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Original article

Spatial scales of foraging in fallow deer: Implications for associational effects in plant defences

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ABSTRACT

Large herbivores select food at several spatial scales: plant communities are chosen at a landscape scale, plant patches are chosen within a plant community, and individual plants within a patch. Foraging decision at the patch level can result in associational effects in plant communities and populations. Several studies have shown that herbivore attack and consumption rates may not only depend on a plant's own defence traits, but also on the defence traits of its neighbours. In the present experiment we investigated whether the spatial scale of the food distribution affects food selection by fallow deer and whether the foraging behaviour gives rise to associational effects in plant defences. In a population of captured wild fallow deer we simulated a natural situation where two separate plant patches are exposed to intense herbivory pressure. We presented different spatial arrangements of low- and high-tannin food to the deer, varying the frequency of the feeder types within and between patches. We found that the deer consumed palatable food among the unpalatable food on average as much as they consumed palatable food among other palatable feeders. However, when unpalatable food occurred among the palatable food it was more consumed than among other unpalatable feeders. Hence, we did not find support for associational defence, but our results supported associational susceptibility. At the between patch level a patch of mainly high-tannin feeders was consumed less when presented near to a patch of mainly low-tannin feeders, suggesting that for well-defended plants having palatable neighbours in a nearby patch might accentuate the effectiveness of their defence.

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1. Introduction

Large herbivores make foraging decision at different spatial scales. These decisions follow a hierarchical order: plant communities are chosen at the landscape scale, plant patches

at the within plant community scale, and individual plants or plant parts at the bite scale within a patch (Senft et al., 1987; Bailey et al., 1996). At the bite scale the feeding decision is based on the characteristics of individual plants (or parts of a plant), e.g., plants having lower levels of phenolics or other

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secondary compounds are preferred over those having higher levels. At the between patch level, however, a herbivore's decision to stay or leave a patch is influenced by the matrix surrounding an individual plant, i.e. the overall composition of conspecific or heterospecific individuals within the patch (Senft et al., 1987; Hjältén et al., 1993; Milchunas and Noy-Meir, 2002; Bergvall et al., 2006). Foraging decisions at the patch level have been explained using optimal foraging theory (e.g., the marginal value theorem), but it has been shown, for example in moose and deer, that the theory can be inadequate (Shipley and Spalinger, 1995; Hanley, 1997; Searle et al., 2005).

Whether herbivores select between patches or within patches can have distinctly different effects on individual target plants and hence eventually also on the population structure of plants. When herbivores select food at the between patch level, the other plants surrounding an individual target plant in the patch can have positive or negative effects on the target plant. Positive effects occur when palatable plants gain protection from their unpalatable neighbours, and this phenomenon is often called *associational defence* (syn. associational resistance, associational plant refuges, plant defence guilds, see e.g. Tahvanainen and Root, 1972; Atsatt and O'Dowd, 1976; McNaughton, 1978; Pfister and Hay, 1988; Danell et al., 1991; Hjältén et al., 1993; Hambäck et al., 2000). Negative effects occur when neighbours have a detrimental influence on target plants. *Associational susceptibility* (syn. associational damage, shared doom) refers to a situation when a defended (unpalatable) plant is consumed more when associated with palatable neighbours (Thomas, 1986; Brown and Ewel, 1987; Hjältén et al., 1993; Wahl and Hay, 1995; Karban, 1997; White and Whitham, 2000).

Unpalatable plants can also gain a particularly large benefit of their defence when they occur among undefended neighbours, due to the contrast to the palatable plants. This phenomenon has been referred to as *neighbour contrast defence* (Bergvall et al., 2006). Such an effect could occur if the herbivores are selective within patches, but not between patches (Hjältén et al., 1993; Tuomi and Augner, 1993; Bergvall et al., 2006). One factor promoting within-patch selectivity could be that the defence traits have signal value for the herbivores, so that they could easily distinguish defended and undefended plants from each other (Augner, 1994; Tuomi et al., 1994). This kind of honest signal could also enhance between patch selectivity if the distance between the patches is short enough to allow accurate comparison of the food sources. Another possible consequence of within-patch selectivity is that palatable plants are particularly susceptible to attack when they occur in a patch with unpalatable neighbours, a situation referred to as *neighbour contrast susceptibility* (Bergvall et al., 2006). There is thus a suite of different associational effects for which the foraging behaviour of herbivores could be a driving force. These effects, when taking place between conspecific neighbours, could influence the evolution of plant defences. In general, stronger within-patch selectivity should favour the evolution of defences, whereas between patch selectivity can counteract the evolution of defences (Tuomi and Augner, 1993; Tuomi et al., 1994; Leimar and Tuomi, 1998).

