Habitat structure, female distribution, and fallow deer Dama dama mating stands

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Male fallow deer *Dama dama* exhibit inter and intrapopulation variation in mating behaviour, including both territorial and non-territorial mating tactics. During 1993 I investigated the relationship between fallow deer mating territory location and female distribution in relation to habitat characteristics at the Ottenby nature reserve in southern Sweden where males defend isolated mating stands during the autumn rut. Mating stands were positively associated with dense canopy cover and the presence of hazel *Corylus avellana* trees, but negatively associated with the number of alder *Alnus glutinosa* trees. Preference for such sites may be connected with the types of display males engage in during the rut as both auditory and olfactory means of communication can be affected by habitat structure. In relation to one another, the stands were randomly dispersed throughout the wooded region and along the perimeter of fields, with no indication of clumping or overdispersion. Female distribution was not associated with any of the habitat characteristics, or with stand location. The idea that males might be defending areas of favoured resources was ruled out as a possible explanation for stand location, although the idea that males might be defending game trails frequented by females remains as a potential determinant of stand locations.

In mammals, female reproductive success is closely related to the amount and quality of resources available to both mother and offspring (Clutton-Brock, Guinness & Albon 1982), while male reproductive success is often dependent on access to sexually receptive females (Trivers 1972). Thus, male dispersion is predicted to follow female distribution, while female dispersion should be most affected by resource distribution (Emlen & Oring 1977). When resources important to females are economically defendable, males would benefit by defending such resources and thus obtain exclusive mating access to the females which visit such a resource-containing territory. Alternatively, in order to monopolise matings when females or resources important to females are not economically defendable, males may pursue other tactics such as defence of display sites or other opportunistic strategies (Clutton-Brock 1989).

Resource defence by males is a common strategy among African antelopes (Gosling 1986). Puku *Kobus vardoni* males defend resource patches favoured by females during the breeding season and thus gain

mating opportunities. However, in addition to being attracted to food resources, female puku are also attracted to certain male phenotypes (Rosser 1992). Defence of mating territories containing resources can also be found among cervids, although this type of strategy is not common. In a red deer *Cervus elaphus* population in Doñana National Park, Spain, some males defend territories which either contain resources or are strategically located between female resting areas and favoured resources (Carranza, Alvarez & Redondo 1990). Some fallow deer *Dama dama* males in Doñana Park also defend resource territories during the October rut, tactics which for both species probably arise through the availability of economically defendable resources (Alvarez, Braza & San Jose 1990).

In some populations of ungulates, two or more male mating tactics may occur simultaneously. Fallow deer males at Petworth Park in England are able to defend stands which contain resources (oak trees), but most females choose instead to visit the lek, a group of clustered smaller territories containing no resources (Clutton-Brock, Green, Hiraiwa-Hasegawa & Albon 1988). Topi *Damaliscus lunatus* male tactics also include both defence of resource territories and defence of lek territories, with resource territories attracting more females than unsuccessful lek territories but fewer than successful lek territories (Gosling & Petrie 1990). Uganda kob *Kobus kob thomasi* males do not defend resource territories at all, but defend lek territories or single mating territories (Leuthold 1966). Recently, a correlation has been discovered between resources and female location in kob, but the resources are not economically defendable for males and the connection between resources, female dispersion and male dispersion breaks down (Deutsch 1994).

Fallow deer exhibit a number of different mating tactics including resource defence, isolated territories (stands), lek territories and other, non-territorial, tactics (Langbein & Thirgood 1989, Thirgood 1990, Apollonio, Festa-Bianchet, Mari, Mattioli & Benedetta 1992, Moore, Kelly, Cahill & Hayden 1995). Many of the earlier studies of fallow deer have focused on populations with lek territories, and have concentrated mainly on male characteristics associated with mating success (Apollonio 1989, Apollonio, Festa-Bianchet & Mari 1989a, 1989b, Apollonio, Festa-Bianchet, Mari & Riva 1990, Apollonio et al. 1992, Clutton-Brock et al. 1988, Clutton-Brock, Hiraiwa-Hasegawa & Robertson 1989, Clutton-Brock, Price

& MacColl 1992, Festa-Bianchet, Apollonio, Mari & Rasola 1990, Thirgood 1990). With the exception of the Petworth Park study (Clutton-Brock et al. 1988), none of these studies have investigated habitat characteristics in relation to lek territory location or to female dispersion. At Ottenby, in southern Sweden, males either defend mating territories smaller than one hectare or attempt to follow females in order to mate. Females visit these isolated mating stands and mate most often with a territorial male (Espmark & Brunner 1974). In this study, I tested whether habitat characteristics affect the distribution of females and the location and spacing of male mating territories.

