Socially informed random walks: incorporating group dynamics into models of population spread and growth

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Simple correlated random walk (CRW) models are rarely sufficient to describe movement of animals over more than the shortest time scales. However, CRW approaches can be used to model more complex animal movement trajectories by assuming individuals move in one of several different behavioural or movement states, each characterized by a different CRW. The spatial and social context an individual experiences may influence the proportion of time spent in different movement states, with subsequent effects on its spatial distribution, survival and fecundity. While methods to study habitat influences on animal movement have been previously developed, social influences have been largely neglected. Here, we fit a ‘socially informed’ movement model to data from a population of over 100 elk (*Cervus canadensis*) reintroduced into a new environment, radio-collared and subsequently tracked over a 4-year period. The analysis shows how elk move further when they are solitary than when they are grouped and incur a higher rate of mortality the further they move away from the release area. We use the model to show how the spatial distribution and growth rate of the population depend on the balance of fission and fusion processes governing the group structure of the population. The results are briefly discussed with respect to the design of species reintroduction programmes.

Keywords: correlated random walk; group dynamics; biphasic movement; radio-collar; Global positioning system data; elk

1. INTRODUCTION

Global positioning system (GPS)–satellite collars can provide frequent and accurate data about the locations of individual animals and have enabled detailed parametrization of animal movement models (Jonsen *et al.* 2003; Morales *et al.* 2004). However, animals move differently as they go about their various activities (Turchin 1998), and temporally sparse location data restrict modelling to an ambiguous ‘average’ movement process that necessarily integrates over these different movement behaviours. Model predictions are sensitive to changes in the mix of behavioural activities that comprise this longer term average. Higher temporal resolution allows modelling of the movement of individuals in different behavioural states, but to use these models at temporal scales relevant for population dynamics requires understanding how often animals change from one movement type to another (Skalski & Gilliam 2003). One clue to predicting how animals move is provided by the landscape context through which animals are moving. Overlaying movement trajectories onto landscape maps (e.g. aerial photographs or classified satellite images) has provided new insights into how animals respond to and move around complex landscapes. This powerful combination of movement and landscape data enables the parametrization of ‘spatially

informed’ movement models that relate the movement behaviour of an individual to the spatial context through which it moves (Jonsen *et al.* 2003; Morales *et al.* 2004).

Spatially informed movement models provide a promising and fast-developing bridge between landscape ecology and the movement of individuals, but most species for which GPS collar data are likely to be available are to some extent social, and the movement of individuals of these species is likely to be heavily dependent on the particular social context experienced by an individual. To understand the distribution of populations over landscapes will require scaling-up from individual movement patterns to groups of individuals, and populations of groups, and this will require the development of socially informed movement models that can incorporate interactions between the group structure of a population and the movement of individuals comprising the population. Spatially informed movement models are a rapidly growing area of ecology (Jonsen *et al.* 2003, 2005; Morales *et al.* 2004) but socially informed movement models remain relatively unexplored, and are the subject of this paper.

The study of group structure and its implications for demography is particularly demanding as it requires tracking the movements of a high proportion of a population, in addition to estimating the effects of group structure on the underlying demographic parameters of

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the population as a whole. Here, we show how it is possible to develop movement models incorporating group structure for a reintroduced population released into a novel environment from a single point. For a reintroduced species, a balance of spread and coalescence processes will determine the broad-scale distribution of individuals over the landscape. If survivorship and fecundity are higher in groups, then population persistence may depend on the coalescence process ultimately dominating and curtailing the spreading process, thereby enabling the establishment of a natural group structure within the designated release area. Only then can population vital rates be normalized and early population losses reversed (Stanley Price 1989; May 1991; Caro 1999). Disrupted group structures are likely to result in both reduced survivorship and fecundity. Fecundity may be reduced as a result of the trauma of translocation and/or the disruption of the population's group structure (Saltz & Rubinstein 1995; Ostermann *et al.* 2001). Rapid development of natural group structure is also likely to stabilize population spread rates and minimize population 'leakage' out of the designated release area. Potential fitness costs of dispersal are commonly described (Belichon *et al.* 1996) and a previous study has shown that the median area of available habitat associated with successful release programmes was five times that of unsuccessful ones (Wolf *et al.* 1996). Thus actions that can be taken to mitigate the disruption to group structure resulting from translocation of small populations will increase the likelihood that reintroduction programmes will be successful.

