Fallow Deer Tactic to Compete Over Food With Red Deer

Luděk Bartoš, Dominika Vaňková, Jiří Šiler, and Soběslav Losos

Ethology Group, Research Institute of Animal Production, Praha, Czech Republic

Small ungulates may compete with larger species through higher mobility, greater aggressiveness, and/or by larger group sizes. We observed a herd of approximately 100 red deer (Cervus elaphus) and 130 fallow deer (Dama dama) at the Žehušice Deer Park during supplemental feeding to determine whether fallow deer can displace red deer at feeding sites and to describe strategies used for displacement. Data were analyzed during the antlered period (AP) when males of both species had hard antlers and the cast period (CP) when all red deer stags had cast antlers, but fallow bucks were still in a hard antler. We conducted 41 observation sessions, 29 during the AP and 12 during the CP. In both periods red deer were more numerous than fallow deer at the feeding sites. Fallow bucks initially waited until red deer arrived at the feeding site, after which they attacked any red deer. Fallow bucks were more aggressive than red deer stags or hinds. When stags retaliated, the bucks turned their attacks toward hinds. During feeding sessions, attacks against hinds intensified, while bucks avoided encounters with stags. As a result, in most cases (90%), red deer vacated the feeding site before the supplementary food was depleted. In contrast, fallow does not compete with the larger red deer and selected other sources of food in the park. © 1996 Wiley-Liss, Inc.

Key words: fallow deer, red deer, aggression, competition

INTRODUCTION

Small social carnivores have developed several tactics which help them compete with larger species. For example, the African wild dog coordinates pack behaviour to capture game and also to protect the prey from hyenas after the kill. In turn, the wild dogs and hyenas compete with lion prides [Wilson, 1975; Fanshawe and Fitzgibbon, 1993]. Various authors have reported the ability of smaller ungulate species to compete with larger species through higher mobility [Raesfeld, 1920; Nebeský, 1956], greater aggressiveness [Logan, 1957; Kiddie, 1962; Bartoš and Žirovnický, 1982], and/or by larger group sizes [Atlimann, 1956], although detailed observational data is rare. At-

Received for publication August 1, 1995; accepted January 31, 1996.
Address reprint requests to Luděk Bartoš, Ethology Group, Research Institute of Animal Production, CZ-104 00 Praha 10-Uhříněves, Czech Republic.

© 1996 Wiley-Liss, Inc.
tempts to introduce wapiti (*Cervus elaphus canadensis*) or Siberian roe deer (*Capreolus capreolus pygargus*) into European populations of red and roe deer have been attempted repeatedly. Although the introduced wapiti bulls or roe deer bucks were much larger [Raesfeld, 1920; Nebeský, 1956] they were unable to compete with local animals. In many areas, introduced sika deer (*Cervus nippon*) have been able to out-compete red deer [Logan, 1957; Kiddle, 1962]. Fights between the two species have been recorded. When sika stags win, it is usually due to high aggressiveness [Bartoš and Žirovnický, 1982]. Under artificial feeding conditions, group effects may play an important role in interspecific competition. Altmann [1956] reported that groups of wapiti approaching salt licks could displace other animals, including much larger moose, simply by the intimidating appearance of the massed approach.

Our previous anecdotal observations have suggested that fallow deer could displace red deer at winter artificial feeding sites in a deer park [Bartoš, 1982]. This study investigated whether fallow deer can displace red deer at feeding sites, and, if so, whether they use any tactic to displace the larger species. We tested the influences of group size, frequency of aggression, location of feeding site, sex, and availability of food on interspecific competition between the two species.

**METHODS**

All observations were done in the Žehušice Deer Park (2.6 km²), Central Bohemia, Czech Republic between 1991 and 1993. During this period, approximately 100 red deer (34% males) and 130 fallow deer (57% males) were present. Supplemental feeding (oats, barley, apples, root vegetables, etc.) were provided regularly throughout the year, allowing the animals to adapt to human presence. During winter, the food was provided daily at five feeding sites, always the same items at all sites. There was also a large hay feeder in the park, where both species fed ad libitum.