Usually in foraging experiments, associational effects have been examined at the community level by testing whether plant species are exposed to either lower or higher herbivory

pressure when associated with more preferred or more repellent heterospecific neighbours. Associational effects within a plant population (i.e., when target individuals are associated with conspecific neighbours) are harder to study since the cues for herbivores to select between species can be much clearer (different species look, smell and taste different) than the cues available to select within species. For example, no visible cues might distinguish palatable individuals from unpalatable ones within a species. Within-species variation poses difficulties also because the level of chemical defence can vary even within individual plants (e.g. between young and old parts) and over the growing season. However, since the spatial distribution of genetic and phenotypic variation in plant defence chemicals can influence both the selective pressure imposed by herbivores and the potential of populations to respond to natural selection (Andrew et al., 2007), it is important to try to understand also the within plant species effects of herbivory.

In the present study we created an artificial world situation that corresponds to within-population associational effects by offering herbivores food that had the same nutritional content and visible cues whether it was palatable or unpalatable. These kinds of functional bioassays have been used previously not only with insects (Erhard et al., 2007) but also with mammals (Bergvall et al., 2006). Our experimental set-ups were intended to simulate a natural situation where two separate plant patches are exposed to intense herbivory pressure from a herd of large mammalian herbivores (fallow deer). We presented different spatial arrangements of food sources, in the form of feeders with low- or high-tannin food, to captured wild deer, varying the frequency of the feeder types between and within patches. This provided a possibility to manipulate both among-patch and within-patch frequencies as well as the spatial scale and to measure the effect on the consumption rates of different food types and to some extent also on the deer foraging behaviour. We had the following main predictions. First, we expected deer to prefer low-tannin food over high-tannin food irrespective of the spatial arrangement. Second, we expected that the spatial arrangement would have an effect on the herbivory pressure on a given food type and that any associational effect would depend on the among-patch frequencies of food types. Assuming that there are different scales of deer foraging decisions and that these are realized as differences in the consumption of low- vs. high-tannin food, we expected to see at least one of the neighbour effects as outlined in Table 1. In terms of deer foraging behaviour, following the expectations of optimal foraging theory, we expected the deer to change less between patches if they have two good patches to select from, or if they started to eat from a good patch. Further we expected the deer to spend more time in set-ups where there was more low tannin food available.

2. Methods

2.1. The herbivore

The fallow deer (*Dama dama* L., Cervidae) is a generalist herbivore having features of both grazer and browser,

Table 1 – Outcome of food selection of low- and high-tannin food in a set-up where herbivores are allowed to forage within and between patches of varying quality (e.g., set-up 1 in Fig. 1)

Associational effect	Between-patch selectivity	Within-patch selectivity	Result of food selection
Associational defence	X		Low is consumed less among high
Associational susceptibility	X		High is consumed more among low
Neighbour contrast defence		X	High is consumed less among low
Neighbour contrast susceptibility		X	Low is consumed more among high

depending on the season. It is one of the most social deer species and can form large herds, sometimes up to 70–100 animals (Putman, 1988). The diet consists of, for example, grass, leaves and bark (Chapman and Chapman, 1975). The experiment was conducted during summer 2002 at Tovetorp zoological station (Stockholm University, Department of Zoology) in south-central Sweden, where a group of captured wild fallow deer was kept in a 20 hectare enclosure where they could move freely. The number of deer was around 30 individuals during winter-early summer and around 40 after calving in the end of June (current summer's calves were not eating the food we offered but occasionally followed their mothers to the experimental area). The deer usually moved and foraged within the enclosure in groups of a few individuals, but occasionally they would gather in larger groups. The group consisted of mainly females with only one mature male (younger males were removed annually from the group before they reached maturity, to avoid inbreeding). All the deer had ad libitum access to their natural feed and water (also during the trials) and were not fasting at any point during the experiment.

2.2. Food manipulation

We manipulated food quality by adding tannic acid (Sigma-Aldrich, CAS #: 1401-55-4, EC NO: 215-753-2, syn. gallotannic acid, gallotannin) to food (pellets). In general, tannins decrease palatability (Bernays et al., 1989) and have a bitter and astringent taste (Robbins et al., 1987). The astringency correlates with the total content of tannin (Mali and Borges, 2003) and can thus serve as a reliable cue to foraging animals to avoid tannin-rich plant material (Prinz and Lucas, 2000). In this experiment the deer could not use visible cues to distinguish the tannin level but they had to either nose or taste the food to make the difference between tannin levels. It seemed that, at least to certain degree, they were able to distinguish the overall quality of a patch by the odour but then again within the patch they had to visit every feeder (and put their nose in the feeder and perhaps taste the food) to make the distinction.

