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Flight distance in roe deer *Capreolus capreolus* and fallow deer *Dama dama* as related to hunting and other factors

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Flight distances in roe deer *Capreolus capreolus* and fallow deer *Dama dama* with respect to a human observer on foot were measured in four nature reserves in the Netherlands: two dune reserves in the western part (the Amsterdam Water Supply Dunes (AWD) and Kennemerduinen (KD)) and two forested areas in the eastern part of the country (Hoge Veluwe (HV) and Kootwijk (KO)). In the four areas there is a gradient in hunting pressure from almost none in the AWD, via an increase in KD, to KO and HV. Fallow deer occur in both of the dune reserves and are not hunted. Of all the factors studied, hunting regime and habitat structure were most strongly related to flight distance. Although the number of individuals per group and most weather conditions also showed some relation to flight distances, their influence was relatively unimportant compared to that of hunting regime and habitat structure. When walking down wind, deer (both roe and fallow deer) flee at longer distances (64.7 ± 5.8 m) than when walking upwind (41.7 ± 3.3 m) or in calm wind (44.2 ± 1.8 m). In the roe deer population of the AWD, flight distances were the shortest among all the studied areas. In both of the dune areas, the flight distances in dense vegetation structures were shorter than in open field. Fallow deer flight distances did not differ between the dune reserves AWD and KD.

Key words: cover, group size, habituation, human disturbance, weather conditions

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In the past decades, recreational pressure in nature reserves has increased. An important aspect for nature visitors is the observation of wildlife, especially the larger (mammalian) species. Meetings with, for example deer, enhance the visitors' experience with nature. A common problem, however, is that deer show a great deal of fear of humans (Jeppesen 1987c, Danilkin & Hewison 1996). This reaction is often interpreted as being

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caused mainly by hunting (Van Bemmel 1983, Büttner 1986). Measurement of flight distance is an accepted methodology for measuring shyness or sensitivity to disturbance. Flight distance is defined as the distance between an animal and an observer at the moment of flight initiation (Phillips 1993). It is expected that deer in hunted populations have longer flight distances than deer in non-hunted populations. In this study, we measured flight distances in roe deer *Capreolus capreolus* and fallow deer *Dama dama* in four areas in the Netherlands. Each of the areas has a different hunting regime and habitat structure. As a result, the present research might contribute to answering the question of whether or not a relation exists between hunting and flight distance in deer.

Apart from effects of hunting on flight distance in deer, other factors may also affect flight distances. Habitat structure is important as cover is essential in moments of danger (Strandgaard 1972, Swenson 1982). Flight distances measured in closed vegetation types are thus expected to be shorter than those of deer in open field (Mitchell, Staines & Welch 1977, Swenson 1982, Mrlik 1987, Kufeld, Bowden & Schrupp 1988, Kramer & Bonenfant 1997). Group size is another factor influencing the degree of safety that deer perceive. Large groups flee at shorter distances than solitary deer (Hamilton 1971, Herbold 1992, Bullock, Kerridge, Hanlon & Arnold 1993), i.e. larger groups have advantages both in risk dilution (each individual having a lower chance of being attacked) and detection (fewer individuals need to be vigilant in order for the group to detect a hunter; Kie 1996). Adult deer are expected to be more alert than younger deer, and as a result show longer flight distances than calves, because they have had more (negative) experiences with man (Van den Bos 1984, Andersen, Linnell & Langvatn 1996). In addition, sex influences cervid behaviour to a great extent. Females show more fear of man than males do (Schoener 1971, Mitchell et al. 1977, Jeppesen 1987a, Bullock et al. 1993). Finally, weather conditions may also play a role. Previous research has shown a relation between flight distance and wind direction: flight distances are expected to be shorter when walking upwind of the deer than when walking downwind (Groot Bruinderink 1987, Danilkin & Hewison 1996, Worm 1998). Also wind force influences cervid behaviour: deer flee at longer distances with strong wind, as their sensory abilities are more hindered than in less strong wind.

Though the effects of hunting regimes on cervid behaviour has been researched before, the knowledge of a direct relationship between hunting and flight distance is limited. Previous research was based mainly on the effects of hunting on group size (Jeppesen 1987b), reproduction (Yarmology, Bayer & Geist 1988), habitat use (Swenson 1982, Langbein & Putman 1992) and home range size (Jeppesen 1987a). Consequently, our research is one of the first attempts to investigate a relationship between flight distance and hunting on deer species.

