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Social 'meltdown' in the demise of an island endemic: Allee effects and the Vancouver Island marmot

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Summary

1. More than 75 years have passed since W.C. Allee proposed that breakdowns in sociality may shift animal populations to inverse density dependence at small sizes and thereby hasten spirals to extinction. Despite decades of attention, empirical evidence of this 'Allee effect' in wild populations remains scarce.

2. Here, we report on findings from a multi-year study of the population ecology and behaviour of the critically endangered Vancouver Island marmot (*Marmota vancouverensis*) and present quantitative evidence of an Allee effect and highlight the mechanisms that drive it.

3. The V.I. marmot is a large, social rodent endemic to Vancouver Island, Canada, and its population has declined by 80–90% since the 1980s. The species currently is represented in the wild by roughly 200 individuals.

4. This study compared characteristics of contemporary V.I. marmots (2002–2005) with (i) animals in the same population at an earlier time period (1973–1975) and (ii) congeners. Specifically, data on time allocation, social activity and ranging behaviour of animals in colonies in the late stages of decline were compared with historical data collected from colonies under more stable demographic conditions.

5. We found that contemporary V.I. marmots had home ranges that were 10–60× larger than historic animals and congeners, interacted with conspecifics at 10% of the historic rate, devoted 10× more time to anti-predator vigilance, and abandoned the bi-modal activity patterns previously described for this and other marmot species. Contemporary marmots also showed an 86% decline in feeding rate, and entered hibernation on average 20 days later than animals in historic populations.

6. Combined with results showing reduced *per capita* survival and reproduction in contemporary marmots, these findings suggest a strong role for Allee effects in the current plight of the Vancouver Island marmot. A positive link between aspects of fitness and population size emphasizes the need to identify threshold colony sizes and densities necessary to promote recovery. We discuss this and other implications of this species' social 'meltdown'.

Key-words: inverse density dependence, mate-searching, movement analysis, population dynamics, predator avoidance, threshold effects

Introduction

Exploring the contributions of density-dependent and independent processes to population persistence is an enduring theme in ecological research (e.g. Chitty 1960; Sinclair 1989; Henle, Sarre & Wiegand 2004; Green 2008). Almost 80 years ago, Allee (1931) speculated that social changes accompanying the attrition of aggregated populations might hasten population decline or prolong recovery time. More recent applied and theoretical efforts have connected this classical notion of 'Allee effects' with investigations of linearity and nonlinearity in rates of population growth (Freckleton *et al.* 2005; Oborny, Meszéna & Szabó 2005; Ferrer & Penteriani 2008). In particular, the idea of threshold relationships, wherein species exhibit abrupt shifts in the pace or direction of demographic change at low population size or density, has become a fundamental topic for those concerned with the management of small populations and the evolution of animal sociality (e.g. Creel & Creel

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1995; Stephens *et al.* 2002; Courchamp, Berec & Gascoigne 2008).

With the exception of biological control and large-scale reintroduction studies, opportunities to investigate the effect of population size on components of fitness in wild populations are limited. Studies of experimentally manipulated populations under a range of ecological scenarios generally support theoretical predictions on the scale and impact of Allee effects (e.g. Hutchings & Reynolds 2004; Berec, Angulo & Courchamp 2007). Yet, attempts to experimentally stimulate Allee effects in natural populations, particularly those of vertebrates, are usually impractical and unethical. Thus, some of the best opportunities to study Allee effects in nature come from 'natural experiments', such as those caused by catastrophic events, or through the intensive study of populations fluctuating greatly in size (Courchamp, Clutton-Brock & Grenfell 1999). Although it is now widely accepted that population density and group size affect population dynamics across a range of taxonomic groups, body sizes and mating systems (Kokko & Sutherland 2001; Gascoigne & Lipcius 2004), few empirical studies have demonstrated the mechanisms that create inverse density dependence in wild populations (Stephens *et al.* 2002; Kramer *et al.* 2009).

Here, we test for empirical evidence of Allee effects in the decline and impaired recovery of the Vancouver Island marmot (*Marmota vancouverensis*; Swarth 1911; hereafter VIM), and attempt to identify the mechanisms that may drive such effects. Like other highly social squirrels, VIM historically occurred in dense colonies where members benefited from group vigilance, anti-predator alarm calls, communal burrow maintenance, and access to mates in neighbouring colonies (Blumstein, Daniel & Bryant 2001). Between 1973 and 2006, the estimated wild population of VIM declined from at least 300 individuals to fewer than 35 (Janz *et al.* 2000), with concurrent declines in colony size from an average of 8·3 animals per colony in 1973 to 3·6 in 2006 (Heard 1977). The 90% decline in population size also drove increased isolation of colonies from a mean inter-colony distance of roughly 3·5 km in the early 1980s to more than 20 km in 2006. In sharp contrast to predictions of density-dependent population growth, *per capita* growth of VIM from 1970 to 2007 was positively correlated with population size (Fig. 1). Furthermore, intensive study of more than 400 known animals from 1986 to 2007 showed *per capita* reproduction also declined at smaller population sizes while mortality due to predation increased significantly (Bryant & Page 2005). As group sizes and proximity to neighbouring colonies declined, possible mechanisms for Allee effects and observed inverse density dependence in this species (and others) include (i) increased ranging behaviour associated with impaired mate-finding, (ii) reduced predator detection/avoidance, and (iii) reduced foraging resulting from increases in vigilance or selection of safer, but less productive habitats (Sutherland 1998; Stephens & Sutherland 2000).

