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Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover

J.U. Jepsen and C.J. Topping

Abstract: The ability of a species to exhibit behavioural plasticity to environmental conditions has consequences for its success in fragmented landscapes. The roe deer, *Capreolus capreolus* (L., 1758), is one of the foremost examples of behavioural flexibility among ungulates. This species has increased rapidly in range from its original forest-mosaic habitat into open agricultural plains. Open-land roe deer populations show distinct differences in spatial and social behaviour, including larger group sizes, compared with forest-living roe deer populations. This is traditionally viewed as an antipredator strategy. The presence of strong behavioural plasticity in species response to landscape structure suggests that this should also be a concern in models attempting to describe effects of landscape change on species distribution. To date the implications of behavioural plasticity for modelling species' response to environmental conditions has received little attention. We used an individual-based model of roe deer to evaluate the consequences of behavioural plasticity for predictions made regarding population response to woodland fragmentation. The inclusion of a flexible behavioural strategy, where increased group size could buffer lack of woodland cover, resulted in significantly higher estimates of population size, population persistence, and the ability of the population to cope with fragmentation. This clearly demonstrates that behavioural plasticity in species response to landscape structure may affect our ability to accurately predict the effects of landscape change and should be a concern to modellers.

Résumé : La capacité que possède une espèce d'avoir une plasticité comportementale en fonction des conditions du milieu affecte son succès dans les paysages fragmentés. Le chevreuil d'Europe, *Capreolus capreolus* (L., 1758), est l'exemple le plus remarquable de cette flexibilité comportementale chez les ongulés. Cette espèce a rapidement étendu sa répartition à partir de son habitat d'origine de mosaïques de forêts jusque dans les plaines agricoles ouvertes. Par comparaison aux chevreuils qui vivent en forêt, les populations des régions ouvertes présentent de nettes différences de comportements spatiaux et sociaux et, en particulier, ils forment des groupes de plus grande taille. Ce comportement est ordinairement interprété comme une stratégie de protection contre les prédateurs. La présence d'une importante plasticité du comportement chez une espèce en réaction à la structure du paysage devrait être une préoccupation pour ceux qui font des modèles pour décrire les effets des changements du paysage sur la répartition de cette espèce. Les conséquences de la plasticité comportementale sur la modélisation de la réaction des espèces aux conditions de l'environnement n'ont encore été que peu étudiées. Nous avons utilisé un modèle basé sur l'individu pour évaluer les conséquences de la plasticité comportementale des chevreuils sur les prédictions faites au sujet de la réaction des populations à la fragmentation des boisés. L'inclusion d'une stratégie comportementale flexible, dans laquelle un accroissement de la taille du groupe peut compenser le manque de couverture forestière, produit des estimations significativement plus élevées de la taille de la population, de sa persistance et de sa capacité de s'accommoder de la fragmentation. Cela démontre clairement que la plasticité comportementale de la réaction d'une espèce à la structure du paysage peut affecter notre capacité de prédire les effets des changements du milieu et qu'elle doit être prise en considération par ceux qui construisent des modèles.

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Introduction

The degree of behavioural plasticity expressed by a given species can be expected to increase with increasing environmental variability (e.g., Morse 1980; de Jong 1995; Komers 1997). The presence of behavioural plasticity in a species has consequences for its ability to deal with for instance predation pressure (e.g., Lima and Dill 1990), habitat alterations (e.g., Boydston et al. 2003), and environmental and resource dynamics (e.g., Maher and Lott 2000; Brashares and Arcese 2002). Field studies documenting behavioural plasticity to environmental conditions require both that the intraspecific variation in social or spatial behaviour of the species be sufficiently large, and that it can be studied over a large gradient of environmental variation. Among ungulate species, however, several recent studies have indicated considerable behavioural plasticity in populations living in contrasting environments (Thirgood et al. 1999; Hewison et al. 2001; Brashares and Arcese 2002). The roe deer, *Capreolus capreolus* (L., 1758), is perhaps the foremost example of behavioural flexibility and adaptive ability in an ungulate species. In the course of the 20th century the roe deer has increased rapidly in range and density across Europe and now inhabits most subalpine regions (Cederlund and Liberg 1995; Danilkin and Hewison 1996; Tellería and Virgós 1997; Linnell et al. 1998). The primary habitat of the roe deer is forest clearings, hedges, and woodland edge (Hansson 1994). Nevertheless, the roe deer has spread into open arable land and grassland, most noticeably in eastern Europe (Kaluzinski 1974; Hewison et al. 1998). In open-land habitat the roe deer show distinct differences in social and spatial behaviour compared with roe deer in woodland habitat, and this has led to a long-standing distinction between “forest” and “field” roe deer. There are, however, no indications that field and forest roe deer differ genetically (Kurt et al. 1993). The recent continued expansion of the species into open agricultural land in western Europe (Cibien et al. 1989) has consolidated the different spatial and social strategies observed in forest and field roe deer as being the result of a strong behavioural plasticity in the species’ response to landscape structure. In woodland habitat and arable-woodland mosaics the roe deer live in association with woodland in a social unit that typically consists of <5 related individuals (Hewison et al. 1998). Open-plain populations aggregate in significantly larger groups, in several cases >50 individuals (Zedja 1978; Bresiński 1982; Mrlik 1991; Gerard et al. 1995; Hewison et al. 1998). Based on comparisons across study regions, it has been suggested that the observed differences in social organization are caused by the availability and configuration of woodland habitat. The roe deer has two main resource requirements: (1) nutrient-rich forage and (2) cover, which offers escape from predators and disturbance (Putman 1986; Cibien et al. 1995; Mysterud and Østbye 1995, 1999; Tufto et al. 1996; San José et al. 1997; Mysterud et al. 1999). In most cases cover is found in the form of tall vegetation or woodland. On the agricultural plains, where woodland structures are scarce or missing, large groups may result in higher group vigilance (amount of time where at least one group member is vigilant) despite a decrease in individual vigilance (Jarman 1974; Ruckstuhl

and Festa-Bianchet 2001). In addition, membership of a larger group may reduce individual predation risk through dilution (Roberts 1996). Which of the two potential mechanisms that is more important for group formation is not clear, but both would allow an increase in group size to buffer the lack of cover habitat for antipredatory reasons.

Recently, Hewison et al. (2001) was able to document a similar effect across a much shorter gradient of woodland configuration. The authors found significant differences both in the degree of association with woodland and in group sizes between study areas with similar total proportion of woodland. When woodland patches were numerous, small, and widely dispersed, roe deer retained a social structure typical for forest roe deer. When woodland patches were clumped with large areas of open field in between, roe deer followed what appears as a typical field roe strategy with little association with woodland and larger group sizes (Hewison et al. 2001). This led the authors to suggest that a certain threshold of woodland configuration might exist above which field behaviour is promoted.

