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Forest habitat use and home-range size in radio-collared fallow deer

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While habitat use by fallow deer has previously been described on the basis of direct observations, this paper presents similar data on radio-collared individuals. Our data show that annual home ranges of males (at 9.75 km^2) appeared much larger than those of females (2.1 km^2). Thickets and meadows were the most often used habitats, while mature forests and young plantations were least utilised. Diurnal and nocturnal habitat selection patterns differed significantly. The primary difference was the use of meadows, which was higher at night than during the day. Results on the representativeness of diurnal habitat use to 24-hour data were equivocal. Although daytime and 24-hour habitat use patterns were similar, day *vs.* night and night *vs.* 24-hour habitat use patterns differed significantly. Our results suggest that when open habitats are involved, the representativeness of daytime data to 24-hour habitat use may be less than complete. This study also indicates that calculations of habitat use by fallow deer based on direct observations are likely to underestimate the use of closed habitats.

Introduction

Although after the last glaciation fallow deer (*Dama dama*) survived in only a few places in Asia Minor and southern Europe (Chapman & Chapman 1997), as a result of human activity the species is now common across Europe and in many localities on all continents. Notwithstanding such a wide distribution, relatively few papers have dealt with the ecology of the species, and those that do, focus predominantly on behaviour and social organisation (Dzięciołowski 1979, Apollonio 1989, Apollonio *et al.* 1989, Thirgood 1996), or on habitat use (Chapman *et al.* 1985, Putman 1986, Thirgood 1995, Apollonio *et al.* 1998).

When studying habitat use, direct observations pose several potential problems. Firstly, where habitats are characterised by different levels of visibility, there may be a tendency to overestimate the use of open habitats as opposed to closed ones. Secondly, unless night vision technology is utilised, direct observation is restricted to daytime. Finally, as direct observations usually focus on active individuals, relatively little information is gathered on habitat use by resting animals. As a consequence, results obtained by observation often differ from those provided by radio-telemetry (Biggins & Pitcher 1978, Borkowski & Furubayashi 1998).

To date, radio-telemetry studies of habitat use by fallow deer have focussed on sexual segregation as a result of human disturbance (Ciuti *et al.* 2004). The existing studies suggest that the species prefers various kinds of open areas and mature — and therefore relatively open — forests (Chapman *et al.* 1985, Putman 1986, Thirgood 1995, Apollonio *et al.* 1998). Given the limitations of direct observations, it is not clear whether and to what extent fallow deer do indeed prefer open habitats, or whether obtained results reflect methodological limitations. In addition, since most studies describe fallow deer habitat use in relatively open habitats, there is much less information on how the species uses typical forest habitats. Finally, there has been little or no information on nighttime habitat use in fallow deer, although it is well known that cervids change their pattern of habitat use depending on the period of the day (Loft *et al.* 1984, Catt & Staines 1987, Mann & Putman 1989) with open habitats usually being visited at night, and closed ones during daytime hours.

An additional question arises as to whether the locations obtained for animals during daytime can serve as a reasonable source of information on the 24-hour habitat use pattern. Opinions to date have been divided. Thus, while Hayes and Krausman (1993), studying mule deer (*Odocoileus hemionus*), and Kernohan *et al.* (1996), studying white-tailed deer (*O. virginianus*), found no differences between diurnal and 24-hour habitat use; Beyer and Haufler (1994), working with American elk (*C. elaphus*), concluded that data collected during the day are not representative of the 24-hour period. However, none of the existing studies invoke habitat structure as a possible factor modifying answers to the question of daytime *vs.* 24-hour habitat use. Because of diurnal/nocturnal dissimilarities in open habitat use by deer, we predict that, in areas where attractive open areas are available, daily and 24-hour habitat use patterns will differ. Alternatively, fallow deer may be a special case because the animal is known to be active both during day and at night (Chapman & Chapman 1997). As such, even in places where open areas are often utilized, its daytime and 24-hour habitat use patterns may be similar.

Direct observations are problematic not only for quantifying habitat use, but also in determining home-range size. Perhaps this is why papers describing home ranges in fallow deer are rare. A few studies of home-range size were done by radio-telemetry (Nugent 1994, Ciuti *et al.* 2003, Davini *et al.* 2004), while others have been based on direct observations of marked individuals (e.g. Putman 1986, Chapman & Chapman 1997).

