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PLANT-ANIMAL INTERACTIONS

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# Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence

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**Abstract** A basic idea of plant defences is that a plant should gain protection from its own defence. In addition, there is evidence that defence traits of the neighbouring plants can influence the degree of protection of an individual plant. These associational effects depend in part on the spatial scale of herbivore selectivity. A strong between-patch selectivity together with a weak within-patch selectivity leads to a situation where a palatable plant could avoid being grazed by growing in a patch with unpalatable plants, which is referred to as associational defence. Quite different associational effects will come about if the herbivore instead is unselective between patches and selective within a patch. We studied these effects in a manipulative experiment where we followed the food choice of fallow deer when they encountered two patches of overall different quality. One of the two patches consisted of pellets with low-tannin concentration in seven out of eight buckets and with high concentration in the remaining bucket. The other patch instead had seven high- and one low-tannin bucket. We performed the experiment both with individuals one at a time and with a group of 16–17 deer. We found that the deer were unselective between patches, but selective within a patch, and that the single low-tannin bucket among seven high-tannin buckets was used more than a low-tannin bucket among other low-tannin buckets. This corresponds to a situation where a palatable plant that grows among unpalatable plants is attacked more than if it was growing among its own kind, and for this effect we suggest the term neighbour contrast susceptibility, which is the opposite of associational defence. We also found that the high-tannin bucket in the less defended patch was less used than the high-tannin buckets in the other patch, which corresponds to neighbour contrast defence. The neighbour contrast susceptibility was present both for individual and group foraging, but the strength of the effect was somewhat weaker for groups due to weaker within-patch selectivity.

**Keywords** Associational effects · *Dama dama* · Fallow deer · Hydrolysable tannin · Plant defences · Tannic acid

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## Introduction

Herbivores can influence the composition of plant communities (Augustine and Mc Naughton 1998), and have most likely had an impact on the evolutionary history and ecology of plants (Bryant et al. 1989). From the point of view of an individual plant, herbivory influences fitness by reducing growth or reproduction, and increasing mortality (Olff et al. 1999). A basic idea of plant defences is that a plant should gain protection from the investment it allocates to its own defence (Rhoades 1979). Plants posses a large number of different defence substances, which can serve to decrease damage from herbivores (Palo and Robbins 1991). There is a vast amount of literature where defence substances have been shown to protect plants from predation by insects (reviewed in Städler 1992) as well as from mammalian herbivores (see examples in Freeland 1991). However, there is also an increasing amount of evidence that defence traits of the neighbouring plants can influence the degree of protection of an individual plant (Atsatt and O'Dowd 1976; Pfister and Hay 1988; Hjältén et al. 1993; Milchunas and Noy-Meir 2002; Callaway et al. 2005). The influence of neighbours depends on the spatial scale of foraging decisions (Brown and Morgan 1995; Morgan et al. 1997; Milchunas and Noy-Meir 2002), which in turn can be influenced by mobility and lifestyle, such as group living in mammalian herbivores (Fritz and De Garine-Wichatitsky 1996; Boissy and Dumont 2002). Herbivores can be selective or non-selective between or within patches of plants and this can give rise to several different associational effects.

One of the effects is expressed when the herbivore makes a foraging decision to leave a patch with highly defended, unpalatable plants. If there are some less defended, palatable plants within the avoided patch, they would then gain protection from the defended plants, and this is referred to as associational defence (syn. associational resistance, associational plant refuge, reviewed in Milchunas and Noy-Meir 2002). On the other hand, if the herbivore that was selective between patches is unselective within a patch of less defended plants, the outcome can be that a highly defended, unpalatable plant among palatable plants will be eaten more than if it occurred in a patch of mainly unpalatable plants, a situation referred to as associational susceptibility (Hjältén et al. 1993). There are examples of associational defence involving insect herbivores (reviewed by Milchunas and Noy-Meir 2002), but the situation differs from those involving mammalian herbivores since insects often utilize a smaller spectrum of food plants. An example of associational defence involving mammalian herbivores is decreased grazing by cattle on grasses *Agrostis* and *Festuca* with an increasing presence of avoided buttercup (*Ranunculus bulbosus*) (Phillips and Pfieffer 1958). A more recent example is a study by Hjältén et al. (1993) with voles (*Microtus agrestis*) and hares (*Lepus timidus*) feeding on rowan (*Sorbus acuparia*), white birch (*Betula pubescens*), and grey alder (*Alnus incana*), where both associational defence and associational susceptibility were found for birch, depending on whether it was presented with preferred rowan or avoided alder.