The presence of behavioural plasticity in species response to landscape structure suggests that behavioural flexibility should also be a concern in models attempting to describe effects of landscape change on species distribution. Effects of large-scale landscape structure or long-term changes in land use on distribution and social organization of larger mammals are rarely documented in the field. This is due to the time span required to detect these effects and the obvious problems involved in performing experimental manipulations at a landscape scale. In many cases spatially explicit simulation models can serve as useful experimental systems. They are able to incorporate the spatial and temporal heterogeneity of real landscapes coupled with information about animal behaviour and response rules to environmental conditions. This means that hypotheses regarding the effects of contrasting environments on population dynamics and animal distribution patterns can be evaluated and perhaps refined. There is already a long tradition for using spatial simulation models to evaluate the consequences of landscape structure on animal movement behaviour, dispersal rates, and hence functional connectivity of landscapes (e.g., Baker 1996; Walters 2001; Goodwin and Fahrig 2002; Marell et al. 2002; Tischendorf et al. 2003; Jepsen et al. 2005). It is only recently, however, that behavioural models have been put to use in investigating the role played by animal behaviour – landscape interactions in shaping population-level patterns such as social structure, disease transmission, or predation risks (e.g., Hebblewhite and Pletscher 2002; Sutherland and Norris 2002; Grimm et al. 2003; Shirley et al. 2003). Individual-based simulation models of animal behaviour are suitable for exploring hypotheses related to behavioural strategies (see for instance Hemelrijk 2002; Ruckstuhl and Kokko 2002). Above all the individual-based structure allows behavioural rules and strategies to be implemented at the natural level of decision-making, namely at the individual animal level. In the language of individual decision-making, the observed behavioural plasticity in roe deer boils down to whether or not the individual deer decides to establish a home range in a given area. The presence of a group size effect, allowing the company of conspecifics to make up

for a lack of cover habitat, will change the acceptance criteria of the individual deer for a potential home range, and thereby the population response to landscape structure. Whether or not behavioural plasticity is considered in models of animal distribution may therefore have consequences for our ability to accurately predict species response to alterations in habitat quality and landscape structure.

This paper is a contribution to the discussion on the role of behavioural plasticity in shaping animal distribution in fragmented habitats. We place special emphasis on the implications of behavioural plasticity for predictive modelling of species in heterogeneous landscapes. We used an individual-based simulation model of roe deer demography and spatial behaviour to address the following questions. (i) How does the presence of behavioural plasticity, in the form of a simple group size effect, influence the spatial distribution of simulated roe deer (home-range size, group size, association with woodland) across a woodland dispersion gradient? (ii) Assuming the presence of a group size effect, at which level of woodland dispersion do roe deer lose the association with woodland habitat? (iii) What is the optimal dispersion level of woodland habitat for model population density, and how is this affected by the presence of a group size effect? We discuss the results in the light of their implications for predictive behavioural modelling.

Methods

The animal, landscape, and man simulation system (ALMaSS)

We used an existing simulation model framework, ALMaSS (Topping et al. 2003a). ALMaSS is a spatially explicit model framework, designed as a versatile decision-support tool for use in answering management questions related to changing landscape structure and land management (Thorbek 2003; Topping et al. 2003a, 2003b; Bilde and Topping 2004; Topping and Odderskær 2004). ALMaSS makes use of individual-based models of animal behaviour to simulate animal movement and population dynamics across a model landscape. The model landscape may be representations of both real landscapes obtained from a GIS or artificially generated raster landscapes. By default ALMaSS contains a simulation of landscape dynamics in the form of realistic agricultural practices, vegetation growth, and weather (Topping et al. 2003a). For the current study the dynamic functionalities in the landscape model were turned off, and the realistic landscape representations commonly used in ALMaSS were substituted by artificially generated neutral landscapes (see below). This was done to be able to control both the amount of woodland and the degree of woodland dispersion in the model landscapes. A series of neutral raster grid landscapes differing in the degree of dispersion of woodland habitat was created. The landscapes consisted of only two habitat types: primary habitat offering both forage and cover (deciduous woodland) and secondary habitat offering only forage (natural grassland). The extent of the landscapes was 10 km × 10 km with a cell size of 10 m. Landscape boundaries were periodic, resulting in a torus-shaped landscape. Landscapes were created according to a simple rule set; an empty grid was seeded with two cen-

tral woodland cells. Additional cells were then randomly chosen and allocated to woodland if they had a minimum of two existing woodland cells as neighbours until the total proportion allocated to woodland reached a predefined value F . A proportion of cells (D) was allowed to escape this rule and was placed at random without considering the values in neighbouring cells. The degree of woodland dispersion could thus be varied from $D = 0$ (all woodland cells in a single central patch) to $D = 100$ (random allocation). All remaining cells were allocated to grassland. We created a total of 22 landscapes setting F to either 10% or 20% to obtain a value on either side of the woodland threshold (15%) used for roe deer home-range establishment (see Roe deer model description below). D was varied in steps of 10 from 0 to 100. Examples of dispersion landscapes are shown in Fig. 1.

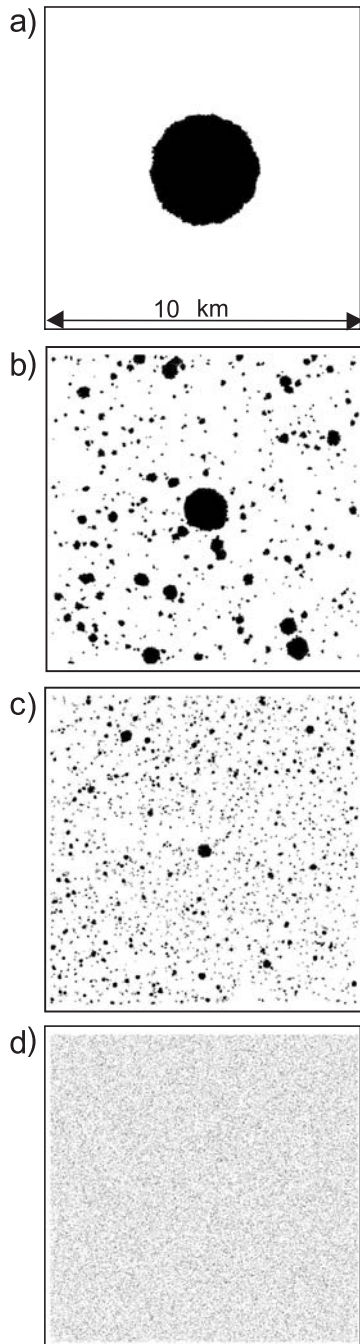
Roe deer model description

All animal models in ALMaSS are built on the same generic framework (Topping et al. 2003a). The animal models are individual-based and build upon a state-transition principle. Relevant animal behaviours (e.g., reproduction, feeding, dispersal) are described as behavioural states and decision rules are formulated for each behaviour. Transitions between states depend on one or more conditions being fulfilled. Conditions may be probabilities or an internal or external event. When these conditions are fulfilled the animal is transferred to a new state containing a new set of decision rules. An animal is divided into one or more object types, which may be determined by sex (male, female) or age class (adult, juvenile). Each object type has its own set of behavioural states and conditional transitions. The roe deer model simulates survival, reproduction, and movements of individual deer in response to habitat quality and external events. Three object types are included: adult males (σ), adult females (φ), and highly simplified juveniles (J). Figure 2 shows the model structure for adults in the form of a state-transition diagram. The majority of time for adult object types is taken up by an alternating cycle of ruminating and feeding, but a number of specialized behaviours are available. This allows individuals to perform intraspecific interactions, such as a communication between mates during reproductive behaviour and territorial interactions between bucks.