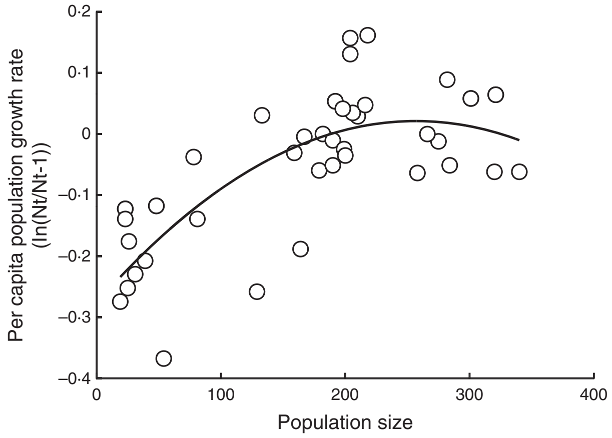

Fig. 1. Annual counts of free-living V. I. marmots reveal strong inverse density dependence in *per capita* population growth from 1970 to 2007. Trend line represents least-squares quadratic fit ($R^2 = 0{\cdot}55$). Data exclude animals introduced from captivity.

We hypothesized that observed reductions in colony size and proximity would affect the time allocation, and movement and social behaviour of individual VIM and, through these changes, contribute to recorded declines in survival and reproduction (Table 1). Specifically, we predicted that relative to congeners and historic VIM, current VIM would exhibit: (i) greater ranging behaviour, presumably as a result of impaired mate-finding, with un-paired adults and males showing the greatest movement; (ii) lower rates of social interaction and cooperative behaviour – even when controlling for differences in group sizes; and (iii) a shift in time allocation towards increased vigilance and reduced foraging and resting time.

Materials and methods

STUDY POPULATION

The V.I. marmot is a large (4–6 kg), fossorial rodent endemic to Vancouver Island, British Columbia, Canada. The species historically occurred widely across the 31 000-km^2 island (Nagorsen, Keddie & Luszcz 1996), but as of 2006 was represented in the wild by only 32 adult animals divided among six colonies. Approximately 170 animals are held in four captive-breeding facilities. The species is distinct from other marmots in skull morphology and pelage (Nagorsen, Keddie & Luszcz 1996; Cardini, Thorington & Polly 2007), behaviour (Heard 1977), and vocalizations (Blumstein 1999). VIM are diurnal, consume a wide variety of grasses and forbs (Martell &

Table 1. Predicted trends in the behaviour and ecology of contemporary Vancouver Island marmots relative to historical colonies and congeners assuming Allee effects

Category	Predicted trend (↑ or ↓)
Movement/home range size	↑ Most pronounced in singles and males
Sociality	↓ Social and cooperative interactions
Time spent in cover	↑ Time underground
Vigilance	↑ Time scanning for threats
Foraging efficiency	↓ Time spent feeding (proportion of total time), ↑ vigilance while foraging

Milko 1986) and use underground burrow systems for rest and escape during the 5-month active season (May–September) prior to hibernation (October–April). They are relatively long-lived, up to 14 years in captivity and 8 years in the wild. There is a single breeding season shortly after emergence from hibernation in early May and one to seven pups (mean 3·4) are born after a gestation of 30–32 days. Young males face reproductive suppression and aggression from adult males and typically disperse to new colonies at *c*. 2–3 years of age (Janz *et al.* 2000).

From April 2002 to May 2005, excluding periods of hibernation, we conducted daily focal observations and radiotelemetry tracking of 38 adult (2 + years) and juvenile marmots (1–2 years) at four colonies (Fig. 2). Our sample size varied from 12 to 18 individuals among years and accounted each year for 50–75% of the total, known wild population. Our research took place at two sites: (i) the largest extant colony, Mt. Washington and (ii) at three adjacent colonies characterized together as the 'Nanaimo Lakes group' [Green Mt., Mt. Moriarty and Heather Mt. (Fig. 2; the relative contribution of data from the two sites is detailed in Table S1)]. These colonies have been continuously inhabited for at least 50 years (Nagorsen, Keddie & Luszcz 1996), and habitat in the area is characterized by steep forested slopes at elevations of 700–1300 m surrounding isolated patches of rock talus and subalpine meadow.