We develop a model of population spread that includes group dynamics to examine the interactions of movement and group cohesion on long-term population growth rate. Our interest is in developing a model framework to think about this problem generally, but we parametrize our model with data from a population of reintroduced Manitoban elk (*Cervus canadensis*). We build on the work of Morales *et al.* (2004) who fit multiple correlated random walks (CRWs) to the movement trajectories of individual elk obtained from GPS collars. The different random walks describe the movement of elk in different behavioural states (an encamped and a ranging state). The switching rates between these behavioural states can be made explicitly dependent on the habitat through which the elk move. Since our focus is the longer term spatio-temporal dynamics of the population, we assume that the natural grain of the landscape imposes switches between these states at fixed average rates. We extend this movement model, applying it to both single and grouped individuals, quantifying the processes of group fission and fusion, the movement rates of groups and estimating the demographic consequences of group and solitary modes of existence. While the fine-scale movement models are parametrized using GPS collar data, the population group structure is determined from more than 7000 locations of mostly VHF-collared elk collected over nearly four years following a release of 120 individuals introduced into east-central Ontario in two consecutive point releases (Rosatte *et al.* 2002, 2007; Yott 2005). Following parametrization of these processes, we then combine them into an individual-based model that demonstrates the sensitivity of medium-term growth rates to the group structure of the population.

2. MATERIAL AND METHODS

(a) *The data*

Elk were translocated from Elk Island National Park, Alberta, to a release area in east-central Ontario on two occasions. The first occasion involved 70 individuals (36 adult females, 14 adult males, 10 juvenile females, 10 juvenile males). They were released immediately on their arrival (a hard release) into the new environment on 7 January 2000. The second occasion involved 50 individuals (20 adult females, 13 adult males, 11 juvenile females, 6 juvenile males) held in a fenced compound for three months before their release (a soft release) from the same point, on 15 April 2001. All individuals were VHF radio-collared and tracked (mostly from the ground, but sometimes from the air) and their location determined to within triangulation error (median 0.6 km) approximately once in every two weeks. The densely forested nature of the release area resulted in very few direct visual sightings of elk. Ten cows from the second release were fitted with GPS collars; data from four of these collars were subsequently recovered between 160 and 220 days post release. In order to avoid complications arising from diurnal movement patterns, only the first fix each day from the GPS collars and all the VHF data (a total of 117 individuals and 6921 locations over 1311 days) were used for analysis.

(b) *The release area*

The release point was located 30 km southeast of Bancroft, Ontario. This area was last inhabited by elk prior to extirpation of eastern elk in the late nineteenth century (Rosatte *et al.* 2007). After lakes are factored out, the habitat was 92% forested, mostly dense and mixed deciduous forest, with some mixed and sparse coniferous cover (Jenkins *et al.* 2007). The remainder is made up of recently cleared forest (4%), cultivated (2%) and settled land (2%). This landscape extends for between 60 and 80 km to the north, east and south (beyond which the proportion of settled and agricultural land increases sharply) and approximately 200 km to the west where it is bounded by Lake Huron. The area is lightly settled throughout, and fragmented by a network of forest roads and small highways.