Description of behavioural states

The roe deer model is divided up into 13 behavioural states (1–13 below) used by at least one object type. In addition the model contains three non-behavioural states (14–16 below), which contains updates of counters, file output routines, etc. Some behavioural states include several specialized behaviours that may differ for the different object types involve. The duration of a behavioural state varies between immediate processing (immediate state) and one full day. Movement behaviour is used in several of the states described below (4, 5, 6, 10, 12). Movement in ALMaSS is implemented as a correlated random walk and defined by three parameters (see also Fig. 5 in Topping et al. 2003a): (1) a directional vector (DV) indicating the preferred direction (one of eight possible directions with 0 indicating north); (2) a weight (W), indicating the strength of the bias

Fig. 1. A total of 11 different neutral dispersion landscapes were created for each degree of woodland cover. Woodland dispersion (D) varied between 0 (a single large patch) and 100 (random allocation). The example below shows dispersion landscapes with 10% woodland habitat (black area) and dispersion degrees of (a) $D = 0$, (b) $D = 10$, (c) $D = 50$, and (d) $D = 100$. A corresponding set was created for 20% woodland cover.



towards the directional vector, which varies between 0 (only preferred direction allowed) and 4 (all eight directions allowed); (3) the number of steps (NST) indicating the maximum allowed distance per time step. Movement rules are linked to behaviours rather than habitat (e.g., the distance covered per time step of feeding is assumed identical

whether feeding takes place in open grassland or forest). If an animal gets stuck (whereby the preferred direction and weight would take them into unsuitable habitat), the directional vector is altered by ± 1 until movement is again possible. See descriptions of behavioural states below for the values of movement parameters.

1. Initiation (σ , φ , J): Immediate state. Parameters are assigned initial values.
2. Maturation (J): Juveniles are assumed to mature on their first birthday (AM, Table 1). The juvenile object is removed from the simulation and a new adult object is created with identical attributes. A maturing object's first attempt at establishing a home range (see Establish range). If not successful it is transferred to Disperse.
3. Assess habitat (σ , φ): Immediate state. Each land-cover type is scored on a relative scale for its value both as cover (C_i) and as forage (F_i). The cover score is used when selecting a suitable place for ruminating. It depends on vegetation type and height (only if a dynamic landscape simulation is used). For the present use of the model we assumed that forest was threefold better than open land with respect to cover, but that forage possibilities were equal between forest and open land.
4. Feeding (σ , φ): The majority of the daily activity is taken up by alternating bouts of feeding and ruminating. The minimum time required for feeding for adults depends on body mass. While feeding within uniform habitat (all neighbouring cells equally good), the animal moves at random (DV = random number between 0 and 7; $W = 4$; NST = maximum 300). When it encounters a boundary between two land-cover types, it selects the highest forage score. When forage score is equal between two neighbouring land-cover types, the boundary is not recognized.
5. Ruminating (σ , φ): After each feeding period the animal needs to ruminate. Minimum time spent ruminating is assumed proportional to the intake during the previous feeding period. The cover score needs to be above a minimum value of 1. If not, the animal will spend 1 time step searching outwards in all directions for a patch with sufficient cover. When a suitable patch is found the animal moves directly towards it (DV = the direction of the suitable patch; $W = 0$; NST = maximum 600).
6. Dispersal (σ , φ): Dispersal from the natal area can happen during the second or third summer (Kurt 1968; Strandgaard 1972; Wahlström and Liberg 1995). First, an animal attempts to establish home range in its natal area. If it fails to find a suitable and (or) vacant area, it disperses. While dispersing, the animal moves with intermediate direction away from the natal home-range centre coordinates while selecting land-cover types with the highest possible cover score (DV = the direction away from natal home-range centre, first step is random if the animal is standing exactly in the home-range centre; $W = 2$; NST = maximum 1200). By the end of each day a dispersing animal evaluates the area it has arrived at and decides whether to keep dispersing or attempt to establish a home range (see Establish range).
7. Establish range (σ , φ): Immediate state. The decision rules for establishing a home range is outlined in Fig. 3.

Fig. 2. State-transition diagrams for (a) male objects and (b) female objects. States inside the broken square boxes describe the roe deer behaviours that take up the majority of time (mainly feeding and ruminating). Remaining states describe specialized behaviours used either for daily updates or for reacting to external events (E). After a specialized behaviour is completed, the animal is returned to the behaviour it was engaged in before the update/external event (R).