The aims of this study were: (i) to examine habitat use by fallow deer in forest environment using radio-telemetry; (ii) to compare daytime habitat-use patterns with those exhibited at night; (iii) to check if habitat structure, i.e. presence of attractive open areas, affects the extent to which daytime radio-telemetric data can provide information on 24-hour habitat use; (iv) to study home-range sizes in fallow deer.

Methods

Study area

The study was done in ca. 4000 ha forest complex that is a part of the Pszczyna Forest District in southern Poland (50°05´N, 18°56´E). The dominant three species is Scots pine (*Pinus silvestris*), which occupies about 75% of the area. The other species are oak (*Quercus robur*), birch (*Betula verrucosa*), and alder (*Alnus glutinosa*). The local climate is relatively wet, with annual precipitation of 800 mm. The growing season lasts on average 213 days, while the number of days with temperatures below 0 °C is not greater than 100. Although the number of days with snow cover is on average 90, the winters during the study period were mild. There are about 30 fallow deer per 1000 ha of forest in Pszczyna Forest District. The other ungulates occurring in the study area are red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), and a few (ca. 15) sika deer (*C. nippon*). There are also about 30 European bison (*Bison bonasus*) living in a 700 ha fenced bison reserve. The reserve area includes high quality meadows (over 23 ha) that, although managed mainly as pasture for the bison, are accessible to other animals. While the European bison reserve is fenced, radio-collared fallow deer often crossed the fence, and thus the presence of the enclosure does not reduce the size of deer home ranges.

Deer capture and tracking

In winter 1999/2000, seven fallow deer were fitted with radio-collars (Televilt, TXE-3). Five of these were tracked (one animal removed the collar and the other was probably soon killed by dogs). In addition, one male (No. 0) was killed by a car in January 2001. In winter 2000/2001, an additional four individuals were caught and radio-collared. As a result, nine fallow deer (five females, three males, and one fawn) were tracked between spring 2000 and winter 2001. The animals were located with a hand-held three-element Yagi antenna, by triangulation, several days a month. Two consecutive locations of the same individual were separated by at least two hours. Male No. 5 was mostly located in a peripheral part of the study area with habitat conditions differing from its center (in that agricultural fields are present). Data obtained for this individual were thus used only for calculating home-range size and not for habitat use.

Data analysis

Habitat selection was analysed using compositional analysis (Aebisher *et al*. 1993), with the denominator in the log-ratios being mature forest since this habitat was present in all the home ranges. Missing values were replaced with value of 0.01%, while those of availability were set to zero (cf. Aebisher *et al*. [1993] appendix 2 option 1). The compositional analysis overcomes many of the problems and violations of assumptions associated with other tests. In this method each individual — and not each radio-location — is considered a sample unit. Influence of a season and part of a day on habitat selection was tested using MANOVA, with the individual and habitat type being dependent variables, while season or part of a day independent one.

A location was used in the habitat-use analysis only if the triangle formed by three bearings fell well within one forest sub-compartment and thus could be assigned to one habitat type. In most cases, this did not create any problems, since the average habitat patch size in the study area was much larger (14.86 ha) than the average triangle formed by three bearings (0.95 ha; confidence interval = 0.10) as calculated on the basis of 200 randomly selected triangles. Home ranges were calculated using the 95% minimum convex polygon method (MCP). Although this method has limitations (White & Garrot 1990), it is still one of the most widely used for estimating home ranges. The independence of data was tested with Schoener's index (Swithart & Slade 1985) and, when necessary, points among consecutive locations separated by the shortest time intervals were sequentially excluded from analysis until data became independent. Seasons were defined as follows: spring: 16 March–15 June, summer: 16 June–15 September, autumn: 16 September–15 December, winter: 16 December–15 March. The analysis of habitat use employed the following forest age classes: young plantation (1–5 years), pre-thicket (6–12 years), thicket (13–35 years), pole-sized forest (36–50 years), and mature forest (> 50 years).

