OIKOS 102: 124–136, 2003

Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*

Volker Grimm, Norbert Dorndorf, Fredy Frey-Roos, Christian Wissel, Tomasz Wyszomirski and Walter Arnold

Grimm, V., Dorndorf, N., Frey-Roos, F., Wissel, C., Wyszomirski, T. and Arnold, W. 2003. Modelling the role of social behavior in the persistence of the alpine marmot *Marmota marmota*. – Oikos 102: 124–136.

A general rule of thumb for biological conservation obtained from simple models of hypothetical species is that for populations with strong environmental noise moderate increases in habitat size or quality do not substantially reduce extinction risk. However, whether this rule also holds for real species with complex behavior, such as social species with breeding units and reproductive suppression, is uncertain. Here we present a population viability analysis of the alpine marmot *Marmota marmota*, which displays marked social behavior, i.e. it lives in social groups of up to twenty individuals. Our analysis is based on a long-term field study carried out in the Bavarian Alps since 1982. During the first fifteen years of this study, 687 marmots were individually marked and the movements and fate of 98 dispersing marmots were recorded with radio-telemetry. Thus, in contrast to most other viability analyses of spatially structured populations, good data about dispersal exist. A model was constructed which is individual-based, spatially explicit at the scale of clusters of neighbouring territories, and spatially implicit at larger scales. The decisive aspect of marmot life history, winter mortality, is described by logistic regression where mortality is increased by age and the severity of winter, and decreased by the number of subdominant individuals present in a group. Model predictions of group size distribution are in good agreement with the results of the field study. The model shows that the effect of sociality on winter mortality is very effective in buffering environmental harshness and fluctuations. This underpins theoretical results stating that the appropriate measure of the strength of environmental noise is the ratio between the variance of population growth rate and the intrinsic rate of increase. The lessons from our study for biological conservation are that simple, unstructured models may not be sufficient to assess the viability of species with complex behavioral traits, and that even moderate increases in habitat capacity may substantially reduce extinction risk even if environmental fluctuations seem high.

V. Grimm, N. Dorndorf and C. Wissel, UFZ Umweltforschungszentrum Leipzig-Halle GmbH, Sektion Ökosystemanalyse, PF 500136, DE-04301 Leipzig, Germany. Present address of VG: UFZ Centre for Environmental Research Leipzig-Halle, Dept of Ecological Modelling, P.O. Box 500163, DE-04301 Leipzig, Germany (vogri@oesa.ufz.de). – F. Frey-Roos and W. Arnold, Forschungsinstitut für Wildtierkunde und Ökologie, Savoyenstrasse 1, AT-1160 Wien, Austria. – T. Wyszomirski, Instytut Botaniki, Uniwersytetu Warszawskiego, Al.Ujazdowskie 4, PL-00-478 Warszawa, Poland.

The risk of population extinction is mainly determined by two aspects: the size or quality of the habitat and the intensity of environmental fluctuations (Goel and Richter-Dyn 1974, Leigh 1981, Goodman 1987, Wissel 1989, Renshaw 1991, Wissel and Stöcker 1991, Burgman et al. 1993, Lande 1993, Foley 1994, Wissel et al. 1994). In small or low-quality habitats, the population size may be so small that populations die out due to demographic variations ("demographic noise"; May 1973), whereas with sharp environmental fluctuations

Accepted 17 January 2003

ISSN 0030-1299

("environmental noise"; May 1973) the population even in larger habitats may occasionally become so small that it is subject to demographic noise. The relationship between habitat capacity, K, environmental noise, and extinction risk is usually depicted in plots of the mean time to extinction, T_m, versus K. For theoretical population models which are simple enough to be tackled analytically, the following results were obtained (Lande 1993, Wissel et al. 1994): without environmental noise this plot is an exponential function, but with environmental noise the increase in T_m with K is only a power function $T_m = cK^{\nabla}$, where c is a constant. The weaker the environmental noise, the larger the exponent ∇. For strong environmental noise, ∇ is very small, leading to just a slight increase in T_m with K, which finally turns into a logarithmic curve for very high environmental noise (Wissel et al. 1994). A rule of thumb for conservation arising from these plots would be that management measures leading to an increase in K are likely to pay only if environmental noise is weak, i.e. if the individuals' performance does not vary too much because of environmental fluctuations (e.g. weather, disturbances, biotic interactions, etc.).

It would, however, be premature to apply this rule of thumb literally in biological conservation because mechanisms may exist that moderate apparently strong environmental fluctuations. For example, sociality or social behaviour are likely to affect extinction risk. However, the relationship between the risk of extinction, capacity K, and environmental fluctuations has still not yet been thoroughly explored for social species. Vucetich et al. (1997) discuss the role of the social structure of the gray wolf in terms of demographic noise and the cyclic variation of its food resource, yet fail to consider environmental noise. They argue that sociality may inflate the significance of demographic noise by restricting the number of breeding units to the number of social groups (Vucetich et al. 1997, Courchamp et al. 1999), thereby leading to an increased extinction risk by amplifying demographic noise. However, one might intuitively argue that sociality buffers environmental noise because communal breeding units, for example, are less susceptible to extreme environmental conditions than isolated individuals. Nevertheless, it is still not clear exactly how this buffering functions; moreover, it is not clear either how strong the effect of sociality is on the risk of extinction. Hence the relationship between sociality and the risk of extinction must be examined both qualitatively and quantitatively before guidelines for managing endangered social species can be worked out.

However, insights into the relationship between sociality and persistence are hard to obtain empirically. Using models of social species therefore seems to be the most promising way to study this relationship. In particular, since differences between individuals are a main feature of sociality, the individual-based approach of ecological modelling (Huston et al. 1988, DeAngelis and Gross 1992, Uchmanski and Grimm 1996, Grimm 1999) is the most appropriate tool in this context because in individual-based models (IBMs) individuals are characterized by features that may differ among individuals (e.g. age, size, rank, location, etc.). With IBMs it is possible to take into account explicitly behavioral traits that may be essential for the dynamics and persistence of the entire population.

Here we present an IBM about the alpine marmot (*Marmota marmota*), which shows marked social behavior. The models is based on long-term field study which started in 1982 (Arnold 1986, 1990a, b, 1993a, 1997, Arnold and Dittami 1997, Frey-Roos 1998). Thus, in contrast to almost all other population viability analyses (PVA; Boyce 1992, Beissinger and Westphal 1998), our model is founded on an exceptionally good database recording not only mortality, fecundity and behavior, but also dispersal. Moreover, the record of group size distribution allows for the validation of the model to an extent which is rarely possible.

Our aim is to use the model to explore the relationship between sociality and persistence in the alpine marmot. We intend to derive general insights from our model that could be, mutatis mutandis, used for the investigation and management of other social species as well. We will show that sociality can be so effective in buffering environmental fluctuations that the plot of T_m (mean time to extinction) versus capacity K again is exponential, as in the case of no environmental noise at all. This finding clearly has wide implications for the management of endangered social species.