The pellets (Viltfor SP, Lantmännen) used in the experiment were of a type intended for wild cervids made of corn, milling and sugarbeet bi-products, minerals, vitamins, fat and vegetable oils having crude protein content of 120 g and 10.5 MJ energy per kg of pellets. The tannin was dissolved into water and sprayed on pellets in proportions of 0.4% and 2% of pellet dry mass (in the following these proportions will be referred to as low- and high-tannin food respectively). After spraying, pellets were allowed to dry overnight at room

temperature before being used in feeding trials. The range of tannin levels used here is within the range found, for example, in tree foliage used by deer. In birch (*Betula pubescens*) and in oak (*Quercus robur*) the level of gallotannins is close to 0% of dry mass (Salminen et al., 2001, 2004) whereas in maple (*Acer platanoides*) the level can be close to six percent (M. Lahtinen et al., unpublished data).

2.3. Experimental design

As feeders we used buckets (vol. 12 litres), placed in wooden support structures to prevent overturning by the deer. Eight feeders containing either low-tannin or high-tannin food (pellets) were positioned in a circle (diameter three meters) making the shortest distance between feeders about one meter. A similar circle of eight feeders was placed nine meters away (Fig. 1). The distance of nine meters was selected because this was enough for the deer to consider the two patches as separate (many of the deer were unwilling to switch to other patch before some of the dominant individuals had already moved there). On the other hand, this distance was not too long to prevent changes between patches altogether. Low- and high-tannin food was

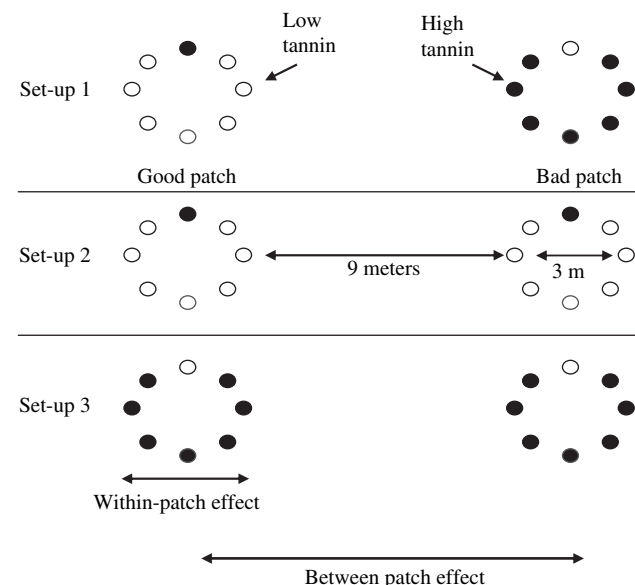


Fig. 1 – Spatial arrangements of the experimental set-ups. A good patch (1 high- and 7 low-tannin feeders) and a bad patch (1 low- and 7 high-tannin feeders) were presented in three combinations (one at the time, i.e. either set-up 1, 2 or 3) to a group of freely foraging fallow deer.

presented in three different arrangements (set-ups 1, 2 and 3 in Fig. 1). In every trial only one of the three set-ups was presented making the three set-ups independent. By the term "good patch" we refer to a patch arrangement where a single high-tannin feeder was presented with seven low-tannin feeders and by the term "bad patch" we refer to an arrangement where a single low-tannin feeder was presented with seven high-tannin feeders. The position of the single low- or high-tannin feeder along the perimeter of the circle was randomised in every trial and the positions of the good and bad patches in set-up 1 were changed between consecutive trials. The amount of food (pellets) offered per feeder varied between 2 and 3 kg, depending on how many deer were expected to take part in the trial (estimated on the basis of the number of deer in sight).

Following our predictions outlined in the Introduction we expected the deer to spend more time in set-up 2 than in set-ups 1 and 3. Further we expected the deer to change less between patches in set-up 2 (and in set-up 1 when the deer start from the good patch) than in set-up 3 (and in set-up 1 when the deer start from the bad patch). If the deer selectivity was to result in associational defence, low-tannin food in the bad patch in set-up 1 should be consumed less than in the good patch, whereas associational susceptibility would be seen as higher consumption of high-tannin food in the good patch compared to the bad patch in set-up 1. Neighbour contrast defence, on the other hand, would be realised if the high-tannin food was consumed less in the good patch than in the bad patch in set-up 1 and respectively neighbour contrast susceptibility if the low-tannin food was consumed more in the bad patch than in the good patch in set-up 1 (Table 1). By comparing consumption in different set-ups (the good patch in set-up 1 and set-up 2, as well as the bad patch in set-up 3 and set-up 1) we wanted to find out if these effects occur also when the deer are facing a situation where there is clear contrast between the two patches vs. when there is no difference in the quality of the two patches. In these comparisons for a given food type, the within-patch neighbourhood remains the same, whereas the patch neighbourhood varies between the set-ups (see Fig. 1).