During 1991, observations were conducted by one observer at one feeding site. During the subsequent two seasons, four observers were located at one of four feeding sites. To avoid any influence of human presence, we used high seats located about 50 m from the feeding site for observations. Observers were in place shortly before the food was delivered by tractor. Deer apparently ignored the high seat and movements in the immediate area of the seat were uninhibited. Food was usually spread over a large area (50 × 50 m) to allow as many animals as possible to feed. The order of food delivery was varied daily. Red deer usually responded to the sound of the tractor, walking behind it and eating the food as soon as it was delivered. Fallow deer were normally nearby. Some red deer stayed at the first feeding site, while others followed the tractor to the next place. After a while some fallow deer joined the first group of red deer, but others carried on to the next feeding site.

For each species we recorded the time of arrival of the first deer after food delivery, the time of the first species to leave the feeding site once both species were present, the number of animals present by sex, and the number of attacks by sex of the instigator and recipient. An ‘attack’ was any activity of one animal (such as direct approach, kick, bite, or antler pushing) which was followed by apparent displacement of the recipient. Aggression was expressed as number of attacks per animal of the attacking species, divided by the number of individuals of the other species at feeding. Only inter-specific attacks were recorded.
Because antlers are a potent weapon in agonistic encounters [Clutton-Brock, 1982], data were analyzed for two periods: "antlered period"—the period when males of both species had hard antlers; the "cast period"—when all red stags had cast their antlers, but fallow bucks were still in a hard antler. The summary of both periods is referred to as "total." Observations when both species had cast antlers, or were in velvet, were not conducted because there was little interest in supplementary food during this period.

The following terms are used throughout the text: "stag"—male red deer; "hind"—female red deer; "buck"—male fallow deer; and "doe"—female fallow deer.

**Statistical Analysis**

Nonparametric statistics were applied using "Statgraphics 4.2" software. All tests were two-tailed. If not otherwise stated, the results are presented as median ± lower and upper quartile. Spearman Rank Correlations were conducted for data from both periods combined, due to the low incidence of red deer attacks.

**RESULTS**

We conducted 41 observation sessions, 29 for the antlered period and 12 for the cast period. In 37 cases (90.0%) feeding sites were visited by both species. During the cast period in two cases (4.0%) only red deer came to feed and in two cases (4.0%) only fallow deer.

**Arrival at the Feeding Sites**

In all cases where the feeding site was approached by both species, red deer arrived first (against equality, $\chi^2 = 24.08, P < 0.001$). Fallow deer always arrived at the feeding site when there was food still available. The time taken for the first fallow deer to join red deer at a feeding site did not differ between the antlered and cast periods (Fig. 1, Mann-Whitney test $z = 1.04, \text{NS}$).

![Graph](image)

**Fig. 1.** Time taken for the first fallow deer to join a group of red deer at the feeding site, and for the last red deer to leave the site after being joined by fallow deer. Striped bars, time which elapsed since red deer started feeding and when the first fallow deer arrived to the feeding site; grey bars, time when red deer left after being joined by fallow deer.
Number of Deer

In total, red deer outnumbered fallow deer (Mann-Whitney test, $z = 6.72, P < 0.001$) at the feeding sites (Fig. 2). During both periods there was a similar trend with red deer being more numerous (Fig. 3), but this was only statistically significant in the antlered period (Mann-Whitney test, $z = 3.46, P < 0.001$). More hinds than stags visited the feeding sites (Wilcoxon test, antlered period $T = 2.28, P < 0.03$; cast period $T = 2.48, P < 0.01$; total $T = 2.47, P < 0.01$). In contrast, fewer does than bucks visited feeding sites (Wilcoxon test, antlered period $T = 4.72, P < 0.001$; cast period $T = 2.48, P < 0.01$; Total $T = 5.50, P < 0.001$). In red deer, the male/female percentage decreased after antler casting from 28.18% (16.67% to 53.85%) to 16.23% (3.00% to 28.18%) (Mann-Whitney test, $z = 2.46, P < 0.01$). However, there were no changes in the ratios of does to bucks during the same period, from 100.00% (83.14% to 100.00%) to 100.00% (82.31% to 100.00%) (Mann-Whitney test, $z = -0.04$, NS).

There were no differences in the numbers of stags and bucks (Mann-Whitney test, antlered period $z = -0.13$, NS; cast period $z = -0.84$, NS; Total $z = -0.80$, NS). While the number of stags declined after antler casting (Mann-Whitney test, $z = -2.29, P < 0.05$), the number of bucks did not change (Mann-Whitney test, $z = -0.72$, NS).