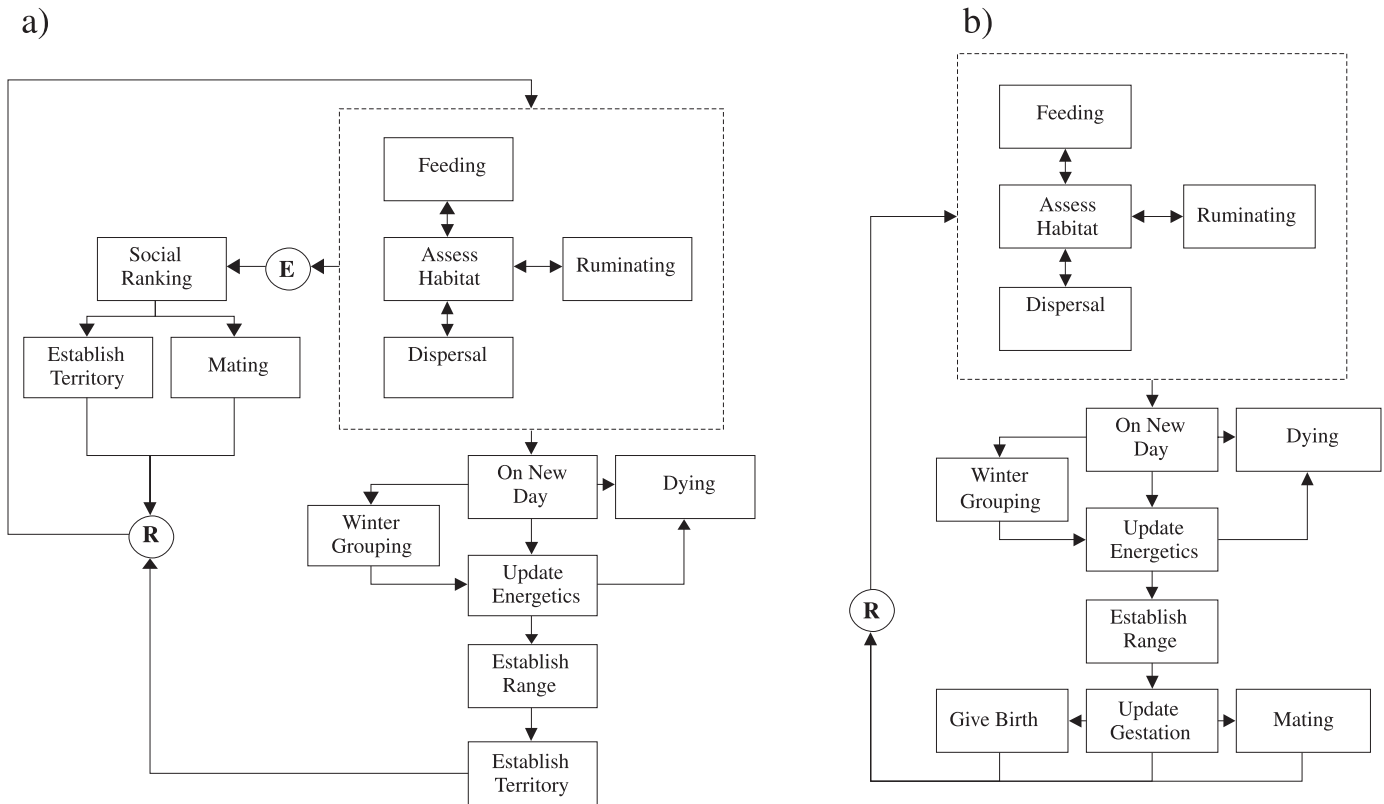
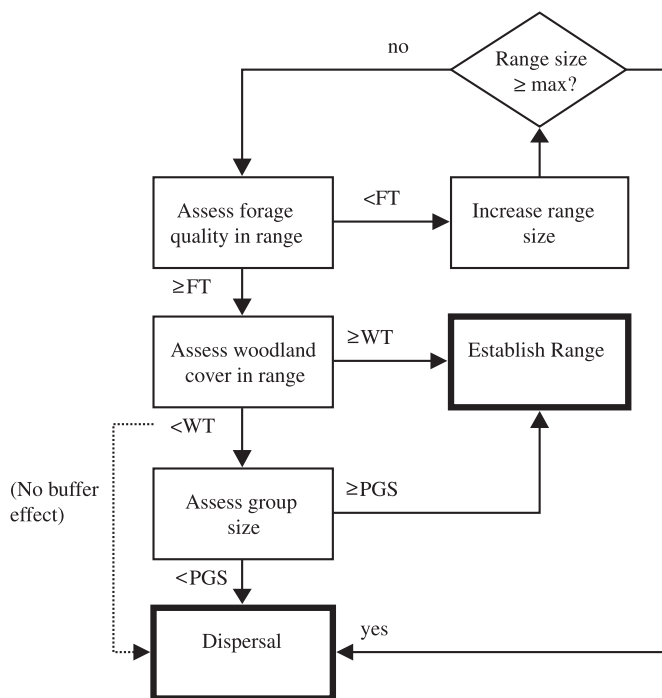


Fig. 3. The decision rules for establishing a roe deer home range. The dotted arrow “no buffer effect” indicates the flow when grouping behaviour is not allowed to buffer a lack of cover in the form of woodland habitat (default setting of the model).



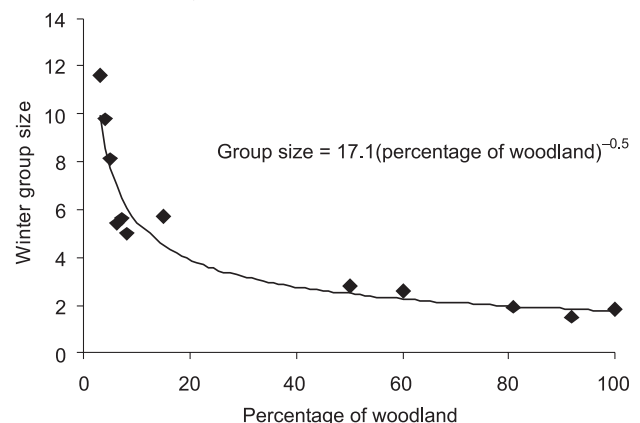
The evaluation of a new potential home range is initially performed for a minimum square area (MinRS, Table 1). The evaluation area is expanded outwards in size until the area is either fulfilling the requirements or has reached a maximum size (MaxRS, Table 1). The decision rules are designed to reflect the assumption that a home range first has to support the energetic needs and second the cover needs of the animal. If the energetic needs are not met, the area is unsuitable and no further evaluation is necessary. To address the questions outlined for the present study we designed the decision rules for home-range establishment (Fig. 3) to explicitly incorporate two different strategies: (1) a default strategy where group size is not allowed to buffer a lack of cover habitat and (2) a buffer strategy where a lack of cover habitat can be buffered by large group sizes. In the default strategy, the need for cover can only be supported by the presence of a minimum proportion of woodland. A potential home range is thus first evaluated with respect to forage and secondly with respect to woodland habitat. If either of these fails to meet the minimum requirements, the home range is unsuitable and the animal continues to disperse. In the buffer strategy, however, the need for cover can be supported either by the presence of woodland habitat or by membership of a sufficiently large social group (\geq preferred group size; see Winter grouping). Consequently, a potential home range is evaluated first with respect to

Table 1. Roe deer, *Capreolus capreolus*, model parameters and thresholds.