FIELD METHODS

Data on ranging, sociality and activity budgets were first collected on VIM in the Nanaimo Lakes area by Heard (1977) in 1973, 1974 and 1975 when populations appeared to be stable ($N \approx 350$). To test for changes in the ecology of VIM that might indicate an Allee effect, we used the same focal sampling methods (Altman 1974) employed by Heard (1977) to gather comparable data on time budgets, social interactions and ranging activity during 2002–2005, a period far into the species' decline ($N \approx 30$). To further minimize bias in comparisons between historic and contemporary data, we used Heard's (1977) ethogram and behavioural categories during our sampling.

Our study was limited to wild marmots individually ear-marked and implanted with radiotransmitters to allow telemetric tracking. Bryant (1998) described the transmitters, and capture and implant techniques. All marmots studied were of known sex and age. Monthly monitoring of implanted individuals has occurred from 1986 through today in a basic effort to document annual mortality, reproduction and distribution of VIM (Janz *et al.* 2000). From 2002 to 2005, 38 individuals were observed on a more intensive schedule from emergence (May 1) to the onset of hibernation (mid-October). This sample represented 70% of the known surviving wild population at the time of the study.

Fig. 2. Map of Vancouver Island, Canada with stars indicating the general location of V. I. marmot subpopulations included in this study.

HOME RANGE ESTIMATION

For both the historic (Heard 1977) and current period, home ranges were estimated using locations collected daily on known individuals across the 5-month active seasons. For 2002–2004, when a marmot was first located each day, the observer recorded its GPS position; measurements were considered accurate to within ±6 m. Data points were plotted using Home Range, Movement and X-tools extensions in ArcView 3.2 (ESRI 1996; Hooge 1999) and the Home Ranger program (Hovey 1998). We used a minimum of 35 distinct locations distributed evenly from May to October (mean = 88, range 35–129) to estimate annual ranges over an active season (Seaman *et al.* 1999). A maximum of one location was gathered per day during 2002 and 2003. In 2004, collection was intensified to characterize range size by month; this entailed a maximum of two measurements per animal per day, each at least 5 h apart (typically in the morning and afternoon). This sampling produced a minimum of 34 location observations per animal per month. The distribution and frequency of our spatial sampling was designed to minimize the potential for temporal or other biases caused by over- or under-sampling (de Solla, Bonduriansky & Brooks 1999). Home ranges were plotted using the fixed nonparametric kernel (density probability) method with a grid resolution of 255. To allow comparison with other studies, home range also was estimated using the minimum convex polygon method.

The minimum linear distance between successive independent locations was used in addition to total range size to assess travel costs and to determine if patterns in movement differed between males and females. This was measured using the formula:

$$d = \sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2},$$

where d is the shortest distance between two successive locations, and x_1, x_2 and y_1, y_2 are the Northing and Easting bearings for each point in Universal Transverse Mercator. Changes in elevation during travel were not included in calculating distance moved.

SOCIALITY AND TIME ALLOCATION

Behavioural data in both the historic and current period were gathered using a focal sampling approach (Altman 1974), thus allowing direct comparisons of data collected from 1973 to 1975 with those from 2002 to 2004. A randomized protocol was used to ensure equal coverage of animals and sample times, and to minimize observer and sampling biases related to the duration, onset and termination times of a sampling event. Instantaneous activity was scored for each animal at 1-min intervals for 60 consecutive minutes. All behaviours were observed from a distance of 40–300 m with 10× binoculars and 60× spotting scopes. Study animals were habituated to human presence and reliably identified from their radiotelemetry frequencies, ear tags and moult patterns.

In every month of the active season, each marmot was observed for > 12 h while the animal's transmitter was active (typically 6 am–

6 PM; transmitters functioned on a 12-h on–off cycle to prolong battery life). The 38 focal individuals were studied for a combined total of more than 1800 observation hours across the multi-year study. Each year, a small number of animals were added to the population (i.e. were discovered and implanted), while others died or were removed to augment captive stocks.

Methods of Martin & Bateson (1993) were applied to both historic and current data to quantify activity budgets for feeding, resting (lying or sitting) and time spent in-burrow. Historic behavioural data from Heard (1977) were analysed from means ± SE for each individual marmot or calculated from raw monthly data for each individual studied. Less frequent behaviours, such as social interactions or alarm calling, were expressed in both historic and current data sets as occurrences per animal per hour of observation. The degree of sociality observed in a marmot colony probably depends on the number of its members, thus, to ensure that interaction rates from the past and present came from similar group sizes, interaction rates from Heard's (1977) two study sites (mean colony size = 8·3; monthly range 4–17, Mt. Haley, Green Mt.) were compared with our largest colony (mean local population size = 12·0; range 5–15, Mt. Washington). Therefore, if colony size biases interaction rates, it should favour higher rates of social behaviour in the current rather than historical population.

