

Model complexity and population predictions. The alpine marmot as a case study

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Summary

1. During the past 15 years, models have been used increasingly in predictive population ecology. Matrix models used for predicting the fates of populations are often extremely basic, ignoring density dependence, spatial scale and behaviour, and often based on one sex only. We tested the importance of some of these omissions for model realism, by comparing the performance of a variety of population models of varying levels of complexity.

2. Detailed data from more than 13 years of behavioural and demographic research on a population of alpine marmots *Marmota marmota* in Berchtesgaden National Park, southern Germany, were used to parameterize four different population models. The models ranged from a simple population-based matrix model, to a spatially explicit behaviour-based model.

3. The performance of the models was judged by their ability to predict basic population dynamics under equilibrium conditions. Only a spatially explicit individual-based model ignoring optimal behaviour predicted dynamics significantly different to those observed in the field, highlighting the importance of considering realistic patterns of behaviour in spatially explicit models.

4. Using realistic levels of environmental and demographic stochasticity, variance in population growth rates predicted by all models was high, even within the range of population densities experienced in the field. This emphasizes the difficulty of using population-level field data to determine overall patterns of density dependence for use in population models.

5. All models were also used to predict potential density-dependent effects on alpine marmot population growth. In this regard, the models differed greatly. It was concluded that the simplest matrix model was adequate for making predictions regarding population sizes or densities under equilibrium conditions, but that for predictions requiring an understanding of transient dynamics only the behavioural model would be adequate.

6. An emergent feature of this study of alpine marmot population dynamics was the prediction of a demographic Allee effect with a profound influence on population dynamics across a very broad range of population sizes. Three mechanisms were identified as underlying this Allee effect: stochastic skews in sex ratio and demographic composition at low population sizes; less efficient social thermoregulation during hibernation in small groups; and difficulties with mate finding during dispersal, even at relatively high population sizes.

Key-words: Allee effects, behaviour-based models, density dependence, individual-based models, matrix models

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Introduction

The need for models to address questions within ecological uncertainty is increasingly apparent (Sutherland & Watkinson 2001). In recent decades, much attention has been paid to models predicting the fates of single populations, either under current conditions or following changes in management or environment. In particular, such models are widely used for population viability analyses (Soulé 1987; Boyce 1992) and to evaluate the likely effects of different management options (Taylor *et al.* 1987; Smith & Trout 1994; Shea & Kelly 1998). Whilst ecological models can aim for either generality or realism and precision, a key feature of predictive population models must be to maximize realism.

Predictive population models are usually based on matrix models (Caswell 2001), in which individuals in a population are classified into different states, usually on the basis of age, stage or a combination of these. Probabilities of reproducing whilst in a given state, or of changing from the current to any other state, are fixed and applied equally to all members of the population in that state. Matrix modelling is a broad term, however, and models may vary from single-sex deterministic models, ignoring phenomena such as density dependence, to spatially structured two-sex stochastic simulations, incorporating detailed feedbacks between population size and survival or fecundity. The degree of sophistication is usually dependent on the quality of data available, and such data (particularly for species of conservation concern) are frequently sparse. This leads to considerable debate regarding the predictive value of matrix modelling, particularly when applied to population viability analysis (Hamilton & Moller 1995; Beissinger & Westphal 1998; Bierzychudek 1999; Brook *et al.* 2000; Coulson *et al.* 2001). In certain situations, however, analytical models may be as informative as more complex individually based and spatially explicit models, yielding virtually identical results (Pacala 1986; Matos, Freckleton & Watkinson 1999).

Of considerable importance for making predictions about novel scenarios, is an understanding of the density-dependent processes to which a population is subject (Boyce 1992; Coulson *et al.* 2001). To incorporate density dependence in matrix models, it is important to be able to parameterize accurate functions describing the density-dependent processes. Alternatively, when more is known of the behaviour of the species, density dependence may be an emergent feature of behaviour-based models (Sutherland 1996). Behavioural modelling has been used to make a wide variety of predictions about population-level processes. For example, for a range of bird species, foraging behaviour has been used to predict patterns of habitat use (Sutherland 1996; Ollason *et al.* 1997), while territorial behaviour has been used to predict cyclicity in grouse *Lagopus lagopus* population dynamics (Hendry *et al.* 1997). The crucial feature of behaviour-based modelling is that move-

ments, transitions or fecundities of individuals in a given state are not modelled according to predetermined probabilities but depend, instead, on some kind of optimization criterion. This criterion is often a simple proxy for fitness (so, for example, individuals behave in a way that maximizes their foraging intake rate, or minimizes their detrimental effects on close relatives) but may also be based on residual fitness, incorporating expected survival, reproductive success and indirect fitness. Residual fitness approaches have the intuitive appeal of simulating behaviours of evident evolutionary stability but may not differ greatly from more obvious and tractable proxies (Ollason & Yearsley 2001). Given that they are based on the solid grounding of natural selection, behaviour-based models are likely to produce patterns of individual behaviour (and therefore patterns of population behaviour) of far greater realism than patterns predicted by simpler population models that lack such a grounding. They can be hard to construct and parameterize, however, and may be thought of as unnecessarily complex for dealing with population-level issues.

In this study, we took advantage of detailed data available from more than 13 years of intensive field research on alpine marmots *Marmota marmota* (L.) (Arnold 1988, 1990a,b, 1995; Arnold & Dittami 1997; Frey-Roos 1998; Hackländer & Arnold 1999) to construct population models of varying levels of complexity. We tested four models (Table 1), each parameterized using field data from the marmot study: 1, a semi-annual population-based matrix model, incorporating environmental stochasticity and density-dependent regulation of fecundity; 2, a development of model 1, in which the population was subdivided into social groups and group-level density dependence was incorporated; 3, a temporally and spatially explicit individual-based model, in which individual fates were based on empirical data; and 4, a behaviour-based version of model 3, in which individual fates were based on residual fitness optimization, rather than on empirically determined probabilities. The models were compared, particularly with respect to their predictions regarding the effect of density dependence on population growth, and three main questions addressed. First, how does density dependence affect the growth of alpine marmot populations and what mechanisms underlie this? Second, regarding the alpine marmot, what predictions of the different models can be treated with confidence? Third, what are the broader implications of this study for predictive ecology?

Background and methods

STUDY SPECIES

Alpine marmots are large, diurnal, burrow-dwelling rodents, found throughout much of the mountainous regions of west and central Europe. They are one of the

Table 1. Summary of model properties

Model	Description	Environmentally stochastic	Demographically stochastic	Density-dependent availability of breeding sites	Group-based density-dependent winter survival	Spatially explicit	Behaviourally based
1	Population-based matrix model	✓	✓	✓	✗	✗	✗
2	Group-based matrix model	✓	✓	✓	✓	✗	✗
3	Individual-based model	✓	✓	✓	✓	✓	✗
4	Behaviour-based model	✓	✓	✓	✓	✓	✓

Table 2. Stage classes of alpine marmots as used in both the field study and the simulation model

Stage class	Age		Description
	Minimum	Maximum	
1	0	10 months	Juveniles, yet to emerge from their first winter
2	11 months	22 months	Yearlings, have survived one winter
3	23 months	34 months	Two-year-olds, have survived two winters, are reproductively mature but have yet to reach full size
4	35 months	12 years	All adults that have survived at least three winters but remain subordinate to the current same-sex dominant in their territory
5	35 months	12 years	Adults dominant within a territory
6	23 months	12 years	Floater, or dispersed adults of any age that have not secured dominance in a territory. These animals live in very poor habitat and are subject to high mortality

most social species of sciurid, living in social groups of up to 20 individuals (Arnold 1990a). Groups are typically composed of a dominant pair and their offspring from 1 or more years, and occupy a territory, defended against same-sex intruders by the dominant male and female (Arnold 1990a). Within their social groups, marmots hibernate communally over winter (Arnold 1990b). Females are receptive for just 1 day within the first 2 weeks after emergence from hibernation and give birth after a gestation period of 34 days (Hackländer & Arnold 1999). Litters are produced on approximately 64% of territories with a dominant female and at least one adult male but, due to male-caused reproductive failure, survive to emergence in only 50% of such territories (Hackländer & Arnold 1999). Juveniles are weaned by approximately 40 days after birth and emerge above ground to live herbivorously like adults within days of weaning. Alpine marmots can reach sexual maturity at 2 years old but rarely reproduce before their third hibernation. Only the dominant female breeds successfully (Hackländer & Arnold 1999), at most once per year. Reproductive suppression in males is less pronounced, particularly when subordinates are closely related to the dominant male (Arnold & Dittami 1997). Subordinate animals of both sexes may inherit their natal territory or disperse to find a territorial vacancy, evict a same-sex dominant from another territory or become a floater (Arnold 1990a,b; Frey-Roos 1998). During the field study, no dominant individuals ever dispersed, except following eviction by another animal. Dispersing subordinates joined established groups or territories only as dominant animals. Floaters do not have a well-defined home range, live solitarily and occupy suboptimal habitat (lacking bur-

rows and escape holes, and often covered by tall vegetation); consequently, floaters suffer high mortality costs from predation, poor-quality hibernacula and the lack of social thermoregulation in the winter (Arnold 1990a,b; Frey-Roos 1998). Dispersal occurs throughout the active period but peaks about 4–5 weeks after emergence. Over the entire study period, annual survival of philopatric (non-dispersing) adults was: dominant males, 0.90 ($n = 108$ marmot years); subordinate males, 0.98 ($n = 164$); dominant females, 0.92 ($n = 114$); subordinate females, 0.97 ($n = 78$).