Biological background and field study

Marmota marmota lives in social groups of up to twenty individuals and spends half the year hibernating (Arnold 1993a). A group occupies a territory which is defended by the dominant couple (hereafter referred to as "territorials"; Arnold 1993a). In autumn the group disappears in a common burrow called a hibernaculum. Mating takes place during the first two weeks after emerging from hibernation in spring and a single litter is produced at most per year. Marmots become sexually mature at the age of two years, but regularly reproduce only as territorials (Arnold 1990a). Among females, subordinates are completely excluded from reproduction and territorials litter on average every second year (Arnold 1990a, Hackländer and Arnold 1999). Reproduction among males is also dominated by territorial animals although subordinate group members participate to some degree (Arnold et al. 1993). Young are born after 32 days of gestation. They are weaned around the beginning of July when first emerging from the natal burrow after about four weeks of lactation. At

Table 1. Age-dependent number and proportions of subordinate animals staying in the natal territory and of dispersed marmots.

Age	Not dispersed	Dispersed
2	129 (79%)	35 (21%)
3	35 (28%)	91 (72%)
4	16 (52%)	15 (48%)
5	1 (1%)	11 (99%)

this time, litter size varies between one and six with a biased sex ratio of 58% towards males (Arnold 1986). Due to predation, newborns and yearlings have a summer mortality of about 10% (51 of 468) and 6% (19 of 289), respectively (Arnold 1993a).

Becoming territorial happens either by occupying a vacant territorial position or via the eviction of a territorial animal (Arnold 1990a). An animal can obtain a territory with low risk either by inheriting its home territory or by occupying a territorial position in a neighbouring territory within a distance of 500 m. Within this distance, subdominant marmots can notice vacant territorial positions during short-term excursions or without leaving the territory at all (Frey-Roos 1998). The alternative option is to leave the home territory permanently and search for available territorial positions in a much larger area. Dispersal from the natal site may occur throughout the year, but peaks in spring. Only adult marmots disperse and the rate of dispersal gradually increases with age (Arnold 1993a, Table 1; cf. Blumstein and Armitage 1999). Wandering marmots are highly mobile and can cover distances of several kilometers in steep mountainous landscape (Frey-Roos 1998). Dispersed animals run a high mortality risk if they do not find a territory during the summer because their chances of surviving the next winter alone are slim (Arnold 1993a, Frey-Roos 1998).

Marmots are subjected to environmental fluctuations in the form of the varying severity of winter. A good indicator of the severity of overwintering conditions in a given year and hibernaculum is the date in spring when the respective territory becomes free of snow.This date changes from year to year and correlates closely with the average soil temperature at a hibernaculum throughout winter (Arnold 1990b). The longer the snow cover lasts in spring, the lower was the average ambient temperature during the preceding hibernation season and the higher was the energy expenditure for a hibernating marmot. Parental animals and juveniles are particularly affected by harsh overwintering conditions. Parents have a higher energy expenditure because they invest in warming juveniles during hibernation (Arnold 1990b, 1993a). Juveniles have lower fat reserves than adults and thus have a higher risk of dying of exhaustion. Their chances of surviving the first hibernation are significantly influenced by the weight achieved at the end of weaning (Table 2), which is apparently a good indicator of physical strength and the amount of fat reserves that can be accumulated during the short period until the beginning of hibernation. Multiple logistic regression analysis shows that besides the date of snow melting, age and weaning weight, the presence of other subdominant animals also affect the winter mortality of parental animals and juveniles (Table 2). Marmots related to the territorials help in warming their young sibs and by doing so reduce the energy costs of the territorials, thus decreasing not only the winter mortality of juveniles but also of territorial animals (Arnold 1990b).

The following model is mainly based on results from a field study in the National Park of Berchtesgaden, located in the most eastern region of the Bavarian Alps, where marmots have been continually studied from 1982 to 1996. The study site at an altitude between

Table 2. Results of a multiple logistic regression analysis for the winter mortality of territorial animals ($n = 536$), yearlings and subordinate adults ($n = 531$) and juveniles ($n = 90$; see also: Arnold 1990a, 1993a, b).

Variable[1]	b	S.E.	WALD	Sig	R	exp(b)
Territorial:						
Winter strength	0.0281	0.0142	3.926	0.0475	0.084	1.029
Age	0.2857	0.0823	12.940	0.0005	0.192	1.331
Number of subdominants[2]	−0.3946	0.1217	10.517	0.0012	−0.176	0.674
Constant	−6.8197	1.8761	13.213	0.0003		
Subdominants[2]						
Winter strength	0.0383	0.0183	4.4015	0.0359	0.110	1.039
Constant	−7.5452	2.1928	11.8400	0.0006		
Juveniles:						
Winter strength	0.0241	0.0138	3.022	0.0821	0.056	1.024
Weaning weight	−0.0081	0.0015	27.43	0.0001	−0.281	0.991
Number of subdominants[3]	−0.614	0.1722	12.703	0.0004	−0.182	0.541
Constant	1.014	1.7187	0.3481	0.5552		

[1] Variable names in eq. (1)–(3): Winter strength: *WS*; Age: *A*; Number of subordinates: *SUBY* (eq. (1)) and *SUB* (eq. (3)); Weaning weight: *WW*.
[2] Including yearlings.
[3] Excluding yearlings.

1,100 and 1,500 m above sea level mostly contains mountain pastures. Almost every marmot living in the main study area during the study period, a population of about 130 animals per year, was individually known. During the fifteen years of this field study, 687 marmots have been marked individually and telemetry data of 98 dispersing marmots were recorded. For a detailed description of this long-term field study and the methods applied, see Arnold (1986, 1990a, b, 1993a, 1997) and Frey-Roos (1998).

The model

Due to the complex social system of marmots the model is individual-based and has a sex, age, social, and spatial structure (Dorndorf 1999; a similar individual-based model, which is based on the same field study as the model presented here but addresses a different question. It was developed by Stephens et al. 2002). The model comprises four hierarchical levels: individual, territory, (meta)population, and environment.

At the bottom level of the hierarchy, individuals are characterized by a suite of attributes, i.e. identity number, age, sex, and identity of the territory where the individual lives. Individuals which have not completed their first winter are referred to as juveniles; one-year-olds as yearlings, and all others as adults. Apart from this, social rank is the main attribute which tells the difference between territorial and subdominant. The next hierarchical level is the territory, which may be occupied by a social group of marmots and which contains one hibernaculum used by this group during winter. A territory is characterized by its identity number, the number and list of individuals present, and its quality. If the number of individuals is zero, the territory is referred to as "empty", i.e. space which has become vacant due to the extinction of a social group. Thus, territories may be recolonized just like empty patches in metapopulations. "Quality" is an attribute characterizing habitat heterogeneity with respect to the harshness of overwintering conditions, indicated by the date in spring when a territory becomes snow-free.

The next hierarchical level is the population composed of several territories or social groups, respectively. Populations are characterized by size, the number of social groups, and the number and list of territories. In addition, a "floater pool" keeps track of both all subdominants which have left their home territory and territorials which have been evicted. The spatial structure is taken into account by specifying the linkages to neighbouring territories. A neighbouring territory is defined as a territory within the above-mentioned distance of 500 m. The number of linkages may vary between zero and six (Fig. 1). Clusters of neighbouring territories compose a local metapopulation because all the attributes of a metapopulation are given (dynamics of social groups are only partly coupled to other social groups and local extinctions and recolonizations occur; see Reich and Grimm 1996, Hanski and Simberloff 1997). Several clusters or local metapopulations, respectively, make up the regional metapopulation of the Alpine marmot (Fig. 1). As distances between clusters are greater than 500 m, only dispersing subdominants will cross this distance. On this spatial scale beyond 500 m the model is not spatially explicit but the dispersers may reach any cluster of territories within the model area. This restricts the extent of the area that can be described by the model to several square kilometers.