Methods

Four study areas in the Netherlands were visited: two along the west coast and two in the eastern part of the country. The reason for choosing the four areas was their differences in hunting regimes and terrain structure. Table 1 summarises some facts for each area. The Amsterdam Water Supply Dunes (AWD) comprise 3,400 ha of dune area along the west coast and has a roe deer population of about 600 individuals, and 325 fallow deer (spring 2000). In 1997, roe deer hunting as a management tool officially stopped, but in spite of that, from 1998 onwards, 20 females have been shot for research purposes each year in February, which was outside the period when we conducted our study. Fallow deer have never been hunted. We consider the AWD to be an area with a low hunting pressure relative to the other areas. The area contains a mixture of high and low brushwood, pine forest, deciduous forest and grassland vegetation. A little north of the AWD, the nature reserve of the Kennemerduinen (KD) is situated. This dune area covers some 1,240 ha with vegetation types quite similar to those in the AWD. The KD lodges about 350 roe deer, of which 40 animals are culled annually, and a fallow

Table 1. Hunting regime (+: hunting; -: no hunting), size (in ha), population density/100 ha, area characteristics and recreation pressure expressed by number of visitors (in thousands/year and ha) for each of the four study areas. Data were not available on density in the KO area.

Area	Species	Hunting	Size	Density	Characteristics	Visitors/year	Visitors/ha	Visitor regulations
AWD	roe	-	3400	17.6	rolling dunes	715	210	Off tracks
	fallow	-		9.6				
KD	roe	+	1250	17.0	rolling dunes	1000	800	On tracks
	fallow	-		2.8				
HV	roe (+ red)	+	5000	3.6	flat and open	650	130	Off tracks
KO	roe (+ red)	+	5000		flat and open	few	few	On tracks

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deer population of about 35 individuals, of which none are culled. The recreational pressure in the KD area is quite high, and with 1.2 million visitors/year it exceeds by 50% the number of visitors in the AWD (800,000 visitors/year). Also the admission regulations differ: in the KD visiting is limited to walkways, whereas in the AWD people are allowed to leave designated foot paths.

The two areas in the east of the country lie on the Veluwe, and both of them hold hunted roe deer populations. The first area, the national park, 'De Hoge Veluwe' (HV), is a completely fenced area of 5,000 ha that lies a little north of Arnhem, and it hosts about 150 roe deer. With 650,000 visitors/year, who are allowed to walk off the designated foot paths in certain parts of the reserve, the HV is a fairly popular nature reserve. In the second area, the Forestry Kootwijk (KO), roe deer counts are not performed, but (as background information) it is assumed that about five roe deer/100 ha of vegetation cover are present. The total KO area covers 5,000 ha which leads to a population estimate of about 250 roe deer. Visitors in the KO are not registered. The two areas on the Veluwe have comparable vegetation types: quite open forests mainly consisting of pines, but open heathland and grass fields are also common in the areas. Overall, the vegetation cover is less pronounced in both of the Veluwe areas than in the dune areas. Apart from roe deer, populations of red deer *Cervus elaphus* and wild boar *Sus scrofa* are present in both of the Veluwe areas, and these populations are also hunted.

During August-December 2000, the four study sites were visited 30-40 times each. During this period, hunting (if any) was carried out until 15 September after which date no hunting was performed. Flight distances were determined in relation to a human observer (Hanneke Y. de Boer) who walked transects of about five kilometres in length in each study area. Transects were walked both in the period around sunrise and around sunset for a total of 2.5 hours (half an hour before sunrise until two hours afterwards and two hours before sunset until half an hour after sunset). Most of the time the same transects were used in each area. When an animal was noticed, the observer approached it. Each animal was approached in the same way, so effects of differences in sampling methods per area were avoided. Flight distances were measured in metres using a Leica Vector 1500 range finder.

We collected data on vegetation type, sex, group size and weather conditions simultaneously with each flight distance measurement. The vegetation type was classified in two categories: open field and closed vegetation structures (e.g. forest, shrubs and brushwood). Sex and age were combined in one variable and were classified as 'adult male', 'adult female', 'fawn' or 'unknown'. For each group, only one flight distance was noted. Wind force was distinguished as 'windless', 'weak wind' and 'strong wind', wind direction as quarters of the compass and as 'downwind', 'upwind' or 'calm wind'. Precipitation was separated into three classes (dry, weak rain and hard rain), and temperature was measured in °C. The factor 'area' provides information about hunting regime and other variables (see Table 1).

Statistical analyses

Flight distances were analysed using SPSS 11.0 for Windows. Initially, data of all areas and of both roe and fallow deer were pooled to analyse the effect of each factor on flight distances separately. The relative importance of each factor was studied by stepwise forward regression using the general linear models (GLM) procedure. For the final analysis of flight distances per area, the data set was split on species and again the GLM procedures with Tukey's post-hoc tests were used.

