

Rutting pit distribution and the significance of fallow deer Dama dama scrapes during the rut

Authors: Stenström, David, Dahlblom, Stina, Jones Fur, Cheryl, and Höglund, Jacob

Source: Wildlife Biology, 6(1): 23-29

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.2000.034

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Rutting pit distribution and the significance of fallow deer *Dama dama* scrapes during the rut

David Stenström, Stina Dahlblom, Cheryl Jones Fur & Jacob Höglund

Stenström, D., Dahlblom, S., Jones Fur, C. & Höglund, J. 2000: Rutting pit distribution and the significance of fallow deer *Dama dama* scrapes during the rut. - Wildl. Biol. 6: 23-29.

We studied the distribution of rutting pits and the role of scraping during the rut in a south Swedish population of fallow deer Dama dama. Pits are large patches of bare soil found at the centre of mating stands where most of the rutting activities take place. The location of rutting pits in the study area was not significantly different from a random distribution in any of the five years of the study. Thus, there was no evidence of aggregation of rutting pits. Scrapes are small patches of bare soil found throughout the areas of deer activity. Only bucks showed any interest in scrapes. Within a 10 day period half the scrapes were rescraped at least once. Larger scrapes were more frequently rescraped than smaller ones. Frayings, i.e. removal of bark and subsequent scent marking on bushes and small trees close to scrapes, also had a positive effect on the frequency of rescraping. Artificial scrapes made close to real scrapes attracted less rescraping than natural scrapes. This might indicate that a scrape is preferentially rescraped by the buck who first created it. We found a tendency that scrapes were made in the direction of other stands/ pits, possibly indicating that they may function as territorial marks. However, the fallow deer bucks in our study do not seem to mark territorial boundaries, rather the intensity of markings tends to decrease with distance from the rutting pit suggesting that scraping may instead be used in male status signalling.

Key words: Dama dama, fallow deer, scent marking, scrapes

David Stenström & Cheryl Jones Fur, Department of Animal Ecology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden - e-mail: David.Stenstrom@zoologi.uu.se Jacob Höglund, Department of Population Biology, Uppsala University, Norbyvägen 18D, SE-752 36 Uppsala, Sweden Stina Dahlblom, Smultronvägen 4, SE-314 32 Hyltebruk, Sweden

Received 9 April 1999, accepted 20 January 2000

Associate Editor: Jean-Michel Gaillard

Among deer (Cervidae) and ungulates in general the production of different types of scent marks is an important part of male behaviour during the rut (Owen-Smith 1977, Gosling 1982). Examples of such markings in fallow deer *Dama dama* are so-called scrapes, i.e. small patches of bare soil (approximately 0.25 m²), from which the marking individual has removed the vegetation with its feet (Chapman & Chapman 1975).

One or more rutting pits, that is larger areas of scraped ground, can generally be found in the centre of a rutting buck's territory. Pits can be quite large (approximately 1-5 m²). Both scrapes and pits are, besides the visual mark, also marked with odour either from urine or from scent glands (Gosling 1982). In addition to scrapes and pits many cervids mark bushes and trees both visually by removing bark and

leaves, and by odour using scent glands on the head. In fallow deer this behaviour is generally referred to as fraying (Chapman & Chapman 1975).

The function of scrapes and pits in fallow deer and other Cervidae is not obvious. Chapman & Chapman (1975) could not find any correlation between the sites where bucks rutted and the distribution of scrapes. In white-tailed deer Odocoileus virginianus contradictory results have been presented with respect to the usual distance between scrapes and frayings (Moore & Marchinton 1974, Kile & Marchinton 1977). In roe deer Capreolus capreolus, scrapes have been shown to function as territorial markings (Johansson, Liberg & Wahlström 1995, Johansson & Liberg 1996). In general, a reasonable hypothesis for the function of pits and scrapes in fallow deer and other cervids is that they serve a role in territorial behaviour and/or sexual advertisement. In this paper we set out to test this hypothesis in a semi-enclosed population of fallow deer.

The mating tactics of fallow deer males commonly varies both within and between populations, and males in different populations have been classified as defending small clustered territories (lekking), dispersed resource defence polygyny, dispersed mating stands without resource defence, and mobile harem defence (reviewed in Thirgood, Langbein & Putman 1999). The population under focus in our study can be described as one where adult males defend dispersed rutting pits that do not contain any obvious resources essential for females (Espmark & Brunner 1974, Jones Fur 1998a).