Methods

I conducted my study during 5-30 October 1993 at Ottenby Nature Reserve located on the Swedish island of Öland (56°13'N, 16°26'E). The fallow deer population has access to the entire 995-ha reserve, but I focused my study on the 250-ha wooded region where the deer are concentrated during the rutting period (Fig. 1). The nature reserve is bordered on three sides by the Baltic Sea and is fenced along the northern perimeter. Three major habitat types occur in the reserve: birch-oak forest, scrub land, and pas-
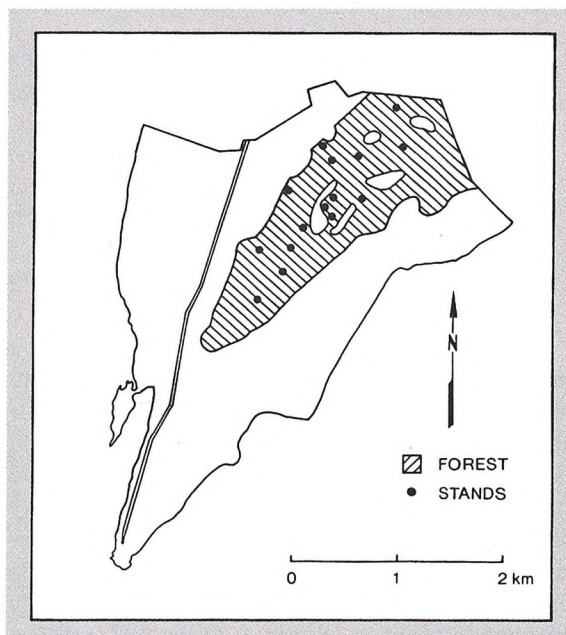

Figure 1. Ottenby Nature Reserve with indication of the forest and the 15 fallow deer mating stands included in this study.

ture. The birch-oak forested region can be subdivided into 10 different communities based on floristic composition as well as species dominance (Larsson 1974, Table 1). A total count of 278 deer was made from a helicopter census conducted during February 1994 covering the northern 700 hectares of the reserve, giving an estimate of 28 deer/100 ha for the entire reserve (approximately 61 antlered bucks, 100 females and 117 juveniles and calves). Females are found in the forested region throughout the year, occasionally venturing out onto the open areas surrounding the forest at dawn or dusk. Males utilise much more of the reserve than females and can be found far out onto the pastures during the summer months, while from autumn to spring males are more often found in the forested area (pers. obs.). Due to this concentration of both males and females in the forest during the rutting period, the density of fallow deer in the study area was expected to be somewhat higher than that reported for the entire reserve.

The investigation of stand characteristics was conducted by comparing habitat structure of 15 mating stands with 15 randomly selected plots. Fallow deer mating stands can be characterised as a defended area, usually less than one hectare, where males groan, scent-mark and scrape. There is usually one scrape which is the focal point of male activity, resulting in a deeper pit than at other scrapes. Temporary stands also occur, requiring that set requirements be fullfilled before a stand could be included in the study as a permanent stand. A stand was considered permanent if a male was seen defending it, or heard groaning from it on two consecutive days during the main rutting period (22-30 October). This did not require that a male defend the same stand throughout the rut. I established stand sample plots by creating a 10 m × 10 m sample area around the central point of the largest scrape at each stand. The random plots were established by randomly selecting centre points on a map of the study area. Within each plot, I counted and identified all trees, estimated shrub cover (>1m) using a scale from one to four (1: 0-25%, 2: 26-50%, 3: 51-75%, 4: 76-100%), and estimated canopy cover directly over the centre point using the same 1-4 percentage scale. I measured grass height at the middle point of the four sides of each plot, and made percent grass cover estimates using 0.5 m × 0.5 m quadrates along the north and south sides. In addition, as many plants as possible were identified within each sample quadrate. For each sample plot I determined community type which was then treated as a categorical variable (see Table 1).

The importance of stand habitat characteristics was investigated by fitting a logistic regression model to the stand and random habitat variables using the SPSS package (Norusis 1990). This method indicates which, if any, variables are important in differentiating the stand and random plots. The floristic species analysis was conducted using canonical correspondence analysis from the CANOCO (Ter Braak 1987) software program. This method tests for relationships between species and a supplied environmental variable, in this case, stand or random. The habitat characteristics which were indicated as significant in the multivariate tests were also investigated using univariate methods.