STATISTICAL ANALYSES

For data from historic and current periods, Kolmogorov–Smirnov tests were used to compare distributions and Mann–Whitney *U*-tests to compare medians when data were not distributed normally. Data were pooled only where within-individual variance was larger than that observed between individuals and sample sizes were similar (Leger & Didrichsons 1994). After confirming that variation between years was greater than that recorded between individuals, observations of individuals from different years were treated as independent (see also Barash 1989; Hoogland 1995; Blumstein & Arnold 1998). Results are presented as means ± SE. In addition to historical data, data from recent studies of other marmot species also were used for comparison (see Blumstein, Daniel & Bryant 2001 for a discussion of this approach).

Results

DEMOGRAPHIC EVIDENCE OF AN ALLEE EFFECT

From 1970 to 2007, wild VIM showed strong inverse density dependence, with annual p*er capita* growth positively correlated with population size ($R^2 = 0·55$, $N = 38$, $P < 0·01$; Fig. 1). Also consistent with an Allee effect, individual VIM observed monthly from 1986 to 2007 showed a positive relationship between *per capita* reproduction and population size ($R^2 = 0·72$, $N = 38$, $P < 0·01$; see also Bryant & Page 2005).

RANGING

Home range estimates for current and historic VIM are summarized in (Table 2). The mean home range of 38 adult males and females from 2002 to 2005 was 88·6 ± 8·1 ha. Home ranges of males were on average 45 times larger than values recorded in 1973–1975 (Table 2; Fig. 3). Home ranges of adult females (including three females that weaned pups) were 30 times larger on average than those recorded in 1973–1975 (Tables 2 and S2). Despite dramatic differences in historic and current home ranges of both male and female marmots, the 90% kernel range size for modern females (73 ha; Table S2) was only 32% smaller than that of modern males (108 ha). Home ranges of contemporary females are an order of magnitude higher than those observed for males in 1973–1975. Minimum distances moved between independent

Table 2. Comparison of marmot activity and behaviour in 1970s and 2000s [1970's data are from Heard 1977. Where appropriate, data are presented as mean ± SE; [range] (*n*)]

Activity	1973–1975	2002–2005	Statistical significance
Ranging			
Home range (ha)	2·4 ± 0·6 [0·5–4·5] (6 ♂, 3♀, 3?)	88·6 ± 8·1 [25–201] (24 ♂, 14♀)	$P < 0·001$
Time budgets[a]			
Daily activity	Bimodal	Unimodal	K–S test; $P < 0·001$
Total time allocated to feeding	25·0 ± 4·5%	3·5 ± 0·4%	$U = 25, n_1 = 5, n_2 = 5, P < 0·001$
Total time allocated to resting	34·3 ± 4·4%	23·4 ± 1·6%	$U = 23, n_1 = 5, n_2 = 23, P = 0·03$
Total time allocated to burrow use	35·0 ± 7·6%	64·0 ± 4·6%	$U = 23, n_1 = 5, n_2 = 23, P = 0·03$
Sociality			
Greeting rate[b]	0·55 ± 0·06	0·05 ± 0·02	$U = 25, n_1 = 5, n_2 = 23, P < 0·001$
Interaction rate[c]	1·12 ± 0·27 (28)	0·18 ± 0·04 (29)	$U = 25, n_1 = 5, n_2 = 23, P < 0·001$
Affiliative : Agonistic interactions	1·68	0·54	$U = 18, n_1 = 5, n_2 = 23, P < 0·05$
Alarm call rate	0·34 h^{-1}	0·07 h^{-1}	$x^2 = 157$, d.f. $= 1, P < 0·01$
Other			
Hibernation date[b]	September 18 [September 16–21] (28)	October 7 [October 3–19] (26)	$U = 710, n_1 = 28, n_2 = 26, P < 0·001$

[a] Tests and standard errors calculated using a single mean for each month which combines all individuals across all years. Heard (1977) did not report standard errors or mean activity budgets for individuals.

[b] Calculated from monthly means. Rates are incidence per animal per hour of observation.

[c] All marmots, all social acts combined. Rates are incidence per animal per hour of observation.