Compared to the above examples, quite different associational effects will come about if the herbivore instead is unselective between patches and selective within a patch. One example of these effects is seen when less attractive plants in a patch tend to escape attack when the patch also contains more attractive plants that are selected by the herbivore. This phenomenon has been suggested to apply to insect herbivory and is referred to as the attractant decoy hypothesis (Atsatt and O'Dowd 1976), as some plants act as decoys attracting the herbivore away from the others. More generally, the situation when an herbivore is unselective between patches and selective within a patch can have two separate effects. First, a defended, unpalatable plant in a patch of mainly palatable plants could be less eaten when the herbivore is selective within the patch. For this effect, we suggest the term neighbour contrast defence, since the contrast perceived by the herbivore between the two types is a prerequisite for this neighbour effect and the outcome is that it enhances the defence of the unpalatable plant. The effect is the opposite of associational susceptibility, in the sense that an unpalatable plant is less attacked instead of more attacked when occurring in a palatable patch. Second, a palatable plant could be eaten more when growing in a patch of mainly less palatable plants, for which we suggest the term neighbour contrast susceptibility. The palatable plant is more susceptible to herbivory through the contrast between itself and its less palatable neighbours, resulting in a situation that is the opposite of associational defence.

The situation described above, with herbivores that are unselective between and selective within patches, has been observed for mammalian herbivory. In cattle pastures with bracken fern (*Pteridium aquilinum*), the degree of utilization of the bracken fern was found to be a function of the relative palatability of the other plants available (Hayakawa 1972, cited in Atsatt and O'Dowd 1976). When growing among palatable plants, the bracken fern was less eaten, which corresponds to neighbour contrast defence. On the other hand, it was more eaten when growing among unpalatable plants, corresponding to neighbour contrast susceptibility. Although neighbour contrast defence and neighbour contrast susceptibility may be commonly occurring in nature, they have been less studied than associational defence and associational susceptibility. Moreover, associational effects have commonly been studied by comparing consumption of palatable and unpalatable plant species in different neighbourhoods. Because species usually differ from each other with respect to many traits that herbivores can, in addition to defensive traits, use as cues in their food choice, heterospecific comparisons may not be as easy to interpret from the point of view of the evolution of plant defences as would be possible if conspecifics were used instead. One of the main goals of our study is to investigate within- and between-patch choice by herbivores, and the resulting associational effects of plant defences. It must be noted that at present we are unable to a priori predict what kind of associational effects could be expected in a particular case.

Optimal foraging theory traditionally dealt with both patch exploitation and diet choice (Stephen and Krebs 1986), and these elements have been combined into a theory of the effect of spatial scale on diet selectivity (Brown and Morgan 1995; Morgan et al. 1997). This kind of model could in principle give predictions about associational effects for different types of food items (Brown and Morgan 1995), although it is not clear that the assumptions of the classical diet choice models hold good for mammalian herbivores. One of the important differences may be that mammalian herbivores continually sample and evaluate food, instead of either consuming or rejecting food items. Therefore, our predictions for the present experimental situation are purely explorative in the sense that they help us to detect whether there are neighbourhood effects, and whether they represent the types described above (associational defence, associational susceptibility, neighbour contrast defence, or neighbour contrast susceptibility).

We investigated associational effects in relation to the food choice of fallow deer exposed to artificial food types, in the form of pellets with different concentrations of hydrolysable tannin. Two circles with buckets containing pellets were placed in an experimental enclosure, with the intention of mimicking a situation where a forager encounters two plant patches of overall different quality. From previous work on food choice (Alm et al. 2002), we know that fallow deer prefer lower concentrations of tannin and hence the food could be seen as more (low-tannin food) or less (high-tannin food) palatable plants for the deer. It has also been shown that the magnitude of the contrast in the defence levels influences herbivore selectivity (Alm Bergvall and Leimar 2005). In order to investigate associational effects, one of the two patches consisted of food with low-tannin concentration in seven of the eight buckets, with high concentration in the remaining bucket (good patch). The other patch instead had seven high- and one low-tannin concentration bucket (bad patch). This allowed us to estimate the consequences of within- and between-patch choices by the fallow deer. Following the above definitions of the possible associational effects, we compared the consumption per bucket and tested: (1) if the low-tannin food in the bad patch was eaten more than in the good patch, which would support the idea of neighbour contrast susceptibility, or instead less than in the good patch, which would support the idea of associational defence, and (2) if the high-tannin food in the good patch was eaten less than in the bad patch, which would support the idea of neighbour contrast defence, or instead more than in the bad patch, which would support the idea of associational susceptibility. Furthermore, we performed two experiments, one with one individual deer at a time, and the other with a group of 16–17 deer in order to study how group foraging might influence the spatial scale of foraging decisions and, hence, possibly also the above associational effects.

## Materials and methods

We used 17 female fallow deer that were between 2 and 10 years old for the study. The deer were hand-raised and could be handled individually. They were kept in a 4-ha enclosure with forest and meadow, situated at Tovetorp Zoological Research Station in south-central Sweden. The deer had ad libitum access to pasture, water, minerals, and salt stone also during the study. The experiments were performed with permission from the Swedish National Board for Laboratory Animals, and took place from May to August 2002.

### Singleton experiment

The experiment was performed with one animal at a time ($n = 10$) in a small quadratic experimental enclosure (100 m$^2$), situated within a larger enclosure where the deer were kept. The entrance had a small vestibule into which an animal could be led. To start a trial, the animal was released from the vestibule into the experimental enclosure where an experimental arrangement was placed. The walls of the experimental enclosure were solid, and 10 m long and 1.4 m high, so that the deer were prevented from seeing other deer through or over the wall. The general procedure corresponded to that used by Alm et al. (2002).