(c) *Analysis of movement and demography with respect to group structure*

(i) *The underlying movement model for solitary individuals*

Movement of socially complex, large mammals over long time scales is unlikely to be well described by simple CRWs. Preliminary examination of the GPS collar data revealed a bimodal distribution of daily displacements indicating that individuals could be in one of the two behavioural states: encamped—occupying a 'camp' (Bailey *et al.* 1996), wherein daily displacements (step lengths) would be small and turning angles large; or a ranging state, in which daily step lengths were larger and turning angles smaller (Morales *et al.* 2004). Movement of solitary individual elk was therefore described using a two-state CRW. Switching between these two states was modelled assuming fixed switching rates contained within a simple transition matrix. The switching rates we used do reflect the spatial characteristics of the landscape, as they are estimated directly from the movement paths of the GPS-collared animals, but do not assume explicit knowledge of a landscape map. Turning angles and step lengths in each movement state were modelled as wrapped Cauchy distributions and Weibull distributions, respectively. Parameters for these distributions corresponding to each movement

state and the switching rates between states were estimated simultaneously from all the daily GPS collar movement trajectories using a hierarchical Bayesian model (the 'double-switch' model developed, and fitted using Markov Chain Monte Carlo methods as described in *Morales et al. 2004*, and in which details of the selection procedures and measures of goodness of fit are described). Because all elk in the region were collared, it was possible to establish that these GPS animals were solitary (no collar within 2 km within four days either side of the date of the fix) for at least three-quarter of all the days for which location data were available, and we go on to assume that the step lengths and turning angles characteristic of each state are applicable to all individuals in the population.

(ii) Group status

In order to classify an individual as solitary or in a group of a particular size, we required a definition of grouping. For each location datum, we asked how many other collars had been tracked within 2 km of this location within four days either side of the date of this fix. Location data around which no other collars were found in this space-time 'envelope' were termed solitary. When a fix was not solitary, it was termed grouped and the number of collars within the envelope enumerated. This definition of grouped is based on our experience of the habits of this herd and its subgroups over the three years of tracking (analysis using temporal windows of 2, 4 and 8 days demonstrated that our qualitative findings were not sensitive to this choice of window size).

In order to calculate daily rates of group fission (individuals leaving groups) and fusion (individuals joining up with groups or other individuals to become groups), we needed to identify changes in the group status of each individual over the duration of the study. For each fix of a grouped individual, we recorded the size of the group of which it was a member and whether the individual was solitary or grouped when its location was next determined. We then computed the number of grouped to solitary (n_{gs}) and grouped to grouped (n_{gg}) transitions for each individual over a range of group sizes, and the average time interval between fixes corresponding to each of these observations ($\bar{t}_{gs}$, $\bar{t}_{gg}$). The average fission rate per day was then estimated as $n_{gs}/(\bar{t}_{gg}n_{gg} + \bar{t}_{gs}n_{gs}/2)$ by which it is assumed that when individuals leave their groups, they do so, on average, midway between observations. These fission rates were computed over a range of different group sizes, so that a function could be estimated describing the dependency of fission rate on group size.

In the same way, daily fusion probabilities can be estimated from $n_{sg}/(\bar{t}_{ss}n_{ss} + \bar{t}_{sg}n_{sg}/2)$ where the number of solitary to grouped (n_{sg}) and solitary to solitary (n_{ss}) transitions are computed over a range of different distances. Distance for individuals that were solitary and became grouped was taken to be the distance from the individual or group with which they grouped at the time of the preceding fix. Distance for individuals that remained solitary was taken to be the distance to the nearest individual at the time of the preceding fix. We restricted the analysis to consecutive fixes acquired within 14 days of each other.

For specified dates, we computed an $n \times n$ inter-elk distance matrix (n = number of elk for which a fix existed within the two weeks of the specified date) on which we performed UPGMA cluster analysis. Using a cut-off of 2 km, this procedure identified elk groups of varying sizes. We computed the

proportion of the overall herd in each group (p_i) and defined the herd fragmentation index (HFI) using the Shannon–Weaver measure of entropy: $HFI = -\sum p_i \ln(p_i)$ (*Shannon & Weaver 1949; Okubo 1986*). This value is high when the groups are numerous and small, reduces as the groups become fewer and large, and is defined to be equal to zero if one group constitutes the entire herd.