To get normally distributed data, analyses were performed with the logarithm of flight distances. However, the results are described as mean flight distances in metres.

Results

Overall effects

A total of 291 deer was observed. Of these, 240 were roe deer and 51 fallow deer. After a first analysis, vegetation structure and study area turned out to be the most important factors, each separately explaining at least 17% of the total variance ($P < 0.05$; Table 2). When combined in a model, they explained almost 35% of the total variance.

Of the other factors, temperature, wind direction, group size, species, precipitation, and the factor up-or-

Table 2. Total explanation of variance (r^2) and significance (P) of the seven factors or combinations of them (data of both roe deer and fallow deer combined).

Factor	r^2	P
Vegetation structure	0.181	0.000
Area	0.170	0.000
Temperature	0.071	0.000
Up/downwind	0.070	0.000
Group size	0.039	0.022
Species (roe/fallow)	0.032	0.002
Precipitation	0.028	0.042
Structure*area	0.349	0.000
Structure*area*up/down wind	0.460	0.000

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downwind also had significant effects on flight distances ($P < 0.05$), but the percentages of explained variance were low ($r^2 < 0.10$). A higher temperature led to shorter flight distances, and so did rain and winds from west-southwest, whereas the opposite effect was found with easternly winds and with increasing group size which both led to longer flight distances.

Fallow deer fled at shorter distances than did roe deer, and rain led to shorter flight distances. Adding these factors to the model did not lead to a significant increase in the explained variance, so they were not analysed any further.

The factor up-or-downwind in itself did not explain a substantial part of the variance, but when added to the model with area and vegetation structure, the r^2 increased considerably (from 0.349 to 0.460; $r^2_{adj} = 0.333$ and 0.416, respectively). Mean flight distances (for roe and fallow deer together) are significantly shorter when walking upwind (41.7 ± 3.3 m) than when walking downwind (64.7 ± 5.8 m) or in no wind (44.2 ± 1.8 m). The effects of up-or-downwind on flight distance were independent of area and vegetation structure. After combining the factors area, vegetation structure and up, down or no wind, not enough replications for each combination were left to run a complete analysis. As the factor up, down or no wind was independent of the other two factors it was omitted in the following analyses.

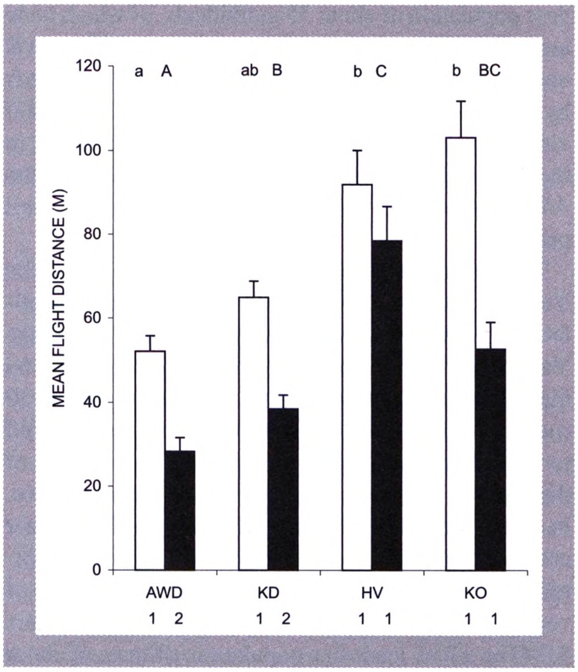

Figure 1. Mean flight distances (± 1 SE) for roe deer in the study areas AWD, KD, HV and KO in relation to open (□) and closed (■) vegetation structure. Mean flight distances with different letter/number differ significantly ($\alpha = 0.05$). Significant differences within areas are symbolised by 1-2, between areas within open field vegetation by a-b and between areas within closed vegetation by A-B-C.

Roe deer flight distances

Roe deer mean flight distances in the vegetation types open and closed in each of the four study areas are shown in Figure 1. On the basis of total means, significant differences were found between the AWD area and the three other study areas; the mean flight distance in the AWD was shorter (39 m). In the KD area, mean distances were significantly shorter than in the HV area (mean = 50 and 85 m, respectively). No differences were found between the two areas on the Veluwe, neither in overall distance nor with respect to flight distances per vegetation structure. Comparison of mean flight distances within the vegetation structure open field, showed significant differences per study area and revealed significant differences between the AWD area and both of the areas on the Veluwe (see Fig. 1). In the closed vegetation structure, flight distances in the AWD area were shorter than in all other areas. As with overall means, flight distances in closed vegetation structures in KD area were shorter than in HV area.