FIELD METHODS AND DATA ANALYSIS

A population of alpine marmots was studied from 1982 to 1996 in Berchtesgaden National Park, south-east Germany. The study covered the area illustrated in Fig. 1 but focused on 21 territories between elevations of 1100 and 1500 m a.s.l., populated by approximately 80–120 individuals annually. Each year, about 95% of the focal population was trapped during the active period, most of them twice. Trapped animals were tattooed for individual identification at first capture and weighed at each capture. Age determination by body mass was possible until the beginning of the third active period, during which the animals reached adult size. Animals were classified into six stage classes, summarized in Table 2. Intensive observation during the last days prior to the onset of hibernation revealed the composition of the resident population. A similar period of intensive observation at the time of emergence revealed which individuals failed to emerge from hibernation and these animals were deemed to have died during the winter. Disappearances of animals during the active

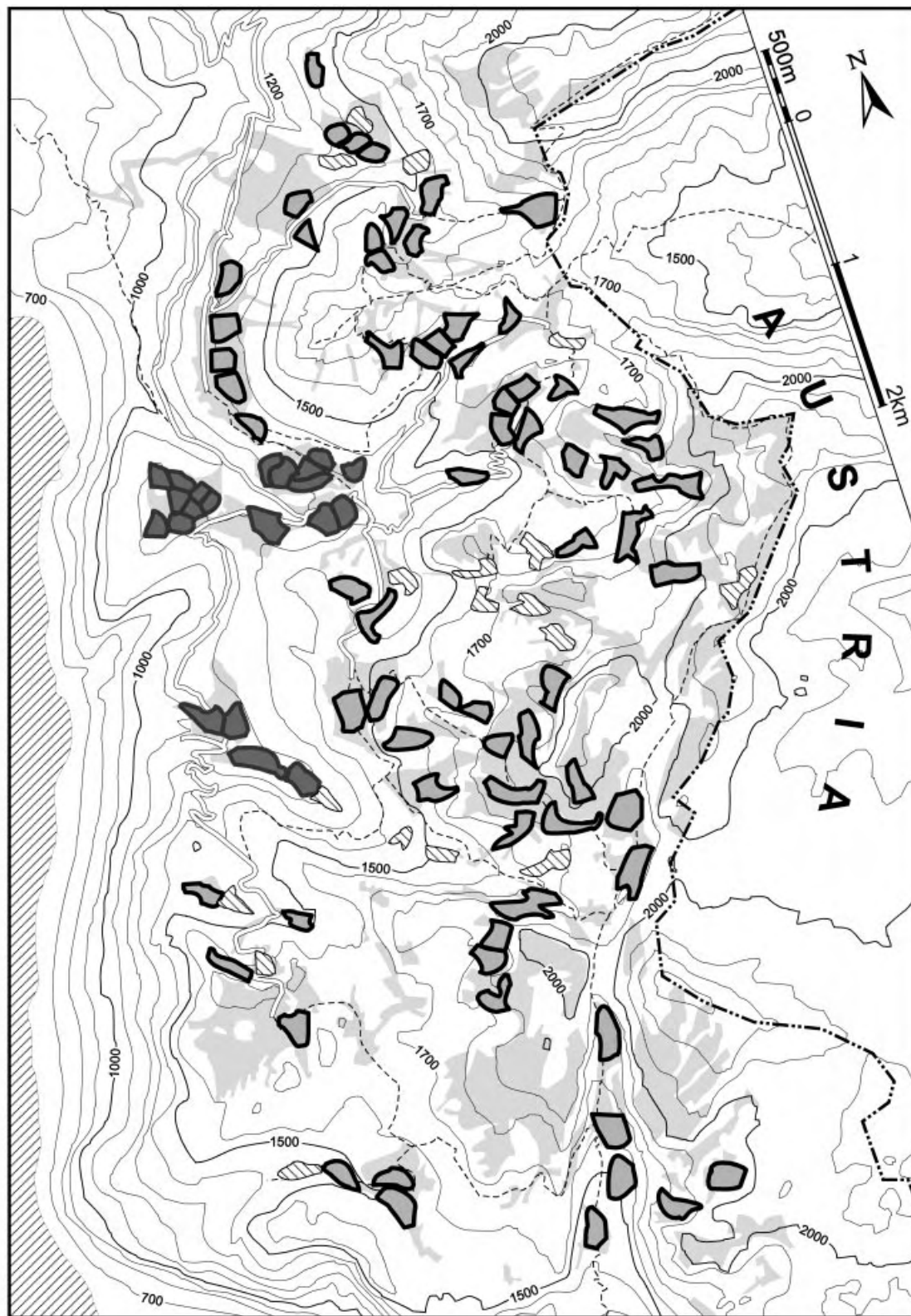


Fig. 1. A map of the study area showing the arrangement and usage of territories from 1993 to 1996. Territories are indicated by black polygons, either used (filled) or abandoned (hatched). Territories of the focal study area are dark filled. Intermediate grey shading indicates areas of optimal short-grass pasture habitat. The hatched area to the west indicates the location of a montane lake. Altitudinal isoclines are indicated by lines intersected with number of metres a.s.l.

period were due to dispersal or mortality. No juveniles or yearlings were ever observed to disperse or trapped as floaters. All disappearances of these animals during the active period were attributed to predation, largely

by red foxes *Vulpes vulpes* (L.). Disappearances of older animals were attributed to predation only with direct evidence. Radio-transmitters were fitted to 89 individuals (including 12 juveniles) and the dispersal

Table 3. Model parameters measured for the Berchtesgaden population 1982–96

Parameter	Description	Value ($\pm$ SD)
T	Total number of territories (Fig. 1)	109
pR	Probability of reproduction when a territorial female and adult male are present on a territory (Hackländer & Arnold 1999)	0.64
$\bar{L}$	Mean litter size ($n = 126$)	3.47 ± 1.47
μ	Primary sex ratio (males/females)*	1.38
M_m	Weaning mass of males ($n = 183$), $e^{(-0.6228 \pm 0.125SD)}$ (kg)	0.54 ± 0.18
M_f	Weaning mass of females ($n = 145$), $e^{(-0.6792 \pm 0.125SD)}$ (kg)	0.51 ± 0.17
l_{xs}	Summer survival of individuals of class: 1	0.8816
	2	0.9191
	3,4	0.9911
	5	0.9933
l_{f1}	Survival of long-distance dispersers immediately after leaving the natal neighbourhood†	0.90
l_{f2}	Survival of long-distance dispersers after travelling through three distant neighbourhoods†	0.76
A_{max}	Maximum age of a marmot (years)‡	12
$\bar{W}$	Mean winter length (days)§	113.90 ± 9.0
l_{6w}	Winter survival of a floater ($n = 7$)	0.56
l_{6ew}	Winter survival of an evicted territorial¶	0.01

*Represents the sex ratio of all litters (437 juveniles in total) at first emergence.

†Summer survival of known long-distance dispersers was 68% (15 of 22). Twenty animals (*c.* 90%) survived the dangers of predation immediately on departing the natal neighbourhood, and the remainder of mortality occurred after the animals had travelled a substantial distance, traversing an average of around three neighbourhoods.

‡During the entire field study, the oldest age-known individuals were 12 ($n = 3$) or 13 ($n = 1$).

§Winter length was measured as the average number of days from the beginning of the year until the territory was 75% free of snow cover. Mean is for 256 territory years.

¶Winter survival of evicted territorials was known to be very low. In addition, none of 33 known evicted territorials re-acquired territorial status (Arnold 1990a) and, hence, these animals are unlikely to make further contributions to the population. The low winter survival of these animals in the simulation models reflected this.

behaviour of these animals was monitored by telemetry. During the spring thaw, all marmot territories were photographed at least every second day. These pictures were used to determine the date by which 75% of the territory was free of snow, coinciding with the approximate onset of vegetation growth. This was deemed to be the date of termination of snow cover. More detailed descriptions of the study area and field methods are given elsewhere (Arnold 1990a,b, 1993; Arnold & Dittami 1997; Frey-Roos 1998).

Analyses of the field data were used to parameterize the simulation models (below and Table 3). Mean summer mortalities were calculated for each stage class based on all mortalities from the active period. Binary logistic regressions of the fates during hibernation, of individuals of known age and body mass, in groups of known composition, were used to estimate winter mortality functions from the field data. Litter size distributions were determined from 126 litters observed at emergence after weaning. Body masses of all juveniles weighed within 11 days following emergence were used to produce weaning mass distributions for male and female juveniles. Data on 483 subordinate animals were used to characterize dispersal behaviours, and to provide validation for the behavioural model output.

MODEL METHODS

All models were closely based around the life history and characteristics of the Berchtesgaden study popu-

lation. Table 3 summarizes the parameters calculated from field data that were incorporated in the model. All models were two-sex and stage based, with individuals assigned to one of six stage classes, according to age and status (Table 2). Each model included environmental stochasticity, represented by the severity of winter conditions (a critical determinant of winter mortality); winter length was drawn from a normal distribution (Table 3). The models were also demographically stochastic. Litter size was drawn from a normal distribution and sex of young was assigned according to the sex ratio at weaning (Table 3). The field study provided no evidence for density-dependent mortality due to food limitation. However, density-dependent restrictions on fecundity arose from restrictions on the number of available territories. During the field study, 91 territories were regularly available for occupancy by a breeding group, and in the models no more than 91 litters could thus be produced in any 1 year. There was no evidence of density dependence in summer survival and probabilities for each class were taken directly from the field study (Table 3). Winter mortality and other aspects unique to each model are described in more detail below. Due to historical bottlenecks, the marmots of Berchtesgaden show limited heterozygosity (Rassmann, Arnold & Tautz 1994) but no evidence of either inbreeding avoidance behaviours or deleterious effects of inbreeding (Bruns & Arnold 1999). Consequently, genetic concerns were not incorporated into any of the models. The principal properties of all