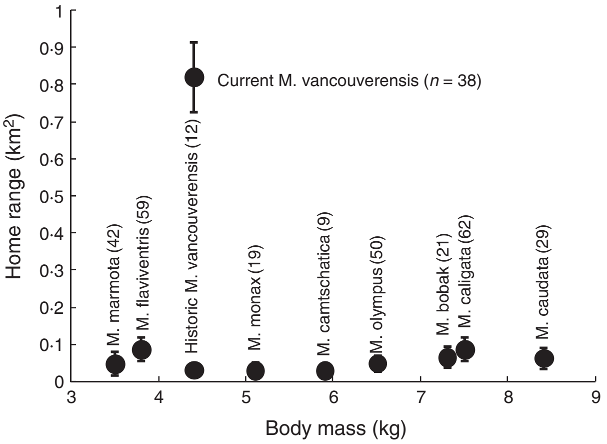

Fig. 3. Home range size (mean ± SE) in relation to average adult body mass for eight species of marmots (*Marmota* sp.). The V. I. marmot (*Marmota vancouverensis*) is divided into estimates of current (2002–2005; this study) and historic home range size (1973–1975; Heard 1977). Sources of data for all other species are provided in Table S2. Estimates were calculated as, or, when possible, converted to, 95% minimum convex polygons to aid comparison.

locations differed by sex, with males moving almost twice as far (Table S2). Except for two adult females whose home ranges were distinct, all 90% annual kernel estimates for colonies showed overlap.

Insufficient variation in group size and low statistical power prevented rigorous tests of an effect of group size on ranging behaviour. Nevertheless, adult male marmots that emerged from hibernation with a female from 2002 to 2005 (highly suggestive of a reproductive pair) showed smaller home ranges than unpaired males (*U*-test: $U = 77, n_1 = 11, n_2 = 9, P < 0{\cdot}01$). Also, despite small samples sizes, females with pups in an active season showed significantly smaller home ranges than non-breeding females ($U = 34, n_1 = 5, n_2 = 8, P = 0{\cdot}05$).

SOCIALITY AND TIME ALLOCATION

Vancouver Island marmot in 2002–2005 showed mean greeting rates one-tenth as frequent as observed in animals during 1973–1975, and modern social interaction rates were less than one-twentieth of historic rates (Table 2). The ratio of greetings to agonistic behaviours also changed significantly over the 30 years between studies. Animals in 2002–2005 showed fewer greetings while engaging in significantly more fighting and chasing (Table 2). The fraction of above-ground time spent near any conspecific (< 100 m; a distance within which marmots are likely to detect alarm calls and maintain visual contact) during 2002–2005 was 38·5%. When nearest neighbours that were below ground were excluded, this value falls to 14·5% (mean distance between conspecifics = 25·5 m, SD = 31·3 m, $n = 7665$ measurements). Seventy-eight anti-predator alarm calls were recorded in more than 1200 h of focal sampling in 2002–2005 (modern call rate = 0·07 h^{-1}), significantly less than the 212 alarm calls in 626 h of observation that were recorded 30 years ago (historic call rate = 0·34 h^{-1}; Table 2).

Analysis of activity data showed that in 2002–2005 VIM entered hibernation in the first week of October, *c.* 3 weeks later than they did 30 years ago ($P > 0{\cdot}001$; Table 2). Immergence dates from the 1980s (September 26–October 3, $n > 70$) fall between these extremes, and, thus, are consistent with a trend towards increasingly delayed immergence (Bryant & Page 2005). Modern VIM not only hibernated for shorter periods, they also fed less than animals observed in the 1970s (Table 2; Fig. 4). Contemporary animals also allocated less time to above-ground activity during the beginning (May–June) and end (September–October) of each active season (Table 2; Fig. 4). The proportion of total time spent each month resting above ground has also decreased over time (Table 2; Fig. 4). Furthermore, the timing of peak activity associated with feeding and movement in 2002–2005 generally correspond to periods of low activity during 1973–1975.

In addition to monthly shifts in time allocation, contemporary marmots also differed from historical colonies in daily time budgets. Modern animals were less active in the morning and evening periods, and more active at midday than in the 1970s (Table 2; Fig. S1). Time spent in the burrow by