(iii) Movement of grouped animals

We assumed that the characteristics of the CRWs describing movement in the encamped and ranging state would not be influenced by group status, but that the switching rates between these behavioural states would be. In order to model the movement of groups, we assumed that individuals in groups move together performing the same biphasic CRW as solitary individuals but with different switching rates. We estimated the two switching rates (ranging to encamped state and encamped to ranging state) that were most likely to give rise to the observed net displacement of 'mostly grouped' (defined as those in groups on at least 80% of occasions they were ever located) VHF-collared individuals. Likelihoods of different switching rates were obtained from direct simulation of the biphasic model to obtain distributions of displacements for different combinations of switching rate.

(d) Survival analysis

Preliminary analysis of survival data showed that some animals died quickly after the reintroduction, but individuals surviving this first period incurred lower mortality rates subsequently. We performed survival regression analysis with a Weibull model using age (juvenile versus adult), release (first versus second), sex, proportion of time solitary, time since release and scaled displacement from the release site (explained below) as covariates. Since we have different observation times for different animals due to mortality and different release dates and varying periods of time between relocations, we scaled displacement as distance (kilometres) from release site at time t divided by t^γ where t corresponded either to time of death or the last observation of an individual and γ is a scaling parameter fitted to all our displacement observations. Displacement for a simple diffusion scales with the square root of time ($\gamma = 0.5$), but we found that $\gamma = 0.44$ had a better fit to our data.

(e) Fecundity

The annual probability of calving was estimated to be 0.34 from the number of cows with calves at heel as determined from annual helicopter surveys over three years.

(f) Model development

The estimated parameters relating to the processes of daily movement, group status, switching between grouped or solitary status, daily risk of mortality dependent on time and scaled displacement, and annual calving were used directly in a stochastic individual-based and spatially explicit simulation model of elk movement and demography. The model assumed the following rules: (i) the movement of both grouped and ungrouped individuals was governed by the same two CRWs corresponding to encamped and ranging states, (ii) the switching rates between the two movement phases differed for grouped and ungrouped individuals, (iii) individuals left groups with a probability dependent on group size, (iv) individuals joined (or formed)

Table 1. Parameters used in the socio-demographic model.

symbol	interpretation	value
a_s	Weibull distribution (encamped state)	2.827
a_f	Weibull distribution (ranging state)	0.033
b_s	Weibull distribution (encamped state)	0.959
b_f	Weibull distribution (ranging state)	1.823
ρ_s	wrapped Cauchy (encamped state)	0.387
ρ_f	wrapped Cauchy (ranging state)	0.441
μ_s	bias (encamped state)	1.801
μ_f	bias (ranging state)	0
q_{sf} (ungrouped)	switching from ranging to encamped state	0.09
q_{fs} (ungrouped)	switching from encamped to ranging state	0.02
q_{sf} (grouped)	switching from ranging to encamped state	0.725
q_{fs} (grouped)	switching from encamped to ranging state	0.0065
	probability of leaving group	0.02–0.002
	probability of joining group	0.14–0.02
b_0	intercept for Weibull survival covariate	8.452
b_1	slope for Weibull survival covariate	–0.237
α	Weibull survival scale parameter	0.803
	fecundity per female	0.34

a group with a probability dependent on distance to the nearest individual, (v) the mortality rate was modelled as an increasing function of scaled displacement rate, (vi) individuals in groups moved together according to a biphasic CRW with grouped switching rates, (vii) females were assumed to calve annually with a fixed probability, and (viii) calves were ‘grouped’ in the mothers group for the first year, after which they could leave groups according to the default group-leaving probabilities. Parameters for all these processes were estimated as described previously and are reported in table 1. The model was run using a daily time step within which individuals had the opportunity to switch behavioural state, move, die, group up or leave groups. The model output was the average population growth rate over a four year period and we explored how this growth rate changed with parameters governing the group structure of the population.

3. RESULTS

The data indicate that elk spread quickly over an extensive area of more than 10 000 km², as shown in figure 1*a*. After 120 days, average ‘straight-line’ displacement from the release site was 13 km (range: 0–62 km) but stabilized shortly after this time, rising to only 27 km after 1000 days (range: 5–97 km). Initially, and by the end of the tracking study, average displacement was similar for males and females, but males moved further from the release point in the second and third years following release (figure 1*a*). Overall, scaled displacement did not differ significantly by

age, sex or release ($F_{1,116}=0.60$, $p=0.805$; $F_{1,116}=2.89$, $p=0.092$; $F_{1,116}=3.07$, $p=0.082$).