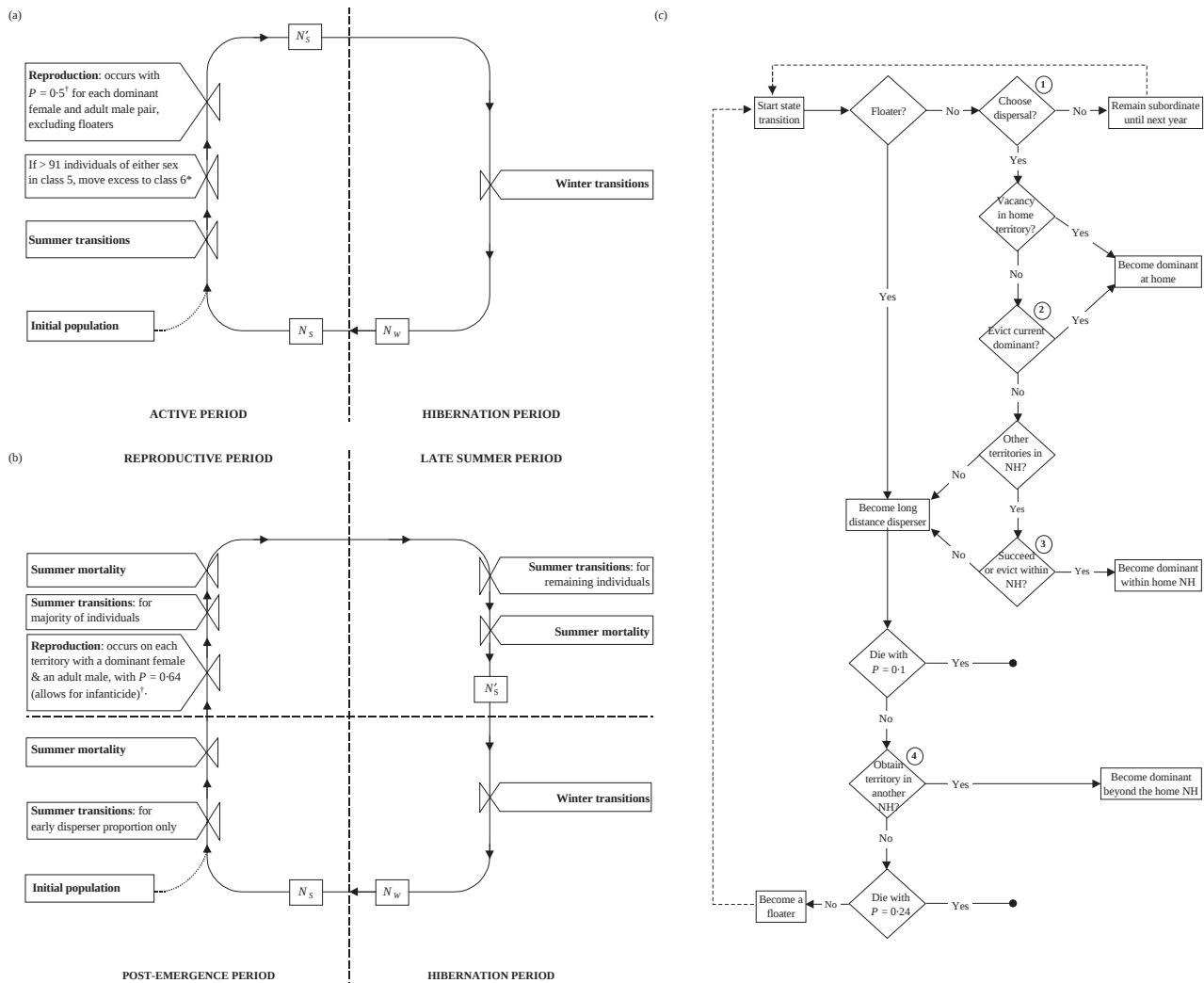


Fig. 2. (a, b) Generalized Forrester diagrams for the population simulations. Forrester diagrams are valid for (a) models 1 and 2, divided into only two periods, and (b) models 3 and 4, divided into four periods. N_S = population at the start of the active period; N'_S = population at the end of the active period; N_W = population at the end of winter. See text for further details. (c) Schematic flow diagram for the dispersal process in model 4. NH = neighbourhood. See text for further details regarding steps labelled 1–4. *This step applies to model 1 only. When moving excess individuals from class 5 to class 6, older animals were moved first in order to replicate the turnover of dominants produced by eviction of older residents by younger subordinates in the natural population. †The lower probability of reproduction in (a) than (b) allows for the fact that, although reproduction occurs on 0.64 of territories with an adult pair, due to male-caused reproductive failure, reproduction is successful in only 0.5 of such territories (Hackländer & Arnold 1999).

four models, their similarities and differences, are set out in Table 1, and model flow is illustrated using Forrester diagrams (Fig. 2a,b) (Haefner 1997) and flow diagrams (Fig. 2c). Specific details relevant to each model are given below.

Population-based matrix model

The fates of marmots during the active period can be described by the formula:

$$N'_S = \mathbf{A}_S N_S \quad \text{eqn 1}$$

where N_S = vector representing numbers in each class at start of active period; N'_S = vector representing numbers in each class at end of active period; $\mathbf{A}_S$ = a transition matrix of the form:

$$\mathbf{A}_S = \begin{pmatrix} P_1 & 0 & 0 & 0 & F_5 & 0 \\ 0 & P_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & P_3 & 0 & 0 & 0 \\ 0 & 0 & G_{3,5} & P_4 & 0 & 0 \\ 0 & 0 & 0 & G_{4,5} & P_5 & G_{6,5} \\ 0 & 0 & G_{3,6} & G_{4,6} & G_{5,6} & P_6 \end{pmatrix} \quad \text{eqn 2}$$

where P_i = the probability of survival and remaining in the same stage class; $G_{i,j}$ = the probability of changing class from stage class i to stage class j ; F_i = the fecundity of mated females in stage class i .

The values of the transition parameters for each sex were taken directly from the field data and are summarized in Table 4. The probability of a litter being produced by a dominant female and adult male and surviving to emergence was set at 0.5 (see study species, above). The number of reproductive attempts

Table 4. Transition matrix parameter values for the active period of model 1

Class	Parameter	Males	Females
1	P_1	0.882	0.882
2	P_2	0.919	0.919
3	P_3	0.882	0.706
	$G_{3,5}$	0.088	0.224
	$G_{3,6}$	0.005	0.013
4*	P_4	0.330	0.290
	$G_{4,5}$	0.476	0.523
	$G_{4,6}$	0.041	0.040
5†	P_5	0.993	0.993
	$G_{5,6}$	$G_{5,6}$	$G_{5,6}$
	F_5	0.000	3.470
6	$G_{6,5}$	0.000	0.000
	P_6	1.000	1.000

*For 7-year-olds of class 4, P_4 was 0.000 and the values of $G_{4,5}$ and $G_{4,6}$ were scaled up accordingly.

†The number of class 5 individuals of either sex could not exceed 91 at any stage and, hence, values of $G_{5,6}$ were density dependent.

was limited to 91, or to the number of dominant females or adult males, whichever was fewer.

Processes occurring during the hibernation period can be described by the formula:

$$N_W = \mathbf{A}_W N'_S \quad \text{eqn 3}$$

where N_W = vector representing numbers in each class at the end of hibernation; $\mathbf{A}_W$ = a transition matrix of the form:

$$\mathbf{A}_W = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 0 \\ G_{1,2} & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{2,3} & 0 & 0 & 0 & 0 \\ 0 & 0 & G_{3,4} & P_4 & 0 & 0 \\ 0 & 0 & 0 & 0 & P_5 & 0 \\ 0 & 0 & 0 & 0 & 0 & P_6 \end{pmatrix} \quad \text{eqn 4}$$

Here, P_i and $G_{i,j}$ are entirely analogous to probabilities of survival over winter. Survival depended on class and, potentially, winter length and age. Winter survival probability functions derived from the field study are summarized in Table 5.

Group-based matrix model

In this model, individuals were classified by territory as well as by stage. Population changes during the active period can be described by a modified version of equation 1:

$$N'_S = \sum_{i=1}^n \mathbf{A}_{S,i} N_{S,i} \quad \text{eqn 5}$$

where $N_{S,i}$ = vector representing the number of individuals of each class in the i th group at the start of the active period; $\mathbf{A}_{S,i}$ = transition matrix describing the fates of group members during the active period; n = number of available territories (= 91).

The transition matrix $\mathbf{A}_{S,i}$ is equivalent to $\mathbf{A}_S$ described by equation 2. Transitions were not only between stages but also, potentially, between territories. Proportions of transitions occurring within and between territories were based on the empirical data (Table 6). Where the number of individuals changing to stage class 5 exceeded the number of vacancies, excess individuals were assigned to stage class 6.

Transitions during the hibernation period are described by a modified version of equation 3:

$$N_W = \sum_{i=1}^n \mathbf{A}_{W,i} N'_{S,i} \quad \text{eqn 6}$$

where $N'_{S,i}$ = vector representing the number of individuals of each class in the i th group at the end of the active period; $\mathbf{A}_{W,i}$ = transition matrix describing the fates of group members during the hibernation period.

The transition matrix $\mathbf{A}_{W,i}$ is equivalent to $\mathbf{A}_W$ described by equation 4. Inclusion of group structure permitted within-group density dependence in winter survival (Table 5). Floaters were not included in any calculation of the membership of individual groups. The field study also provided evidence for winter mortality arising in two further ways. First, where standard mortality resulted in a sole surviving adult or yearling in a group, the group was subjected to a further risk of mortality of 0.66 (six of nine groups in this condition died out during the field study). Juveniles in groups with no surviving adults or yearlings also died out. In addition, all groups faced a risk of catastrophic mortality of 0.004 (equivalent to 1 out of 256 group years in which the group was eradicated by the collapse of their hibernaculum during the Berchtesgaden study).

Spatially explicit individual-based model

The structure of this model is illustrated in Fig. 2b. Both summer transitions and summer mortality were staggered throughout the three active periods. All individuals were exposed to stochastic summer mortality divided between the three sections of the active period, in the ratio 2 : 12 : 12, corresponding to the approximate number of weeks in each of the subsections. Components of summer mortality were set so that cumulative survival was equivalent to that used in models 1 and 2.

In reality, the exact timing of dispersal is difficult to ascertain in the field, although it is known that relatively little occurs in the period immediately post-emergence, whilst the majority occurs soon after the period of reproduction. In the model, the proportion dispersing immediately after emergence (the 'early disperser proportion') was varied throughout a wide range of values, only a small subset of which gave a frequency of reproduction in line with empirical data. A figure of 0.18 was thus used. Field observations indicated that, without dispersing, subordinate marmots can assess other territories within an approximate 500-m

Table 5. Coefficients used in the winter survival functions

Stage class	Factors influencing winter survival function†	Coefficient	Model fit		
			χ^2	d.f.	Significance‡
Model 1					
1	Winter length (days)§	-0.0338	11.594	1	***
	Constant	4.8440			
2	Constant	2.8084	—	—	—
3,4	Constant	4.1392	—	—	—
5¶	Age/years	-0.1992			
	Winter length (days)	-0.0437	11.672	2	**
	Constant	8.7531			
Model 2					
1	Winter length (days)	-0.0315			
	Adults in the group††	0.5130	29.043	2	***
	Constant	3.2707			
2	Yearlings in the group	0.3354	4.654	1	*
	Constant	1.6603			
3,4	Constant	4.1392	—	—	—
5	Age/years	-0.2675			
	Winter length (days)	-0.0391			
	Adults in the group	0.4858	24.881	4	***
	Yearlings in the group	0.3255			
	Constant	7.0495			
Models 3 and 4					
1	Winter length (days)	-0.0389			
	Adults in the group††	0.7425	73.398	3	***
	Weaning mass (kg)	6.3000			
2	Yearlings in the group	0.3354	4.654	1	*
	Constant	1.6603			
3,4	Constant	4.1392	—	—	—
5	Age (years)	-0.2675			
	Winter length (days)	-0.0391			
	Adults in the group	0.4858	24.881	4	***
	Yearlings in the group	0.3255			
	Constant	7.0495			

†Survival functions were based on logistic probability distribution functions and took the form: $l_w = 1 - \frac{1}{1 + e^{(C_1Q_1 + C_2Q_2 + \dots + C_iQ_i)}}$

where l_w = probability of winter survival; C_1 to C_i = coefficients 1 to i ; Q_1 to Q_i = factors 1 to i .

All age classes were tested with as many of the following factors as was appropriate within the confines of the relevant model: winter length, numbers of juveniles, numbers of yearlings, numbers of subordinate adults and number of adults in the group, as well as age. Non-significant terms were removed.

‡Significance given as: * ≤ 0.05 ; ** ≤ 0.01 ; *** ≤ 0.001 .

§Winter length measured as the number of days from the first of January to the first clearing of snow from the territory.

¶In all models, survival of adults during their thirteenth winter was zero, thus ensuring that no individual exceeded the maximum age ($A_{\max}$) of 12 years (Table 3).

††Sample sizes for juveniles in groups with more than five adults were very low and hence juvenile survival is calculated as though there are a maximum of five adults in the group.

Table 6. Probabilities of different fates for known individuals changing states during the active period in Berchtesgaden 1982–96, as used in models 2 and 3

Sex	Class	Sample size	Become territorial*				
			In home territory	Elsewhere in neighbourhood†	Beyond neighbourhood	Immerge as floater	Die
Male	3	15	0.133	0.400	0.276	0.042	0.148
	4	114	0.079	0.237	0.404	0.062	0.218
Female	3	27	0.259	0.222	0.306	0.047	0.165
	4	58	0.172	0.207	0.367	0.056	0.197

*In the spatially non-explicit model 2, there is no distinction between the destinations of animals becoming territorial and, thus, these probabilities are pooled.

†Neighbourhood refers to all territories within a 500-m radius (see text for further details).