The highest hierarchical level in the model is the abiotic environment and its fluctuations. Since the severity of winter, indicated by the date when territories become snow-free, is by far the most important aspect in the life of marmots, the abiotic environment in the model is characterized by this date. In general model analysis, the date when a territory becomes snow-free (referred to as "winter strength") is drawn from a normal distribution with a empirically determined mean and standard deviation (mean = 117 d of the year for territories in the main study area in Berchtesgaden, s = 10.2 d). This overall winter strength is modified by differences in overwintering conditions among territories. The indicator of differences in winter strength between territories is derived from the remaining variation in the date of becoming snow-free in the studied territories after subtracting the annual mean, i.e. from a normal distribution with a mean of zero and a standard deviation of 8.4 d. This means that territories which have a higher quality than the mean become snow-free a certain number of days earlier than specified by the overall winter strength, whereas territories of lower quality become snow-free later.

The model proceeds in annual time steps. Within each year or time step, seven modules or phases are processed in the following order: winter mortality, eviction, inheritance, dispersal, recolonization of vacant territorial positions, reproduction, and summer mortality. These seven modules are explained below.

Winter mortality

For each of the three classes of individuals, i.e. territorials, juveniles, and subdominants (including yearlings), the major determinants of winter mortality were identified by logistic regression (Table 2). Initially, the variables winter strength, number of juveniles, yearlings, or adults in the hibernating group were entered in the regression analysis and insignificant variables were removed step by step. When analyzing territorials, the factor "age" was considered in addition and in the case of juveniles the factor "weaning weight".

For territorials, winter mortality – interpreted as the probability of dying in a certain winter – is:

$$P_{ter} = [1 + \exp(6.82\text{-}0.286\ \ A - 0.028\ \ WS + 0.395\ \ SUBY)]^{-1} \quad (1)$$

where A is the age, WS winter strength, and $SUBY$ the number of subdominants (including yearlings) present in a group. Eq. (1) states that the winter mortality of dominants increases with the severity of overwintering conditions and with age, but decreases with the number of subdominants and yearlings.

Similarly, winter mortality for subdominants (including yearlings) is:

$$P_{sub} = [1 + \exp(7.545 - 0.038\ \ WS)]^{-1} \quad (2)$$

For juveniles, we found in addition a significant influence of weaning weight on winter mortality:

$$P_{new} = [1 + \exp(-1.014 - 0.024\ \ WS + 0.008\ \ WW + 0.613\ \ SUB)]^{-1} \quad (3)$$

with WW being the weaning weight (see below, Reproduction) and SUB the number of subdominants (excluding yearlings). Thus, the place where sociality comes into play in our model is in eq. (1) and (3) via the variable SUB.

Two additional model rules take into account further processes affecting mortality. Firstly, in groups without subdominants and yearlings, the territorial couple had a higher risk of mortality than specified by eq. (1). In nine out of fifty such groups, either one or both dominants died, which in six of these nine cases led to the extinction of the entire group. Therefore, we introduced the following probabilistic rule: In groups without yearlings and subdominants, whether the first territorial (which is chosen randomly) dies or survives is determined according to the mortality specified in eq. (1). If it dies – and this is the additional rule – its partner has the increased probability of dying of $P' = 0.66$ (i.e. 6/9). If this partner dies as well, the newborns – if present – will also die in turn. However, this rule introduces an additional mortality of territorials which in total would be higher than the mortality specified in eq. (1) and would therefore no longer match the results from logistic regression. Therefore, should the first territorial not die, the mortality of the partner territorial has to be reduced relative to P_{ter} from eq. (1). This reduced mortality P'' can be determined from the following bookkeeping of probabilities of dying,

$$P_{ter} = P_{ter}P'(1 - P_{ter})P'' \quad (4)$$

which says that the probability of dying P_{ter} of a certain territorial in the original model (l.h.s. of eq. (4)) has – in the modified model – to be equal to the sum of two conditional probabilities: first, the territorial may die (P') in the case that the partner has died (P_{ter}), or second (second term on r.h.s.), the territorial may die (P'') in the case that the partner has survived ($(1 - P_{ter})$). From eq. (4), P'' can easily be calculated as

$$P'' = P_{ter}(1 - P')(1 - P_{ter}). \quad (5)$$

The analogous modification of the mortality of newborns, $P_{newborn}$, was not introduced because the effect on model results was negligible.

The second model modification concerning winter mortality introduces the probability P_C, which takes into account the extinction of entire social groups due to local catastrophes during winter. In the field study, where the hibernation of 256 groups was observed, one such event occurred in which a group consisting of five adults and one yearling died out. Since all these animals bore transmitters for telemetry, this catastrophe is well documented. The collapse of the hibernaculum seemed to be the cause of this extinction. In the model, we use a value of $P_C = 0.004$.

Finally, the winter mortality of floaters which failed to take over a new territory during the summer is rather high though poorly quantified (Arnold 1990a; Frey-Roos 1998). We assume a mortality of $P_{floatwinter} = 0.9$.

Eviction

Territorial positions may become vacant not only due to winter mortality but also because the territorial has been evicted by a subdominant group member or an intruder. About 60% of the take-overs of territorial positions are due to eviction (Arnold 1990a). However, there are no data concerning the preconditions for successful eviction. All we know is that during summer 15% of the territorials disappear. We therefore assume that territorials are evicted with a probability of $P_{EV} = 0.15$ and that all evicted animals enter the floater pool.

The following three modules of the model describe how territorial positions which became vacant due to winter mortality and eviction are reoccupied by subdominants or dispersers.

Inheritance

In about 22% of the territory take-overs, a subdominant marmot inherits the territorial position in its home territory (Frey-Roos 1998). In the model, the oldest subdominant animal has a probability of $P_{IN} = 0.22$ of taking the territorial position. If this animal fails or if there is no subdominant in the territory, the territorial position remains vacant.

Dispersal

Most of the subdominants willing to disperse leave their home territory in spring. The probability of leaving depends on age (Arnold 1993a) and is directly taken from Table 1. Dispersed animals are compiled in a list called the ''floater pool''. This list is used to handle the assignment of free territorial positions to floaters. Note that the floater pool contains both true floaters which disperse beyond 500 m and are subject to a dispersal mortality during summer, and animals which will take over a territorial position in the neighbourhood.

Recolonization

Apart from the inheritance of home territories, 53% of the territory takeovers ($n = 116$) were effected by marmots from the immediate neighbourhood and about 25% by animals which had previously dispersed and were thus exposed as floaters to an extra mortality risk (Frey-Roos 1998). About 30% of the floaters died during the summer (Frey-Roos 1998).

In the model, recolonization is implemented by the following suite of rules. The first rule decides with a probability of $R_N = 0.5$ whether a vacant territorial position is reoccupied by a marmot that comes from a neighbouring territory. If this is the case, the floater pool is searched (in a random order) for such an animal, and if no animal is found the territorial position remains vacant. After repeating this procedure for each vacant territorial position, the remaining animals in the floater pool are treated as true floaters and have a dispersal mortality of $P_D = 0.3$, i.e. about 30% of the remaining floaters die before the next model rules are applied.