Aggression

A total of 712 agonistic interactions were recorded ($n = 656$ antlered period, $n = 56$ cast period). When a fallow deer was displaced, it often returned immediately. We observed various unusual behaviours such as bucks attacking red deer with their antlers from behind. There were marked differences between the sexes in inter-specific attacks. Does rarely attacked any red deer. There was significant variation among stags, hinds, and bucks (Fig. 4) during the antlered period (Kruskal-Wallis ANOVA, $n = 29$, $H = 6.07, P < 0.001$), the cast period (Kruskal-Wallis ANOVA, $n = 8$, $H = 13.43, P < 0.001$), and the total (Kruskal-Wallis ANOVA, $n = 37$, $H = 14.36, P < 0.001$). During all periods, bucks attacked others more frequently than stags (Wilcoxon test, antlered period $T = 2.46, P < 0.01$; cast period $T = 2.11, P < 0.03$; total $T = 3.04, P < 0.001$) or than hinds (Wilcoxon test, antlered period $T = 1.93, P < 0.05$; cast period $T = 2.26, P < 0.02$; total $T = 2.03, P < 0.05$).
The number of attacks against fallow deer did not differ between stags and hinds (Wilcoxon test, antlered period $T = 0.75$, NS; cast period $T = 0.71$, NS; total $T = 1.00$, NS).

We compared aggression against all categories of the other species (Fig. 5). In this case, aggression was expressed as the number of attacks per animal of the attacking category present, divided by the number of individuals of the attacked sex. (These expressions also were used for calculating correlations.) In general, red deer of both sexes seldom attacked other conspecifics. Stags attacked bucks more frequently than does in the antlered period (Wilcoxon test, $T = 3.62$, $P < 0.001$), but not during the cast period. In contrast, hinds attacked bucks and does equally (Wilcoxon test, antlered period $T = 0.00$, NS; cast period $T = 0.71$, NS; total $T = 0.00$, NS). Bucks attacked stags more than hinds in the antlered period only (Wilcoxon test, antlered period $T = 2.92$, $P < 0.01$; cast period $T = 0.00$, NS; total $T = 0.88$, NS).

After antler casting, stags reduced the frequency of attacks against bucks (Mann-Whitney test, $z = -2.47$, $P < 0.01$), while hinds instigated relatively few attacks against bucks (Mann-Whitney test, $z = 1$, NS). The frequency of attacks against does did not
Fig. 5. Number of attacks produced per animal of the attacking category divided by number of individuals of the attacked sex.

change between the antlered and cast periods (Mann-Whitney test, stags z = 1.00, NS; hinds z = 1.00, NS).

Generally, frequent attacks by bucks resulted in frequent attacks by stags (r = 0.58, n = 37, P < 0.001). Increased attacks by bucks against hinds did not correspond to an increase in attacks by hinds against bucks (r = -0.13, n = 37, NS). In contrast, frequent attacks by stags against bucks did not correspond to more frequent attacks by bucks against stags (r = 0.29, n = 37, NS), but did for hinds (r = 0.38, n = 37, P < 0.05). With
increasing time at feeding sites, buck attacks increased against hinds \((r_s = 0.42, n = 37, P < 0.01)\), but not against stags \((r_s = 0.14, n = 37, NS)\).

**Feeding Sites**

We tested for variations in the numbers of deer visiting the five feeding sites using data when four feeding sites were monitored simultaneously. After food delivery, 53% and 30% of feeding sites in the antlered and cast period respectively were not visited during the observation session (about 1 hr). Some sites were visited more frequently than others (Table I, antlered period \(\chi^2_{(4)} = 8.00, P = 0.09\); cast period \(\chi^2_{(4)} = 15.24, P < 0.01\)) and each site was vacant at least once.

The number of deer of each species at a feeding site did not differ among observation sessions in the antlered period (Kruskal-Wallis ANOVA, \(n = 8\), red deer \(H = 10.05, NS\); fallow deer \(H = 6.48, NS\)), or cast period (Kruskal-Wallis ANOVA, \(n = 4\), red deer \(H = 2.21, NS\); fallow deer \(H = 0.07, NS\)). Similarly, the numbers of stags and hinds did not differ at the four feeding sites during the antlered period (Kruskal-Wallis ANOVA, stags, \(n = 4\), \(H = 4.27, NS\); hinds, \(n = 4\), \(H = 4.19, NS\)). In contrast, there were differences in occupation of the four feeding sites during the antlered period by bucks (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 7.98, P < 0.05\)) and does (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 6.68, P = 0.08\)). In the cast period, stags (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 2.60, NS\)) and does (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 5.03, NS\)) did not show variation in occupying the feeding sites, while hinds (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 10.54, P < 0.01\)) and bucks (Kruskal-Wallis ANOVA, \(n = 4\), \(H = 10.88, P < 0.01\)) did vary (Fig. 6).