Consumption (per feeder) was computed as the difference between the amount (weight) of pellets before and after the trial. Spillage of feed was insignificant due to the large feeders and the wooden supports. Trials were conducted between late May and late September and only during dry weather to avoid weight changes from rain water. At most two trials per day were conducted (one in the morning and the other in the afternoon). We conducted 26 trials of set-up 1 and 12 trials of both set-ups 2 and 3. Trials of set-ups 2 and 3 were arranged in between the trials of set-up 1 to avoid deer to get used to the set-up 1. Because in five trials of set-up 1 all the low-tannin food was consumed (i.e. leaving no alternative for high-tannin food), we disregarded these trials (although including them in the analysis did not affect the interpretations we made). Thus the total number of trials in set-up 1 was 21, and 45 altogether in all three different set-ups. In most of the trials in set-up 3 all the low-tannin food (from the two feeders) was consumed, but we regarded this as a natural consequence of the food arrangement and, hence, we did not disregard these trials from further analyses.

2.4. Observation of deer behaviour

Because we used wild deer in this experiment we were not able to control the feeding but let the deer start and end trials freely. A trial was considered to start when the first deer started to eat, and when the last deer left the feeding station or when no eating was observed for a minute the trial was finished. In almost all the trials the arriving animals started to eat from the patch at which the first deer arrived. Every trial was recorded onto a videotape that was later analysed to measure the number of animals that changed between the two patches. Within-patch (i.e. between feeders in the same patch) changes were not possible to follow either from video or in the field.

Because in some trials individual deer joined the eating group in the middle of the trial and because, occasionally, some deer in the herd were not eating (usually calves) we estimated the number of deer eating in every trial in the following manner. The number of deer eating from the patches was counted in even minutes starting from the patch that the deer started, i.e. after one minute from the start of the trial the number of deer eating was counted from the patch the deer started eating, a minute after that (two minutes after starting) deer were counted from the other patch, a minute after that (three minutes after starting) deer were counted again from where they started eating etc. To make the three different set-ups comparable, number of deer eating in different patches was related to the total amount of deer observed eating in that particular trial. The number of deer taking part in the trials was on average 21 ± 1.1 (no significant difference between the set-ups: $F_{2,42} = 1.86$, $p = 0.168$), but not all deer were eating during the whole trial, which is the reason for the above procedure to estimate the number of deer eating in both patches. The average amount of tannin eaten by an individual deer in each trial was estimated by relating the total amount of tannin consumed in the trial to the number of deer participating in the trial.

2.5. Data analysis

Because the number of animals participating in the feeding trials could not be controlled and, further, because food intake varied (in addition to deer number) due to various natural reasons, the consumption from the feeders was related to the overall consumption (average of all set-ups) to make the different set-ups comparable. Here we aimed to have comparison to the bad and the good patch in set-up 1 and hence for each trial in set-up 2 and set-up 3, we pooled the data from the two patches because they had identical spatial configurations (Fig. 2).

For statistical analysis of our predictions, we tested a null hypothesis that consumption per feeder only depends on the food type and not on the spatial arrangements in the different set-ups (H_0 : consumption of given food type is the same irrespective of arrangement). To test this we computed differences of least square means between different set-ups under a mixed model analysis of variance using unstructured covariance matrix and REML as estimation method. As data points for the tests we computed trial averages of consumption for different types of feeders in each trial. In the model we had tannin (low vs. high), patch quality (bad vs. good),

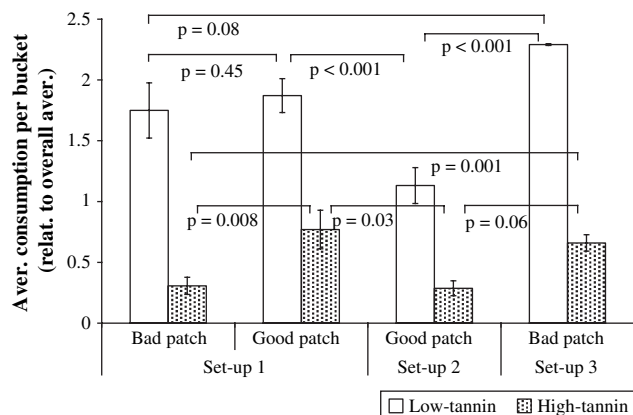


Fig. 2 – The average (± 1 S.E.) amount of low-tannin and high-tannin pellets eaten per feeder in a good and a bad patch during a trial in the three different set-ups in the experiment, relative to the average consumption in all set-ups. In set-ups 2 and 3 data from the two patches are pooled. The bars connected with lines are compared by differences of least square means under a mixed model ANOVA (see Section 2 for details).