The next rule is analogous to the first rule, but this time only the floaters that do not come from the neighbourhood are allowed to occupy the available territorial positions. The probability R_F that one of these animals takes over a certain vacant territorial position is 0.5. This value is a compromise between the 25% mentioned in the paragraph above and telemetric data in which 13 out of 22 marked floaters became dominant at a distance beyond 500 m, indicating a recolonization probability greater than 0.25.

Finally, the last rule of this module checks territories where the territorial positions are still unoccupied for the presence of sexually mature animals. If this is the case the oldest subdominant animal moves into the territorial position.

Reproduction

Only when a territorial male and female are present in a territory can reproduction take place. The probability of a territorial female having offspring is 0.64 (Hackländer and Arnold 1999). The mean litter size (L) is 3.3 and standard deviation is 1.43. The mean weaning weight (WW_{mean}) is 536 g (s = 126.3 g) but decreases with litter size. Therefore a regression model is used to assess a mean weaning weight depending on litter size L ($WW_{mean} = 680.23 - 35.24\ L$, $R^2 = 0.143$, $p < 0.001$). In the model, litter size and weaning weight are drawn from normal distributions (in the case of litter size, discretized and truncated to the interval [1,6]) with the means and standard deviations specified. The sex of offspring is determined by chance with a bias of 0.58 towards males. It was observed that reproduction was virtually absent if a change of the territorial male has occurred after the mating season of the current year (Hackländer and Arnold 1999). Interruption of gestation or infanticide caused by the new territorial male is very likely to be the reason for this. Most changes in territorial positions occur after the mating season, thus, the model features no reproduction if the holder of a male territorial position has changed during the current year.

Summer mortality

Summer mortality rates are only known from the field for juveniles and yearlings. Summer mortality of resident adults is low but hard to quantify because when an animal has disappeared from the study site it is usually uncertain whether this is because it has dispersed or because it has died. The summer mortality of adults is thus indirectly and implicitly taken into account in the probabilities of eviction and dispersal mortality. Newborns and yearlings die during summer with a probability of 0.11 and 0.07, respectively.

The full model

Table 3 gives an overview of the processes of the model, the related parameters and their default values. With the exception of the winter mortality of floaters, all parameters were derived from the data from the long-term field study. Fig. 2 shows the life history of the model marmot, i.e. the transitions between different ages and social stages. In the simulation program, both individuals and territories were processed in a random sequence in order to avoid peculiar effects due to synchronization (Ruxton and Saravia 1998). Computer-generated random numbers were used to take the numerous probabilities discussed so far into account (Burgman et al. 1993). The spatial configuration of the study population in Berchtesgaden was mimicked in the model (Fig. 1).

For each combination of parameters investigated, the mean time to extinction, T_m, was determined from the

Table 3. Overview of processes, parameters and default values of parameters of the model. If not otherwise specified, these default values are used.

Parameter	Value
Number of territories	22
Age of sexual maturity	2
Winter mortality:	
Mean of the winter strength distribution	117
Standard deviation of the winter strength distribution	10.2
Mean of the territory quality distribution	0
Standard deviation of territory quality distribution	8.4
Mean of the weaning date distribution	185.5
Standard deviation of the weaning date distribution	6.6
Winter mortality of floaters	0.9
Recolonization:	
Dispersal probability at age 2	0.2
Dispersal probability at age 3	0.7
Dispersal probability at age 4	0.5
Dispersal probability at age 5	1
Probability to inherit a vacant territorial position at home	0.2
Probability to occupy a vacant territorial position in the neighbourhood	0.3
Probability to occupy a vacant territorial position further away than 500m	0.5
Eviction:	
Eviction probability of territorial animal	0.15
Reproduction:	
Reproduction probability of a territorial female	0.64
Mean of the litter size distribution	3.3
Standard deviation of the litter size distribution	1.43
Sex ratio in a litter	0.58
Summer mortality:	
Summer survival of juveniles	0.9
Summer survival of yearlings	0.94

distribution of extinction times resulting from 1,000 runs lasting for 300 years at maximum using the "$\ln(1-P_0)-$plot" (Stelter et al. 1997). This plot is based on the general relationship

$$P_0(t) = 1 - c\,\exp(-t/T_m) \quad (6)$$

which holds for times t larger than a certain transient time which is usually very short (Wissel et al. 1994). C is the probability that a population reaches the so-called "established state", i.e. a state which is within the typical range of fluctuations of the population and which is characterized by the fact that the risk of extinction per year is constant ($=1/T_m$). $P_0(t)$ is the risk of extinction by time t.

We used an approximation of eq. (6) to assess the minimum habitat requirements for minimum viability: for small values of $P_0(t)$ and if simulations start with an established state (i.e. $C=1$), eq. (6) can be approximated by $P_0(t) = t/T_m$ (Wissel et al. 1994). This means that the minimum capacity K_{min} required for a maximum risk of extinction of 5% in 100 years can be

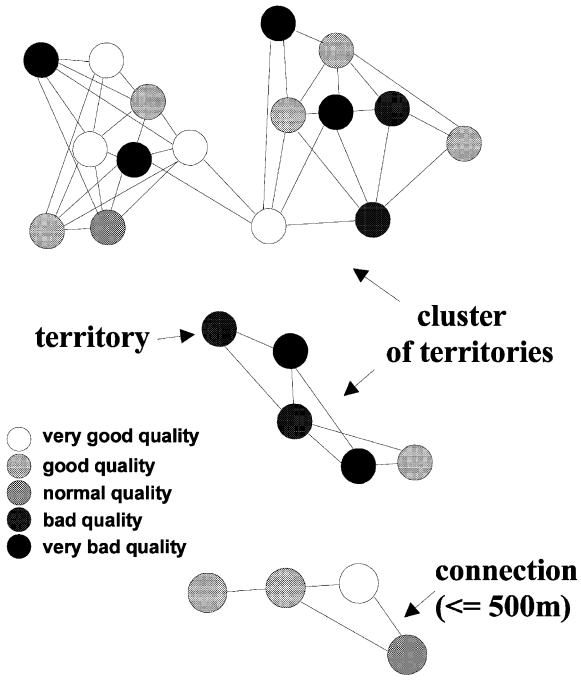

Fig. 1. Spatial arrangement of territories in the model. Territories which are closer than 500 m to each other are linked by lines, indicating the chance of subdominants recolonizing vacant territorial positions within this neighbourhood without undertaking long-distance dispersal. The different gray scales of the territories indicate different habitat qualities of the territories.

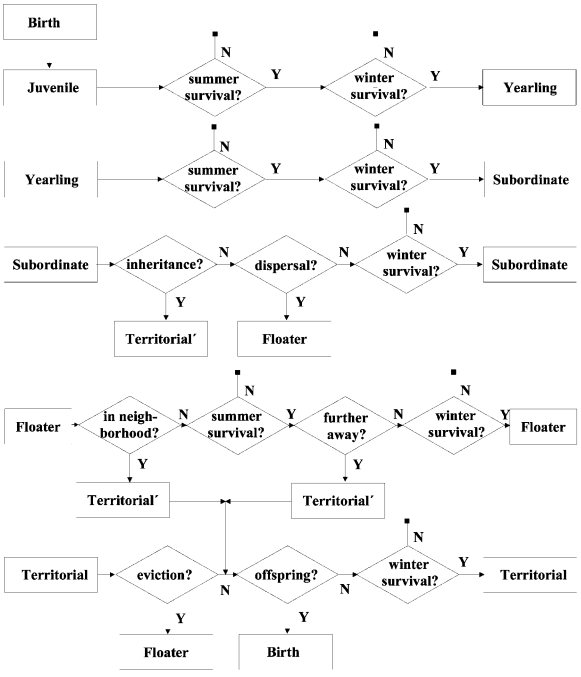

Fig. 2. Life history of the model marmot showing the transitions between different age and social classes, as well as the processes which cause these transitions.