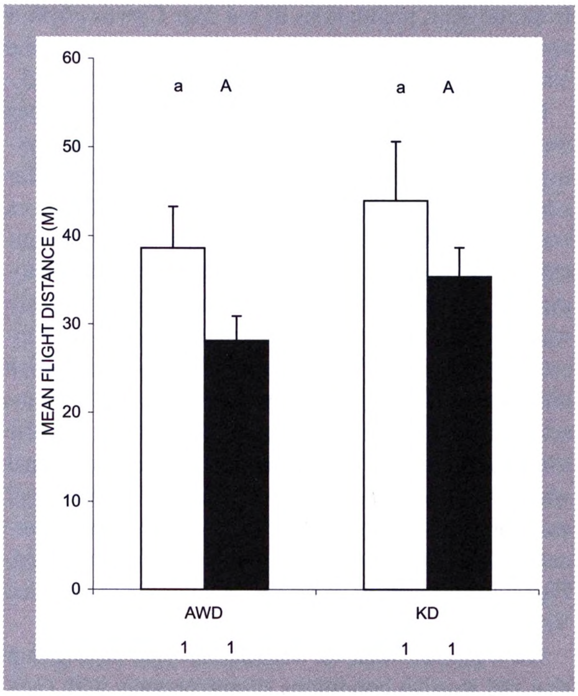

Figure 2. Mean flight distances (± 1 SE) for fallow deer in the AWD and the KD in relation to open (□) and closed (■) vegetation structure. Mean flight distances with different letter/number differ significantly ($\alpha = 0.05$).

Fallow deer flight distances

Fallow deer live only in the two dune areas (AWD and KD) that were visited in our study, and mean flight

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distances per vegetation structure in these areas and the significance of the comparison are shown in Figure 2.

Fallow deer mean flight distances in the AWD and KD areas did not differ significantly, but the total numbers of observations in the vegetation structure open field were rather low in both of these areas (N = 8 and 4, respectively).

Discussion

Overall effects

The data set did not allow for a thorough analysis of all weather conditions, many of which probably are correlated in some way (e.g. clouds with rain). Our study indicates that weather conditions do influence flight distances, but that this influence is relatively unimportant compared to those of the area characteristics and vegetation structure.

The significant effect of group size on flight distance that we found is not in accordance with findings of MacArthur, Geist & Johnston (1982) in mountain sheep *Ovis canadensis* and of Recarte, Vincent & Hewison (1998) in fallow deer.

Both studies found that animals in larger groups are less frightened than solitary ones. Neither do our results support the ideas expressed by Hamilton (1971). It might be the case that single individuals more often were surprised by the observer than groups were; the variation in flight distances of single individuals was large. If we temporarily excluded the solitary individuals, the relationship between group size and flight distance was no longer significant. Further analyses revealed only a significantly longer flight distance for groups of two animals when compared to a single individual. Furthermore, we admit that the sample size of groups of ≥ 4 animals was very small.

The absence of a relation between age and sex and flight distance is also surprising as Van den Bos (1984), Langbein & Putman (1992) and Recarte et al. (1998) reported females to be more vigilant towards humans than males. The small number of observations in our study may have contributed to this absence.

Roe deer flight distances

For roe deer, the mean flight distances in the AWD area are significantly shorther than in the three other areas. As roe deer in the AWD are hardly hunted, in contrast to the situation in the other study areas, a relation between hunting and flight distance in roe deer seems evident. Results presented by Büker, Scheibe, Streich, Eichhorn & Scheibe (1999) support this finding. They found that visual exposure decreased when the hunting pressure was high. Closer inspection of our results reveals reasons for discussion. In both dune areas (AWD and KD), flight distances in open field were longer than in closed vegetation types. This is in agreement with findings of Root, Fritzell & Giessman (1998), who state that deer are more at ease in areas with more vegetation cover than in open field. But in both dune areas, flight distances in the open field did not differ significantly. This is a surprising result, as it was expected that the effects of flight distance would be more obvious in open field than in closed vegetation (Mitchell et al. 1977, Swenson 1982, Mrlik 1987, Kufeld, Bowden & Schrupp 1988, Kramer & Bonenfant 1997). This finding does not support the idea of a possible relation between hunting and flight distance. Notably, in the AWD area, visitors can walk freely through the terrain, i.e. they can leave roads and paths wherever they like. Roe deer may have become accustomed to this human behaviour and consequently were less surprised when seeing the observer leaving the transect route. In the KD area, roe deer are not used to people off roads, and consequently could have been more surprised seeing the observer walking directly through the vegetation (Poutsma 1986, Herbold 1992). This could have led to the longer flight distances we found in the KD area than in the AWD area. Possibly, on the longer flight distances we measured in open field, effects of the observer's behaviour may not have been very obvious, and this may explain why no difference in mean flight distance in the open field vegetation structure of AWD and KD was found.