neighbouring patch quality (neighbouring patch either good [for a bad patch in set-up 1 and a good patch in set-up 2] or bad [for a good patch in set-up 1 and a bad patch in set-up 3]) as factors. Because patches and tannin levels within the trials were not independent we considered tannin \times patch quality as a repeated (within subject) factor in the model and trial as a subject. We report the result of the whole ANOVA-model in Table 2 and the statistical significances of the differences of least square means between different patch quality/neighbourhood/tannin combinations in Fig. 2.

The proportion of the deer participating in the trial that fed in different patches was tested with a paired sample t-test within each set-up. The average duration of trials, the number of changes between patches and the amount of tannin eaten in different set-ups were analysed by means of one-way ANOVA (followed by Tukey's test when comparing the amounts of tannin eaten). When examining the duration of trials we split the data in set-up 1 into trials in which: (i) the deer started eating from the bad patch; and (ii) the deer started

from the good patch (cf. Fig. 3). A χ^2 -test was employed to examine whether there was a difference in the number of trials in which the deer started to eat from the good patch vs. those in which the start was from the bad patch (in set-up 1). The relationship between the number of the deer eating and the amount of food consumed was studied by means of Pearson's correlation coefficient (r).

The mixed model analysis of variance (with the differences of least square means) was performed with SAS (Proc Mixed) System for Windows release 8.01. All other analyses were performed with SPSS for Windows ver. 11.5.

3. Results

The deer clearly preferred low-tannin food over high-tannin food. The consumption per feeder of low-tannin food was on average 3.5 times higher than that of high-tannin food (1529 ± 92 g of low-tannin vs. 438 ± 40 g of high-tannin food on average per feeder per trial \pm SE). This difference, however, was strongly dependent on the patch quality (significant tannin patch quality interaction, Table 2, Fig. 2). Further the consumption was dependent on the neighbouring patch quality (Table 2). Hence, there seemed to be complex within- and between patch effects behind the food consumption that in turn were caused by the deer foraging behaviour.

3.1. Within- and between patch effects on food consumption

In set-up 1 the patch quality did not affect the consumption per feeder of low-tannin food (Fig. 2). In contrast the consumption of high-tannin food differed depending on the within-patch neighbourhood quality. High-tannin food was consumed significantly more when combined with low-tannin food than when it was presented among other high-tannin feeders (set-up 1 in Fig. 2).

For both low- and high-tannin food, the overall quality of the neighbouring patch clearly had an effect on herbivory pressure (i.e., a between patch effect). For high-tannin food situated in a bad patch consumption was lower if the neighbouring patch was good (set-up 1) than if the neighbouring patch was bad (set-up 3, Fig. 2). For low-tannin food this difference was not quite statistically significant (Fig. 2: $p = 0.08$). For low- and high-tannin food in a good patch the situation was similar: consumption was lower if the neighbouring patch was good (set-up 2) than if it was bad (set-up 1).

When the deer had two bad patches to choose from (set-up 3) they ate about twice as much tannin (10.8 ± 0.8 g per deer) than if two good patches (set-up 2) were presented (5.2 ± 0.3 g). If the two patches presented were of different quality (set-up 1) the amount of tannin eaten was intermediate (7.3 ± 0.6 g; $F_{2,42} = 18.78$, $p < 0.001$; all treatments differed significantly from each other at $p < 0.05$ according to Tukey's HSD test).