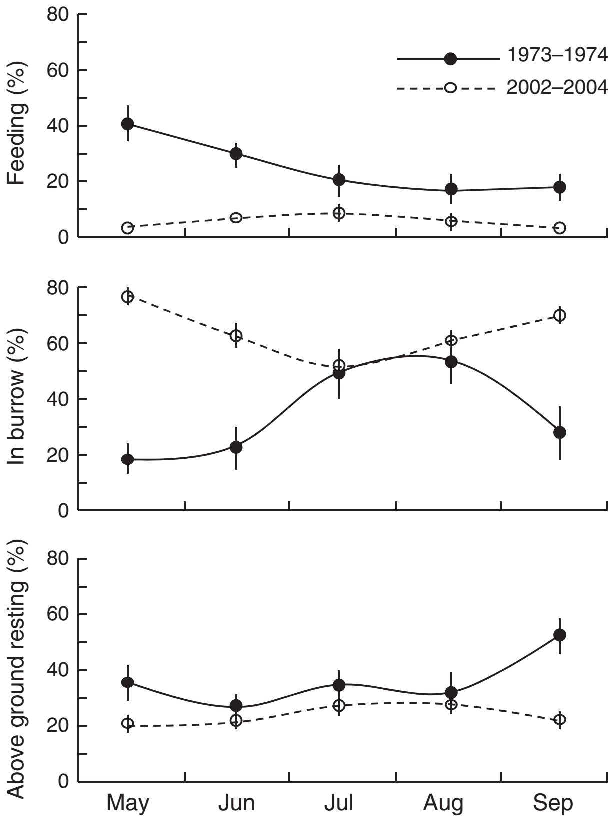

Fig. 4. Percentage of total time that historic ($n = 626$ h; solid line) and modern ($n = 1724$ h; dotted line) V. I. marmots devoted to feeding, below-ground activity, and resting (sitting and/or lying) above ground from May through September (bars are ± SE calculated from hourly means for all marmots in a given month).

contemporary VIM accounted for 63 ± 2·5% of all observations. Only 6·3 ± 0·3% of above-ground activity was spent moving. Far more time above ground was devoted to vigilance ('head-up' = 66 ± 2·2%) than non-vigilance ('head-down' = 34 ± 1·8%). Time allocated to feeding represented 3·5 ± 0·4% of all activity and 7·5 ± 0·7% of above-ground activity. The percentage of time spent vigilant during foraging bouts was 60·1 ± 2·14. In total, the amount of time VIM devoted to feeding in 2002–2005 was < 15% of that observed in the 1970s (Table 2).

Discussion

Empirical evidence of Allee effects acting on small populations is notoriously and inherently elusive (Courchamp, Berec & Gascoigne 2008). Small sample sizes combined with complex additive and synergistic effects of changes in such factors as movement ecology, mating systems, predator–prey interactions and habitat selection at low animal densities often undermine efforts to isolate Allee effects from environmental or other stochasticity (Courchamp, Berec & Gascoigne 2008; Gascoigne *et al.* 2009). Nevertheless, our long-term monitoring data (Fig. 1) and comparisons of ranging, sociality and time budgets between current and historical VIM support our predictions (Tables 1 and 2) and provide strong evidence of Allee effects in this critically endangered species. The significance and scale of aberrations in contemporary VIM ecology and behaviour are made more apparent by comparisons with closely related species. Our findings show home ranges of VIM from 2002 to 2005 were more than 10 times larger than that observed in any study of a social marmot (Fig. 3). This pattern was observed not only in males, which may be expected to travel greater distances in mate-searching at low population densities, but also female marmots, which are typically philopatric (Barash 1989). Comparisons of activity patterns and social behaviour for historic and contemporary VIM, and congeners, paint a similarly striking picture of the behaviour of current VIM. VIM today show significantly lower rates of social interaction and alarm calling and higher rates of intraspecific aggression and vigilance. Daily activity budgets of modern VIM also deviate from the pattern of bimodal activity reported for hoary marmots (*Marmota caligata*), a sister species, and virtually every other montane marmot species (Barash 1989). We elaborate on these results and their implications below.

RANGING

Detailed studies of marmot ecology (e.g. Armitage 1962; Barash 1989; Blumstein & Arnold 1998) report movements of > 200 m by focal animals, but these movements are rare and nearly always attributed to mate-searching or dispersal by subadults early or late in the active season. In contrast, extremely large home range size and movements were exhibited by adults in each month of our study. We directly observed a total of 54 cases in which an adult marmot moved at least 500 m within a 2-h period, and repeated sightings over consecutive days suggested even greater movements (e.g. 15·8 km over 6 days). Reduction in the size and number of colonies, changes in colony composition, and an increase in the distance between colonies all may explain today's larger territories. Increases in ranging come with higher energetic costs and risk of predation; marmots engaged in long-distance travel are more likely to visit unfamiliar areas or areas without escape burrows and thereby expose themselves to predators. This supposition is supported by our observations of marmots hiding under logs, in snow depressions and around tree bases and sometimes fleeing in the open for distances > 600 m without pause when faced with a threat. Taken together, these large increases in home range size observed at low animal density reflect an Allee effect in VIM and suggest direct costs associated with this effect.