First, we investigated the spatial distribution of rutting pits in our study area. In particular we wanted to test if rutting pits showed evidence of clustering, were randomly distributed or showed evidence of over-dispersion. Second, we studied the distribution of scrapes in relation to the location of rutting pits. Third, we tested experimentally whether scrapes were rescraped or not. Finally, we added artificial scrapes to test whether scrapes were re-visited by the buck that made them or if also other bucks re-mark already present scrapes.

Study area and methods

Our field-work was done in the Ottenby Nature Reserve from 9 October to 2 November in 1995. In addition, we used data on the location of rutting pits collected in the same area during each year in the fiveyear period from 1993 to 1997. The 1,000 ha reserve is situated at the southern tip of the island of Öland (56°14'N, 16°26'E) in the Baltic Sea proper off the Swedish east coast. The area is fenced off to the north and surrounded by the sea in all other directions. The enclosure contains approximately 350 hectares of continuous deciduous forest surrounded by a mixture of grazed pastures and thickets (Larsson 1974). During the rut, most of the deer gather in the forested area, and it is also here that all rutting stands can be found (Fig.1).

The density and composition of the population were determined by a helicopter census in February 1994. A total of 270 fallow deer were counted. Out of these 60 were antlered bucks and 93 were adult does, yielding a total density of 27 deer/100 ha and densities of 6 bucks/100 ha and 9 does/100 ha, respectively. Some culling takes place annually in addition to naturally induced mortality. However, we do not have exact figures to calculate the size and composition of the population in the autumn of 1995, so we had to assume that the population had stayed approximately the same and we used these numbers as an index of density and composition.

Rutting stands and pits were located by daily searching the woods for groaning males. Groaning males can be heard from a distance of approximately 500 m in favourable weather conditions. We plotted the location of pits on to scale maps of the study area. We then used these pit locations as well as previously collect-



Figure 1. The Ottenby forest study area and the distribution of the 27 fallow deer rutting pits observed in 1995.

ed data on pit locations from the period 1993-1997 in the same area to perform a nearest neighbour analysis of their distribution using the Clark-Evans test with the Donnelly modification (Krebs 1989).

Behavioural observations

The collection of behavioural observations was either done from hides and hunting towers, or on foot. The latter technique was predominantly used at the peak of the rut when especially the bucks are less vigilant than normally. Occasionally the deer were studied from cars. For each individual male the frequency of scraping as well as the time of appearance and disappearance of other deer on the stand was noted.

Binoculars and a telescope were used for identification of the bucks. All observed bucks were individually recognisable through antler characteristics. The deer were divided into the following categories: adult bucks, young bucks, juvenile bucks, adult does and fawns. Bucks were considered to be adult when the antlers were fully palmated. Young bucks (2-3 years) did not have full palms, but the antlers were branched and larger than the small, unbranched spikes of juvenile bucks. As pointed out by Chapman & Chapman (1975) the use of antler characteristics is not an exact method for ageing fallow deer, although it may be useful for broadly separating the males into age groups. Previous studies have shown that fallow deer males three years old and younger normally can be regarded as socially immature and that they rarely participate actively in the rut (Langbein & Thirgood 1989, Moore, Kelly, Cahill & Hayden 1995, Komers, Pélabon & Stenström 1997).

Experimental study

To investigate if scrapes were rescraped, 95 fresh scrapes were marked with numbered tags and received a light powdering of sieved sand. The scrapes were checked on the first, third, fifth, and tenth day after the first powdering. If a scrape had been rescraped, it was given a fresh powdering of sand. We also checked whether there was any fraying within a 5 m radius of the scrapes. Based on their diameter the scrapes were divided into small (< 40 cm), medium (40-80 cm) and large (> 80 cm) scrapes, and we tested if the frequency of rescraping was dependent on the size of the scrape. A number of roads traversing the study area functioned as transects, which presumably ran through the territories of several different bucks (see Fig.1).

Twenty pairs of artificial scrapes were made near

fresh natural scrapes. To test whether or not scent was important in determining the frequency of rescraping one of each pair of the artificial scrapes was provided with some top soil from the natural scrape. Both kinds of scrapes were also given a light powdering of sieved sand. Artificial scrapes were made approximately 50 cm in diameter and placed at an equal distance of 1-2 m from the natural scrapes.