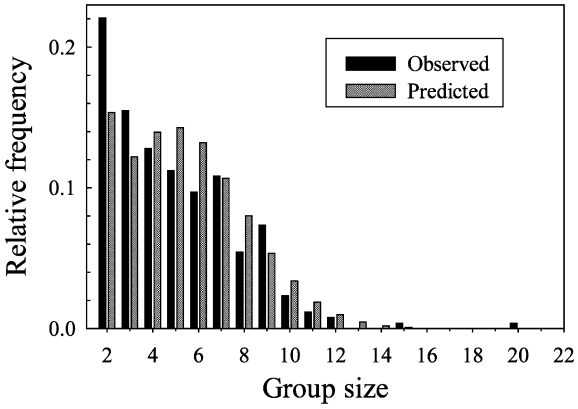

Fig. 3. Comparison of observed (black bars) and predicted (light gray bars) group size distributions. The predicted distribution was recorded during 500 simulations which were performed as described in the text.

inferred from a plot of T_m versus K: T_m must in this case be at least $t/T_m = 100/0.05 = 2000$ years.

Group sizes were counted at the beginning of hibernation when the animals gathered in the burrows.

The overall distribution of group sizes showed high resemblance between empirical an simulated data (Fig. 3). At a more detailed level, mean group sizes were compared. Three extreme cases appeared: for 1983 and 1991, where empirical mean group sizes were about the 1st percentile of the simulated distribution (due to the predominance of small groups and the lack of very big ones in empirical data) and for 1985, where it was about the 99th percentile (due to the appearance of a large group). For the remaining years, empirical mean group sizes were between the 4th and 83rd percentiles of the simulated distribution and no systematic bias was detected towards excessively large or small groups.

We conclude that observed and predicted group size distribution match quite well, which is important because the focus of our model is on social behavior and group living. The group size distribution is the integrated outcome of all the demographic and behavioural processes included in the model and therefore the model seems to capture the essence of these processes of the real population.

Results

Validation

To compare the the structure of the model population with the empirical data recorded at Berchtesgaden, the mean of 500 runs performed under the same, empirically recorded climatic regime of winter strengths was taken. However, the effects of unrealistic initial conditions had to be avoided. Therefore, the model was first run using a randomly chosen climatic regime until the population size was equal (i.e. 122) or close to (i.e. 121 or 123) the size of the real population in the first year of the field study. This state of the population was then used as the initial condition for one run lasting 14 years using the empirical time series of winter strength.

Persistence

To assess the influence of environmental conditions on the marmot population, both mean winter strength, equivalent to the severity of a winter, and the standard deviation of winter strength were varied and the mean time to extinction T_m was computed for various capacities K of the habitat, i.e. numbers of territories (Fig. 4). When changing territory numbers, territories were added to or removed from randomly selected clusters of territories (Fig. 1).

The harsher the environment, the weaker the increase in the mean time to extinction with habitat capacity K (Fig. 4A). For a mean winter strength of 107 d, the

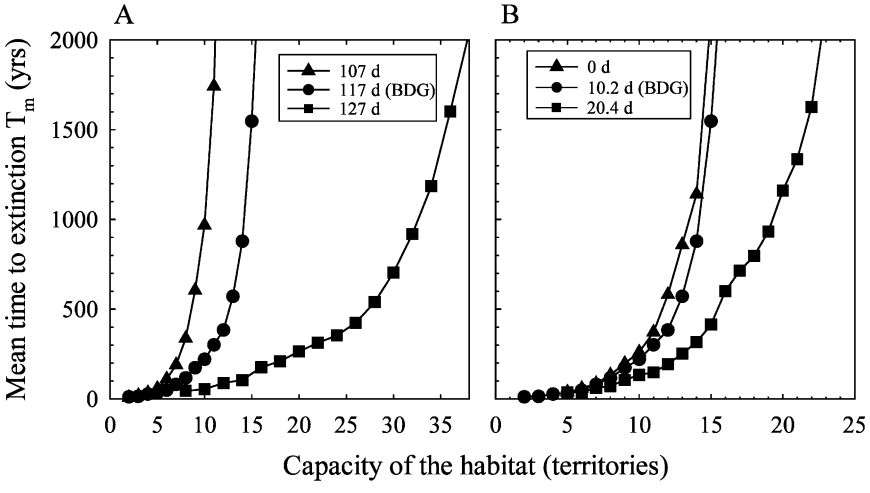

Fig. 4. Mean time to extinction, T_m, versus capacity of the habitat, K, i.e. number of available territories for different environments. (A) Constant standard deviation of winter strength (10.2 d) and varying mean winter strength (triangle: 107; circle: 117 d [Berchtesgaden]; square: 127 d). (B) Constant mean winter strength (117 d) and varying standard deviation of winter strength (triangle: 0 d; circle: 10.2 d [Berchtesgaden]; square: 20.4 d).

minimum capacity for viability, K_{min} (see definition above), is about 10 territories, whereas for 127 d it is about 35 territories. Since the severity of winter is correlated with the altitude of a habitat, this result of the model can be translated into the prediction that the higher up in the mountains a marmot population lives, the larger the minimum number of territories required for long-term persistence.

The effect of the changing strength of environmental noise, i.e. the standard deviation of winter strength, is shown in Fig. 4B. For a given winter strength, for example 117 d as in Berchtesgaden, T_m increases more slowly with K with increasing environmental noise. This effect of environmental noise is well-known from theoretical analyses (see Introduction and the literature cited therein) and would be even more pronounced in harsher environments. Again, the T_m-versus-K-plot shows that the Berchtesgaden population lives under almost optimal conditions because the environmental noise ($s = 10.2$ d) and its effect is so small that they are almost negligible. The plot also shows the strong influence of demographic stochasticity ($s = 0$) at even comparatively high population sizes. At $K = 15$ territories, the population averages around 85 animals but there is still a 5% risk of extinction merely due to demographic noise. This is considerably larger than predicted by traditional models in which the effect of demographic stochasticity is unimportant except at very small numbers (Boyce 1992, McCarthy et al. 1994, Kokko and Ebenhard 1996).

Sociality

To understand the effect of sociality on persistence, it would have been desirable to compare our model with a truly non-social version of the model. However, this is impossible because it would require us to parameterize an imaginary solitary alpine marmot. We can only try to find a conservative approximation to the truly non-social version. 'Conservative' means that the partly non-social version we test should yield higher persistence than the truly non-social version so that all claims we make about the effect of sociality on persistence would be even more pronounced in a truly non-social version.