Name	Description	Values	References and comments
Reproduction and development			
MA	Mating season	15 July – 15 August	Strandgaard 1972
GP	Gestation period	300 days	Strandgaard 1972
LS	Litter size	$0.15W - 0.68$	Hewison 1996; W is maternal mass in kg
SR	Sex ratio at birth	1:1	Strandgaard 1972
AM	Age at maturity	1 year	Strandgaard 1972
AS	Age at onset of senescence	7 years	Gaillard et al. 1993; Strandgaard 1972
Spatial behaviour			
MinRS	Minimum range size	15 ha	
MaxRS	Maximum range size	100 ha	
PGS	Preferred group size	$17.1(\text{percentage of woodland})^{-0.5}$	Hewison et al. 1998 and references therein
FT	Forage threshold	4 000	Fitted value
WT	Woodland threshold	15% of range	Intermediate to woodland cover in landscapes (10% and 20%)
Mortality			
FM	Female background mortality: $FM_{[0]} = 1-2$ years, $FM_{[1]} = 2-7$ years, $FM_{[2]} = 7-10$ years, $FM_{[3]} = >10$ years	0.16, 0.02, 0.19, 0.8	Values assumed proportional to those in Gaillard et al. 1993, 1998
MM	Male background mortality: $MM_{[0]} = 1-2$ years, $MM_{[1]} = 2-7$ years, $MM_{[2]} = 7-10$ years, $MM_{[3]} = >10$ years	0.18, 0.1, 0.13, 0.8	Values assumed proportional to those in Gaillard et al. 1993, 1998
FAM	Juvenile background mortality: $FAM_{[0]} = 0-6$ months, $FAM_{[1]} = 6-12$ months	0.39, 0.11	Values assumed proportional to those in Gaillard et al. 1993, 1998
Energetics			
RMR	Adult resting metabolic rate	4 935 ^a	Mauget et al. 1997; measured in kJ/day for a 22-kg roe and value assumed identical for males and females
AMR	Adult activity metabolic rate: $AMR_{[0]} = \text{stand}$, $AMR_{[1]} = \text{walk}$, $AMR_{[2]} = \text{run}$	842, 1027, 5 537 ^a	Weiner 1977; Olesen et al. 1998; measured in cal./min for a 22-kg roe
CAT	Energy gained / g fat metabolized	9 400 cal.	Energetic value of fat
ANA	Cost of storing 1 g of fat	13 186 cal.	Vigh-Larsen 1987
INR	Intake rate (monthly averages)	8.7, 8.9, 11.7, 13.2, 31.8, 33, 24.7, 23.8, 22.4, 18.8, 11.9, 9.5	Calculated from Drozd 1979; measured in g dry mass / time step spent feeding

^aRecalculated to as cal./(time step·kg body mass)⁻¹ and where 1 cal. = 4.1868 J.

forage, second with respect to woodland, and third — if the minimum requirements for woodland are not met — the area is searched for the presence of groups. If no sufficiently large groups are present, the home range is unsuitable and the animals continue to disperse. The perception range of the individual vary with the size of the home range, i.e., an individual with a large home range is “aware” of the presence of other individuals in a larger area than an individual with a small home range. For these simple decision rules to work three thresholds are required: (1) a forage threshold, which sets the minimum amount of forage required in a home range (FT, Table 1); (2) a woodland threshold, which sets the minimum proportion of woodland (WT, Table 1); and (3) a group size threshold, which sets the minimum group size needed to buffer a given (insufficient) proportion of woodland (PGS, Table 1; see Winter grouping). The forage threshold and the woodland threshold are assumed equal for all individuals. The group size threshold is assumed to depend on the

Fig. 4. The observed relationship between group size and the amount of woodland in the surroundings (data from Table 9.2 in Hewison et al. 1998).

amount of woodland present in the home range. The smaller the amount of woodland, the larger the group size needed to make up for it (Fig. 4).

8. Establish territory (σ): Immediate state. When older than 2 years, a male can attempt to establish a territory (Strandgaard 1972; Liberg et al. 1998). It can achieve this by (i) taking over a territory when the owner dies, (ii) expelling the present territory owner (by having a higher social rank; see Social ranking), or (iii) establishing a new territory in a vacant area (see Establish range). During the territorial season (1 March – 1 September), all territory holders actively scan their surroundings for the presence of other males.
9. Social ranking (σ): Immediate state. A social rank order exists between males living in the same area. Once established the ranking persists until the end of that year. Although territories are persistent between years, all rankings are assumed to be re-established anew every year (Strandgaard 1972; Johansson 1996; Linnell and Andersen 1998). Ranks are established (i) when more than one male wishes to attend the same oestrous female (see Mating) or (ii) when males meet during the territorial season. Ranks depend on age, size, and whether or not the male is within his own territory at the time of the fight. Older age is only an advantage until the onset of senescence (AS, Table 1).
10. Mating (σ , φ): Females are assumed to be monoestrous (Hoffmann et al. 1978). Each female can go into oestrous with a small daily probability every day during the mating period (MA, Table 1). During that period the female sends messages to all males in her vicinity. Males respond by walking to the female's location (DV = direction of the females coordinates; W = 4; NST = maximum 600) unless they are already attending another oestrous female. If more than one male is available, the male with the highest social rank attends the female (see Social ranking). When a male is attending an oestrous female, he stays next to her (e.g., Cederlund and Liberg 1995). No other activities are allowed until the mate-guarding period is interrupted or mating has occurred successfully. If the attending male is successful, mating occurs at the end of that day. After mating the female is recorded pregnant and the gestation counter (see Update gestation) is initiated.
11. Give birth (φ): Immediate state. A pregnant female gives birth (creates a suitable number of juvenile objects) after a constant gestation period (GP, Table 1). Litter size is assumed to depend on maternal mass (LS, Table 1). Sex ratio at birth is 1:1 (SR, Table 1). The new juvenile objects are supplied with information about the identity of their mother and their litter mates.
12. Winter grouping (σ , φ): Each animal belongs to a social group all year, but the groups are only active during winter (1 October – 1 April). During this time the home-range centre (see Establish range) of all group members is shifted to a joint home-range centre (chosen as the home-range centre of the oldest animal in the group). When groups are dissolved in spring all group members return to their previous home range. Juveniles belong to their mothers' groups. The function of social groups is assumed to be predator avoidance, hence

groups represent an alternative to cover in the form of closed habitat (here woodland). The tendency of the individual animal to socialize will therefore depend on the amount of woodland cover in the surroundings. This is incorporated by assigning a preferred group size (PFG, Table 1; Fig. 4) to each animal calculated from the observed empirical relation between woodland cover and observed group sizes (Table 9.2 in Hewison et al. 1998). Groups are designed as dynamic structures in which group members attempt to obtain a group size as close as possible to their preferred group size. Individual group members may join or depart from groups in this process resulting in a fission–fusion system typical for ungulate social structure (e.g., Lot and Minta 1983; Barette 1991; Danilkin and Hewison 1996; Hewison et al. 1998).

13. Dying (σ , φ , J): Immediate state. The animal object is removed from the simulation.
14. On new day (σ , φ , J): Immediate daily update. Age is updated. Background mortality is applied (FM, MM, FAM; Table 1). Dispersing objects are transferred to Update range to attempt to establish a home range at the location they have arrived at. Group counter is updated to determine if it is time to re-establish winter groups. If that is so, the object is transferred to Winter grouping.
15. Update energetics (σ , φ , J): Immediate daily update. A simplified energy budget is kept for adult individuals to determine adult body mass. The time spent feeding in different land-cover types is recorded during the day and summarized in this state. The energetic return is calculated depending on the forage score (F_i) of the relevant land-cover type and the seasonal intake rates (INR, Table 1). Thus, the return of 1 day's feeding in land cover i during month j equals $F_i \times \text{INR}_j \times M_i$, where M_i is the number of time steps spent feeding in land-cover type i . The maintenance cost of 1 day's activity is calculated from the resting metabolic rate (RMR, Table 1) and the activity metabolic rate (AMR, Table 1). If the energetic return is positive, the animal puts on mass; if it is negative, it loses mass (CAT, ANA; Table 1).
16. Update gestation (φ): Immediate daily update. Gestation counter is updated. If gestation period has ended, the object is transferred to Give birth. Mating counter is updated to determine whether it is mating season or not (MA, Table 1). If it is mating season, the object is transferred to Mating.