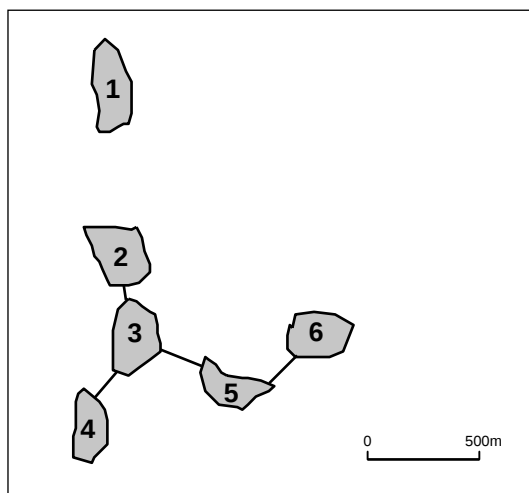


Fig. 3. Map demonstrating linkages between six territories from the south-eastern part of the study area. The neighbourhood of territory 3 comprises territories 2, 3, 4 and 5, while the neighbourhood of territory 5 consists only of territories 3, 5 and 6.

radius of their natal territory (Frey-Roos 1998). For this reason, a given territory, together with all others within 500 m of it, are said to comprise a 'neighbourhood' (Fig. 3) and the distinction was made between dispersal within, and dispersal beyond, the neighbourhood (Table 6). Older subordinates were permitted to disperse first and the fates of all dispersers were determined stochastically. Marmots dispersing beyond the neighbourhood appear to move in a largely random fashion, potentially over great distances, and, hence, the destinations of long distance dispersers were selected randomly.

Of the remaining individuals with the potential to change state, 85% were given the opportunity to do so during the reproductive period. Where state transitions resulted in a male becoming dominant in a territory in which he was unrelated to the previous dominant male or any unweaned juveniles, reproductive failure occurred (Hackländer & Arnold 1999) and no young were produced on that territory in that year.

Winter transitions in model 3 included winter mortality and, for the survivors, age/stage increases. All individuals were exposed to stochastic winter mortality, with probabilities calculated using the functions detailed in Table 5. Spatial structure permitted territories to be assigned different qualities in model 3. In Berchtesgaden, some territories regularly deviated by as much as 11 days, either above or below the mean date of snow-clearance in the spring. In the model, territories were randomly assigned one of three different qualities, fixed throughout all simulations: normal (no difference from annual mean); poor (7 days greater than annual mean); and good (7 days fewer than annual mean). Each type represented approximately one-third of all territories. Throughout the field study, there were no marmots living in a proportion of the territories, although presence of burrows and escape holes indicated previous occupation. These territories were

marked as 'abandoned' (Fig. 1), assumed to be unavailable (mostly due to encroachment by trees and shrubs) and hence were not included in the model. Differences between juveniles (in terms of weaning masses) permitted the inclusion of these as a factor underlying the probability of winter survival. The individual basis of the model also permitted the origins of floaters to be recorded, allowing the distinction between class 6 animals that had failed to acquire a territory and those that were evicted territorials. Winter survival probabilities for these animals are given in Table 2.

Spatially explicit behaviour-based model

Model 4 represented a crucial development over model 3, in that state transitions no longer occurred according to the empirically measured probabilities given in Table 6 but, instead, were modelled according to an ideal free, behaviour-based, rule of fitness optimization (Fretwell 1972; Sutherland 1996). This meant that individual decisions in model 4 were not random events but were generated by an evolutionarily stable approach of maximizing individuals' fitness. As such, behaviours predicted by this model were likely to mirror behaviours evolved through natural selection and, thus, were likely to have greater biological realism than the probabilistic behaviours seen in models 1–3.

The process of state transitions is illustrated in Fig. 2c. Specifically, individuals other than floaters 'chose' to disperse (point 1 in Fig. 2c) only where the inequality:

$$w_{d[A]} > w_s \quad \text{eqn 7}$$

was satisfied, where $w_{d[A]}$ was a measure of the future lifetime fitness expected from an immediate transition at the current age (A), and w_s was the lifetime fitness expected from remaining subordinate for another year and changing state thereafter. Strictly, the fitness accruing from an immediate transition should have been greater than the fitness resulting from any possible period of deferment of transitions, and inequality 7 should thus have been:

$$w_{d[A]} > w_{s,i}$$

where $w_{s,i}$ = the fitness accruing from deferring for i years before making a state transition; $i = 1, 2, 3 \dots A_{\max} - A$ (where $A_{\max}$ is the maximum age).

However, this would be necessary only if the relationship between age and expected fitness was not monotonic, such that, for example, making an immediate transition would be better than deferring for 1 year, but deferring for 2 years would be better than either. As there is no evidence for a relationship of this sort in alpine marmots, the single inequality 7 was deemed sufficient. Calculation of the two components of the inequality is described in detail in the Appendix. In brief, however, the fitness accruing from making an

immediate state transition depended on the probabilities of acquiring dominant status in a territory of a given quality, and the residual reproductive values expected from being dominant in that type of territory. The fitness accruing from deferring a state transition for another year depended on direct benefits (in terms of reproductive opportunities as a subordinate and the expected fitness from making a state transition the next year) and indirect benefits (in terms of increased survival of related individuals in the natal territory). Eviction of a dominant (point 2 in Fig. 2c) was a stochastic process and is also described in greater detail in the Appendix.

If dispersing individuals failed to secure dominant status in their home territory, the two territories within the neighbourhood (if two were available) with the highest individual pay-off values for $w_{d[A]}$ were also tried (point 3 in Fig. 2c). If this was unsuccessful, however, surviving long-distance dispersers were permitted to try between three and five further neighbourhoods chosen at random from a uniform distribution (point 4 in Fig. 2c). Within each neighbourhood, the disperser could succeed into any territorial vacancy, or try to evict the resident dominant from a territory chosen at random. Remaining floaters wintered alone (with associated high risks of mortality) before having the chance to disperse again. Evicted animals also became floaters but faced an even higher risk of mortality during the following winter.

MODEL DATA COLLECTION AND ANALYSIS

In all cases, data on population sizes, demographic composition and individual behaviour were taken from the models only after a 20-year stabilization period. Following stabilization, basic population parameters were collected over a 1000-year period, using winter lengths based on the empirically observed distribution. For data representative of a broad range of population densities, periods during which each successive winter was of prolonged duration (145–175 days, depending on the resilience of the model population) were used to reduce the population in as natural a manner as possible. No data were collected during these periods. Statistical comparisons of empirical and model population densities used Welch's approximate t for samples with unequal variance (Zar 1996).

Results

The basic demography of the study population was compared with that predicted by the four models (Table 7 and Fig. 4). Under stable conditions, models 1, 2 and 4 conformed well to the field data, predicting densities not significantly different from those observed in the field (Welch's approximate $t < 1.782$, d.f. = 12, $P > 0.1$). In contrast, model 3 tended to predict a low incidence of successful reproduction, low overwinter survival and population densities significantly lower than those observed in the field

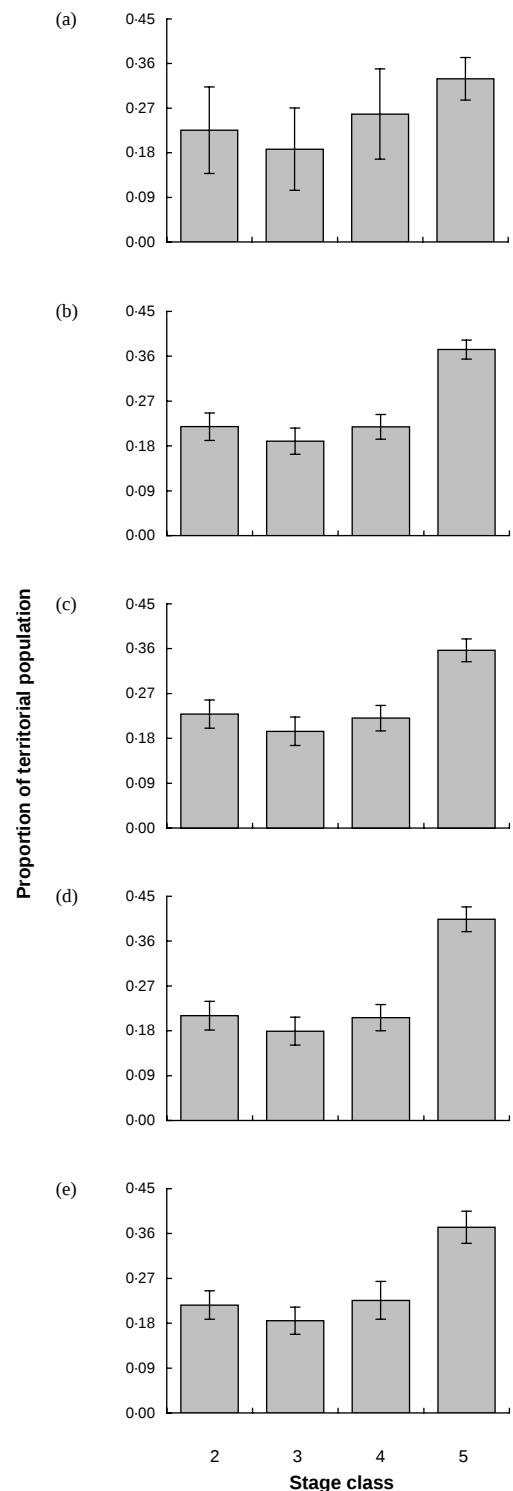


Fig. 4. Breakdowns of emergence population size by stage class for (a) annual figures for field data and predictions from (b) model 1, (c) model 2, (d) model 3, (e) model 4. Model results are averaged over 1000 years following a 20-year stabilization period. Error bars show standard deviations (hence the apparently larger error for the empirical results, measured over a shorter time span).

(emergence: $t = 2.291$, d.f. = 12, $P < 0.05$; immigration: $t = 2.120$, d.f. = 12, $P = 0.07$).

Differences between the models' predictions of density dependence over a wide range of population sizes

Table 7. Comparison of empirical population characteristics (mean $\pm$ SD*) with those predicted by the four models

Parameter	Empirical value	Model 1	Model 2	Model 3	Model 4
Annual population density (per territory)† at:					
emergence	4.84 $\pm$ 0.63	5.04 $\pm$ 0.29	4.69 $\pm$ 0.33	4.50 $\pm$ 0.33	4.84 $\pm$ 0.47
immersion	5.56 $\pm$ 0.65	5.68 $\pm$ 0.29	5.57 $\pm$ 0.30	5.24 $\pm$ 0.31	5.57 $\pm$ 0.45
Annual number of litters weaned per territory	0.50 $\pm$ 0.11	0.50 $\pm$ 0.05	0.50 $\pm$ 0.05	0.46 $\pm$ 0.05	0.49 $\pm$ 0.06

*Larger standard deviations for the empirical data arise because the field data are based on only the 23 most intensively studied territories.

†Excluding floaters.