Herd fragmentation increased over the first five months, as fission processes dominated, but then started to decline again as solitary individuals died and groups coalesced. Fragmentation increased sharply with the release of the second group, but then declined as for the first cycle (figure 1*b*). Thirty days after the first and second releases, the proportion of individuals from these releases that were classified as ungrouped was 18 and 17%, respectively. There was a strong positive relationship between the proportion of time that an individual was solitary and its scaled rate of displacement (figure 2*a*), but no relationship between displacement and group size (data not shown).

We did not find significant effects of age ($p=0.27$), sex ($p=0.63$) or release ($p=0.10$) on survival rates. The only significant covariate was scaled displacement rate ($p=0.0003$), so that the hazard function used in the simulation was $h(t)=\alpha t^{\alpha-1} \exp(-\alpha(b_0+b_1\delta))$, where t is time since release, δ is scaled displacement rate and α , b_0 and b_1 are fitted parameters ($\alpha=0.803$, s.e. 0.148; $b_0=8.452$, s.e. 0.355; $b_1=-0.237$, s.e. 0.0694, figure 2*b*).

Survival rates from hard and soft releases were indistinguishable from each other, and the average proportion of time individuals spent in a solitary state subsequent to release was actually higher (but not significantly so) for those from the soft release relative to the hard release (0.293 versus 0.257). The survival function indicated a substantial drop in the baseline mortality rate after the first year. For example, disregarding the influence of displacement, the mortality rate was estimated at 19.0% in the first year, 10.6% in the second year and 8.1% in the third year. Including the effects of herd displacement would exaggerate these differences still further as outlying individuals die off and surviving groups persist closer to the release point. The hazard function increased by 21% per unit scaled displacement rate (km d^{–0.44}).

The probability of leaving small groups was approximately 0.015 per day, but this fell rapidly to less than a fifth of this value as group size increased to 10 individuals (figure 2*c*). The probability of joining a group varied depending on the distance of a solitary individual from the group. Solitary animals just over 2 km from a group centroid joined with probability 0.14 per day, but this probability dropped off to less than 0.01 at a distance of 50 km (figure 2*d*).

The consequences of simple fission–fusion models for equilibrium population group numbers and sizes have been previously described (Holgate 1967; Gueron 1998; Durrett *et al.* 1999). Here, we extended these approaches by combining group dynamics into an individually based spatially explicit model of movement that included empirically estimated group-dependent demographic processes. Average daily rates of displacement in the ranging and encamped states were estimated to be 5.77 and 0.34 km, respectively. Individuals located in groups switched to the ranging state less often than solitary individuals and consequently spent on average 99.1% of their time in an encamped state, while solitary individuals switched more often into the ranging state, spending 18.8% of their time ranging.

Figure 1. (a) Displacement over time. The graph combines two groups of animals, one released on 7 January 2000 and the other on 15 April 2001. The graph contains data for all animals including those that died over the period of the tracking study (typically those individuals that moved the furthest away). Thick solid line, average for males; thin solid line, average for females. (b) Herd fragmentation through time. Fragmentation is measured using the Shannon–Weaver metric (see §2).

The model generated a wide distribution of median individual displacement distances, but observed median displacements always fell centrally within 95% percentile intervals (PIs) calculated at yearly intervals. We went on to use this model to study the impact of group structure and its rate of normalization on population fragmentation and the long-term population growth rate (the actual growth rate remains unknown due to the difficulty of counting uncollared individuals born into this population). We examined the medium-term demographic consequences of four different release scenarios: releasing animals (i) ungrouped in a ranging state, (ii) ungrouped in a ranging state and precluding subsequent group formation, (iii) in one large group in an encamped state, and (iv) in one large group in an encamped state and precluding subsequent group formation. The model predicted that the size of an ungrouped population would increase by 80% (PIs 50–111%) over four years (and this scenario most closely reflected the observed proportion of animals in groups 30 days post release, PIs 0.786–0.957), and that precluding subsequent grouping reduced this growth rate to 44%

(PIs 13–74%). For sets of grouped individuals, growth rate averaged 85% (PIs 46–120%) and under these circumstances precluding subsequent grouping made little difference to the growth rate (76%, PIs 33–115%).