Distribution of scrapes

The distribution of scrapes was mapped in circular areas around seven rutting pits. To avoid overlap with other stands nearby the radius of the circles was restricted to 50 m. In some cases other pits could be found as close as 100 m from the central pit. Three maps were made by first putting a measuring tape on the ground to the north from the centre of the pit. Then the area of 22.5° west to 22.5° east of the measuring tape was systematically searched for scrapes. The scrapes found were plotted on a map. The measuring tape was then moved 45° and the same procedure was repeated, until the whole area was covered. This method was time consuming, but could be conducted by a single person. The rest of the maps were made by a different method when assistance was available. One person stood in the middle of the rutting pit with a sighting compass while others were systematically searching the area for scrapes. When a scrape was found, the direction from the central pit was taken and the distance measured as the number of steps. The number of steps could later be converted to metres since it was known how many steps each person took when walking 50 m. We tested whether there was any significant difference (χ^2 , one-sample test) between the distribution of scrapes in the inner and outer half of the area around the pits. If scrapes are used in communication between males one would expect a higher density of scrapes in the direction of neighbouring stands. To test this the areas were also divided into four sectors (1-90°, 91-180°, 181-270°, 271-360°) and tested for differences in the distribution of scrapes between different directions $(\chi^2, \text{ one-sample test})$. Fisher's combined probability test was used to test the significance if all circles were used as one sample.

Results

Distribution of rutting pits

The rutting pits were randomly distributed in the forest habitat in all of the five years of study (Table 1). Some

Table 1. Nearest neighbour analysis of the fallow deer rutting pits in the Ottenby study area during 1993-1997. Index of dispersion (R), number of pits (N), z-score and P-values of nearest neighbour distances in all five years of the study are based on Clark-Evans test with the Donnelly modification (Krebs 1989). R approaches zero if the population is overdispersed, 1 if random and 2.15 if clustered.

Year	R	N	Z	Р
1003	1.11	13	0.80	0.42
1994	1.00	11	0.01	0.98
1995	1.02	17	0.11	0.91
1996	1.20	18	1.44	0.15
1997	1.16	15	1.07	0.28

of the pits were used in all years and were found in the same location. Others were more temporary with a few being used in only one of the years (see Fig. 1, Table 2).

Behavioural observations

In total, 652 minutes of deer behaviour were recorded. Adult bucks were observed for 528 minutes in total (mean observation time per buck = 10.6 minutes). They were observed together with other adult bucks for 15 minutes, with young bucks for 217 minutes, with juvenile bucks for 94 minutes and with adult does for 269 minutes. The presence of adult bucks, juvenile bucks or adult does did not influence the frequency of scraping (Mann-Whitney U-test: $\chi^2 = 0.35$, $N_1 = 49$, $N_2 = 4$, N.S.; $\chi^2 = 0.12$, $N_1 = 44$, $N_2 = 9$, N.S. and $\chi^2 = 0.62$, $N_1 = 26$, $N_2 = 27$, N.S.). The frequency of scraping was lower when young bucks were present than when they were absent (Mann-Whitney U-test: $\chi^2 = 5.0$, $N_1 = 43$, $N_2 = 10$, P < 0.05).

Experimental study

On day 1 after first being examined 22% of the tagged scrapes had been rescraped and after three days 31%. After five days 42% and after 10 days 52% of the scrapes had been rescraped at least once. Among large scrapes most became rescraped, whereas the opposite was true for small scrapes: 77% of the large, 50% of the medium, but only 20% of the small scrapes were rescraped ($\chi^2 = 9.02$, df = 2, P < 0.02). Large scrapes were also more frequently rescraped more than once: 52% of the large scrapes (N = 30), 20% of medium sized (N = 49) and 7% of small scrapes (N = 13) were rescraped more than once during a 10 day period ($\chi^2 = 13.30$, df = 2, P < 0.01).

Of all scrapes, 17% had frayings within a 5 m radius. Among large scrapes 16% had frayings close to them. The figures for medium sized and small scrapes were 20 and 8%, respectively ($\chi^2 = 0.85$, df = 2, N.S.). Twenty-

Table 2. The 27 fallow deer rutting pits observed in the Ottenby study area during 1993-1997 and their respective years of occupancy. For pit locations see Figure 1.

Pit number	1993	1994	1995	1996	1997
1			Х		
2			х	Х	Х
3	х		Х	Х	
4	X	Х	Х		Х
5				Х	Х
6			Х	Х	Х
7	Х			Х	
8	х	Х		Х	
9				Х	Х
10			Х		
11	Х	Х		Х	Х
12			Х		
13	Х	х			
14	Х	X	Х	х	Х
15	х	х	х	х	
16	х	х	х	х	
17			х		
18				Х	
19		X			Х
20	х	Х	Х		Х
21	х	х	х	х	х
22				х	
23	х				
24				х	
25					Х
26	х	х	х	х	Х
27			х		

five percent of the scrapes that had been rescraped, but only 10% of the scrapes that were never rescraped, had frayings within a 5 m radius ($\chi^2 = 4.24$, df = 1, P < 0.05).