The location of stands in relation to each other may be important in describing the degree of competition between males. Spatial analysis of stand location was carried out using the Clark-Evans test with the Donnelly modification (Krebs 1989). This measure of

Table 1. Description of vegetation communities found within Ottenby Forest, Öland. (*Hazel trees were not common and were clumped in their distribution. This community was not found along any of the transects.)

Community	Characteristics
Carex vesicaria - Iris pseudacorus	Low lying areas. When trees are present they are mostly alder.
Filipendula ulmaria - Geum rivale	An open, grassy community. Birch trees are the most common tree species.
Betula pubescens - Calamagrostis canescens	Low lying areas. Both birch and alder present.
Quercus robur - Molinia coerulea (typ)	Birch and oak forest almost completely lacking bushes.
Quercus robur - Molinia coerulea (Rubus idaeus)	Birch and oak forest with a well developed shrub layer.
Quercus robur - Agrostis tenuis (Vaccinium myrtillus)	Contains oaks, but also birch and aspen. Much of the grasses replaced by blueberry.
Quercus robur - Agrostis tenuis (typ)	Dominated by oak trees and grasses.
Quercus robur - Deschampsia flexuosa	An open area with few oaks and birches. Rich in grass species.
*Corylus avellana - Geum urbanum**	Hazel groves.

spatial patterning relies on a simple nearest-neigh-bour distance method, resulting in an index of aggre-gation (R) where 1 = not different from random, <1 = aggregated, and >1 = uniform distribution.

The investigation of the influence of habitat char-acteristics on female distribution was conducted dur-ing the same time period as the male mating territory study. I collected female distribution data from observations conducted along four strip transects (300 m × 150 m), each covering 4.5 ha, where each transect was divided into nine 100 m × 50 m plots. I walked through the middle of each transect 13 times over a 25-day period, noting the sex and numbers in each group encountered as well as in which plot the group was found. The deer watched me as I walked by, but more often than not, they returned to previous activities when I had passed by. In those cases where the deer were disturbed and ran away, care was taken not to recount them in the adjacent transect plot. Within each sample plot, I counted and identified trees along a 50-m line which dissected the centre of each plot. Amount of shrub cover >1 m high was also approximated along this line using the previously described 1-4 percentage scale. The amount of canopy cover was established from the centre of each plot using the same 1-4 percentage scale as for shrub cover. At a random point along the 50 m line within each plot, I measured grass height and a 0.5 m × 0.5 m quadrate was randomly thrown out. Within the quadrate, percent green grass, dry grass and total grass cover was estimated using the 1-4 percentage scale as above, and all plants within the quadrate were identified and recorded. I established communi-ty type for each plot and entered community as a cat-egorical variable. I also recorded the distance from the centre of each plot to the nearest stand.

In order to take into account that female distribu-tion is most likely to be influenced by several factors simultaneously, I applied a step-wise multiple regres-sion to determine which factors might have an effect on the distribution. This method allows investigation of the effect of each variable independently of the other variables. A generalised linear model was fitted because of the highly skewed frequency distribution of females and the presence of categorical data. I used the GENSTAT (Payne & Lane 1993) mainframe package and a maximum likelihood model based on a Poisson error distribution and a logarithmic link function. The data were also examined using univari-ate methods.

Results

In the multivariate analysis of stand characteristics, the multiple measurements of the proportion of grass cover, green grass, and dry grass, as well as grass height were each pooled within each stand and ran-dom plot after testing for differences using the Wilcoxon Signed Rank test (% grass cover: z = 0.08, N = 19, ns; % green: z = 1.6, N = 10, ns; % dry: z = 0.2, N = 13, ns) and the Friedman Two-way analysis of variance (grass height: χ^2 = 0.65, df = 3, ns). The logistic regression model producing the best fit included canopy cover, total number of hazel *Corylus avellana* and total number of alder *Alnus glutinosa* as significant variables (Table 2). Stands were found to be positively associated with canopy cover and the number of hazel trees, and negatively associated with the number of alder trees. No relationship was found between specific herbs or grass species and stands. Univariate analyses indicated that canopy cover was positively associated with stands (U = 47.0, N = 15, P < 0.005; Fig. 2), while results for hazel and alder were not significant (hazel: U = 90.0, N = 15, P < 0.073; alder: U = 104.50, N = 15, P < 0.722; see Fig. 2). Grass height was eliminated from the multivariate analysis as it is most likely trampled down on stands as a result of male activity concentrated in these areas.