A trivial approximation would be to realize that the fat reserves of juvenile marmots are by no means sufficient to survive winters solitarily. This follows from telemetric observations of hibernations and from metabolic rates determined in the laboratory at different temperatures (Ruf and Arnold, unpubl.). Thus, a population of solitary alpine marmots could evidently not persist. Another approximation is to deactivate group living completely. This was done in a model scenario where all marmots leave their home territory when they mature (i.e. dispersal at age 2 is 1.0; all other parameters as specified in Table 3). In this scenario, for a capacity of the system of 16 territories, the mean time to extinction is 213 yrs compared to 2638 yrs with the default parameter set.

In the following, we study in more detail a third approximation between the extremes of the first two approximations: we analyse four model variants which differ in the degree of "sociality" which comes into play in eq. (1) and (3): (1) only related subdominants have an effect; (2) only adults (related and unrelated) have an effect, i.e. yearlings have no effect; (3) no social effect for territorials at all ($SUBY = 0$ in eq. (1)); (4) neither a social effect for territorials nor a social effect for newborns ($SUB = 0$ in eq. (3)). In the first two variants, "effect" means that only the specified class of individuals is taken into account in the variable SUB and $SUBY$, respectively, in eq. (1) and (2).

One could argue that these model variants do not address the effect of sociality on persistence per se, but only indirectly via the effect of sociality on individual survival. However, sociality cannot exert a 'direct' effect on persistence, only on individual demographic rates. Birth and death rates are the 'interface' between individual behavior and population level properties as persistence, they are the 'currency' which converts individual behavior to population level properties (a point strongly made by Fahse et al. 1998).

Social behavior (as specified in our third approximation) has a strong positive effect on the persistence of the marmot population (Fig. 5). The difference of the T_m-versus-K-plot between the full model and the variant (3) and (4) without social effect is the same as the

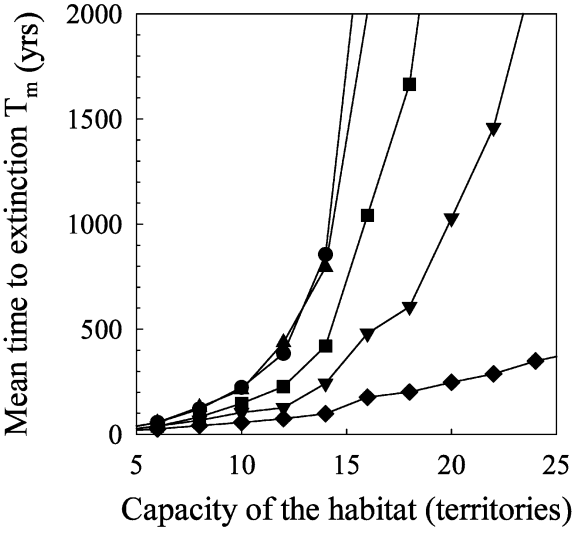

Fig. 5. Mean time to extinction, T_m, versus capacity of the habitat, K, i.e. number of available territories for different degrees of sociality (circles: full model; triangles: only related subdominants have an effect; squares: only adult subdominants have an effect; triangle upside down: no social effect for territorials; diamonds: no social effect at all). Mean winter strength: 127 d. The differences between the curves are similar for a mean winter strength of 117 d but less marked.

difference between two environments of different harshness would be. If only related subdominants are effective, persistence is almost as high as in the full model. This means that social groups indeed consist mainly of animals related to the territorial couple. The effect of social behavior is markedly smaller if only adults (related and unrelated) are effective. Since the difference between this case and the former one is that now unrelated adults are included, but related yearlings are excluded, it becomes clear that related yearlings considerably contribute to the social effect.

How does the strong effect of sociality on persistence emerge? Although a complicated, barely comprehensible synergistic mechanism could easily be assumed, the main mechanism is actually very simple: the sociality of marmots decreases the winter mortality of the territorial couple and has, as can be seen in eq. (1), an effect which is analogous to the effect of changing the environment to more favorable conditions. One additional subdominant in the hibernaculum can increase the winter survival of a territorial by sometimes more than 30%, and a second additional subdominant can even boost winter survival by more than 50%.

Moreover, sociality also buffers the range of environmental conditions as experienced by the territorials, i.e. the variance of winter mortality is much smaller with social effects than without (Fig. 6). What cannot be inferred from eq. (1) is the relative frequency of groups with one, two or more subdominants, because this distribution emerges from the interplay of the seven processes or modules of the model described above. Fig. 7 shows that both for the situation in Berchtesgaden and in harsher environments there are always more than 70% of the groups which have at least one helping, socially effective subdominant.

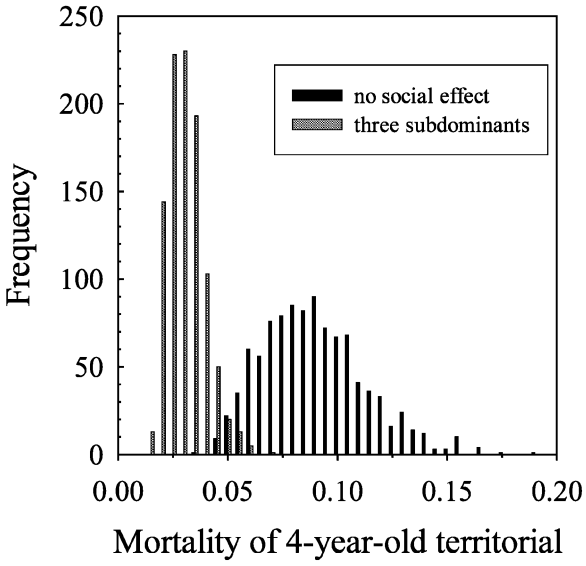

Fig. 6. Effect of sociality on variation in winter mortality of a four-year-old territorial for the case of no sociality at all (black bars) and for three socially effective subdominants (gray bars). The distributions are derived from a run over 100 years and are calculated using eq. (1) and a normally distributed winter strength (see model description and Table 3).

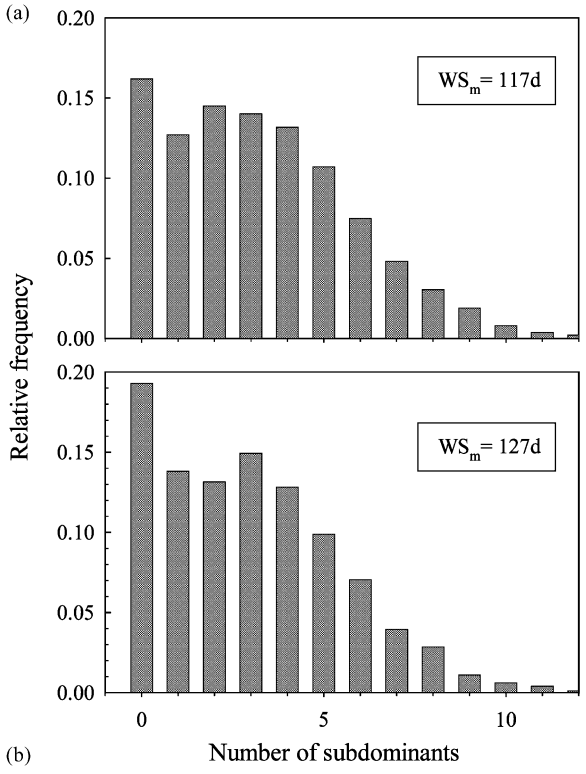

Fig. 7. Relative frequency of the number of subdominants in a social group of model marmots. (a) mean winter strength 117 d; (b) mean winter strength 127 d.