The artificial scrapes were not rescraped as frequently as the natural scrapes. During a five day period (24-29 or 25-30 October) 7.5% of the artificial scrapes (N = 40) were rescraped. Among natural scrapes (N = 95) 35% were rescraped during a comparable five day period (22-27, 23-28 or 24-29 October) (χ^2 = 40.33, df = 1, P < 0.001). During the last period, 24-29 October, the difference between artificial and natural scrapes was even greater; 5% (N = 20) of the artificial and 36% (N = 14) of the natural scrapes were rescraped (χ^2 = 5.34, df = 1, P < 0.05). Since only a total of three out of the 40 artificial scrapes were rescraped it was not possible to test for any effect of the soil added from natural scrapes (two scrapes with added soil, one without).

Distribution of scrapes

The distribution of scrapes around the rutting pits showed a trend of being directed towards the location of other nearby bucks. If data from all pits were combined, the distribution of scrapes was significantly different between different directions as well as closer to the

Table 3. Scrapes around seven different fallow deer rutting pits in the Ottenby study area in 1995 and the different distribution between their inner/outer circle or different directions (N-S-E-W); χ^2 , one-sample test.

Pit number	Inner > Outer circle	Different directions	
1	_	-	
4	**	-	
11	*	**	
17	-	_	
19	_	*	
21	**	**	
27	***	-	
Fisher's combined pr	obability test ***	**	

- N.S.; * P < 0.05; ** P < 0.01; *** P < 0.001

centre compared to the outer half of the area (Table 3). Around four pits (11, 27, 4 and 21 in Figure 1) there were significantly (P < 0.05) more scrapes close to the centre of the area than in the outer half of the area. Two of those pits (11 and 27) also had a significantly (P < 0.01) unequal distribution of scrapes between different sectors (N-S-W-E). At pit 19 we found a significantly unequal distribution of scrapes between different directions but no significant difference between the inner and outer half of the area (see Table 3). Scrapes were aggregated in the direction of other nearby pits around pit 11 and 19. Pit 27 also showed this tendency, even though a substantial part of the scrapes were directed towards the south (see Table 3).

Discussion

Distribution of rutting pits

We found the distribution of the rutting pits to be random in all of the study years. This means that there are no indications of aggregation in the population studied. Other studies of fallow deer have shown that fallow deer bucks may aggregate and form leks during the rut (Schaal 1986, Pemberton & Balmford 1987, Clutton-Brock, Green, Hariawa-Hasegawa & Albon 1988, Apollonio, Festa-Bianchet & Mari 1989, Langbein & Thirgood 1989), and this behaviour has been suggested to be associated with a high density of bucks (Apollonio 1989, Langbein & Thirgood 1989). The population density of mature bucks in our study area falls within the low range reported by Langbein & Thirgood (1989), and it is therefore no surprise that we observed no indications of clustering in our study population and the nearest neighbour analyses did not reveal significant clustering in any year.

The location of mating stands and hence of rutting pits is likely to depend on a range of factors such as proximity to does, distance to other competing bucks, and tradition. In a study in the same area, Jones Fur (1998b) failed to find any vegetation characteristics discriminating between stands and random sites apart from stands being characterised by having a more closed canopy layer. This does not mean, however, that bucks are unable to predict female movements. A comparison of radio-tracking data from two does collected during the rut of 1994/95 at Ottenby suggests that does have home ranges of approximately 40 ha and that these are very stable between years (D. Stenström, pers. obs.). Thus, it is likely that bucks are capable of locating places that are better than others with respect to the probability of encountering does within the forest habitat. If bucks somehow can tell where does are most likely to be encountered, it would clearly be profitable for them to defend stands as such sites. So we would expect the strongest and most dominant bucks to defend the most popular stands, and competition to be most intense for such sites. While we have no direct evidence for this being the case, the fact that some stands/pits were used in all years of the study and others more seldomly suggests indirectly that some sites are indeed more profitable.

The function of scraping

We found no difference when comparing the frequency of scraping with and without adult males, juvenile bucks or adult does present on the stand. However, these non-significant results may be due to small sample sizes. The important thing to note in the present context is that bucks scrape both when other individuals are present, and when they are alone at the stand. This finding shows that scraping in itself is unlikely to be a visual display, even though the resulting scrape may well be so.