Stand distribution during the height of the mating period was found to be randomly dispersed, with no

Table 2. Logistic regression model of stand habitat characteristics versus available sites. Birch, alder and hazel are based on tree counts (average number of trees), while canopy, dry grass and grass cover are reported as percentages.

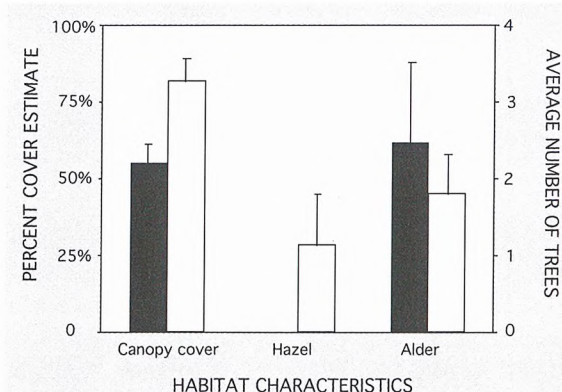| Variable	Slope	Log Likelihood	-2 Log LR	df	Significance of Log LR
Birch	-0.7716	-14.230	2.815	1	.0934
Alder	-0.4209	-15.333	5.021	1	.0250
Hazel	3.8141	-14.906	4.167	1	.0412
Canopy cover	1.4409	-16.329	7.013	1	.0081
Dry grass	-3.1708	-13.972	2.299	1	.1295
Grass cover	2.6655	-14.131	2.616	1	.1058

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Figure 2. Percentage scale scores for canopy cover and average number of trees for hazel and alder on random plots and stands. Canopy was the only variable found significant in univariate analysis (U = 47.0, N = 15, P < 0.005). Filled bars represent random plots and open bars represent stands.

indication of overdispersion or clumping (R = 1, see Fig. 1).

A total of 176 female sightings were made along the transects, with an average of 3.18 ± 2.74 females per transect walked. The number of females in each group ranged from zero to six females. There was a significant difference between the transects in the number of females observed (H = 9.747, df = 3, P < 0.02; Fig. 3). The multiple regression model rejected any significant relationship between the habitat characteristics measured in this study (including distance to the nearest stand) and female distribution. This result was also upheld by non-significant results of a Spearman correlation analysis of female numbers
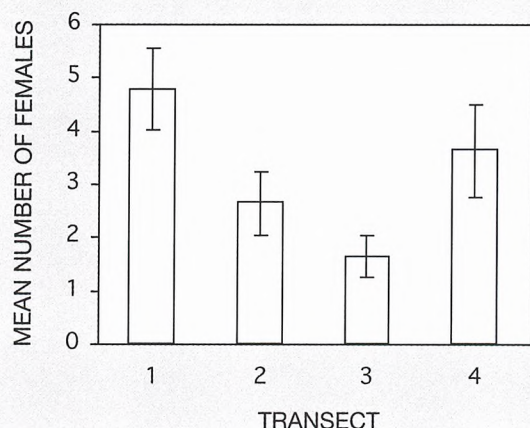

Figure 3. Mean number of females (±SE) observed along four transects in Ottenby forest (H = 9.747, N = 14, P < 0.02).

and the habitat characteristics which were found to be associated with mating stands (canopy cover, r_s = 0.073, ns; hazel, r_s = 0.019, ns; alder, r_s = -0.223, ns; N = 36).

Discussion

Male mating stands were positively associated with dense canopy cover and number of hazel trees, while they were negatively associated with the number of alder trees. In relation to each other, the stands were not overly dispersed or clumped, but were located randomly within the wooded area of the reserve. Female distributions showed no relationship with the habitat characteristics associated with male mating stands, or with any of the other habitat characteristics investigated. What then can explain the random dispersion of mating stands as well as their association with dense canopy cover? Female influence on male mating patterns is most often thought to be a result of female dispersion in response to resource distribution and habitat structure (Jarman 1974, Emlen & Oring 1977). Where this correlation exists, males often defend resource territories or other patches of habitat favoured by females. Although there is a coarse preference by females for the forested region over the open pastures, the results of this study indicate that there was no relationship between habitat characteristics and female distributions within the forest. Habitat structure within the study area varied from small fields to thickets and forest, with females occurring in all habitat types. Resources, in the form of sweet and coarse grasses favoured by fallow deer are abundant throughout much of Ottenby forest, and thus, resources are not likely to be a limiting factor and are not dispersed so that males would find them economically defendable.