3.2. Spatial arrangement and deer foraging behaviour

The abundance of low-tannin food clearly affected the foraging activity of the deer. If two good patches were presented

Table 2 – Analysis of the amount of pellets consumed per feeder: ANOVA results for the studied effects (tannin level, patch quality, and neighbouring patch quality) and their interactions. In all cases the effect $df = 1$ and error $df = 44$

Effect	F	p
Tannin	205.98	<0.001
Patch quality	3.60	0.064
Neighbouring patch quality	17.96	<0.001
Tannin \times Patch quality	12.95	<0.001
Tannin \times Neighb. patch quality	2.02	0.162
Patch quality \times Neighb. patch quality	0.37	0.546
Tannin \times Patch quality \times Neighb. patch quality	0.04	0.845

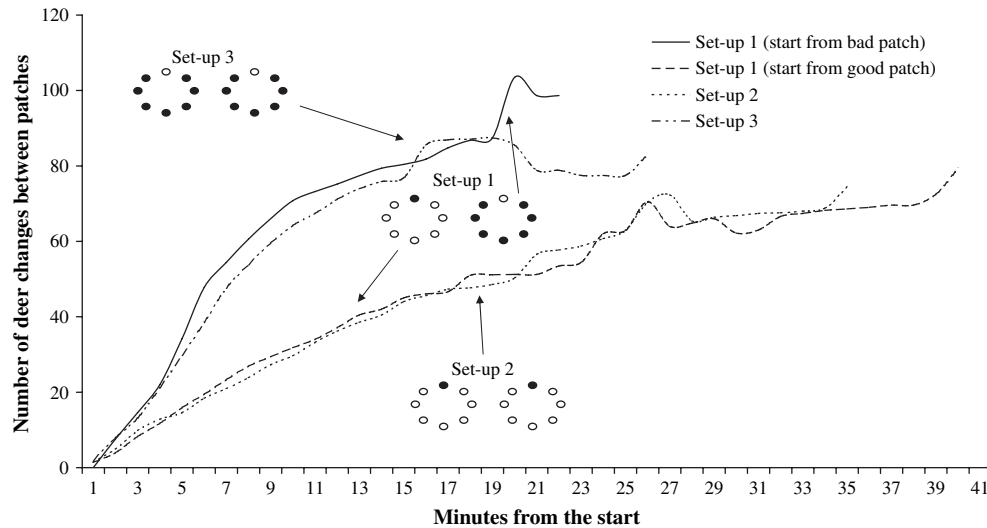


Fig. 3 – The number (cumulative sum) of deer changes between the two patches as a function of time (minutes from the start of the trial). The trials of set-up 1 are split into two groups depending on whether the deer started eating from the good or the bad patch, and separate curves for these groups are plotted in the figure. Data are presented only for the cases where at least three data points (trials) were available to present for every time point; that is why a curve can sometimes decline even though it represents a cumulative sum.

(set-up 2) or if the deer arrived first at the good patch in set-up 1, they changed less between patches than they did if the patches were both bad (set-up 3) or if the deer started from the bad patch in set-up 1 (Fig. 3; after 15 min from the start of the trial: $F_{3,39} = 4.08$, $p = 0.013$). The total amount of changes, however, was not significantly different between above four cases ($F_{3,39} = 2.16$, $p = 0.108$) because the deer kept foraging longer in set-up 2 and set-up 1 when the start was from good patch (Fig. 3).

The fact that in set-up 1 the deer changed less if they started to eat from the good patch was mirrored also in the number of deer eating from the different patches. The number of deer eating from the good patch was on average over four times higher than the number eating from the bad patch (data not shown). This difference, however, arises partly from the fact that deer spent more time in the patch where they first arrived. The proportion of deer observed in the patch where they first arrived was over 70% in set-up 2 (difference to the other patch: $t_9 = 3.37$, $p = 0.008$) and over 60% in set-up 3 respectively ($t_{10} = 2.07$, $p = 0.065$). In set-up 1 over 80% of deer were found on the good patch if that was the patch they started from ($t_{14} = 6.25$, $p < 0.001$). If the start was from the bad patch slightly over 60% of the deer were observed to eat from the good patch (i.e. less than 40% were observed in bad patch, $t_4 = 2.7$, $p = 0.054$). Furthermore, in most of the trials the deer started to eat from the good patch in set-up 1 (in 15 trials the start was from good and in 5 trials from bad: $\chi^2 = 5$, $df = 1$, $p = 0.025$, in one trial the deer started simultaneously from the two patches). The number of the deer participating in a trial was mirrored in the food preference but only when there was very limited amount of low tannin food available (i.e., set-up 3): the ratio of consumed low-/high-tannin food had a clear negative correlation with the number of deer participating in a trial ($r = -0.672$, $p = 0.017$).

The time the deer spent in the trials in set-up 1 was on average 27 min (± 2.5 min) when they started from the good patch and 22 min (± 2 min) when they started from the bad patch. In set-up 2 the average time spent in the trial was 26 min (± 2.5 min) and for set-up 3 the time was 21 min (± 1.5 min). The average time the deer ate in the different set-ups did not differ significantly ($F_{3,40} = 1.73$, $p > 0.1$).

