Roe Deer Model Description

The model simulates survival, reproduction and movements of individual deer in response to habitat quality and external events. Three object-types are included; adult males (bucks), adult females (roes) and fawns. Figure 1 show the structure of each model in the form of a state-transition diagram. The majority of time for all object types is taken up by an alternating cycle of ruminating and feeding, but a number of specialised behaviours are available for each object type. This allows individuals to perform simple intra-specific interactions, such as a coupling of doe and fawn behaviour, communication between mates during reproductive behaviour and territorial interactions between bucks.

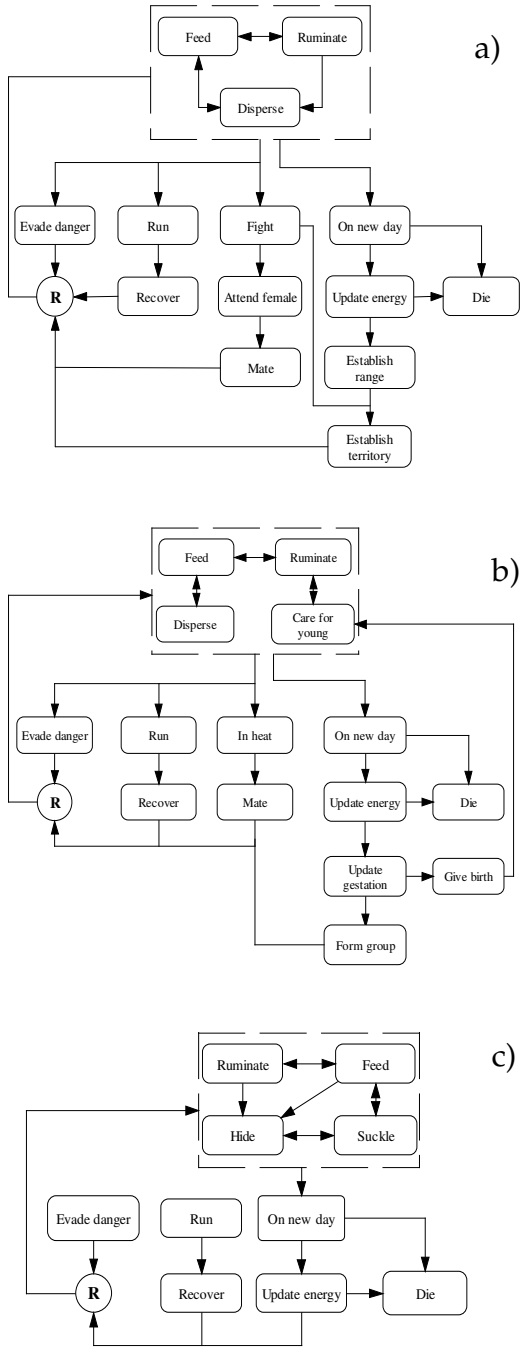

Figure 1. State-transition diagrams for a) male, b) female and c) fawn objects. States inside the square box describe the behaviours that take up the majority of time (mainly feeding and ruminating). Remaining states describes specialised behaviours used either for daily updates or for reacting to external events. After a specialised behaviour is completed, the animal is in most cases returned to the activity in which it was engaged before the event happened (symbolised here by "**R**").

Movements. Animal movement was defined by three parameters: 1) a directional vector, indicating the preferred direction, 2) a weight, indicating the strength of the bias towards the directional vector and 3) the number of steps, indicating the maximum allowed distance per time step. Movement rules were linked to behaviours rather than habitat (e.g. the distance covered per timestep of feeding is assumed identical whether feeding takes place in open grassland or forest).

Evaluate habitat.
Habitat can be evaluated with regard to both cover and feeding quality. *Cover* values are used when selecting a suitable place for ruminating/hiding and are scored based on vegetation characteristics. High cover values are found in young forest, scrubby vegetation and natural grass and crops with high vegetation. Intermediate values are found in short grass/crops and mature forests, while low values are found in open fields and very short grass (e.g. grazed meadows). *Feeding quality* is based on the relative energetic quality of a habitat type. Since no absolute estimate of the energetic content of natural food is available for roe deer, a crude relative score was developed, that incorporates both differences between major habitat types and seasonal variation in quality.

Mature. Fawns were assumed to mature on their first birthday (Strandgaard 1972). The fawn object is removed from the simulation and a new adult object is created with identical attributes.

Feed. The majority of the daily activity is taken up by alternating bouts of feeding and ruminating. The minimum time required for feeding was calculated daily based on empirical data on weight-specific feeding requirements. During feeding the animal selects polygons to maximise the energetic gain.

Ruminate. After each feeding period the animal needs to ruminate. Minimum time spent ruminating was assumed proportional to the intake during the proceeding feeding period. If the cover of the habitat is above a minimum value the animals chooses to ruminate at its present location. If cover is insufficient the animal spends one time-step searching outwards in all eight directions for a patch of suitable habitat. If not found, the animal will ruminate in open habitat.

Hide. While less than two months of age, the fawn spends most of its time in hiding. It will leave this state only when the mother is in the vicinity (Linnell 1994, Andersen et al. 1998, Linnell et al. 1998). Above two months of age fawns are assumed to follow their mothers and never seek hide. Before hiding a suitable bed site is selected based on vegetation height (Linnell 1994, Linnell et al. 1999).