At Ottenby, the does did not show any obvious interest in scrapes, i.e. they were never observed to smell them. In contrast, bucks were often observed smelling scrapes, which suggests that scrapes are likely to be signals primarily directed towards other bucks. However, it is still possible that the does may be affected by the scrapes. In white-tailed deer it has been suggested that scrapes attract does and that the bucks return to their old scrapes to check for waiting does (Moore & Marchinton 1974). Furthermore, in the same species, females have been reported to respond to both rubs and scrapes (Sawyer, Marchinton & Miller 1989).

The scrapes around the mapped rutting pits showed no obvious pattern unless all maps were used as one

sample in a combined probability test (see Table 3). Chapman & Chapman (1975) had the same difficulty in finding any pattern of scrapes made by fallow deer in a 3 ha area. Moore & Marchinton (1974) found that white-tailed deer scrapes were made in conspicuous places and that their location generally coincided with areas of high densities of frayings. Kile & Marchinton (1977) found that white-tailed deer scrapes were clumped, but not at the same sites where clumps of frayings were found. An explanation of these contradictory results could be that scrapes are made where the soil is easily scraped independently of the presence of young trees suitable for fraying. That scrapes around rutting pits in our study in some cases were more frequent in the directions towards other pits could indicate that the scrapes are used in territoriality. However, if scrapes are territorial markings this may be hard to prove by mapping the scrapes since surrounding bucks might change the location of their territory during the rut and as a result confuse the pattern.

Gosling (1990) proposed that the principal function of scent marking by resource holding males should be status advertisement, providing a means of assessment to potential competitors, thereby reducing the cost of agonistic encounters. Whether scraping is used for status advertisement in fallow deer is not fully known. However, male dominance rank has a profound effect on the frequency of both scent marking in general, and scraping, in fallow deer (Jones Fur 1998a, Komers et al. 1997). Further, the spatial pattern of scraping observed in our study seems to suggest that this could be the case. The fallow deer bucks in our study do not seem to mark territorial boundaries, rather the intensity of markings tends to decrease with distance from the rutting pit.

Rescraping was common, and as many as half the tagged scrapes were rescraped within a 10 day period. No observations were made to identify the individual that did the rescraping. Ozoga & Verme (1985) found that prime aged male white-tailed deer rescraped as often as they made a new scrape. Yearling bucks were responsible for 31-44% of the rescraping events.

That artificial scrapes were less frequently rescraped than natural ones may have different reasons. They could either have such a strong human smell that they were avoided, or they could be placed in very specific locations. That the artificial scrapes should be avoided simply because of human smell seems unlikely. Natural scrapes were frequently checked, and when doing so human smell must have been left also at these sites. The artificial scrapes were placed very close (1-2 m) to natural scrapes, but of course there is still a possibility that the deer would not have chosen those particular locations, even though this also seems unlikely. Another explanation could be that scrapes are preferentially rescraped by the buck who first made them.

That large scrapes were rescraped more frequently seems obvious both if scrapes are visual markings and if they are scent marks. This is because large scrapes are likely both to be more conspicuous and to contain more scent. Scrapes that are rescraped more often probably will also become larger with time. It is impossible to tell how many times a given scrape had been scraped when it was first found, tagged and measured.

Scrapes close to frayings were more often rescraped than other scrapes, maybe because they were more often visited. If this is correct, it might indicate that these scrapes were of a greater strategical importance than others, for instance as territorial marks or signposts for status signalling. However, the frayings could also attract deer and make the area more often visited independently of any strategical importance.

In conclusion, the function of scraping seems to be communicative primarily towards other bucks. It is probably the scrape itself and not the scraping activity that functions as a visual as well as an olfactory signal. We suggest that scrapes primarily serve as signposts for status signalling. Very little seems to indicate any function for scrapes in territoriality. However, we cannot exclude the possibility that scrapes may play a role for does when choosing a buck to mate with.

Acknowledgements - we thank Håkan Ignell, Maria Levin and Gunlög Fur for valuable assistance in the field. His Majesty King Carl XVI Gustaf of Sweden kindly gave us permission to work with his deer. Financial support for our study was provided by The Royal Swedish Academy of Sciences and Zoologiska Stiftelsen (D. Stenström and C. Jones Fur) and Swedish Natural Sciences Research Council (J. Höglund).