4. Discussion

The spatial arrangement of food sources clearly affected foraging behaviour of the fallow deer, which in turn was mirrored in the consumption of the different foods. Since it has been shown in earlier bioassay studies that foraging decisions of fallow deer follow the same pattern whether the bioassays are carried out with artificial food or real plants (Bergvall et al., 2006, in press), it seems reasonable to regard the present results as support for the idea that the herbivore pressure on a single plant does not only depend on its own defences but also, at least to some extent, on the defence level of other plants growing around it. The consequences appear to be complex, however, because the neighbour effects on the target food source may not only depend on the structure of a focal patch (within-patch effects) but also on the quality of neighbouring patches (between patch effects).

4.1. Foraging behaviour

Even though the deer preferred low tannin food over high tannin food, their food selection was not optimal. In most cases the deer seemed to be able to distinguish the overall patch quality when they started to eat in the good patch (set-up 1) but they still were moving often between patches.

The maximum number of deer participating in a trial in set-up 1 was on average 21.4 ± 1.6 and the total number of changes between the good and the bad patch was around 80 (Fig. 3), which means that on average every deer changed patch several times. Also the fact that the time deer spent foraging in different set-ups was more or less the same suggests that deer were not optimal in their foraging. There were some indications that the deer did not change as willingly if they had two good patches to choose from, or if they started to eat from a good patch in set-up 1 (Fig. 3), but even in these cases on average every deer changed several times. This kind of seemingly non-optimal changes between patches might be explained by information collection (Dall et al., 2005). On the other hand, effects of social cohesion in the herd were clearly visible, suggesting that the individual deer were not completely free to make foraging decisions.

The effect of social factors was clearly seen in between patch choices: with few exceptions, the arriving animals started eating from the same patch as the first deer, irrespectively of the quality of the arrival patch. Most of the deer were also unwilling to switch between patches before one or a few dominant (older) deer had already moved to the other patch. Furthermore, the herd usually finished eating either simultaneously or immediately after a few (or only one) dominant deer did. Dumont and Boissy (2000) observed with sheep that an individual sheep did not leave its group to reach a preferred feeding site located further away unless it was accompanied by several peers. Similarly, in our study only a few (older) deer were willing to change to the other patch if no other deer was there. Only after the first one(s) were already exploring the patch others were ready to follow. The behaviour that a dominant individual is the first to leave a patch in order to move to another patch of unknown quality has also been seen in experiments with sheep (Hewitson et al., 2007). However, in our study, it seemed like all individuals were free to move between patches when both patches had at least a few foraging deer. This would be in accordance with the concept of "combined decision making" (Conradt and Roper, 2005), where individuals make decisions without consensus with others but in a manner which is not completely free from the effects of the others' decisions. Social factors were also present in the within-patch selection, because individual deer often preferred those feeders that were already occupied even when there were free feeders nearby.

In addition to social facilitation, competition also seemed to influence foraging decisions. If the herd started to eat from the bad patch (in set-up 1), the single low-tannin feeder was crowded rapidly and, hence, the deer switched to another patch more quickly than if they started from the good patch (as revealed in Fig. 3). This is similar to the observation by McNaughton (1978) that wildebeest (*Connochaetes taurinus albojubatus*) moved rapidly through stands where unpalatable forage was concentrated. However, contrary to the results of White and Whitham (2000), herbivory pressure in our study was not determined – at least not predominantly – by the unavailability of palatable food, since we disregarded the trials in which the low-tannin food was totally exhausted (in set-up 1, though including these trials did not change the results) and, further, only in nine trials out of 21 the palatable

food was totally consumed in the bad patch (set-up 1). Thus in most of the cases the deer could find palatable food in both patches, so the foraging activity was not related to the availability of palatable food as such. On the other hand, if there was competition for access to the palatable food items, this might force some deer to change to food of lower quality (i.e., high-tannin pellets). This is supported by the fact that when the palatable food was rare (set-up 3), the ratio of consumed low-/high-tannin food had a clear negative correlation with the maximum number of deer participating in a trial, which indicates a decreased selectivity with increasing herd size. This is in accordance with Crawley (1983) and Smit et al. (2007) who observed that increased grazing pressure reduces the selectivity of herbivores as the availability of preferred food declines and, consequently, less preferred (unpalatable) plant species are consumed more frequently. Our observations are also in agreement with lower selectivity for group foraging compared to solitary foraging found in experiments with hand-raised fallow deer (Bergvall et al., 2006).