In his study of Uganda kob, Deutsch (1994) found that although females were associated with certain habitat types, these favoured habitats were, for males, not defensible. Instead, males defend small lek territories which the females visit in order to mate. He concludes that these display territories are a default strategy pursued when females or their resources are not economically defendable (Deutsch 1994). At Ottenby, although females are predictably found within the forest during the mating season, habitat preferences within the forest are not discernible, and therefore not defensible. For fallow deer at Ottenby, there are several explanations to

why, despite the lack of correlation between female distribution and habitat characteristics, males defend mating territories. One explanation is similar in kind to Deutsch's reasoning. Males have no way to predict female location, so by default, they defend small mating territories. Although this is compatible with the random distribution of stands, it does not help to explain the correlation of mating stand location with dense canopy cover.

Another possibility is that mating stands serve as display sites which might then have a function in male-male competition or in female choice situations, or both. During the rut, males scent-urinate and groan at the stand locations. One possible explanation for the establishment of mating territories at sites with closed canopy is that tight canopy cover is helpful in keeping the scent and sound from dissipating away from the area, concentrating it instead on just that particular male's territory. The information contained in these signals would then be obtainable by males and/or females nearby or on the stand. The random distribution of stands is then explained by the random distribution of sites which satisfy the environmental constraints of a display site (Alberts 1992).

White-tailed deer *Odocoileus virginianus* males also create scrapes which are most often found in open forested areas under an overhanging branch (Kile & Marchinton 1977). Although white-tailed deer are usually not territorial, these scrapes may serve as a source of communication between males and females, or males and other males, and therefore, function as a type of display site. It has also been suggested that in fallow deer, pheromones from male scent-urination may help to induce oestrous in females (Kennaugh, Chapman & Chapman 1977). This seems to be the case for moose *Alces alces* display sites, where female moose actively seek out, and sometimes defend sites where males have scent-urinated into pits (Miquelle 1991). In order to understand the significance of tight canopy cover at display sites more research is needed as to the function of groaning and scent urination in fallow deer.

Although active male display may play an important role in male competition and/or female choice, the ability to successfully defend a territory may be the most important determinant of male reproductive success in fallow deer populations. Of the four different mating tactics observed in a population of fallow deer in Dublin, Ireland (high-fidelity territorial, low-fidelity territorial, satellites, followers), high-fidelity territorial males had the highest mating success (Moore et al. 1995). Studies of lekking populations of fallow deer have also concluded that female preference for (certain) territories may lead to male-male competition and insure mating with a socially dominant male (Apollonio et al. 1990, Festa-Bianchet et al. 1990) Thus, dispersed display sites might be more than a default strategy for fallow deer as well as for other cervids.

A third possible explanation for why males might defend mating territories is that male fallow deer might, in fact, be able to predict female location. Even though female distribution was not predictable based on habitat characteristics, males might have other means of identifying areas of high female density, such as knowing where female home ranges overlap (Clutton-Brock 1989). The differences found between transects in the mean number of females observed indicate that females are not evenly dispersed throughout the Ottenby forest, and therefore it may be possible for males to use cues other than habitat characteristics to predict areas of high female density. One problem with this line of reasoning is that it contradicts the findings of an absence of relationship between female distribution and distance to the nearest male mating stand. However, if males were to establish mating stands along frequently used game trails, the flow of females between feeding areas and resting areas could result in a high encounter rate for males while not necessarily being reflected in a relationship between female distribution and distance to the nearest stand. This is the case for red deer in Doñana, Spain, where some males defend resource territories while other males defend territories which are situated on paths frequently used by females (Carranza et al. 1990, Carranza 1995). A similar situation occurs at a fallow deer lek in central Italy, where females seem to prefer lek territories situated near a path used by females entering the lek (Apollonio et al. 1990). Further investigations into the possible relationship between game trails, flow of females and mating stand location would be beneficial in understanding the function of mating stands in fallow deer populations.

An individual males' choice of mating tactic, such as defence of a mating stand, should be based on both the population structure and habitat conditions, as well as the individuals own condition. That fallow deer exhibit a great intraspecific variability in available tactics may therefore be a reflection of the varying environmental circumstances in which different

populations are found, as well as the relative costs and benefits of each tactic in relation to current population parameters. Consideration of the variation in habitat and population characteristics is therefore an especially important aspect of describing mating patterns in those species which exhibit inter and intra-specific variation in mating tactics.

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