The average four-year growth rate was relatively sensitive to the coefficient relating scaled displacement rate to mortality (b_1 in the hazard function). For example, growth rates corresponding to the lower and upper 95 CI of this parameter corresponded to 62 and 95%. The growth rate is more sensitive to interactions between this parameter and those governing group formation. For example, if a distance threshold is introduced beyond which individuals are unable to travel to join up or form groups, then growth rates collapse quickly as b_1 increases (figure 3).

The faster rate of movement in the ranging state results in ranging individuals incurring a significantly higher mortality rate as a result of their greater displacement. However, because the average time spent in the ranging state is given by $q_{fs}/(q_{sf} + q_{fs})$ and $q_{fs} \ll q_{sf}$, overall population growth rates are relatively insensitive to a plausible range of switching rates. The effects of different

Figure 2. (a) Relationship between the proportion of fixes that were classified as solitary and the scaled rate of displacement. The equation for the regression line is $y = 6.33x$ and is significantly positive ($F_{1,116} = 53.63$, $p < 0.0001$). (b) Deaths shown as a function of scaled displacement rate (1, dead; 0, alive). The solid curve illustrates the increase in the hazard function with scaled displacement rate and is fitted using Weibull survival regression (see §2). (c) The daily probability of leaving a group as a function of group size (2 s.e. shown around each point). The solid curve is a Weibull distribution ($a = 0.0753$, $b = 0.3006$) and the dotted line is a closer fit to the data modelled with a quartic polynomial but simulations adopting this alternative function yield population growth rates indistinguishable from the monotonically declining function. (d) The probability of a solitary individual grouping up with another animal (moving within 2 km of each other) as a function of the distance between them at the time of the last acquired location (2 s.e. shown around each point). The fitted curve is a four-parameter exponential model: probability of leaving group = $0.5604e^{-0.7224x} + 0.0480e^{-0.0342x}$.

combinations of switching rates of both ungrouped and grouped animals sampled over the full range of possible values is shown in figure 4a,b.

4. DISCUSSION

Ungulate group structure has been described in both sedentary and migratory populations (Knight 1970; Franklin & Lieb 1979; Shoesmith 1979; Clutton-Brock *et al.* 1982; Jenkins & Starkey 1982) and can be very dynamic (Bender & Haufler 1999), but the factors important to the rate of normalization of population structure following release into novel environments and how changing patterns of group structure interact with movement and demography have received much less attention. Opportunities to study these processes are unusual for a number of reasons. Determination of group status requires that a high proportion of individuals in the population are collared, and all individuals tracked for a long period of time. It also requires that a large number of individuals be released so that group-level

parameters may be estimated with at least some statistical precision. Finally, the importance of group status will be most profound in social and highly cognitive animals, and the release and subsequent monitoring of large numbers of these often highly vagile species is very resource intensive.

This study has demonstrated that over at least medium time scales, elk movement can be represented as biphasic, with individuals switching between movement 'modes' corresponding to an encamped and ranging behavioural state. However, the switching rates from the encamped to the ranging state is higher, and from the ranging to the encamped states lower for single animals, with the result that ungrouped individuals move greater distances than grouped animals. Grouped animals are more likely to leave small groups, than larger groups, and single individuals are more likely to join close groups than distant groups.