Results

In total, 1620 location points (648 in 2000 and 972 in 2001) were registered. There were slightly more (937; 58%) location points obtained during daytime than at night (683; 42%). Habitat use analysis was based on 26–35 and 25–32 location points per individual per season in 2000 and 2001, respectively. The analysis was performed on the combined dataset. Habitat use by fallow deer was not proportional to habitat availability (Table 1), either at the scale of the study area, i.e. choice of a home range within a landscape (second order of Johnson's (1980) selection), or at the scale of the home range, i.e. habitat use within a home range (third order of Johnson's [1980] selection). The results obtained at the two scales were quite different (Table 1). Although at both scales young forest plantations were strongly avoided, at the scale of the study area pre-thickets and mature forests were selected, while these habitats were of low rank at the home-range scale. Highly selected habitats within home ranges were thickets and meadows (Table 1).

Second order of Johnson's (1980) selection depends on the demarcation of study area boundaries. Such demarcation is especially difficult when animals are studied within a large, continuous forest tract, as was the case in the present study. Therefore, the most meaningful result is likely the third order selection, and further analyses were confined to the home-range scale. For all seasons, habitat use by fallow deer was not proportional to habitat availability (Table 1). However, habitat rankings in spring, summer, and autumn did not differ significantly (MANOVA: each pair of seasons $p > 0.05$). Winter habitat ranking was different than that for all other seasons (MANOVA: each pair of seasons $p < 0.05$): the winter habitats of highest ranks were meadows and pole-sized stands, while those of lowest ranks were young forest plantations and pre-thickets.

The day and night habitat use by fallow deer differed significantly (MANOVA: Hotelling-Lawley trace = 1.9, $F_{5,10} = 3.8$, $p < 0.05$; Table 1). Although habitat rankings were similar for daytime and 24 hours (MANOVA: Hotelling-Lawley trace = 0.7, $F_{5,10} = 1.5$, $p > 0.05$), they differed for 24 hours and nighttime (MANOVA: Hotelling-Lawley trace = 2.4, $F_{5,10} = 4.8$, $p < 0.05$).

Fallow deer home ranges were analysed on the basis of the data gathered between 16 December 2000 and 15 December 2001, when there was a maximum number of located animals. This allowed for a comparison between sexes. The only exception was male No. 0, which was included in the analysis (the data available only for the year 2000). Home ranges (95% MCP) were calculated on the basis of 734 location points (on average 92 location points/individual/year).

Table 1. Habitat rankings obtained by compositional analysis for different spatial scales, seasons, and periods of day. M = meadow, YP = young plantation, PT = prethicket, T = thicket, PS = pole-sized forest, MF = mature forest; ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	Habitat ranking	Chi^2 (df = 5)
Spatial scale		
Study area	PT ≥ MF ≥ T ≥ PS ≥ YP ≥ M	24.9***
Home range	T ≥ M ≥ PS ≥ PT > MF > YP	13.3*
Season		
Spring	T ≥ PT ≥ PS ≥ MF ≥ M > YP	12.9*
Summer	PS ≥ M ≥ T ≥ MF ≥ PT ≥ YP	17.8*
Autumn	T > M ≥ PS ≥ PT > MF > YP	24.1***
Winter	M ≥ PS ≥ T > MF ≥ YP > PT	30.8***
Part of a day		
Day	T ≥ PS ≥ MF > M ≥ PT > YP	17.2*
Night	T ≥ M ≥ PT ≥ PS > MF ≥ YP	15.5*

Although the limited number of radio-collared individuals in the present study precluded statistical analysis, male home ranges seem to be larger than those of females (Table 1). The average yearly home range of females was only 2.1 km^2, i.e. around one-fifth of that of males (9.75 km^2) (Table 2). The maximum mean female seasonal home-range size was recorded in spring (1.44 km^2), and the minimum in autumn and winter. In contrast, autumn was the season of maximum mean home-range size in males (6.6 km^2). The minimum mean home range for males was recorded in winter (1.72 km^2). Location of the home ranges in the study area are shown in Fig. 1.

Discussion

As mentioned previously, at the study area scale, composition of available habitats depends heavily on demarcation of study area boundaries. As such, this approach may often lead to erroneous conclusions. For example, our results show that meadows were the habitat of lowest rank at the scale of the study area, while meadows were significantly more important at the home-range scale. We will, therefore, focus the discussion on the home-range scale.