When taking both areas on the Veluwe (HV and KO) into account as well, the effect of hunting on flight distance again becomes more plausible. As in the AWD area, visitors of the HV are allowed to walk freely through the terrain. Flight distances in the HV area are significantly longer than those found in the AWD, however. This lack of relation between human behaviour and deer habituation is reinforced by data on recreation pressure (in terms of number of visitors/ha in one year; see Table 1) in the study areas. The KD is visited by 316 persons/ha/year, but flight distances are longer than in the AWD, which has 210 visitors/ha/year. This result does not show decreasing flight distances as the number of visitors increases. In the HV area, the recreation pressure is even smaller than in the AWD area, but flight distances are longer. The numbers of visitors per year are unknown for KO, but on the basis of the three other areas, habituation of deer to humans seems unlikely.

Flight distances in the KD are shorter than in the

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HV, which could be due to the higher hunting activity (not only on roe deer) in the HV. This outcome is in accordance with findings of Minnaard (1972), who states that roe deer on the Veluwe can hardly be approached when compared to roe deer in other parts of the Netherlands. An alternative explanation could be differences in cover: on the Veluwe, where forests are less developed than in the rest of the Netherlands, less cover is available. Besides, the open fields of the Veluwe are quite flat and large and offer no cover at all, whereas those in the dune areas are more rolling so roe deer can easily 'disappear'. This may also explain why flight distances in open field and closed vegetation on the Veluwe did not differ. The absence of differences between the KD and KO areas remains unexplained.

Overall, our study shows a relation between hunting and flight distances for roe deer, with roe deer in areas with hunting being more fearfull of man than those in areas without hunting. However, other factors, which we did not incorporate in our study, may influence flight distances as well. Intra- or interspecific competition could play a part in the differences found. In the AWD area, for example, the carrying capacity of the system seems to have been reached for roe deer. In spite of the fact that hunting has stopped, roe deer numbers seem to be stable (L. Van Breukelen, S.E. van Wieren & R.S. Schoon, unpubl. data). Animals living in densely populated areas need more time to forage and consequently take more risks to get their daily energy needs met which may result in shorter flight distances. Female mule deer *Odocoileus hemionus*, for example, spent more time foraging when their home ranges were heavily grazed by cattle, than with moderate or no grazing (Kie, Evens, Loft & Menke 1991, Kie 1996). Furthermore, mule deer have to forage more during relatively dangerous times of the day with heavy cattle grazing (Kie 1996). Another reason for roe deer having to spend more time foraging might be found in the exponential growth seen for the fallow deer population in the AWD (Van Breukelen, Groot Bruinderink, van Wieren, Schoon, Hootsmans & van der Hoek 2000). Latham (1999) states that forage strategies and resource use can change as a result of interspecific competition. Further research on both deer populations in the AWD might elucidate this phenomenon. Information about population density in relation to carrying capacity is unknown for the other three areas in our study.

Fallow deer flight distances

Our study did not show differences in flight distances for fallow deer in the AWD and KD areas. In these areas, fallow deer populations are not hunted and live under the same environmental conditions as do roe deer. The area characteristics are identical for roe deer and fallow deer and could hardly have caused the different outcome of flight distances for roe deer and fallow deer. Therefore we need to look at other factors to explain the different findings of flight distances for roe deer and fallow deer in the AWD and the KD areas. Hunting of roe deer is the only known factor that differs for roe and fallow deer in the KD area. As a result, it seems plausible that hunting causes the difference in flight distances between roe deer in the AWD and the KD areas, which is not found for fallow deer. This result supports the hypothesis that there is a positive relation between hunting and flight distance in cervids. A weakness in our results on fallow deer flight distances is the low number of observations (especially in open field). This low observation number may have contributed to the result that we found no significant difference in fallow deer flight distance in open field and closed vegetation structures for the two dune areas. However, previous research did not show a relation between vegetation structure and the degree of disturbance either (Langbein & Putman 1992, Thirgood 1996.

Recapitulating, our study indicates a relationship between flight distance in roe deer and hunting. Flight distance is not determined by hunting alone, however. Vegetation structure affects flight distances as well. Further research, involving data on population density in relation to carrying capacity and recreation pressure per ha each year is essential to further elucidate these relationships.

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