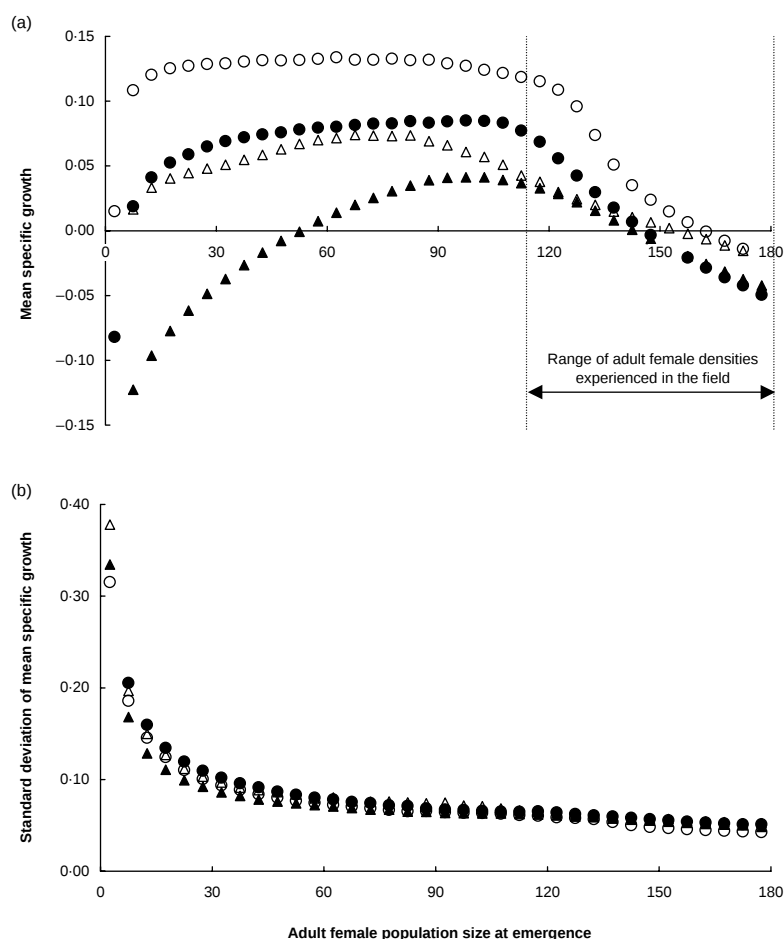


Fig. 5. (a) Mean and (b) standard deviation of specific (or per capita) population growth predicted across a broad range of adult female emergence population sizes by model 1 (open circles), model 2 (closed circles), model 3 (black triangles), model 4 (open triangles). In (a), each point is the mean of minimum 1500 data points (mean > 55 000 data points).

were more marked (Fig. 5a). Although the carrying capacity predicted by the models was broadly similar, the effects of population density on population growth below the carrying capacity varied widely, even within the range of densities experienced in the field. Model 1 predicted that growth rates would rise sharply as the population dropped below the carrying capacity, rapidly reaching a maximum mean value of around 13.2% per annum. This mean growth rate was seen at all population sizes down to about 10–15 adult females, below which it declined, as a result of demographic

stochasticity in sex ratios. Model 2 predicted a similar pattern of density-dependent population growth to model 1. However, the maximum mean growth rate was lower (peaking at approximately 8.5% per annum) and a decline in growth rates was more pronounced, occurring once the population dropped below about 50 adult females. Models 3 and 4 both predicted a stronger effect of negative density dependence, causing a decline in mean growth rates above a population of only 100 or 80 adult females, respectively. Maximum mean growth rates were also lower in these models (4.1%

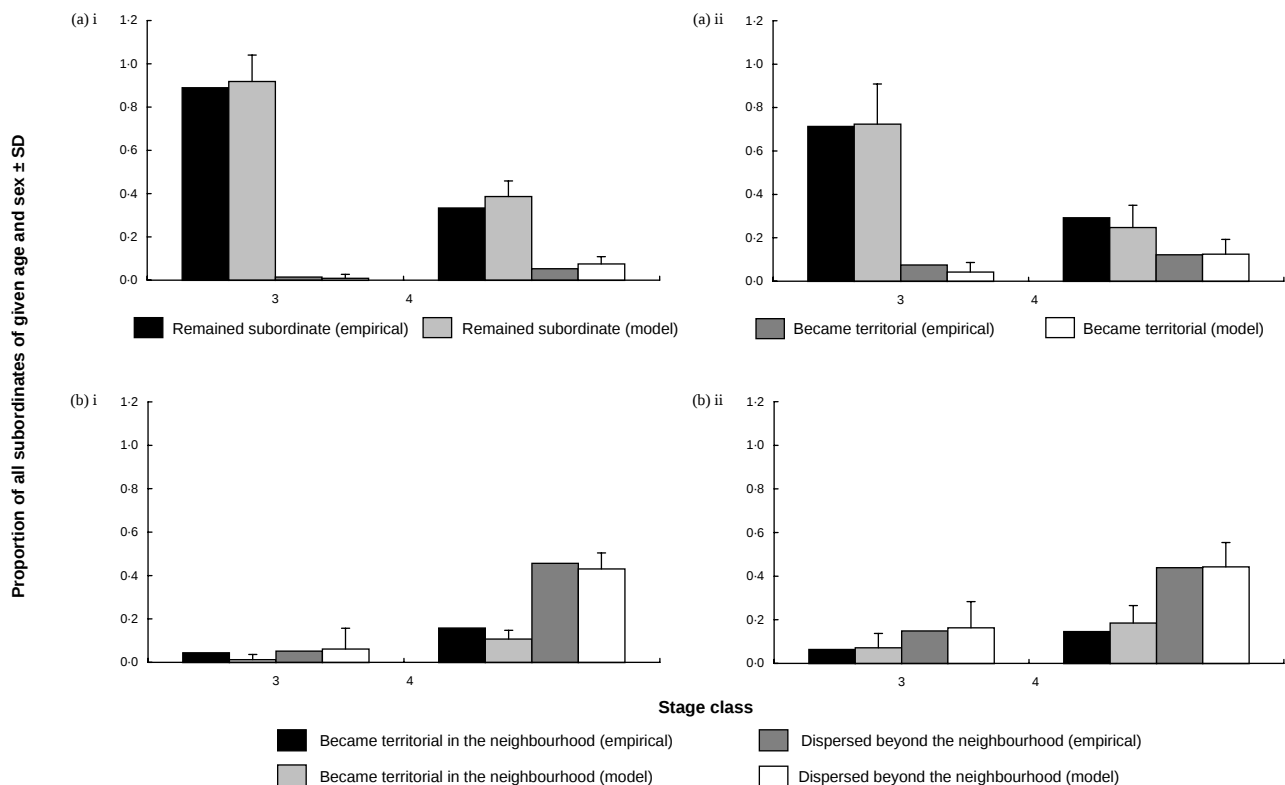


Fig. 6. Fates of subordinate animals by sex and stage predicted by model 4. (a) Remained in natal territory (i, males; ii, females), (b) dispersed from natal territory (i, males; ii, females). Model results are averaged over 1000 years following a 20-year stabilization period.

and 7.4%, respectively), while declines in growth rates at lower population sizes were most pronounced in model 3 (with negative mean growth rates below about 50 adult females) but marked in model 4 also. Due to the stochastic nature of the model and the relatively small population size considered, variance in mean growth rates was large but consistent across all models, again, even within the range of densities experienced in the field (Fig. 5b).

The performance of the behavioural model (model 4) was examined by comparison with several aspects of behaviour and demography from the field and was shown to provide accurate predictions of dispersal behaviour (Fig. 6) and group size distributions (Fig. 7), when compared with the data from the empirical study. Rates of turnover of dominant animals were also similar: dominant male mean tenure and standard deviation, 3.14 ± 2.38 (simulation), 3.02 ± 2.34 (field study); dominant female, 3.60 ± 2.49 (simulation), 3.63 ± 2.04 (field study). These are key comparisons, as all of these properties of the population are emergent features of the rules used to determine dispersal behaviour (see the Appendix) rather than being derived directly from the parameterization of the model.

Discussion

Our results indicate that models of a variety of levels of complexity are capable of predicting equilibrium population sizes of alpine marmots with some precision.

For predicting populations or assessing management strategies, behaviour-based modelling has, in the past, been applied successfully only to species with relatively simple life histories, primarily several species of birds, including oystercatchers *Haematopus ostragalus* (Goss-Custard *et al.* 1995), bean geese *Anser fabalis* (Sutherland 1994), barnacle and brent geese *Branta leucopsis* and *B. bernicla* (Pettifor *et al.* 2000) and black-tailed godwits *Limosa limosa* (Gill, Sutherland & Norris 2001). Our results show that this approach can also be applied to more complex social species, accurately predicting dispersal behaviour, group dynamics and overall population dynamics. The results also show that a range of models parameterized using the same data set can provide markedly different predictions about the nature of density dependence, even within the range of densities experienced in the field. The models predicted maximum mean growth rates ranging from approximately 4% per annum to almost 14% per annum; upper, stable equilibrium population sizes of between 140 and 160 adult females; and levels of depensation ranging in severity from a drop off to lower (but still positive) mean growth rates when the population dropped below about 10 adult females, to a marked reduction in growth rates below relatively high population sizes (over 90 adult females in model 3), leading to negative mean growth rates when populations dropped below 50 adult females. These results will be discussed in light of the three principal questions posed in the introduction.

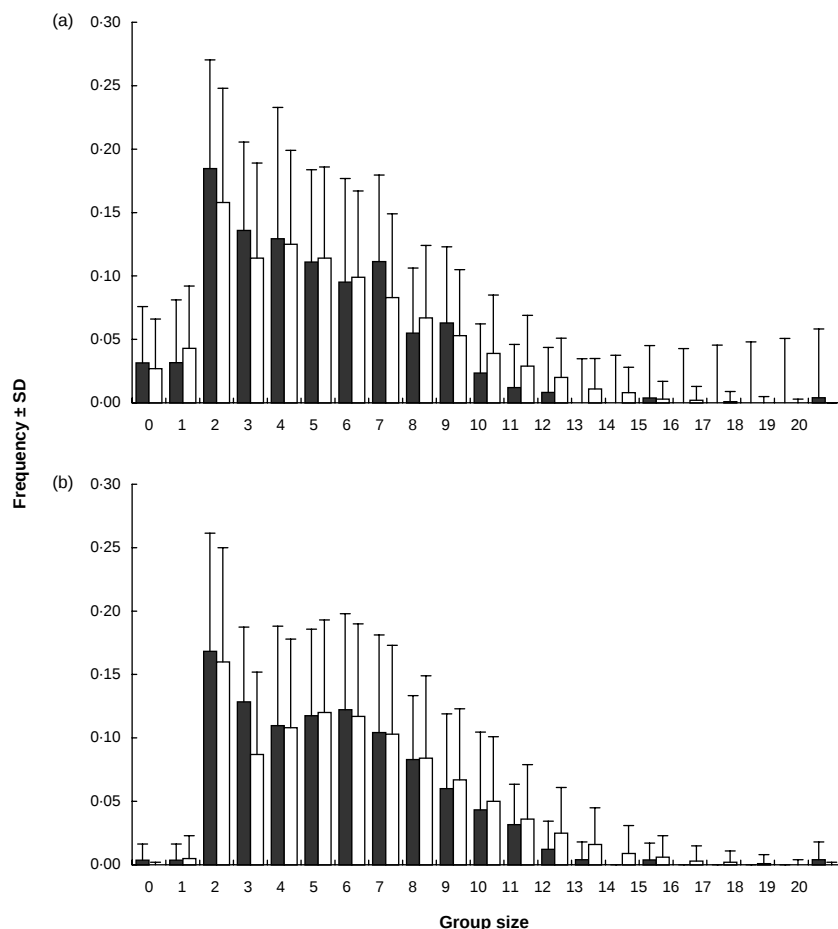


Fig. 7. Group size distributions at (a) emergence and (b) immergence, for empirical data (filled bars) and model 4 predictions (light bars). Model results are averaged over 1000 years following a 20-year stabilization period.