There were two sorts of open habitats in Pszczyna: meadows and young forest plantations. In general, the latter were used much less often than the former. Such a situation may arise due to

Table 2. Seasonal and yearly home ranges (mean ± confidence interval; km^2) of fallow deer in Pszczyna

	Females	Males
Spring	1.44 ± 0.69	4.96 ± 3.2
Summer	1.03 ± 0.87	3.3 ± 1.2
Autumn	0.55 ± 0.19	6.6 ± 3.5
Winter	0.64 ± 0.46	1.72 ± 0.6
Yearly average	2.06 ± 0.88	9.75 ± 5.6

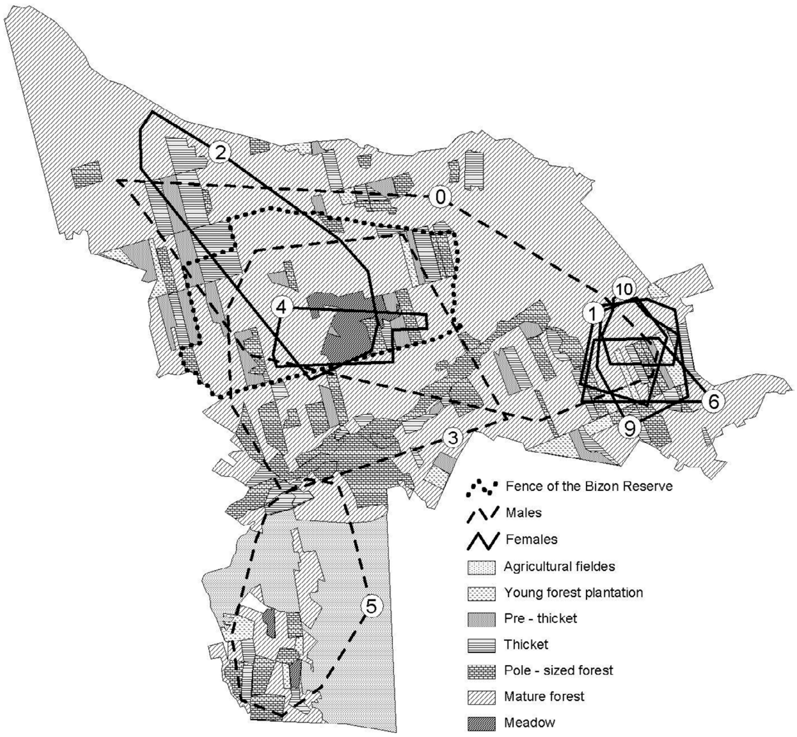

Fig. 1. Yearly home ranges of radio-collared fallow deer in Pszczyna. The respective number of each individual is given in the circle.

food availability. Food biomass in young forest plantations was very low (Borkowski 2003), while meadows were characterised by grasses of high biomass and quality. The fallow deer diet is known to be dominated by grasses (Caldwell *et al.* 1983, Jackson 1997). In Pszczyna, grasses were the main component of the fallow deer diet in the autumn and winter, with a share reaching nearly 50% on average (Borkowski & Obidziński 2003). As might be expected, open grasslands have been reported as habitats preferred by fallow deer (Thirgood 1995, Apollonio *et al.* 1998).

While meadow use is easily understood, the interpretation of the pattern to forest habitat use — especially the unexpectedly high rank of thickets — is less intuitive. Although both pre-thickets and thickets may offer favourable cover conditions, fallow deer used heavily only thickets, while pre-thickets were rarely used. This result may be have been influenced by the presence of food — thickets had a greater abundance of food (ground vegetation) than pre-thickets (Borkowski 2003). Moreover, due to clearing (removal of some trees for better growth of a stand), the stem density in thickets is lower than in pre-thickets, while the light conditions — especially in coniferous stands (most of Pszczyna forest) — ensure that lower branches are dead. Because of this, deer locomotion may be easier in thickets, which may combined with higher food availability make thickets more attractive than pre-thickets.

One potentially surprising result was the low rank of mature forests. With a relatively high food biomass (Borkowski 2003), mature forests would have been predicted to be more attractive to fallow deer. Mature pine stands were important habitat to red and roe deer in forest located not far from Pszczyna (J. Borkowski unpubl. data). However, mature forest use was dependent on cover conditions and understorey density. Mature forests in Pszczyna have relatively poor understorey and this could make them unattractive to fallow deer.

Diet analysis of Polish fallow deer (Borkowski & Obidziński 2003) has suggested that damage caused by fallow deer to forestry is of marginal importance. This study supports that finding, since young forest plantations were the habitat of lowest rank in every season. Moreover, in winter, when debarking of pine pre-thickets by deer is usually the most intense, the use of this habitat by fallow deer was very low.