References

- Apollonio, M. 1989: Lekking in fallow deer: just a matter of density? - Ethology Ecology and Evolution 1: 291-294.
- Apollonio, M., Festa-Bianchet, M. & Mari, F. 1989: Correlates of copulatory success in a fallow deer lek. - Behavioral Ecology and Sociobiology 25: 89-97.
- Chapman, D. & Chapman, N. 1975: Fallow Deer, their history, distribution and biology. Terence Dalton Ltd, Lavenham, 271 pp.

- Clutton-Brock, T.H., Green, D., Hariawa-Hasegawa, M. & Albon, S.D. 1988: Passing the buck: resource defence, lek breeding and mate choice in fallow deer. Behavioral Ecology and Sociobiology 23: 281-296.
- Espmark, Y. & Brunner, W. 1974: Observations on rutting behaviour in fallow deer, (Dama dama). - Säugetierkundliche Mitteilungen 22: 135-142.
- Gosling, L.M. 1982: A reassessment of the function of scent marking in territories. - Zeitschrift f
 ür Tierpsychologie 60: 89-118.
- Gosling, L.M. 1990: Scent marking by resource holders: Alternative mechanisms for advertising the costs of competition. - In: Macdonald, D., Müller-Schwarze, D. & Natynczuk, S. (Eds.); Chemical signals in Vertebrates 5. Oxford University Press, Oxford, pp. 315-328.
- Johansson, A. & Liberg, O. 1996: Functional aspects of marking behavior by male roe deer (Capreolus capreolus).
 Journal of Mammalogy 77: 558-567.
- Johansson, A., Liberg, O. & Wahlström, L.K. 1995: Temporal and physical characteristics of scraping and rubbing in roe deer (Capreolus capreolus). - Journal of Mammalogy 76: 123-129.
- Jones Fur, C. 1998a: Ecology, sexual selection and variable mating tactics in fallow deer Dama dama. - PhD thesis, Uppsala University, Uppsala, 151 pp.
- Jones Fur, C. 1998b: Habitat structure, female distribution, and fallow deer (Dama dama) mating stands. - Wildlife Biology 4: 185-192.
- Kile, T. & Marchinton, L. 1977: White-tailed deer rubs and scrapes: spatial, temporal and physical characteristics and social role. - The American Midland Naturalist 97: 257-266.
- Komers, P.E., Pélabon, C. & Stenström, D. 1997: Age at maturity in male fallow deer: age-specific versus dominancespecific behaviors. - Behavioral Ecology 8: 456-462.

- Krebs, C.J. 1989: Ecological Methodology. Harper & Row, New York, 620 pp.
- Langbein, J. & Thirgood, S.J. 1989: Variation in mating systems of fallow deer (Dama dama) in relation to ecology. - Ethology 83: 195-214.
- Larsson, A. 1974: Ottenby natureservat, vegetation och markanvändning. - University of Lund, Lund, 70 pp. (In Swedish).
- Moore, G. & Marchinton, L. 1974: Marking behaviour and its social function in white tailed deer. - In: Geist, V. & Walter, F. (Eds.); The behaviour of ungulates and its relation to management. Morges, Switzerland, pp. 447-456.
- Moore, N.P., Kelly, P.F., Cahill, J.P. & Hayden, T.J. 1995: Mating strategies and mating success of fallow (Dama dama) bucks in a non-lekking population. - Behavioral Ecology and Sociobiology 36: 91-100.
- Owen-Smith, N. 1977: On territoriality in ungulates and an evolutionary model. - The Quarterly Review of Biology 52: 1-38.
- Ozoga, J. & Verme, L. 1985: Comparative breeding behaviour and performance of yearling vs. prime-aged white-tailed bucks. - Journal of Wildlife Management 49: 364-372.
- Pemberton, J.M. & Balmford, A.P. 1987: Lekking in fallow deer. Journal of Zoology (London) 213: 762-765.
- Sawyer, T.G., Marchinton, R.L. & Miller, K.V. 1989: Response of female white-tailed deer to scrapes and antler rubs. - Journal of Mammalogy 70: 431-433.
- Schaal, A. 1986: Mise en évidence d'un compartement de reproduction en arène chez le Daim d'Europe (Dama d. dama). - Comptes Rendus de l'Academie des Sciences de Paris 303: 729-732. (In French).
- Thirgood, S., Langbein, J. & Putman, R.J. 1999: Intraspecific variation in ungulate mating strategies: The case of the flexible fallow deer. - Advances in the study of behaviour 28: 333-361.