DENSITY DEPENDENCE IN THE ALPINE MARMOT

Contrary to the implications of the logistic model, it is predicted that for most vertebrates, density dependence will be non-linear, with populations exhibiting most population regulation at levels close to the carrying capacity (Fowler 1981). For mammals, there is abundant evidence to show that this may be due to non-linear negative relationships between fecundity, juvenile survival, adult survival (or a combination of these) and population size (reviewed by Fowler 1987). All of our models for the alpine marmot are consistent with this, showing strong negative density dependence only above intermediate population sizes (90–100 adult females), owing to the limited number of territories available in the model. Alpine terrain is highly dissected and, typically, characterized by precipitous slopes, rocky outcrops, loose scree and forest. In Berchtesgaden, only about 10% of the area is suitable for marmot habitation (Frey-Roos 1998). Within this area, territories are closely packed and annual variation in their size, number and location is minimal. Among females, reproduction is limited to territorial animals (Arnold 1990a) and, consequently, competition for the limited breeding sites is fierce. Subordinate adults of both sexes

have two choices: they may either remain subordinate on a territory, or they may disperse. Those that remain subordinate are unlikely to contribute to reproduction. Dispersing females may acquire a territory but, due to competition, this becomes less likely at higher population sizes. Failure to acquire a territory forces the animal to become a non-breeding floater, subject to extremely high mortality. Although there is no evidence for food limitation in alpine marmots, negative density dependence does arise from two processes. First, as the population increases, so too do the proportions of subordinate adults and floaters, leading to reduced mean fecundity. Secondly, increasing numbers of floaters also reduces mean survival as the population grows. Both of these effects are directly attributable to the restricted availability of breeding territories.

Less well recognized are mechanisms affecting density dependence when populations are at low densities. Early conservation literature emphasized the importance of inbreeding depression, birth, death and environmental stochasticity at low population sizes. In recent years, however, there has been increasing interest in the Allee effect as a manifestation of density dependence. Allee effects are positive relationships between components of individual fitness and population size or density (Stephens, Sutherland &

Freckleton 1999) and may have profound consequences for many aspects of behaviour, ecology and conservation (Stephens & Sutherland 1999, 2000). Numerous empirical studies have shown that a wide range of behavioural mechanisms can lead to positive relationships between some component of fitness and population size or density, and that these effects can manifest at a range of scales, including groups, larger aggregations and populations (reviewed by Stephens & Sutherland 2000). In spite of this body of evidence, few empirical studies of animals have demonstrated clearly that such component Allee effects (positive relationships between some aspect of individual fitness and population size or density) lead to demographic Allee effects (manifested in a positive relationship between overall population growth and population size or density).

All of our models predicted some form of demographic Allee effect for the alpine marmot population, but it was in this area that the most striking differences between the models were seen. Patterns of density dependence in Fig. 5 allow the mechanisms underlying the demographic Allee effect to be elucidated. The weak Allee effect predicted by model 1 arose from demographic stochasticity. Specifically, skews in the sex ratio and demographic make-up of the population at small population sizes (Caughley 1994; Stephens *et al.* 1999) reduced fecundity through their effects on effective population size (Creel 1998). Incorporating group structure and the lower capacity for social thermoregulation in smaller groups (model 2) had striking effects, including a higher population size below which mean growth declined abruptly (25 adult females, as opposed to 10 in model 1); a stronger reduction in growth (leading to negative mean growth rates below approximately five adult females); and a reduction in growth rates not restricted to very low population sizes (as is often believed to be the case for Allee effects), even reducing the maximum growth rate by over 50% from that predicted by model 1. Finally, model 2 also predicted a lower carrying capacity of approximately 145 adult females (cf. more than 160 adult females in model 1). The lower carrying capacity can be explained by the heterogeneous group structure: while some groups contain fewer than the mean number of individuals (thus being subject to greater over-winter mortality), others are higher than the mean group size (and thus have a greater number of individuals that are not contributing to reproduction). Introducing spatial structure (models 3 and 4) affected the density-dependent dynamics still further. Model 3 did not produce realistic results (see further below) and, hence, will not be discussed here. Model 4, however, predicted an even more pronounced demographic Allee effect than that arising from model 2. The introduction of spatial scale led to a mate-finding component Allee effect, perhaps the most widely cited mechanism of the Allee effect (Allee 1931; Dennis 1989; Hopper & Roush 1993; McCarthy 1997; Amarasekare 1998), which arises

when potentially reproductive individuals of each sex fail to meet up, necessarily foregoing reproduction for another year. The seemingly random nature of long-distance dispersal in marmots means that this mechanism has a strong effect on the overall dynamics of the species. In particular, the mate-finding Allee effect resulted in an even lower maximum growth rate than was apparent from the spatially non-explicit model 2 (mean of 7.3%, cf. 8.5% in model 2), and reduced growth rates at all population sizes below the carrying capacity.

In summary, our models suggest that a demographic Allee effect is very likely in a relatively closed population of alpine marmots, such as that of Berchtesgaden. The mechanisms underlying this effect include skews in sex ratio and demographic composition at very low population sizes; less effective social thermoregulation in smaller groups found predominately at low, but also at intermediate and even high, population sizes; and difficulties in finding reproductive vacancies for individuals in populations distributed throughout a spatially diverse landscape. The importance of the thermoregulatory mechanism of the Allee effect underlines the potential of group-level Allee effects to produce population-level Allee effects, in agreement with recent findings from the study of meerkats *Suricata suricatta* (Clutton-Brock *et al.* 1999) and recent heuristic models that have examined this possibility (Courchamp, Grenfell & Clutton-Brock 2000). The thermoregulatory mechanism of the Allee effect is likely to be the major motivation for group living in the alpine marmot (Arnold 1990b). As prey of a generalist predator, marmots may also be subject to another mechanism of the Allee effect, that of increased per capita predation at low densities (Sinclair *et al.* 1998). However, little is known of the relative dependence of predators on marmots and this mechanism is not considered here.

MODEL COMPLEXITY AND THE ALPINE MARMOT

Attempts to prove that the predictions of models are 'true' or 'false' are misguided (McCarthy *et al.* 2001). Even with regard to the models' predictions of the shape of density dependence, only a detailed independent data set recording mean specific growth rates of marmot populations for a range of population densities would permit identification of one set of predictions as correct and the others as erroneous. Such a data set is not available and could only be obtained by extensive long-term monitoring of an (ideally) hunted marmot population, in order to ensure a wide range of population sizes. Even with such a data set, the levels of variance shown in Fig. 5b illustrate the inherent difficulties of establishing accurate patterns of density dependence for a population from census data alone. It is only possible, therefore, to make qualitative judgements on the merits of each model, based on their

performance under stable conditions and their flexibility for prediction under novel circumstances.

Only one model (model 3) predicted equilibrium population densities significantly different from observed densities. Model 3 also provided the most pessimistic predictions of potential growth rates. It seems likely that a spatially explicit model that distinguishes between individuals but ignores behaviour is highly unrealistic. If state transitions are dictated solely on the basis of empirical probabilities, then the behaviour of individuals is essentially random. As a result, it is entirely possible that an individual in a territory with a reproductive vacancy will disperse beyond that territory within this type of modelling framework. Similarly, an individual may disperse over a long distance (facing high potential mortality), even though reproductive vacancies exist within the home neighbourhood. Moreover, probabilistic dispersal may lead to individuals dispersing even when reproductive opportunities are few, and when their own fitness could better be served by remaining in the natal territory and increasing the survival prospects of related siblings. Such examples highlight the need to consider realistic patterns of behaviour in spatial models.

Of the remaining models tested, all three predicted realistic densities of marmots under stable conditions. This suggests that any of the models would be adequate for answering questions such as how much area is necessary to support a given number of individuals? In this situation, there would be no requirement for a highly complex model; rather, the simplest of the matrix models (model 1) would be favoured. This observation is in agreement with the findings of other authors who have compared a range of models of increasing complexity (Pascual, Kareiva & Hilborn 1997). In contrast, the differences between the models' predictions of population variability and density dependence suggest that not all would be appropriate for questions regarding the stability of the population, for predicting the consequences of processes that lead to increased mortality (such as hunting, climate change or reduced habitat quality), or for assessing transient dynamics (such as colonization events). For predictions regarding these processes, we believe that the behavioural model would be the most appropriate, based on four lines of reasoning.

First, although models 1, 2 and 4 all predicted mean population sizes similar to those measured in the empirical study, a more important element of the predictions is variability in predictions (McCarthy *et al.* 2001). Only model 4 approached the levels of population size variance observed in the field study (Table 7). Secondly, models 1 and 2 were prone to errors regarding the strength of winter mortality. Model 1 had a tendency to underestimate winter mortality, due to the fact that over-winter dependency on social thermoregulation within groups could not be incorporated into a population-based matrix. This tendency is likely to be more pronounced at low densities, when average group

sizes are lower (Fig. 5a). Model 2, on the other hand, had a tendency to overestimate winter mortality. This is likely to be due to the probabilistic nature of state transitions, as previously discussed with respect to model 3. In reality, sociality buffers the effects of winter mortality but if state transitions are based on probabilities alone, then individual marmots will be unlikely to remain in groups, even where they may increase the survival of their siblings by doing so. The result is an unrealistically even distribution of group sizes. In contrast, the behavioural model provided highly accurate estimates of both group size distributions, and of winter mortality. The third reason for favouring model 4, is the inclusion of spatial structure. If dispersal is relatively free and the scale of dispersal is large, then the inclusion of spatial scale may be unimportant (Pacala & Silander 1985). However, one of the important outcomes of the comparison of models was the potential importance of mate finding as a mechanism of the Allee effect. Only a spatially explicit model can give an indication of the relative importance of this mechanism to the transient dynamics of the population. Finally, it is also likely that, of the models tested, the behavioural model will be the most flexible for making predictions about novel conditions. Despite abundant evidence to suggest that dispersal behaviour is affected by density and competition (Fowler & Baker 1991), these processes are poorly understood for the majority of species (Ims & Hjermann 2001; Lambin, Aars & Piernay 2001). Emerging evidence suggests that optimality models may provide the most accurate method for predicting these relationships (Sutherland & Gill 2001). Clearly, using fixed rates of dispersal, as in models 1–3, is likely to provide misleading estimates of population growth in changing densities. In contrast, the accuracy with which the optimality rule used in model 4 predicts rates of dispersal and group-size distributions (including rates of seasonal territory occupancy and extinction, a good test of a model with metapopulation-type structure; Hanski 1997; McCarthy *et al.* 2001) under current conditions, inspires considerable confidence in its ability to do so for novel conditions.