The proportion of deer species varied at all except one feeding site in both periods during the successive observation sessions. (Table I. Tested by contingency table or by Fisher exact probability test. For statistical analysis, sessions when no animals arrived were omitted.)

<table>
<thead>
<tr>
<th>Observation session</th>
<th>Site A % (n)</th>
<th>Site B % (n)</th>
<th>Site C % (n)</th>
<th>Site D % (n)</th>
<th>Site E % (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Antlered period</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>66.67% (120)</td>
<td>25% (4)</td>
<td>-</td>
<td>27.69% (65)</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>75.47% (53)</td>
<td>-</td>
<td>-</td>
<td>54.17% (24)</td>
<td>95.59% (68)</td>
</tr>
<tr>
<td>3</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>66.67% (45)</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>57.10% (31)</td>
<td>-</td>
<td>75.00% (16)</td>
<td>91.80% (61)</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>96% (25)</td>
<td>-</td>
<td>-</td>
<td>25.00% (32)</td>
<td>-</td>
</tr>
<tr>
<td>6</td>
<td>10.11% (89)</td>
<td>91.94% (62)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>-</td>
<td>54.55% (33)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>44.93% (69)</td>
<td>78.95% (38)</td>
<td>91.95% (87)</td>
<td>70.59% (68)</td>
<td>-</td>
</tr>
<tr>
<td>(\chi^2)</td>
<td>143.98*</td>
<td>23.6*</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Cast period</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>87.72% (57)</td>
<td>11.11% (9)</td>
<td>100.00% (22)</td>
<td>63.64% (110)</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>37.50% (80)</td>
<td>0.00% (9)</td>
<td>100.00% (22)</td>
<td>92.59% (54)</td>
<td>-</td>
</tr>
<tr>
<td>3</td>
<td>59.70% (67)</td>
<td>0.00% (6)</td>
<td>-</td>
<td>70.37% (27)</td>
<td>-</td>
</tr>
<tr>
<td>4</td>
<td>29.41% (85)</td>
<td>75.00% (36)</td>
<td>-</td>
<td>92.59% (54)</td>
<td>-</td>
</tr>
<tr>
<td>(\chi^2)</td>
<td>58.34*</td>
<td>29.31*</td>
<td>-</td>
<td>26.70*</td>
<td>-</td>
</tr>
</tbody>
</table>

*\(P < 0.001\).

\(^1\)Fisher exact probability test used.
Fig. 6. Mean numbers of the deer at the four feeding sites during antlered and cast periods. a: Red deer stags; b: red deer hinds; c: fallow deer bucks; d: fallow deer does.
During the antlered period, fallow deer tended to visit the same feeding sites as red
deer (n = 32, stags vs. bucks $r_s = 0.84, P < 0.001$, stags vs. does $r_s = 0.48, P < 0.01$, hinds
vs. bucks $r_s = 0.80, P < 0.001$, hinds vs. does $r_s = 0.45, P < 0.01$). In both species males
and females stayed together (red deer $r_s = 0.82, P < 0.001$; fallow deer $r_s = 0.76, P <
0.001$). In the cast period (n = 16) stags and hinds occurred together less frequently ($r_s
= 0.35, NS$). Bucks associated with feeding sites containing a higher proportion of
hinds ($r_s = 0.51, P < 0.05$), than stags ($r_s = -0.08, NS$). There was no relationship be-
tween the numbers of does at feeding sites and bucks ($r_s = 0.38, NS$), stags ($r_s = -0.23,
NS$), or hinds ($r_s = 0.13, NS$).

**Leaving Feeding Sites**

In 34 cases (91.9%), red deer left the feeding site before the depletion of the supple-
mentary food (red vs. fallow deer $\chi^2 = 15.63, P < 0.001$). In the antlered period, red deer
left first in 26 cases (89%, red vs. fallow deer $\chi^2 = 10.94, P < 0.001$) and in eight cases
in the cast period (100%, the sign test, $P < 0.01$). In the antlered period, hinds tended to
leave earlier than the stags. In 22 cases (71.0%) the hinds left first ($\chi^2 = 2.89, P = 0.09$).
During the cast period the difference between the sexes diminished. Hinds left the feeding
site in only five cases (55.6%) before depletion of the feed (Fisher exact probability
test, NS).

