insight from a long-term study (1962–2001). *Oecologia*, **136**, 543–550.

Oli MK, Armitage KB (2004) Yellow-bellied marmot population dynamics: demographic mechanisms of growth and decline. *Ecology*, **85**, 2446–2455.

Oli MK, Armitage KB (2008) Indirect fitness benefits do not compensate for the loss of direct fitness in yellow-bellied marmots. *Journal of Mammalogy*, **89**, 874–881.

Oli MK, Slade NA, Dobson FS (2001) Effect of density reduction on Uinta ground squirrels: analysis of life table response experiments. *Ecology*, **82**, 1921–1929.

Ozgul A, Armitage KB, Blumstein DT, Oli MK (2006) Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. *Ecology*, **87**, 1027–1037.

Ozgul A, Childs DZ, Oli MK *et al.* (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, **466**, 482–485.

Salsbury CM, Armitage KB (1994) Home range size and exploratory excursions of adult, male yellow-bellied marmots. *Journal of Mammalogy*, **75**, 648–656.

Schwartz OA, Armitage KB (2003) Population biology of yellow-belled marmots: a 40 year perspective. In: *Adaptive Strategies and Diversity in Marmot* (eds Ramousse R, Allainé D, Le Berre M), pp. 207–212. International Network on Marmots, Lyon.

Schwartz OA, Armitage KB, Van Vuren D (1998) A 32-year demography of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Zoology London*, **246**, 337–346.

Silk JB (2007) The adaptive value of sociality in mammalian groups. *Philosophical Transactions of The Royal Society B*, **362**, 539–559.

Svendsen GE (1974) Behavioral and environmental factors in spatial distribution and population dynamics of a yellow-bellied marmot population. *Ecology*, **55**, 760–771.

Van Vuren DH (2001) Predation on yellow-bellied marmots (*Marmota flaviventris*). *American Midland Naturalist*, **145**, 94–100.

Van Vuren D, Armitage KB (1991) Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. *Canadian Journal of Zoology*, **69**, 1755–1758.

Van Vuren D, Armitage KB (1994) Survival of dispersing and philopatric yellow-bellied marmots: what is the cost of dispersal? *Oikos*, **69**, 179–181.

Wolff JO (1997) Population regulation in mammals: an evolutionary perspective. *Journal of Animal Ecology*, **66**, 1–13.

Woods BC, Armitage KB (2003) Effects of food addition on life history of yellow-bellied marmots. *Oecologia Montana*, **12**, 29–36.

Woods BC, Brown CL, Cobb MA (2009) Elevation variation in life-history characteristics of populations of yellow-bellied marmots (*Marmota flaviventris*). *Ethology Ecology & Evolution*, **21**, 381–392.

Wynne-Edwards VC (1965) Self-regulating systems in populations of animals. *Science*, **147**, 1543–1548.

K.B.A's interest is on the biology of ground-dwelling squirrels with emphasis on social behavior and fitness strategies. K.B.A. focused on a 40-year study of yellow-bellied marmots that included social behavior and structure, habitat use, hibernation, temperature regulation and water balance, thermal energy exchange, body mass and growth, reproductive success and population dynamics

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Data accessibility

Available by request through the Rocky Mountain Biological Laboratory (RMBL): http://www.rmbl.org.

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