The fact that we used a group of deer can naturally give rise to several differences compared to foraging studies using individual herbivores, because the social interactions pose constraints on the decisions made by individuals (e.g. Boissy and Dumont, 2002; Conradt and Roper, 2005). As an example, according to the ideal free distribution (Fretwell, 1972), for an individual herbivore it might be more profitable to move to a poorer patch when the good patch is already crowded. Also for an individual herbivore it might be profitable to collect information from several patches (Dall et al., 2005). However, group cohesion as described above can constrain these behaviours.

4.2. Implications for associational effects in plant defences

Assuming that our results in this artificial world experiment are applicable to the real world situation, we did not find support for the idea that palatable plants would gain defence by associating with unpalatable (or less palatable) plants (e.g., Tahvanainen and Root, 1972; Atsatt and O'Dowd, 1976). The fallow deer in our study were able to find palatable (low-tannin) food among the unpalatable (high-tannin) food and consumed it on average as much as palatable food among other palatable feeders. On the basis of our results from set-up 1, where between patch choices concentrated herbivory to the good patch, more was consumed from an unpalatable feeder if the within-patch neighbours were palatable than if it occurred among feeders of its own kind, which would support the phenomenon of associational susceptibility (Table 1) observed by, for example, Hjältén et al. (1993), Karban (1997), and White and Whitham (2000).

We did not observe neighbour contrast effects in set-up 1, but if one compares the different set-ups (in Fig. 2) one can find support also for these effects. Low-tannin food in set-up 3 was consumed much more (per feeder) than in set-up 2 and marginally more compared to low-tannin food in the bad patch in set-up 1, supporting neighbour contrast susceptibility. Also neighbour contrast defence gets support from the set-up comparisons, since high-tannin food was

consumed much less in set-up 2 than in the good patch in set-up 1 and marginally less compared to high-tannin food in set-up 3. These set-up comparisons correspond to a situation where herbivores encounter different spatial configurations of plant types on separate occasions, e.g. in another meadow or forest.

Another perspective on the set-up comparisons is that without the possibility of a choice between good and bad patches, there was a tendency for the deer to eat more high-tannin food, suggesting that unpalatable plants could suffer more in a situation resembling set-up 3, where most of the neighbours are unpalatable (cf. Crawley, 1983; Smit et al., 2007). Thus, the between patch effects when comparing set-ups 1, 2 and 3 did not follow the same pattern as the within-patch effects in set-up 1 (Fig. 2). First, two good patches seemed to gain advantage from each other: the consumption per patch decreased if both patches were good (set-up 2) as compared to the consumption from a good patch presented with a bad patch (set-up 1). This has been referred to as safety in numbers (Connell, 2000), as prey can get protection by occurring in large groups. Alternatively one can claim that neighbour contrast susceptibility (Bergvall et al., 2006) can work also on between patches if they are close enough to allow reliable comparison: a patch of low tannin food is consumed more if there is a bad patch nearby to be compared to. Second, for a patch of high-tannin food (defended plants) it was better to have a patch of low-tannin food (palatable plants) as neighbour (set-up 1) since deer ate more high-tannin food if both patches were bad (set-up 3). Furthermore, the deer were prepared to eat more tannin when most food items present were high in tannin (low-tannin food was either rare or consumed). This suggests that the power of even an effective defence might be limited if all the neighbours have an equally good defence. Conversely, for well-defended plants, palatable neighbours in a nearby patch or population might accentuate the defence capability, which suggests that also the neighbour contrast defence (Bergvall et al., 2006) could work at the between patch level if the patches are close enough to allow accurate comparison.

The associational effects we observed have implications for the evolution of plant defences as well. Our results, in conjunction with previous results for fallow deer (Alm et al., 2002; Bergvall and Leimar, 2005; Bergvall et al., 2006, 2007, in press), illustrate that herbivore selectivity is likely to depend on a number of factors that may act to increase or decrease selectivity at either the within-patch or the between patch level. These kinds of neighbour effects are important in patchily distributed plant populations and may either promote or counteract the evolution of plant defences depending on herbivore selectivity between or within patches (Tuomi and Augner, 1993; Augner, 1994; Tuomi et al., 1994, 1996; Leimar and Tuomi, 1998; Bergvall et al., 2006, in press). Our results suggest that the neighbourhood structure can be especially important for the signal value of plant chemical defences. The taste and the odour of the defensive substances allow fast comparison of food sources within and between patches. If, as our results tend to suggest, the contrast of food sources located close to each other is a key determinant of herbivores' foraging decisions, it is highly likely that plant defences have evolved as honest signals that allow reliable comparison of

food sources (e.g. Augner, 1994). Thus the effect of defensive substances depends not only on their toxicity as such, but also on the neighbourhood context that determines the signal contrasts directing herbivores' decision making.

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