**DISCUSSION**

Generally, both species visited the feeding sites. Red deer arrived first, almost imme-
diately after food delivery. Fallow deer joined the red deer later, before the food supply
had been exhausted. In a previous study at the same park [Bartoš, 1986], we observed
that red deer remained at feeding sites for an average of more than 50 min if no fallow
deer approached the site. We suggest that the delay of fallow deer to approach a feeding
site containing red deer be a tactic associated with a reduction in the red deer’s motiva-
tion to fight [comp. Leyhausen, 1973].

In most cases, red deer outnumbered fallow deer at the feeding sites, although differ-
ences occurred between the antlered and cast periods. During the antlered period, the
sex ratio at feeding sites was similar to that within the entire herd. During the antlered
period, similar numbers of stags and bucks were present but only a small proportion of
does visited the feeding sites, suggesting that few female fallow deer herd received
supplementary feeding. During the cast period, fewer stags visited the feeding sites.
Fallow deer usually visited the same feeding places as red deer and avoided unoccupied
sites, even though supplementary food was available. Thus, the presence of red deer
may indicate to fallow the availability of food.

Since feeding did not occur at regular times, it may be more beneficial for fallow
deer to compete with red deer, rather than losing time by seeking sites with no supple-
mentary food.

In the antlered period, red deer visited individual feeding sites proportionally across
observation sessions, while fallow deer did not. Since red deer always arrived first at the
feeding sites, fallow deer chose the most suitable place to join their competitors.
Since red stags and hinds kept together in the antlered period, bucks could not avoid
places with antlered stags. Selection of feeding sites by bucks probably was based on
criteria other than the presence/absence of stags. This trend changed during the cast period, when stags and hinds tended to feed at different sites. Bucks then preferred those feeding sites with a higher proportion of hinds.

Fallow bucks were more aggressive than red deer stags or hinds. After arrival at the feeding site, bucks attacked any red deer. When stags increased their defense against bucks, bucks subsequently attacked hinds. As the time spent feeding progressed, attacks against hinds intensified, while bucks avoided encounters with stags. These attacks were not severe and were not always successful. Nevertheless, the disturbance caused by these attacks may have red deer to depart the feeding sites. Hinds were more vulnerable to attacks from bucks in hard antlers and therefore more likely to leave the feeding site first. After casting antlers, stags were less successful at defending attacks from antlered bucks. Therefore, during the cast period the latency between stags and hinds leaving the feeding site diminished.

In the antlered period stags attacked bucks more frequently than does. However, this probably reflects the defensive behaviour of stags against attacks by bucks, because the number of attacks instigated by stags against bucks correlated to the number instigated by bucks against stags.

Attacking a competitor with antlers from behind was used by bucks, but not stags. This tactic has been described for sika stags when fighting with red deer [Bartoš and Žírovnický, 1982], and also when red deer stags were fighting against wapiti bulls [Raesfeld, 1920]. Perhaps when faced with a competitor of a larger species, deer become less conservative in fighting style.

The decrease in the number of stags visiting the feeding sites after antler casting may be due to a loss of the ability to defend against attacking bucks. Consequently stags may avoid any encounter while bucks are in a hard antler. In the park, bachelor groups break up much later [Bartoš, 1985; Bartoš and Perner, 1985] when compared to other populations [Bützler, 1974]. Moreover, unantlered stags, if present, displayed almost no aggression against bucks.

In conclusion, fallow deer adopted a simple tactic to compete with red deer at feeding sites. Bucks waited until red deer had arrived at the feeding site. If the composition of the red deer group was suitable, the bucks joined them. Otherwise, they moved to another feeding site. Thus, bucks selected a feeding site according to the composition or sex ratio of red deer. Nevertheless, bucks attacked any competitor although as feeding time progressed, or when stags increased the number of attacks against bucks, bucks focused their aggression toward hinds. As a result, in over 90% of cases, red deer vacated the feeding site before the supplementary food was depleted. In contrast, fallow does did not spend energy competing with much larger red deer and instead selecting other sources of food in the park.

ACKNOWLEDGMENTS

We are grateful to Jaroslav Madlafousek, Marek Špinka, and two anonymous referees for their constructive comments and discussions. We thank Alison Hanlon and Karl V. Miller for assistance with preparation of the English version.
REFERENCES


Kiddie DG (1962): “The Sika Deer (Cervus nippon) in New Zealand.” New Zealand Forest Service, Information Series No. 44.