Run. A response pattern to danger and disturbance was built into the model to allow for future implementation of human activities and/or explicit predator models. The animal is assumed to respond by running if the danger is acute e.g. within a threshold distance. It moves in as straight a line as possible away from the danger and attempts to stay in habitats offering good cover. It continues to run until more than a minimum safety distance to the danger has been attained. The disturbance thresholds depend on season and habitat (Jeppesen 1987, Olesen et al. 1998). Fawns always follow their mother (Mrlik 1991).

Evade danger. If danger is less acute (beyond a threshold distance) the animal tries to evade it by walking away in a suitable direction.

Recover. After running the animal needs to recover before it can return to normal activity. During this time it rests in a suitable bed site (Olesen et al 1998).

Disperse. 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 selects habitat types with the highest possible cover values. 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.

Establish range. A potential home range is evaluated with regard to i) distance to natal area, ii) habitat quality and iii) presence of other individuals of the same sex. Initially the animal evaluates a minimum square area. If the area fails to fulfil the requirements, the size is gradually increased towards an upper limit. If still insufficient the area is abandoned and the animal continues to disperse the next day. Young males have an additional constraint on their choice of area. Having found a suitable area they position themselves in the matrix of existing male territories according to one of two strategies. The strategies mimic a high-risk-high-gain strategy ("satellite" males) and a low-risk-low-gain strategy ("peripheral" males) (Cederlund and Liberg 1995). A satellite male is assumed to choose the oldest established male in the area as his "host" and establish his home range centre close to that of the old male. If the old males dies or is out-competed the satellite male is given an advantage over other males in taking over the territory. A peripheral male chooses his home range centre as far away as possible from established males and stands less of a chance of taking over the neighbouring territories. The resulting home range is defined by two parameters. i) the location of the home range centre and ii) the radius of the evaluated square. During all regular activities (excluding dispersal) the animals evaluates the distance to the home range centre before each step. When it reaches the radius of the evaluated square, the animal is gradually weighted back towards the centre. The model contains no built-in assumptions about the shape and location of home ranges or territory borders and the spacing system of males and females were assumed to be independent (Bramley 1970).

Establish and defend territory. When older than two years, a male can attempt to establish a territory (Liberg et al. 1998, Strandgaard 1972). It can achieve this by i) taking over a territory when the owner dies, ii) expelling the present territory owner, or iii) establishing a new territory in a vacant area. During the territorial season all territory holders actively scan their surroundings for the presence of male intruders.

Fight. 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 et al. 1996, Linnell and Andersen 1998). Ranks are established i) when more than one male wishes to attend the same oestrous female, or ii) when males meet during the territorial season. Ranks depend on age, size, a measure of "experience" expressed as the number of previous matings and the number of previous fights, and whether or not the male is within his own territory at the time of the fight.

Suckle. Every time-step a non-weaned fawn evaluates whether the amount of time it has been nursed during the last hour is below an age-specific threshold. If so, fawn is transferred to this state and sends a message to its mother in order to initiate a new care period.

Care for young. When receiving a message from one of her fawns the female evaluates her own physical condition. Unless she is below a critical threshold, she allows the fawn to be nursed and is transferred to this state. The fawn walks to the female and is nursed for the rest of that time step.

In oestrous. 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. During that period the female sends messages to all males in her vicinity. Males respond by walking to the female's location unless they are already attending another oestrous female. Roe deer females actively choose their mates, but the cues they base their choice upon remains unclear (Liberg et al. 1998). For use in this model males were ranked and the strongest male was chosen to attend the female.

Attend female. When a male is attending an oestrous female, he follows her closely wherever she goes (e.g. Cederlund and Liberg 1995). No other activities are allowed until the guarding period is interrupted or mating has occurred successfully. If the attending male is successful, mating occurs at the end of that day.

Mate. The mutual pointers between the attending male and the female are deleted. The female is recorded pregnant and a gestation counter is initiated.

Give birth. A pregnant female gives birth (i.e. creates a suitable number of fawn objects) after a gestation period that is assumed constant (Strandgaard 1972). Litter size and birth weights are assumed to depend on maternal weight (Oftedal 1985, Hewison 1996, Hewison and Gaillard 2001). The new fawn objects are supplied with information about the identity of their mother and their littermates.

Form group. Female and fawn aggregate in family groups during autumn and winter. The preferred group size for an animal is assumed inversely proportional to the amount of wooded habitat in the animal's range (e.g. Hewison et al. 1998 and references herein). An animal keeps a reference to all other animals in its group and a fawn always belongs to its mother's group. When groups are formed in autumn each animal evaluates whether its current group size is suitable. If not, the animal can attempt to join a neighbouring group. A potential new group member is evaluated by all present group members. If it is a close relative (parent or offspring) to any member in the group, it is always accepted. Strangers are only accepted if the size of the group is less than the preferred size. While the group persists all members substitute their own range centre with a shared group range centre. When the groups are dissolved in spring, the members regain their old range centres. The result is a highly simplified, but dynamic group structure where each group predominantly consists of related individuals.

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