These movement processes are shown to influence the demography of the population: ungrouped individuals experience higher mortality and mortality was substantially elevated in the first year following release. As a result

Figure 3. The sensitivity of population growth rate (shown as contours, and averaged over the four-year period, and measured as the proportion increase relative to the starting population size) to variation in the scaled displacement-dependent mortality (y -axis), and the threshold (km) beyond which the probability of grouping up is set to zero (x -axis). Individuals are released in an ungrouped ranging state.

of the interaction between movement and demography, the population as a whole demonstrates an initial increase in spatial fragmentation fuelled by movement and group fission, followed by coalescence, arising from group fusion and mortality. These dynamics strongly suggest that the growth rate of the population will be sensitive to the initial group status of the released population and the subsequent ability of individuals to group up. As a result of the dependency of survival on scaled displacement rate, modifying the switching rates to cause individuals to spend a higher proportion of time in the ranging state will reduce population growth rate, but this growth rate is more sensitive to the switching behaviour of grouped individuals as the majority of individuals are grouped most of time (figure 4*a,b*).

The model predicts that the medium-term growth rates of this population depends critically on either the group status prior to release or the capacity of individuals to form groups subsequent to release. However, the survival rates from hard and soft releases are indistinguishable from each other. This suggests that the additional three months that individuals were retained in the release compound did not result in an increased level of grouping relative to that achieved by an instantaneous release. In both cases, the more important determinant of grouping may be the relatedness of individuals captured from the source population (Elk Island, Alberta), and their shared experiences while undergoing identical translocation procedures prior to arrival at the release compound.

We do not know whether the increased mortality rate in the ranging state results from individuals incurring additional risk factors arising directly from moving, or whether the increased risk arises from a greater likelihood of being in unsuitable habitat as a result of having moved further. The former mechanism relates to the risk of animals moving and their interactions with unfamiliar environments, i.e. the direct costs of movement, while the

Figure 4. Sensitivity of population growth rate (shown as contours, and averaged over the four-year period, and measured as the proportion increase relative to the starting population size) to different combinations of switching rate between encamped and ranging state for (a) ungrouped animals and (b) grouped animals. Individuals are released in an ungrouped ranging state. The filled circle indicates estimated switching rates for ungrouped and grouped individuals respectively.

latter can be expected to increase as individuals are released into areas of smaller core habitat. Our current parametrization of displacement-dependent mortality cannot tease apart these two hypotheses.

Our analysis is forced to make a number of assumptions. While all released individuals were radio-collared, those born into the population could not be collared and those that lost their collars could not be re-collared, so the fraction of individuals in our study population that were collared started off high (100%), but declined through time. This would tend to introduce a bias—acting to underestimate group size, overestimate the proportion of solitary individuals and underestimate the differences in demographic processes associated with grouped and ungrouped individuals. We also assumed that the switching rate of the group leader between encamped and ranging states is independent of group size—we suspect

that rates of switching to the ranging state decline with group size, but we do not have enough groups to measure this effect. We assume that individuals in groups leave them at a rate inversely proportional to group size—and measure this rate directly from the data. An equally plausible way to model this process would be to assume that individuals leave groups as a direct result of switching to the ranging state. Reassuringly, either approach yields similar answers (groups switch to the ranging state with probability 0.0065 per day, while individuals leave groups with a probability ranging from 0.002 to 0.02 depending on group size).

Features of the landscape and configuration of landscape heterogeneities are also likely to play an important role in the interaction between movement, group structure and resulting site fidelity (Larkin *et al.* 2004). Here, we have made the parameters of the movement model conditional only on the ranging or encamped state of individuals. However, the same methodology can be used to parametrize a spatially informed CRW in which the parameters of the movement model may be made contextually dependent on features of the local landscape through which the animal is moving (e.g. the individuals proximity to sites containing higher quality forage as might be identified from satellite imagery; Morales *et al.* 2004). Using such an approach, it would be possible to predict the possible outcomes of population reintroductions in different landscapes (Macdonald & Rushton 2003). Closer linkage of landscape ecology and population biology will require an appreciation of the complex interactions between landscape heterogeneities, animal behaviour, movement, population growth rate and persistence. These interactions are an important and general feature of the demographic process that affects the dynamics of both endangered and invasive species, and merit greater empirical study.

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