IMPLICATIONS FOR MODELLING AND PREDICTIVE ECOLOGY

This study has several important implications for predictive ecology. First, comparisons of simple computer models allow us to identify minimal sets of assumptions that lead to observed phenomena (Pacala 1989). Our comparison indicates that overlooking spatial scale and realistic behaviour would have precluded the identification and characterization of the Allee effects to which alpine marmots may be subject. Our modelling indicates that the Allee effect is capable of altering the dynamics of a species across a broad range of population sizes and even of altering the potential carrying capacity of a population. Density dependence is often ignored in applied species-specific matrix models

(Smith & Trout 1994; Wielgus *et al.* 2001) and, where it is included, is generally restricted to the inclusion of a finite number of territories (Zhou & Pan 1997; Loison, Strand & Linnell 2001) or overall carrying capacity (Forys & Humphrey 1999; Kelly & Durant 2000), both of which introduce an upper limit to the population size. Even more elaborate treatments of density dependence, such as the effects of density on both age at first reproduction and calving interval in the African elephant *Loxodonta africana* (Fowler & Smith 1973), only allow for negative effects of density on population processes. In view of the growing body of evidence supporting the importance of Allee effects, our findings concur with other recent work (Dennis 2002) recommending that modellers should be careful to consider the role of Allee effects in their study species. In particular, the range of social species now shown to be subject to Allee effects, indicates that models of social species should concentrate attention on these phenomena, while empiricists should continue to gather data which may help such effects to be modelled with greater realism.

This study has emphasized the potential importance of mate-finding Allee effects that could affect a much greater variety of species. As stated previously, this is the most widely studied mechanism of the Allee effect and its consequences are not restricted to social species. The majority of matrix models do not incorporate spatial scale and many are restricted to modelling the abundance of females only. The potential importance of mate-finding Allee effects, even at high densities, suggests that two-sex spatially explicit models may be preferable for examining issues concerned with the transient dynamics of populations. Finally, our study has also shown that the approach of behaviour-based modelling can be applied to species with relatively complex life histories. It is evident that spatially explicit models that ignore behaviour may be prone to inaccuracies when applied to predictive population dynamics. The apparent accuracy of the behavioural modelling approach, together with its potential flexibility, highlights the importance of this method as a tool for predictive ecologists.

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References

- Allee, W.C. (1931) *Animal Aggregations, a Study in General Sociology*. University of Chicago Press, Chicago, IL.
- Amarasekare, P. (1998) Allee effects in metapopulation dynamics. *American Naturalist*, **152**, 298–302.
- Arnold, W. (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology*, **158**, 151–156.
- Arnold, W. (1990a) The evolution of marmot sociality. I. Why disperse late? *Behavioral Ecology and Sociobiology*, **27**, 229–237.
- Arnold, W. (1990b) The evolution of marmot sociality. II. Costs and benefits of joint hibernation. *Behavioral Ecology and Sociobiology*, **27**, 239–246.
- Arnold, W. (1993) Energetics of social hibernation. *Life in the Cold: Ecological, Physiological and Molecular Mechanisms* (eds C. Carey, G.L. Florant, B.A. Wunder & B. Horwitz), pp. 65–80. Westview Press, San Francisco, CA.
- Arnold, W. (1995) Social behaviour and telemetric assessment of thermoregulation in hibernating marmots. *Behavioural Brain Research in Naturalistic and Semi-Naturalistic Settings* (eds E. Alleva, A. Fasolo, H.-P. Lipp, L. Nadel & L. Ricceri), pp. 395–411. Kluwer Academic Publishers, Amsterdam, The Netherlands.
- Arnold, W. & Dittami, J. (1997) Reproductive suppression in male alpine marmots. *Animal Behaviour*, **53**, 53–66.
- Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.
- Bierzychudek, P. (1999) Looking backwards: assessing the projections of a transition matrix model. *Ecological Applications*, **9**, 1278–1287.
- Boyce, M.S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics*, **23**, 481–506.
- Brook, B.W., O'Grady, J.J., Chapman, A.P., Burgman, M.A., Akçakaya, H.R. & Frankham, R. (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature*, **404**, 385–387.
- Bruns, U. & Arnold, W. (1999) Social marmots – cooperative polyandry and inbreeding. *Zoology*, **102** (Suppl. II (DZG 92.1)), 13.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.
- Clutton-Brock, T.H., Gaynor, D., McIlrath, G.M., MacColl, A.D.C., Kinsky, R., Chadwick, P., Manser, M., Skinner, J.D. & Brotherton, P.N.M. (1999) Predation, group size and mortality in a co-operative mongoose *Suricata suricatta*. *Journal of Animal Ecology*, **68**, 672–683.
- Coulson, T., Mace, G.M., Hudson, E. & Possingham, H.P. (2001) The use and abuse of population viability analysis. *Trends in Ecology and Evolution*, **16**, 219–221.
- Courchamp, F., Grenfell, B.T. & Clutton-Brock, T.H. (2000) Impact of natural enemies on obligately cooperative breeders. *Oikos*, **91**, 311–322.
- Creel, S. (1998) Social organization and effective population size in carnivores. *Behavioral Ecology and Conservation Biology* (ed. T.M. Caro), pp. 246–265. Oxford University Press, Oxford, UK.
- Dennis, B. (1989) Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modelling*, **3**, 481–538.
- Dennis, B. (2002) Allee effects in stochastic populations. *Oikos*, **96**, (in press).

- Forys, E.A. & Humphrey, S.R. (1999) Use of population viability analysis to evaluate management options for the endangered Lower Keys marsh rabbit. *Journal of Wildlife Management*, **63**, 251–260.
- Fowler, C.W. (1981) Density dependence as related to life history strategy. *Ecology*, **62**, 602–610.
- Fowler, C.W. (1987) A review of density dependence in populations of large mammals. *Current Mammalogy* (ed. H. Genoways), pp. 401–441. Plenum Press, New York, NY.
- Fowler, C.W. & Baker, J.D. (1991) A review of animal population dynamics at extremely reduced population levels. *Report to the International Whaling Commission*, **41**, 545–554.
- Fowler, C.W. & Smith, T. (1973) Characterising stable populations: an application to the African elephant population. *Journal of Wildlife Management*, **37**, 513–523.
- Fretwell, S.D. (1972) *Populations in a Seasonal Environment*. Princeton University Press, Princeton, NJ.
- Frey-Roos, F. (1998) *Geschlechtsspezifisches Abwanderungsmuster beim Alpenmurmeltier (Marmota marmota)*. PhD Thesis. Philipps University, Marburg, Germany.
- Gill, J.A., Sutherland, W.J. & Norris, K. (2001) Depletion models can predict shorebird distribution at different spatial scales. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **268**, 369–376.
- Goss-Custard, J.D., Caldow, R.W.G., Clarke, R.T., Durell, S., Urfi, J. & West, A.D. (1995) Consequences of habitat loss and change to populations of wintering migratory birds – predicting the local and global effects from studies of individuals. *Ibis*, **137**, S56–S66.
- Hackländer, K. & Arnold, W. (1999) Male-caused failure of female reproduction and its adaptive value in alpine marmots (*Marmota marmota*). *Behavioral Ecology*, **10**, 592–597.
- Haefner, J.W. (1997) *Modeling Biological Systems: Principles and Applications*. Chapman & Hall, New York, NY.
- Hamilton, S. & Moller, H. (1995) Can PVA models using computer packages offer useful conservation advice? Sooty shearwaters *Puffinus griseus* in New Zealand as a case-study. *Biological Conservation*, **73**, 107–117.
- Hanski, I. (1997) Metapopulation dynamics: from concepts and observations to predictive models. *Metapopulation Biology: Ecology, Genetics and Evolution* (eds I. Hanski & M.E. Gilpin). Academic Press, San Diego, CA.
- Hendry, R., Bacon, P.J., Moss, R., Palmer, S.C.F. & McGlade, J. (1997) A two-dimensional individual-based model of territorial behaviour: possible population consequences of kinship in red grouse. *Ecological Modelling*, **105**, 23–39.
- Hopper, K.R. & Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological-control introductions. *Ecological Entomology*, **18**, 321–331.
- Ims, R.A. & Hjermann, D.Ø. (2001) Condition dependent dispersal. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 203–216. Oxford University Press, Oxford, UK.
- Kelly, M.J. & Durant, S.M. (2000) Viability of the Serengeti cheetah population. *Conservation Biology*, **14**, 786–797.
- Lambin, X., Aars, J. & Piertney, S.B. (2001) Dispersal, intraspecific competition, kin competition and kin facilitation: a review of the empirical evidence. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhondt & J.D. Nichols), pp. 110–122. Oxford University Press, Oxford, UK.
- Loison, A., Strand, O. & Linnell, J.D.C. (2001) Effect of temporal variation in reproduction on models of population viability: a case study for remnant arctic fox (*Alopex lagopus*) populations in Scandinavia. *Biological Conservation*, **97**, 347–359.
- McCarthy, M.A. (1997) The Allee effect, finding mates and theoretical models. *Ecological Modelling*, **103**, 99–102.
- McCarthy, M.A., Possingham, H.P., Day, J.R. & Tyre, A.J. (2001) Testing the accuracy of population viability analysis. *Conservation Biology*, **15**, 1030–1038.
- Matos, D.M.S., Freckleton, R.P. & Watkinson, A.R. (1999) The role of density dependence in the population dynamics of a tropical palm. *Ecology*, **80**, 2635–2650.
- Ollason, J.G., Bryant, A.D., Davis, P.M., Scott, B.E. & Tasker, M.L. (1997) Predicted seabird distributions in the North Sea: the consequences of being hungry. *Ices Journal of Marine Science*, **54**, 507–517.
- Ollason, J.G. & Yearsley, J.M. (2001) The approximately ideal, more or less free distribution. *Theoretical Population Biology*, **59**, 87–105.
- Pacala, S.W. (1986) Neighborhood models of plant population dynamics. IV. Single-species and multispecies models of annuals with dormant seeds. *American Naturalist*, **128**, 859–878.
- Pacala, S.W. (1989) Plant population dynamic theory. *Perspectives in Ecological Theory* (eds J. Roughgarden, R. May & S. Levin), pp. 54–67. Princeton University Press, Princeton, NJ.
- Pacala, S.W. & Silander, J.A. (1985) Neighborhood models of plant population dynamics. I. Single-species models of annuals. *American Naturalist*, **125**, 385–411.
- Pascual, M.A., Kareiva, P. & Hilborn, R. (1997) The influence of model structure on conclusions about the viability and harvesting of Serengeti wildebeest. *Conservation Biology*, **11**, 966–976.
- Pettifor, R.A., Caldow, R.W.G., Rowcliffe, J.M., Goss-Custard, J.D., Black, J.M., Hodder, K.H., Houston, A.I., Lang, A. & Webb, J. (2000) Spatially explicit, individual-based, behavioural models of the annual cycle of two migratory goose populations. *Journal of Applied Ecology*, **37**, 103–135.
- Rassmann, K., Arnold, W. & Tautz, D. (1994) Low genetic variability in a natural alpine marmot population (*Marmota marmota*, Sciuridae) revealed by DNA fingerprinting. *Molecular Ecology*, **3**, 347–353.
- Shea, K. & Kelly, D. (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications*, **8**, 824–832.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P. & Newsome, A.E. (1998) Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, **12**, 564–575.
- Smith, G.C. & Trout, R.C. (1994) Using Leslie matrices to determine wild rabbit population growth and the potential for control. *Journal of Applied Ecology*, **31**, 223–230.
- Soulé, M.E. (1987) *Viable Populations for Conservation*. Cambridge University Press, Cambridge, UK.
- Stephens, P.A. & Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution*, **14**, 401–405.
- Stephens, P.A. & Sutherland, W.J. (2000) Vertebrate mating systems, Allee effects and conservation. *Vertebrate Mating Systems* (eds M. Apollonio, M. Festa-Bianchet & D. Mainardi), pp. 186–213. World Scientific Publishing, London, Erci, Italy.
- Stephens, P.A., Sutherland, W.J. & Freckleton, R.P. (1999) What is the Allee effect? *Oikos*, **87**, 185–190.
- Sutherland, W.J. (1994) Depletion models and their consequences for conservation. *Individuals, Populations and Patterns in Ecology* (eds S. Leather & A.D. Watt), pp. 337–345. Intercept Press, Andover, UK.
- Sutherland, W.J. (1996) *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford, UK.
- Sutherland, W.J. & Gill, J.A. (2001) The role of behaviour in studying sustainable exploitation. *Conservation of Exploited Species* (eds J.D. Reynolds, G.M. Mace, K.H. Redford & J.G. Robinson), pp. 259–280. Cambridge University Press, Cambridge, UK.
- Sutherland, W.J. & Watkinson, A.R. (2001) Policy making within ecological uncertainty: lessons from badgers and GM crops. *Trends in Ecology and Evolution*, **16**, 261–263.