Discussion

We presented an individual-based model designed to reflect the essence of the population dynamics of the alpine marmot. Since persistence, i.e. the mean time to extinction, is the main currency used in our model analysis (Grimm et al. 1999), our investigation may be considered as a population viability analysis (PVA). In contrast to most PVA, our model is based on an exceptionally good database which results from a detailed long-term field study (but see Neuert et al. 1995, Letcher et al. 1998). The original purpose of this field study was not a PVA but to achieve a thorough analysis of the social behavior of the alpine marmot, insights into the costs and benefits of this behavior and, in turn, an understanding of the selective forces driving the evolution of social behavior in the alpine marmot (Arnold 1986, 1990a, b, 1993a, 1997, Frey-Roos 1998).

It seems likely that there are many other long-term field studies addressing behavioral issues which could

also provide unique databases for PVA. PVA of certain species usually address threatened populations for which databases are slim. Our study suggests that PVA could achieve many important insights if it mined the fascinating databases of behavioral ecology more frequently. Two different kinds of insights could be achieved from these PVAs. Firstly, models like that presented here represent "best-case-scenarios" of PVA because of their good database. They provide insights into the shortcomings of PVA which are based on much weaker databases. This is important because there is some concern about the risk of oversimplification in many PVA models dealing with species which are known to display complex behavior, for example social behavior (Harcourt 1996, Yahner and Mahan 1997, Beissinger and Westphal 1998, Caro 1998). Secondly, these database models provide insights into the previously obscure ambivalent relationship of social behavior and population persistence.

As to the first type of insights which may be gained from PVA of populations that have been thoroughly studied and therefore allow very detailed models, McCarthy et al. (1994) presented five different models for the helmeted honey-eater augmenting the degree of realism (sex structure, territoriality, limited reproduction, density-dependent survival). They found that with each additional aspect, the demographic uncertainty and in turn the risk of extinction increased. All these details can be found in our model too. A female needs a male, as well as a territory so that they can reproduce. Hence reproduction depends on the chance of both finding a mate and a vacant territory. Furthermore, reproduction is limited by the assumptions that the juveniles die when both parents die during hibernation and that reproduction can fail because of infanticide. Furthermore, the survival of a parent can depend on the survival of its partner. All these details and several others like, for example, the dispersal and recolonization of empty territories, are realized as chance events for single individuals which increase the effect of demographic uncertainty beyond the small numbers predicted as being relevant by simplified models. Therefore the predictive power of PVA models can be substantially obscured by ignorance of demographic details of endangered species, and users must be warned of the shortcomings of PVA models which lack realism (McCarthy et al. 1994).

As to the second type of insights, apart from the various aspects of individual behavior, we also addressed here the question of how social behavior affects population persistence in the alpine marmot and, if possible, in general. We know of only one model addressing a similar question: a PVA of a small population (< 50 individuals) of gray wolves on the Isle Royal in Lake Superior. Depending on the amount of resources (old moose) and, in turn, population size, the wolf population is divided into varying numbers of packs (1 to 5 packs) which, like the marmots, have only one reproductive couple (Vucetich et al. 1997). In this study, it is argued that social structure inflates the importance of demographic stochasticity. The reasoning behind this is that demographic noise is known to increase as the number of reproductive units decreases. Since, for example, "a larger wolf population (e.g. 45 in 1976) divided into a few packs (three) has the same reproductive potential (one litter per pack per year) as a smaller wolf population (e.g. 14 in 1982) divided into the same number of packs" (Vucetich et al. 1997), it is argued that the social structure constrains the number of reproductive units and, in turn, the mean time to extinction. Vucetich et al. conclude that, "populations that are characterized by reproductive suppression and comprise a moderate number of individuals, and thus a small number of social groups, will suffer significant extinction risk due to demographic stochasticity alone".

In the light of our own model about the alpine marmot, we agree to a certain extent with this conclusion. We doubt, however, whether this conclusion always holds and if it really does reflect the entire relationship between social behavior (linked to reproductive suppression) and population persistence. One could even argue that the conclusion of Vucetich et al. (1997) neglects the well-known importance of kin-selection in the evolution of complex animal societies with reproductive suppression. It seems unlikely that social systems exist without any, albeit small, reproductive benefits for subdominants in terms of enhanced frequencies of at least some proportion of their genes (Cockburn 1991). If this is so, some social or helping effect of subdominants on reproduction ought in general to be expected. This will then increase offspring survival or, as in the case of marmots, the survival of the reproducing couple. Consequently, the social or helping effect increases population growth rate.

Our model shows that there are at least three mechanisms of how the social behavior increases population persistence in alpine marmots. Firstly, increasing the growth rate decreases the strength of environmental noise. The term "environmental noise" is extremely misleading because it is not the fluctuation of the environment per se which is relevant for persistence, but the fluctuations of the population growth rate, i.e. the fluctuations as perceived by the population. A measure of the strength of environmental noise is the ratio of the variance of population growth rate and the intrinsic rate of increase (Wissel et al. 1994). A higher intrinsic rate of increase thus lowers the strength of the environmental noise. The marmot model allows these phenomenological considerations to be translated into real mechanisms: winter strength is the crucial aspect of the marmot environment, and this aspect varies considerably from year to year. Sub-

dominants increase the survival of the reproducing couple and their offspring and thereby increase the growth rate. Consequently, the population will recover much faster from small sizes which may occasionally result due to bad environmental conditions (Wiegand et al. 1998).

The effect of increasing population growth rate on the T_m-versus-K-plot is the same as if strong environmental fluctuations are buffered so effectively that they can almost be neglected. This is significant for endangered populations with social behavior, because it means that for such species an increase in habitat (or reserve) size would substantially reduce the risk of extinction (see Introduction). This buffer effect of sociality demonstrated with the marmot model may play a siminlar role in the persistence of other species with social structure and reproductive suppression.

The second mechanism of how sociality may increase persistence comprises the increase in survival of the reproductive couple being combined with a decrease in variation in the survival rate (Fig. 6) with consequences analogous to those of decreased winter mortality. And thirdly, the social and spatial structure of the marmot population provides mechanisms to quickly fill in territorial positions which have become vacant due to winter mortality. Thus, although the number of reproductive units is reduced if compared to a hypothetical scenario where all fertile animals reproduced, the complete failure of a reproductive unit is usually prevented in contrast to the non-social scenario. Sociality introduces a reliability at the level of reproductive units (Pulliam 1988, Kokko and Sutherland 1998) which should by far counteract the apparent increase in the importance of demographic noise. In fact, Vucetich et al. (1997) also have these mechanisms in their model: if a wolf pack becomes extinct, a new pack is immediately constructed by the youngest male from the pack with the most males and the youngest female from the pack with the most females.

From a management point of view, the ambivalent effects of social behavior on the persistence of a population have the following consequences. PVA models for endangered species ignoring complex social structures should not be relied upon without careful tests and thorough evaluation. Management decisions should be examined to see whether they have a negative affect on the social behavior of a species. Inadequate hunting, for example, might not affect the occupancy of the territories and thus the number of reproductive units but might change the size of social groups and the number of dispersers and therefore increase the risk of extinction.

Acknowledgements – We thank Eloy Revilla for valuable comments on an earlier draft, along with Flurin Filli for providing us with relevant literature and information.