Model evaluation

Our main concern in the model evaluation is to ensure that the model produces population-level patterns that are realistic and comparable with observed patterns in real populations. The study is conducted in artificial stylized landscapes. This is justified by the aim of the study, which is to explore the interaction between a behavioural strategy and landscape structure, and how this shapes overall patterns of space use. The consequence, however, is that it makes little use to compare some types of numeric output (such as population size) to real data. We therefore chose a set of population-level patterns, which could be expected to have a limited sensitivity to the specific landscape configuration,

Table 2. Roe deer model evaluation using the mean values of all replicates in all landscapes extracted for the entire population in simulation year 30.

Variable	Mean model value (range)	Range in literature values	References
Age structure	See Fig. 7	See Fig. 7	
Dispersal distance (km)	2.4 (0.3–8.1)	0.8–2.9	Linnell 1994 (Norway); Wahlström and Liberg 1995 (Sweden); Strandgaard 1972 (Denmark)
Territory tenure (years)	5.3 (1–11)	5–7; life time	Johansson 1996 (Sweden); Strandgaard 1972 (Denmark)
Reproducing females (%)	65* (61–72)	60 [†] , 85 [‡]	Hewison 1996 (UK)
Litter size at birth	1.9* (1–3)	2.0–2.2	Andersen et al. 1995 (Norway); Andersen 1953 (Denmark); Strandgaard 1972 (Denmark)
Adult sex ratio ($\sigma^{\circ}:\varphi$)	1.4:1 (1.2:1–1.5:1)	1.9:1	Strandgaard (Denmark)

*, Adults + yearlings; [†], yearlings only; [‡], adults only.

and compared their mean values and range of variation with values reported in the literature. This to ensure that the demographic and spatial components of the model produce results within realistic bounds. The patterns examined were population age structure, adult sex ratio, number of fawns per female, proportion of reproducing females, male territory tenure, and dispersal distance. Data from Danish populations were used whenever possible and supplemented with data from northwestern Europe when needed.

Model scenarios

Each behavioural strategy was simulated in each of the 22 dispersion landscapes. The two levels of woodland cover (10% and 20%) were chosen to be on either side of the threshold for territory establishment (WT, Table 1). For each run, the model was seeded with an initial population of 200 adult individuals of each sex and run for a time period of 40 simulation years with 5 replicate runs of each scenario. It took approximately 10 simulation years before a stable population structure was obtained. Output information was thus only collected from year 11 onwards (total sample period 30 years). Information was sampled once a year on total population size (N_{total}), group size (GS), individual home-range size, and the proportion of woodland habitat in individual home ranges (HR_{size} , HR_{wood}). To evaluate the three objectives outlined in the Introduction, we compared the predictions made regarding total population size, group size, and home-range size based on each behavioural strategy across the entire range of woodland dispersion and at each level of woodland cover. The mean proportion of woodland in home ranges was used as a measure of roe deer association with woodland.

Results

Scenarios

The presence of behavioural plasticity had a very large impact on model predictions regarding the effects of woodland dispersion on roe deer spatial distribution and group size. The difference between the two behavioural strategies was most pronounced when average woodland cover was low. At 0% woodland dispersion (Fig. 1a), there is a minimum of edge habitat available. Following the default strategy, the population is confined to the wooded fraction of the landscape setting up home ranges with high woodland cover (Fig. 5a) and small size (Fig. 5b). When the option exists of

switching to the buffer strategy when woodland cover is insufficient, the majority of home ranges are established in the open land (Fig. 5a, black bars) and are 2–3 times larger (Fig. 5b) than under the default strategy. Hence, the presence of behavioural plasticity enables a significant proportion of the population to loose the association with woodland at the lowest woodland dispersion levels.

As the degree of random woodland dispersion increase, the larger patches of woodland quickly break down and become scattered across the landscape. Following the default strategy, home-range sizes increase drastically in response to this (Fig. 5b). Behavioural plasticity act to stabilize home ranges at an intermediate value in return for a large increase in mean group size (Fig. 5c).

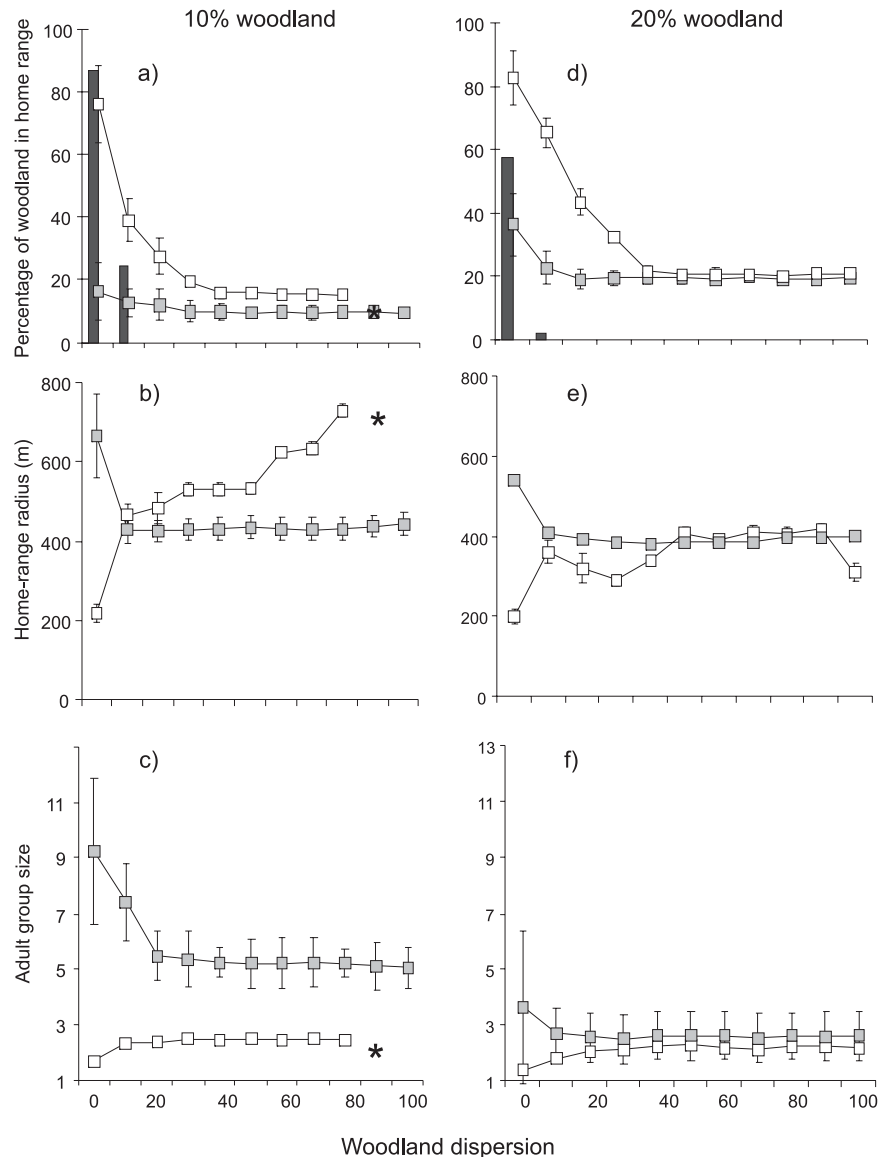
When the average woodland cover in the landscape is above the requirements of the individual animal (20%), a smaller proportion of home ranges are established in open land (Fig. 5d). Home-range sizes stabilize around an intermediate value at a low degree of woodland dispersion (Fig. 5e) even in the absence of behavioural plasticity. There is no significant difference in model predictions regarding group size under the two strategies (Fig. 5f).