Dramatic differences in historic and contemporary VIM home ranges are interpreted here as strong evidence of increased mate-searching and a deviation from 'normal' marmot ecology; however, there are three alternative explanations for this result. First, it is possible that differences in methods used in 1972–1974 and 2002–2005 create a misleading result. Secondly, it is possible that the extensive ranging observed in current VIM is not due to increased mate-searching, but instead a result of changes in forage quality or distribution. Thirdly, a majority of individuals (Table S1) in this study are from colonies 100 km from the site of Heard's (1977) study and it is possible that limited geographical overlap between the two time periods has created a misleading result. Each of these alternatives were considered and tested at length. First, Heard (1977) quantified VIM home ranges without the use of radiotelemetry and, thus, may have underestimated animal movements. Yet, an analysis limited to a subset of five individuals for which we had sufficient observations without the use of telemetry, produced estimates that fell within the range of our other results. Lastly, Heard's (1977) historic VIM range estimates are very similar to those reported for studies of other marmot species in which radiotelemetry was used (e.g. Salsbury & Armitage 1994; Blumstein, Daniel & Bryant 2001; Griffin 2007; Kyle *et al.* 2007; Maher 2009; Fig. 3), which strongly suggests that the differences in ranging we report are genuine (see also Fig. S2).

Secondly, changes in resource abundance or distribution, perhaps driven by climate change, also may explain the differences in ranging we observed between historical and contemporary VIM. However, vegetation surveys in historically occupied habitats indicate that these meadows have high abundance and diversity of known food plants. Although some sites have experienced moderate tree encroachment (Laroque, Lewis & Smith 2001), descriptions and photographs of plant communities at both Mt. Washington and Haley Mt. have changed little from the early 1970s (Heard 1977), through the 1980s (Martell & Milko 1986), 1990s (Demarchi *et al.* 1996) and early 2000s. Moreover, our own assessment of the abundance and distribution of known food plants, based on repeated monitoring of plant sampling plots (J.S. Brahares, unpublished results), showed no difference in preferred foods between extinct and extant colony sites or between the starting and ending points of long-distance marmot movements. Lastly, the fact that unpaired adult males and females showed the largest home ranges further suggests that the unusual ranging of contemporary VIM is better explained by observed changes in demography than shifting habitat quality.

Thirdly, countless studies have shown that behaviour, including ranging, will be influenced by local conditions. The differences we observe in VIM ranging and other behaviours between the two time periods may partly be explained by the fact that current sampling included the large Mt. Washington colony that was not considered by Heard (1977). However, a comparison of activity, ranging, alarm calling and social behaviour between current marmots at the Mt. Washington and Nanaimo Lakes colonies reveals no statistical differences ($N = 9$ and 29; $P > 0{\cdot}10$ for all comparisons; Table S1). In fact, contrary to the argument that geography rather than Allee effects explains our results, current ranging distances were qualitatively, although not statistically, higher for animals in the Nanaimo Lakes region where Heard conducted his work than at Mt Washington (mean = 104 vs. 86 ha). Lastly, the colonies included in this study occur within the same mountain range and at matching elevations, slopes and aspects. Furthermore, the diet of marmots was indistinguishable across sites as was, more broadly, the composition of local flora and fauna, including predators.

SOCIALITY AND TIME ALLOCATION

In contrast to other social marmots where roughly 90% of time is spent within 20 m of other colony members (K. B. Armitage, pers. comm.), contemporary VIM lead solitary lives and we observed no stable social groups from 2002 to 2005 (i.e. cases where an adult marmot regularly spent time within 20 m of one or more adult conspecific). Almost every animal in our study remained alone despite a demonstrated awareness of others. Alarm calling in response to a perceived threat, long held as a signature characteristic of marmot sociality (Barash 1989; Blumstein, Daniel & Bryant 2001), is notably rare in contemporary VIM (Table 2) and, combined with increases in rates of agonistic interactions and declines in affiliative behaviour, suggests a general decline of sociality in this species. The current rarity of alarm calling cannot be explained by a decline in predators or predation as both increased between 1970 and 2008 (Bryant & Page 2005). It is important to recognize that changes in VIM over time may reflect behavioural plasticity (adjustments to low density) or phenotypic shifts in mean 'personality' created by sharp selection against certain personality types, in this case, animals predisposed to affiliative and alarm-calling behaviour.