Taylor, M.K., DeMaster, D.P., Bunnell, F.L. & Schweinsburg, R.E. (1987) Modeling the sustainable harvest of female polar bears. *Journal of Wildlife Management*, **51**, 811–820.
Wielgus, R.B., Sarrazin, F., Ferriere, R. & Clobert, J. (2001) Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models. *Biological Conservation*, **98**, 293–303.

Zar, J.H. (1996) *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.
Zhou, Z.H. & Pan, W.S. (1997) Analysis of the viability of a giant panda population. *Journal of Applied Ecology*, **34**, 363–374.

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Appendix: calculation of the residual fitness benefits of state transitions

EXPECTED LIFETIME FITNESS FROM AN IMMEDIATE TRANSITION

The residual fitness of a state transition was calculated as shown in equation A1. The four terms on the right-hand side of the equation represent: (i) the probability of acquiring the home territory, multiplied by the residual reproductive value of being dominant in that territory; (ii) the probability of acquiring the next most desirable territory in the neighbourhood, multiplied by the residual reproductive value of being dominant in that territory; (iii) as (ii) but for the next most desirable territory (assuming there is one); and (iv) the probability that no territory is acquired in the home neighbourhood but one is acquired elsewhere, multiplied by the residual reproductive value of being dominant in an average territory.

$$w_{d[A]} = pA_1 \sum_{x=0}^{\infty} l_{x1} m_{x1} + (1 - pA_1) \cdot pA_2 \sum_{x=0}^{\infty} l_{x2} m_{x2} + (1 - (1 - pA_1)pA_2) \cdot pA_3 \sum_{x=0}^{\infty} l_{x3} m_{x3} + (1 - (1 - (1 - pA_1)pA_2)pA_3) \cdot pA_f \cdot l_f \sum_{x=0}^{\infty} l_{xf} m_{xf}$$

eqn A1

where pA_i = probability of acquiring territory i , either by succession (if the territory has no current dominant of the disperser's sex, in which case $pA = 1$) or by eviction of the current dominant (in which case pA was sex and age specific, equivalent to pE , the probability of eviction; see further below); l_{xi} = probability of surviving as the dominant to year x in territory i ; this probability incorporated age-specific summer and winter mortality risks (assuming average conditions and an average group composition) as well as the density-dependent annual probability of eviction from a territory in a neighbourhood of given size (see further below); sub-

script f denotes average survival in a territory outside the neighbourhood; m_{xi} = average number of young raised to yearling annually in territory i , assuming average winter conditions, average group compositions and incorporating the annual probability of reproduction, as well as both summer and winter survival for juveniles in a territory with given quality; m also includes relatedness, assuming that the young are direct offspring; subscript f denotes average number of young raised to yearling in a territory outside the neighbourhood (see further, below); pA_f = probability of acquiring an average territory outside the immediate neighbourhood, accounting for the relative availability of territorial vacancies and the number of territories that a dispersing marmot can visit; l_f = survival of long-distance dispersers (Table 3).

Three of the parameters listed above were not directly available from the field data. First, as observed above, if acquisition of a territory required eviction of the current same-sex dominant, then the probability of acquisition, pA , was equivalent to pE , the probability of eviction. In the field, an eviction attempt is hard to classify, as much assessment may be indirect, through scent marking, for example. Thus, the sex-specific probabilities of a subordinate evicting a dominant in a single attempt (pE) could not be ascertained directly from the field data. Instead, using a version of the behavioural model in which age-specific probabilities of a state transition were fixed at empirically observed values, the eviction parameters were varied through a wide range, only a small subset of which gave realistic model predictions (based on a variety of comparators, including mean population densities at emergence and emergence, mean numbers of litters per territory, and mean proportions of class 4 dispersers becoming dominant). The parameters were thus assigned the values shown in Table A1. Incorporating these values into the behavioural model did not distinguish between the competitive abilities of 2-year-olds and older subordinates. However, 2-year-olds are not yet of full adult size and are likely to have lower eviction abilities. Reducing

Table A1. Model parameters derived indirectly, or by simulation in a fixed dispersal rate version of model 4

Parameter	Description	Value
m_x	Mean number of young raised annually to yearling on a territory of quality (x), incorporating pR , relatedness to parent and survival of the juveniles through both summer and an average winter, in a group of average composition	0.647 (1) 0.584 (2) 0.519 (3)
pE_m	Probability of eviction of a male dominant by a male subordinate of class 4	0.09
pE_f	Probability of eviction of a female dominant by a female subordinate of class 4	0.14
pE_{m2}	Probability of eviction of a male dominant by a male subordinate of class 3	0.082
pE_{f2}	Probability of eviction of a female dominant by a female subordinate of class 3	0.125

the eviction abilities of 2-year-olds to approximately 90% of the values used for older subordinates, yielded dispersal rates for these animals that more closely matched behaviour observed in the field. For dispersal in the home neighbourhood, territory acquisition in the home territory and two others was attempted. This was also set by experiment, to avoid an exaggerated tendency to settle in the home neighbourhood.

Secondly, the probability of surviving as the dominant in a given territory, l_{xi} , was partly dependent on the density-dependent annual probability of eviction from a territory in a neighbourhood of given size. In order to assess this, the fixed dispersal rate version of the behavioural model was used again. Logistic regression analyses of output from the fixed dispersal rate model were used to determine the effects on annual probabilities of dominant displacement, of densities of competing subordinate adults of the same sex globally, in the neighbourhood, and in the home territory. The resultant probability distribution functions were then used in the behavioural model. As they inevitably affected dispersal rates (and, consequently, the probabilities of eviction that they described), the same analyses were performed iteratively, using the output from the behavioural model. The process was iterated 30 times, until coefficient values for the probability functions were approximately stable (within the limits of a stochastic program) and any slight inconsistencies did not affect the frequency of dominant evictions. The final probability functions produced by this process were (males: model $\chi^2 = 5886$, d.f. = 6, $P < 0.0001$; females: model $\chi^2 = 7970$, d.f. = 7, $P < 0.0001$; only significant coefficients were retained):

$$pD_m = \frac{1}{1 + e^{(2.8 - 0.08t - 0.006G - 0.1N - 0.06H + 0.01tN + 0.001tNH)}} \quad \text{eqn A2}$$

$$pD_f = \frac{1}{1 + e^{(2.7 - 0.03t - 0.007G - 0.2N - 0.13H + 0.02tN - 0.024tH + 0.003tNH)}} \quad \text{eqn A3}$$

where pD = annual probability of displacement by eviction for male (m) and female (f) dominants; t = number of useable territories linked to the focal territory; G , N , H = number of potential dispersers of the relevant sex at the start of the year, throughout the whole population, in the neighbourhood and in the home territory, respectively.

Finally, the average number of young raised to yearling annually in a territory of given quality, m_{xi} , was calculated as:

$$m_{xi} = pR \times r \times \bar{L} \times l_{js} \times l_{jw} \quad \text{eqn A4}$$

where pR = probability of reproduction (Table 3); r = relatedness of parent to offspring (= 0.5); $\bar{L}$ = mean litter size (Table 3); l_{js} = summer survival of juveniles (Table 3); l_{jw} = winter survival of an average juvenile,

assuming average weaning mass and the presence of two adults in the territory, and accounting for the territory quality (and its effect on mean winter length).

EXPECTED LIFETIME FITNESS FROM DEFERRING A TRANSITION FOR 1 YEAR

Survival of dominants and juveniles is affected by the presence of subordinate adults (Table 5). The benefits of remaining subordinate therefore included the increased survival of related juveniles, assuming these were present (only applicable during the second and third of the active periods). The fitness benefits of remaining subordinate also incorporated the potential of making a state transition in the following year, calculated as in equation A4 but based on the animal being 1 year older. The benefits of remaining subordinate were thus summarized as follows:

$$w_S = j \cdot r_j \cdot l_{js}(l_{jw_a} - l_{jw_{a-1}}) + l_S w_{d[A+1]} \quad \text{eqn A5}$$

where j = number of juveniles present in the natal territory; r_j = relatedness of the subordinate to the juveniles; l_{js} = juvenile summer survival; l_{jw} = juvenile winter survival in the current territory, in a group containing n adults; l_S = annual survival of subordinate adults; $w_{d[A+1]}$ = total fitness from dispersing next year, assuming the same conditions as are available this year, except that the individual will be 1 year older.

DIFFERENCES IN FITNESS CALCULATIONS ACCORDING TO TIMING OF STATE TRANSITION

The process of state transitions was the same during each active period, with the exception that the reproductive and late summer periods differed from the post-emergence period in two ways. First, by this stage any young have been born, dispersers could not reproduce until the following year, and hence residual reproductive value for any territory was calculated as

$\sum_{x=0}^{\infty} l_x m_x$ rather than $\sum_{x=0}^{\infty} l_x m_x$ (see equation A1). Secondly, for individuals making a transition in the reproductive or late summer periods, $w_{d[A]}$ is based on their first potential reproduction taking place during next year's reproductive season. If, however, they were likely to be in the next year's early disperser proportion, the benefits of staying could also incorporate the benefits of reproducing next year. The total number of next year's potential dispersers (including all remaining subordinate adults and this year's yearlings) was expected to reduce by death or dispersal, while there would also be some randomized sorting of animals of equal ages. For simplicity, therefore, it was assumed that if a given subordinate was likely to be in the top 10% of next year's queue, then calculations of $w_{d[A+1]}$ would be based on dispersing during the post-emergence period in the next year, with first potential reproduction in the same year.

* should read
x = 1