A very clear optimal level of woodland dispersion ($D = 10$) for roe deer density was predicted under the default strategy. This was evident at both levels of woodland cover (Fig. 6a, 6b). An optimal dispersion level was also evident when behavioural plasticity was included, but only at low woodland cover. At this dispersion level the model population was able to make optimal use of the landscape, whether behavioural plasticity was an option or not, and there was no difference in the population size obtained following either strategy (Fig. 6a, 6b). At higher levels of woodland dispersion, however, the different strategies produce markedly different predictions. At low woodland cover the default strategy predicts extinction, while the buffer strategy predicts a stable intermediate population size (Fig. 6a). At high woodland cover the default strategy predicts a significantly lower population size at intermediate levels of woodland dispersion, but an increase to the level of the buffer strategy as woodland dispersion approaches a random distribution (Fig. 6b).

Model evaluation

The aim of the model evaluation was to ensure that the demographic and spatial components of the model produce population-level patterns that are realistic and comparable

Fig. 5. The effect of woodland dispersion on the spatial and social patterns of a roe deer population that follows each of the two behavioural strategies. (a) and (d), Mean (± 1.0 SE) percentage of woodland in individual home ranges with solid bars indicating the percentage of home ranges with no woodland association ($<1\%$ woodland cover); (b) and (e), mean (± 1.0 SE) home-range size; and (c) and (f), mean (± 1.0 SE) adult group size. Open squares indicate the default strategy, shaded squares indicate the buffer strategy, and asterisks indicate scenarios where the population is predicted to go extinct (see Fig. 6).



with observed patterns in real populations. The results of the model evaluation are shown in Table 2 and Fig. 7. The population age structure (Fig. 7) and adult sex ratio (Table 2) gives a good indication of whether or not the demographic components (mortality and fecundity) of the model are realistic and balanced. It was compared up against data from a local Danish population (Strandgaard 1972) and indicated a good match between model and data. All females go into oestrous once during the mating period (MA, Table 1). Whether or not they are mated and produce fawns, however, depends on the proximity of a suitable male and a successful mating behaviour (see Roe deer model description, state 10). The predicted percentage of reproducing females (Table 2) is in good agreement with data, and hence, indicates that the

decision rules for mating behaviour are reasonably realistic. Litter size in the model is a product of female body mass (LS, Table 1). This parameter obviously contains little room for variation, since it is constrained to an integer value between 1 and 4. However, a mean predicted litter size in agreement with data shows that variation in female body mass in the model are within reasonable bounds. Territory tenure is the average length of time a male maintains the same territory. In the model, a male roe deer can loose his territory by death or by being evicted by a stronger male during the territory season (see Roe deer model description, state 9). Empirical data on territory tenure is rare, as it requires long time series of monitoring the same population. The predicted territory tenure (5.3 years) is, however, in

Fig. 6. The effect of woodland dispersion on the total population size (± 1.0 SE) of roe deer obtained under each of the two behavioural strategies. The population did not persist at the highest degrees of woodland dispersion following the default strategy. Open squares indicate the default strategy and shaded squares indicate the buffer strategy.

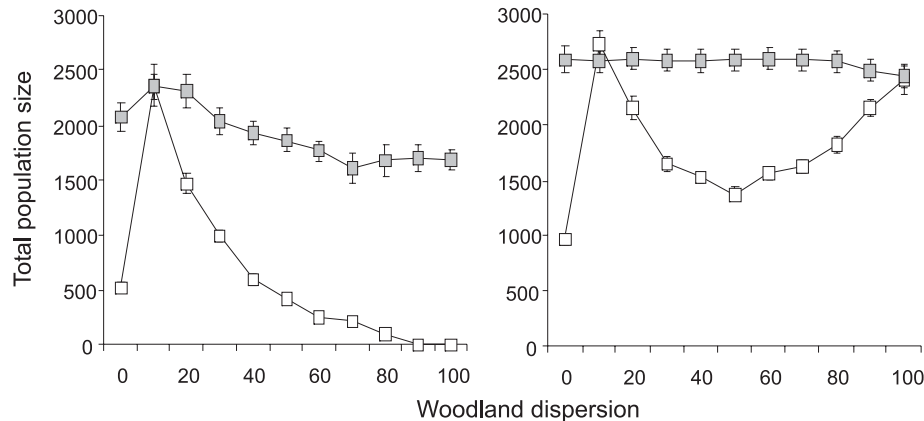
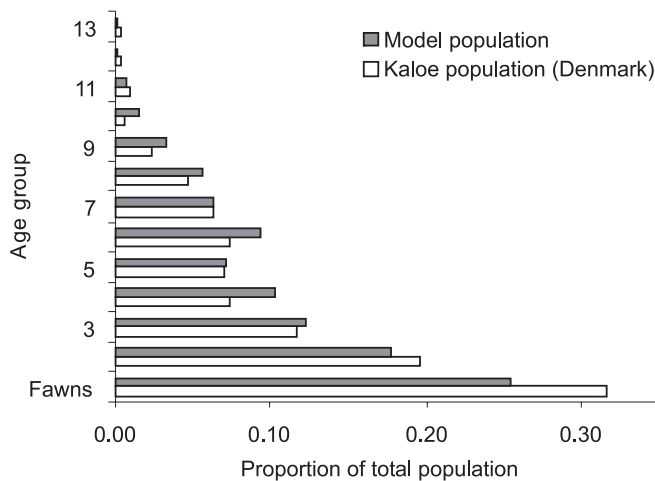


Fig. 7. The mean age structure of the model roe deer population compared with a local Danish population ($n = 300$ from Table 26 in Strandgaard 1972). Model values are means of all replicates in all landscapes extracted for the entire population in simulation year 30. Differences in medians between the two samples were nonsignificant (Wilcoxon's test for paired samples, $Z = -0.864$, $p = 0.388$).



agreement with the few values reported in the literature. The measures of dispersal distance extracted from the model are straight-line distances measured from the centre of the natal home range. They are subject to the inherent limitations imposed by landscape size. The model landscape was 10 km \times 10 km with periodic boundaries. The vast majority (83%) of dispersal event was, however, <4 km with a mean of 2.4 km. This is in good agreement with empirical data on roe deer in southern Scandinavia (Table 2).