In addition to striking changes in social behaviour, VIM spent less time feeding in 2002–2005 (3·5% of all activity) than they did in 1973–1975 (25% of all activity), and also less than any other marmot species. Armitage *et al.* (1996), for example, reported foraging as a major activity for *Marmota flaviventris*, which occupied between 12% and 23% of each day, and *Marmota caudata* and *M. caligata* spend upwards of 30% of their time feeding (Blumstein & Arnold 1998; Karels, Kopel & Hik 2004). The decline in feeding rate observed in VIM may partly be explained by increases in anti-predator behaviour. Contemporary VIM spend nearly two-thirds of their time above-ground scanning for predators; nearly twice the rate observed in any other marmot species (Table S4). Such vigilance reduces time available for foraging and/or reduces foraging efficiency (Carey & Moore 1986; Blumstein *et al.* 2004) and might be expected to reduce body mass gain during the active season. Low mass gain, in turn, can delay hibernation (Shubin, Abelentsev & Semichatova 1978) and lead to high over-winter mortality (Barash 1989). Barash (1973) observed similar costs to solitary life in *Marmota olympus*; solitary marmots doubled the time they devoted to vigilance and scanning compared to colonial individuals. Schwartz & Armitage (1997) found that group-living raised lifetime reproductive fitness in yellow-bellied marmots. Interestingly, Blumstein, Daniel & Bryant (2001) reported slightly lower, but still high levels of vigilance (40%) in VIM in 1998 when the species was in the process of decline and represented by *c.* 100 animals in the wild.

Contemporary VIM show major shifts in circadian and circannual activity patterns that suggest far-reaching effects of low population density on their ecology (Table 2; Figs 4 and S1). We hypothesize that significant declines in feeding rates and a delay in hibernation are a direct result of increased ranging and anti-predator behaviour. However, shifts in hibernation period, in particular, have been linked to climate change for other marmot species (Inouye *et al.* 2000) and may play a role in the patterns we observe.

ALLEE EFFECTS

Researchers have struggled with a framework for understanding and comparing the contribution of Allee effects to population dynamics (Courchamp, Berec & Gascoigne 2008). For example, the terms 'strong' and 'weak' or 'critical' and 'non-critical' have been proposed to distinguish Allee effects where *per capita* growth is positively related to population size from those where it is not, or cases where *per capita* growth becomes negative (indicating extinction thresholds) from situations where it does not (Taylor & Hastings 2005; Courchamp, Berec & Gascoigne 2008). In the case of VIM, our results here and other work show strong inverse density dependence in *per capita* growth (Fig. 1; Bryant & Page 2005) and our behavioural studies suggest mechanisms by which Allee effects may drive reduced reproduction and increased rates of mortality with declining animal density. However, determining the full strength of Allee effects and their specific implications for future recovery of VIM will only be possible through experimental reintroductions in conjunction with intensive study of VIM demography. The potential for just such an experiment increases each year thanks to the early success of efforts to reintroduce captive-born marmots to the wild. The VIM reintroduction programme has begun to re-establish recently extinct colonies while augmenting surviving colonies with released individuals (D. Doyle, pers. comm.). If current rates of re-establishment are maintained, it will be less than a decade before VIM return to densities and colony sizes observed by Heard (1977) in the early 1970s. There should be no doubt, due to the work of many, that the species will be pulled away from the brink of extinction, but whether VIM can move back over the population threshold and rediscover 'natural' social behaviour is a question that can only be answered by future researchers.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Diurnal activity patterns of current and historic Vancouver Island marmots (VIM) and a sister species, *Marmota caligata* (*M. caligata* data adapted from Barash 1989; historic VIM data adapted from Heard 1977).

Fig. S2. Demographic composition of historical and recent VIM study populations. Question mark denotes the individuals that Heard (1977) was unable to sex in his study area. The inset figure shows the combined male and female age structure. Differences in age or sex ratios between time periods could confound efforts to compare the two periods, however, the age and sex structure is similar in the two studies.

Fig. S3. An example of 90% and 50% kernel home range estimates for two marmots included in this study. The first estimate (green, light green) shows a 5·15-km^2 home range of an adult male as determined using 48 observations collected from May to August 2003. The second estimate (shades of purple) shows the 0·64-km^2 home range of an adult female with pups as determined using 31 observations from May to August 2003.

Fig. S4. Potential feedback mechanisms associated with an Allee effect in marmots and other social animals.

Fig. S5. Habitat of the Vancouver Island marmot in the Nanaimo Lakes region, British Columbia (photo by J. Werner).

Fig. S6. Vancouver Island marmot, *Marmota vancouverensis* (photo by J. Werner).

Table S1. Relative contribution of data on current (2002–2005) Vancouver Island marmots from the Nanaimo Lakes and Mt. Washington subpopulations used in this study. Statistical comparisons test for differences between marmots at these two sites in 2002–2005 and also for each site in 2002–2005 with data collected in the Nanaimo Lakes subpopulation in 1973–1975.

Table S2. Comparison of kernel range estimates and minimum recorded distances between successive independent locations for males and females from 2002 to 2005 (range shown in brackets).

Table S3. Sources of data for comparisons of home range estimates across species of the genus *Marmota*.

Table S4. Proportion of time dedicated to anti-predator behaviour for seven species of marmots.