References

Arnold, W. 1986. Ökosoziologie des Alpenmurmeltieres (Marmota marmota, Linné 1758). – PhD thesis, Ludwig-Maximilian-Univ. of Munich.
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. 1993a. Social evolution in marmots and the adaptive value of joint hibernation. – Verh. Deutsch. Zool. Ges. 86: 79–93.
Arnold, W. 1993b. Energetics of social hibernation. – In: Carey, C., Florant, G. L., Wunder, B. A. and Horwitz, B. (eds), Life in the cold. Westview Press, pp. 65–80.
Arnold, W. 1997. Verzögerte Abwanderung und soziales Leben bei Murmeltieren: Strategien des Überlebens im alpinen Lebensraum. – In: Frank, D. (ed.), Verhaltensbiologie. Thieme, pp. 156–160.
Arnold, W. and Dittami, J. 1997. Reproductive suppression in male alpine marmots. – Anim. Behav. 53: 53–66.
Arnold, W., Klinkicht, M., Raßmann, K. and Tautz, D. 1993. Molecular analysis of the mating system of alpine marmots (*Marmota marmota*). – Verh. Deutsch. Zool. Ges. 86: 79.
Beissinger, S. R. and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. – J. Wildl. Manag. 62: 821–841.
Blumstein, D. T. and Armitage, K. B. 1999. Cooperative breeding in marmots. – Oikos 84: 369–382.
Boyce, M. S. 1992. Populaton viability analysis. – Annu. Rev. Ecol. Syst. 23: 481–506.
Burgman, M. A., Ferson, S. and Akçakaya, H. R. 1993. Risk assessment in conservation biology. – Chapman and Hall.
Caro, T. (ed.) 1998. Behavioral ecology and conservation biology. – Oxford Univ. Press.
Cockburn, A. 1991. An introduction to evolutionary ecology. – Blackwell Scientific Publishers.
Courchamp, F., Grenfell, B. and Clutton-Brock, R. 1999. Population dynamics of obligate cooperators. – Proc. R. Soc. Lond. B 266: 557–563.
DeAngelis, D. L. and Gross, L. J. (eds) 1992. Individual-based models and approaches in ecology. – Chapman and Hall.
Dorndorf, N. 1999. Zur Populationsdynamik des Alpenmurmeltieres: Modellierung, Gefährdungsanalyse und Bedeutung des Sozialverhaltens für die Überlebensfähigkeit. – PhD thesis, Philipps-University, Marburg.
Fahse, L., Wissel, C. and Grimm, V. 1998. Reconciling classical and individual-based approaches of theoretical population ecology: a protocol to extract population parameters from individual-based models. – Am. Nat. 152: 838–852.
Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. – Conserv. Biol. 8: 124–137.
Frey-Roos, F. 1998. Geschlechtsspezifisches Abwanderungsmuster beim Alpenmurmeltier (Marmota marmota). – PhD thesis, Philipps-University Marburg, Germany.
Goel, N. S. and Richter-Dyn, N. 1974. Stochastic models in biology. – Academic Press.
Goodman, D. 1987. How do any species persist? Lessons for conservation biology. – Conserv. Biol. 1: 59–62.
Grimm, V. 1999. Ten years of individual-based modelling in ecology: what have we learned, and what could we learn in the future? – Ecol. Model. 115: 129–148.
Grimm, V., Wyszomirski, T., Aikman, D. and Uchmanski, J. 1999. Individual-based modelling and ecological theory: synthesis of a workshop. – Ecol. Model. 115: 75–282.
Hackländer, K. and Arnold, W. 1999. Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). – Behav. Ecol. 10: 592–597.
Hanski, I. and Simberloff, D. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. – In: Hanski, I. and Gilpin, M. E. (eds),

Metapopulation biology: ecology, genetics, and evolution. Academic Press, pp. 5–26.
Harcourt, A. H. 1996. Is the gorilla a threatened species? How should we judge? – Biol. Conserv. 75: 165–176.
Huston, M., DeAngelis, D. and Post, W. 1988. New computer models unify ecological theory. – BioScience 38: 682–691.
Kokko, H. and Ebenhard, T. 1996. Measuring the strength of demographic stochasticity. – J. Theor. Biol. 183: 169–178.
Kokko, H. and Sutherland, W. J. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. – Am. Nat. 152: 354–366.
Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. – Am. Nat. 142: 911–927.
Leigh, E. G., Jr. 1981. The average lifetime of a population in a varying environment. – J. Theor. Biol. 90: 213–239.
Letcher, B. H., Priddy, J. A., Walters, J. R. and Crowder, L. B. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. – Biol. Conserv. 86: 1–14.
May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press.
McCarthy, M. A., Franklin, D. C. and Burgman, M. A. 1994. The importance of demographic uncertainty: an example from the helmeted honeyeater *Lichonostomus melanops cassidix*. – Biol. Conserv. 67: 135–142.
Neuert, C., Du Plessis, M. A., Grimm, V. and Wissel, C. 1995. Welche ökologischen Faktoren bestimmen die Gruppengröße bei *Phoeniculus purpureus* (Gemeiner Baumhopf) in Südafrika? Ein individuenbasiertes Modell. – Verh. Ges. Ökol. 24: 145–149.
Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.
Reich, M. and Grimm, V. 1996. Das Metapopulationskonzept in Ökologie und Naturschutz: Eine kritische Bestandsaufnahme. – Z. Ökol. Natursch. 5: 123–139.
Renshaw, E. 1991. Modelling biological populations in space and time. – Cambridge Univ. Press.
Ruxton, G. D. and Saravia, L. A. 1998. The need for biological realism in the updating of cellular automata models. – Ecol. Model. 107: 105–112.
Stelter, C., Reich, M., Grimm, V. and Wissel, C. 1997. Modelling persistence in dynamic landscapes: lesson from a metapopulation of the grasshopper *Bryodema tuberculata*. – J. Anim. Ecol. 66: 508–518.
Stephan, T. 1993. Stochastische Modelle zur Extinktion von Populationen. – PhD thesis, Philipps-University, Marburg.
Stephens, P. A., Frey-Roos, F., Arnold, W. and Sutherland, W. J. 2002. Model complexity and population persistence. The alpine marmot as a case study. – J. Anim. Ecol. 71: 343–361.
Uchmanski, J. and Grimm, V. 1996. Individual-based modelling in ecology: what makes the difference? – Trends Ecol. Evol 11: 437–441.
Vucetich, J. A., Peterson, R. O. and Waite, T. A. 1997. Effects of social structure and prey dynamics on extinction risk in gray wolves. – Conserv. Biol. 11: 957–965.
Wiegand, T., Naves, J., Stephan, T. and Fernandez, A. 1998. Assessing the risk of extinction for the brown bear (*Ursus arctos*) in the Cordillera Cantabrica, Spain. – Ecol. Monogr. 68: 539–570.
Wissel, C. 1989. Theoretische Ökologie-Eine Einführung. – Springer-Verlag.
Wissel, C. and Stöcker, S. 1991. Extinction of populations by random influences. – Theor. Popul. Biol. 39: 315–328.
Wissel, C., Stephan, T. and Zaschke, S.-H. 1994. Modelling extinction and survival of small populations. – In: Remmert, H. (ed.), Minimum animal populations. Springer-Verlag, pp. 67–103.
Yahner, R. H. and Mahan, C. G. 1997. Behavioral considerations in fragmented landscapes. – Conserv. Biol. 11: 569–570.