Discussion

The implications of behavioural plasticity for modelling species' response to environmental conditions have received little attention to date (Komers 1997; Henein et al. 1998; Hewison et al. 2001). However, as this study clearly demonstrates, the degree to which a species is able to exhibit behavioural plasticity in its response to environmental condi-

tions could have a major impact on the animal's distribution and abundance, and should therefore be of concern to modellers. With a view to the three objectives outlined in the Introduction, we conclude that ignoring behavioural plasticity in the current model resulted in significantly lower estimates of population size, population persistence, and the ability to cope with increased woodland dispersion. Most noticeably the clear optimal dispersion level predicted to be present under the default strategy is less pronounced or missing under the buffer strategy.

With a view to demonstrating this effect, we have contrasted two rather extreme behavioural strategies, both based on the assumptions that cover is a necessary resource for roe deer. In the default strategy the spatial behaviour of all individuals is fixed to a certain environmental cue (proportion of woodland habitat). In the buffer strategy, all individuals have the option of switching to an alternative cue, not determined by landscape attributes (presence of conspecifics). Although this framework is useful for demonstrating the implications of ignoring a strong behavioural plasticity in a model, it is obviously much less flexible than behavioural plasticity shown by a real species. There are therefore a number of simplifications, the inclusion of which would probably have an impact on the results. These include the fact that all adult individuals are assumed to have the same requirements to home-range quality and cover regardless of age, size, and sex (woodland threshold and forage threshold assumed equal to all individuals). We also implemented all or nothing strategies, whereby all individuals are assumed to switch to alternative strategy, if their requirements for cover are not fulfilled. In roe deer, the tendency to group appears to be affected by age and sex. Roe deer females show a stronger tendency to group than males (San José et al. 1997), probably because many are in the company of offspring. In addition, it is not uncommon in ungulates that older animals of both sexes are more solitary than younger animals (e.g., Carranza and Arias de Reyna 1987; Gerard and Loisel 1995). Furthermore, we assume a fixed proportion of woodland rather than a fixed area as a threshold for home-range establishment. Hence, individuals living in large home ranges have larger absolute requirements for cover than individuals in small home ranges. However, based on the as-

sumption that the main function of woodland is cover and the most important attribute of cover is proximity, we consider this to be reasonable. A final simplification is that the degree of plasticity is constant among individuals, but in reality some individuals may be more "risk-prone" than others (McNamara 1996; Bateson 2002).

The view on the mechanisms and motivation behind the spacing patterns of roe deer (and of ungulates in general) is currently undergoing a change. Traditionally, grouping in ungulates has been viewed as an adaptive response to predation pressure, and hence the mechanism at work is natural selection (Hewison et al. 1998; Brashares and Arcese 2002; a recent review in Caro et al. 2004). Large group sizes are suggested to reduce predation pressure either through increased group vigilance or through an effect of dilution. The exact mechanism, however, is unclear (Roberts 1996). Jarman (1974) first noted that because habitat cover serves the same function as large group sizes in predator defence predation pressure should interact with habitat openness to shape group size. Consequently, individuals living in open habitats should show a higher tendency to aggregate than forest-living individuals. This has been shown true for many ungulate species including the roe deer (e.g., Bresiński 1982; Maublanc et al. 1987; Cibien et al. 1989; San José et al. 1997; Hewison et al. 1998; Caro et al. 2004). The speed at which the transition from forest to field behaviour has happened in roe deer indicates, however, that the presence of larger groups in open environments is probably not a result of natural selection (Gerard et al. 2002). Theoretical model studies have shown that grouping patterns, similar to those observed in roe deer, may come simply from instability of groups and variation in detection distance with habitat openness, hence be an emergent pattern (Gerard and Loisel 1995; Gueron et al. 1996). These models build on classical "swarming" models (Gueron and Levin 1995; Gueron et al. 1996), which have been successful in demonstrating how complex large-scale patterns can emerge from local interactions and simple decision rules. The model of Gerard and Loisel (1995) clearly support the idea that a genetically encoded mechanism behind grouping in herbivores is not needed (Gerard et al. 1995, 2002).

However, even for an emergent pattern such as this, there is a requirement for an underlying motivation of the individual decisions shaping the pattern. Several motivating factors have been suggested for the roe deer. Even without a selective pressure acting upon it, the advantage of dilution and (or) joint vigilance, and hence, increased feeding time for the individual may be sufficient for the individual deer to seek company when this is available (e.g., Sieber 1995; Beauchamp 2003a, 2003b). Empirical evidence indicates that group size may influence the predation rate on ungulates (Hebblewhite and Pletscher 2002). Alternatively, an uneven distribution of resources can cause passive aggregation of individuals (e.g., Focardi and Toso 1987), and possibly enhance grouping through effects on individual movement patterns. The presence of conspecifics may thus be a cue for the individual, indicating the presence of resources. Resource distribution is known to affect the spacing patterns of ungulates (e.g., Maher 2000; DePerno et al. 2003; Focardi et al. 2003; Palmer et al. 2003). Brashares and Arcese (2002) studied another small ungulate species, which exhibits sig-

nificant behavioural plasticity (the oribi, *Ourebia ourebi* (Zimmermann, 1783)). They found that forage abundance and forage quality were the main determinants of both female home-range size and group size, while habitat openness (canopy cover and visibility) had no effect.

The aim of the current study was not to evaluate plausible mechanisms shaping the transition from forest to field roe deer. Rather we wished to illustrate the implications of ignoring or including the presence of behavioural plasticity in a behavioural model of roe deer spacing patterns. We assumed that the first concern of an individual roe deer is food resources and the second concern is cover. We further assumed that the tendency of the individual roe deer to group depends on the degree of openness of the habitat. Although these assumptions are supported by the ecological literature, further effort is clearly needed to document the motivation behind the individual choice, the role of perception of environmental cues in decision-making behaviour (e.g., Lima and Zollner 1996; Zollner and Lima 1999), and the possible fitness consequences of choosing one strategy over the other (e.g., Gerard et al. 2002; Caro et al. 2004). Development and application of individual-based behavioural models in management is advancing rapidly. Their usefulness as experimental systems in which hypothesis regarding the effects of contrasting environments on population dynamics and animal distribution patterns can be evaluated is firmly established (Hemelrijk 2002; Ruckstuhl and Kokko 2002; Stephens et al. 2002; Stillman et al. 2002; Sutherland and Norris 2002; Grimm et al. 2003; Shirley et al. 2003). Contrary to this, the identification and implementation of behavioural plasticity and the implications of this for predictive modelling of behaviourally plastic species has received very little attention and should be advocated as a priority research area in the future.

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