Habitat selection in winter was different than in all other seasons. The major difference comes from use of meadows, which was the habitat of highest rank only during the winter. During the period of this study, snow cover was absent or shallow and the meadows with relatively abundant grasses attracted fallow deer. In general, however, habitat use by fallow deer was similar among the seasons. For instance, in each season (with a slight difference in spring only) the same three habitats — thickets, meadows, and pole-sized stands — were of highest ranks.

The habitat selection rankings of fallow deer differed between daytime and nighttime. Again, use of meadows contributed to this difference. Fallow deer utilised meadows more often at night than during days. As previously mentioned, different use of open areas depending on the period of the day is quite common in cervids (*see* Introduction for references).

The results of this study regarding representativeness of day time radio-telemetry data to 24-hour habitat use were equivocal. On the one hand, there was no difference in habitat rankings for day time and 24-hour data. On the other hand, the night and 24-hour habitat rankings differed significantly. Importantly, the day and night rankings of habitat selection were significantly different. Thus, although it is difficult to draw a clear conclusion, our data suggests that when open habitats are involved, the representativeness of daytime data for 24-hour habitat use may not be complete. It is possible that for deer whose home ranges do not encompass open habitats, the daytime and 24-hour habitat uses differ less than in the cases where individuals have open areas within their home ranges. Unfortunately, the relatively low number of radio-collared fallow deer in this study made such comparison impossible.

Our radio-telemetry based analysis confirmed the importance of open grassy areas to fallow deer in Pszczyna. The rank of meadows was high during most seasons. It must be mentioned, however, that meadows in Pszczyna were managed as pastures, which could have made their attractiveness especially high. Our results also indicate that the importance of open areas for fallow deer diurnal habitat use might have been overestimated when relying on data gathered by direct observations (*see* Introduction for references). First of all, direct observations are usually conducted during daytime and these were closed habitats which predominated in the daytime habitat use by radio-collared fallow deer, while the open habitats were relatively less important. The conclusion that the open area use is overestimated when using only directly observed fallow deer seems to be supported by the fact that activity of radio-collared fallow deer in the open areas was higher than in the other habitats (J. Borkowski unpubl. data) and these were mostly active (i.e. standing or walking and therefore easier to be noticed) individuals, which were recorded during direct observations. Thus, forest habitats are likely to be more important to fallow deer than can be determined using only directly observed individuals. In the case of radio-collared fallow deer in Pszczyna, thickets were the habitat of the highest rank. Due to their close character (and consequent poor visibility), if this study was done on the basis of direct observations, the rank of thickets would have been lower. Similarly, the ranks of mature forests and young plantations (open in character, with good visibility) would have been higher. Our interpretations are supported by Ciuti *et al.* (2004), who showed that woods were an important habitat of radio-collared fallow deer. Clearly, more radio telemetry studies are needed for better understanding of fallow deer ecology in forest habitats.

The home ranges of male fallow deer were larger than those of females. Although an absence of sex-related differences in home-range sizes has also been reported (Knight 1970, Clutton-Brock *et al.* 1982, Eberhardt *et al.* 1984), the males of cervids often have larger home ranges than the females (Darling 1937, Cederlund 1983, Beier & McCullough 1990). Indeed, the home ranges of males are also larger among New Zealand fallow deer (Nugent 1994). Two factors are believed to influence this phenomenon. Firstly, because of their larger sizes, males have higher energy requirements and thus forage within larger areas (Harestad & Bunnell 1979). Secondly, males may cover longer distances in order to obtain knowledge about the distribution of females and potential rivals (Beier & McCullough 1990). Because males may travel into mating areas, Clutton-Brock *et al*. (1982) suggested that sex-related differences may or may not be noticed, depending on whether such areas are included in the calculation of home ranges. In this study, the autumn (mating season) home ranges of males were the largest, and this season may have the most influence on annual home-range size. However, two out of three radio-collared males were not located in autumn beyond the home ranges determined on the basis of location points from the other seasons. The third male did show a larger home range in autumn, but this difference was rather incidental in relation to outlying data (lying outside the 95% MCP home range), so these location points were not included in the home-range calculation. As such, in this study at least, the mating season movements of males did not have much influence on sex-related differences in the sizes of annual home ranges.

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