The experimental arrangement consisted of two patches positioned on each side in the experimental enclosure. The distance between the patches was 7 m, and each patch consisted of eight numbered buckets (1–8, vol. 1 l), placed equally spaced along the perimeter of a circle with a diameter of 3 m. The buckets contained food in the form of pellets with different concentrations of hydrolysable tannins (tannic acid, Sigma-Aldrich, CAS No.: 1401-55-4, EC No.: 215-753-2). The low concentration food had 0.3% tannin (per weight) and the high concentration was 1.5% (i.e. five times the low concentration). An important property of tannin is that it causes a sensation of astringency that is correlated with the concentration in a particular plant (Mali and Borges 2003), which means that the defence trait has signal value so that herbivores can distinguish defended and undefended plants from each other (Tuomi et al. 1994). The concentrations used correspond to those detected in wild plants: total tannin content varies between 0.1 and 6.0% of dry mass (Tixier et al. 1997), but plant parts can contain up to 40% tannin (Matthews et al. 1997). The pellets used were of a type intended for wild cervids and contained 10.5 MJ digestible energy and 120 g crude protein per kilogram. The tannin was dissolved in water and sprayed over the pellets. After spraying, the pellets were allowed to dry in room temperature overnight.

In one of the two patches (hereafter referred to as the good patch), the food with low-tannin concentration occurred in seven of the eight buckets, with high-tannin concentration in the remaining bucket. The other patch (the bad patch) instead had seven high- and one low-tannin concentration bucket. The position of the single bucket in a patch containing the dissimilar tannin concentration was changed for every trial and, further, the position of the good and the bad patch was changed between every trial. At the start of a trial, each bucket contained 500 g pellets and the amount remaining in the buckets was weighed at the end of the trial. During each trial, the number of changes the deer made between the patches and between buckets within both patches, as well as the time the deer spent on each bucket it visited, was recorded using a hand-held computer. A trial was considered finished when the animal stopped eating for more than a minute. Each deer performed in a total of eight trials.

### Group experiment

The second experiment followed a similar procedure as the singleton experiment, but was conducted with a group of animals ($n = 16$–17). The group included ten individuals from the singleton experiment. The reason for adding more individuals was to increase the competition for food during a trial. We performed ten trials in total with this group of deer. The buckets (vol. 12 l) were positioned in the same way as in the singleton experiment, but each bucket was placed in a wooden structure to prevent the deer from overturning it when competing for food. We used the same arrangement of good and bad patches as in the singleton experiment. The duration of a trial was 20 min and we performed two trials per day. At the start of a trial each bucket contained 2,000 g pellets. The amount remaining in each bucket was weighed at the end of the trial, and the individual consumption per food type and patch was estimated by relating the total amount eaten food with the total number of individuals (16–17) participating in the trial.

In order to study how individuals behaved while foraging in the group, compared to when they where alone, we recorded the trials with the deer group using digital video cameras. The animals were marked with coloured patches of cloth to allow identification from the video. From these videos, we measured the number of changes between patches for each of the ten individuals used in the singleton experiment (using four randomly selected group trials for each individual).

### Data analysis

From each trial, we obtained four measurements of consumption per bucket: the consumption per low- and high-tannin bucket in both the good and the bad patches. We analysed these measures using food type (low- and high-tannin concentration) and patch type (good and bad) as two crossed repeated measures factors (i.e. within-subject factors, the individual deer or the trial being the subject). For the singleton experiment, we used the individual deer as unit ($n = 10$ individuals), by averaging the consumption over the eight trials an individual performed. For the group experiment, we could not determine each individual's consumption. To obtain replication for a statistical test, we instead used the consumption per individual in a trial (= total consumption divided by number of deer) to get a data point ($n = 10$ trials). Using the trial as a unit of observation in the group experiment is a statistically valid procedure in the sense that the trials represent independent observations of the overall behaviour of this group of animals at different points in time. We used the logarithmic transformation of the measures for all statistical tests and in the figures. In addition to the repeated measures analysis of variance, we used Fisher's LSD, corrected by the sequential Bonferroni procedure (Quinn and Keough 2002) for post hoc comparisons in order to compare treatment means. We used a paired *t*-test (*t*-test for dependent samples) to compare the number of changes between patches (per individual per trial) in the singleton and group experiment, based on information from the individuals that took part in the singleton experiment ($n = 10$). For the total time spent on the patch types, we used the average time per trial on the patches for each individual from the singleton experiment, and compared these with a paired *t*-test. We have reported data as mean ± SE.

## Results

In the singleton experiment, there was an overall preference for low-tannin food (Table 1, Fig. 1), supporting our terminology of good and bad patches, and the consumption per low- and high-tannin buckets was higher in the bad patch (Table 1, Fig. 1). Note that the latter does not reflect total consumption from the patches (see below), since there were different numbers of low- and high-tannin buckets in the two patches. Statistical testing revealed that the consumption from the single low-tannin bucket in the bad patch was significantly higher than the consumption per low-tannin bucket in the good patch (seq. Bonferroni corrected LSD: $P = 0.006$; Fig. 1), giving support to neighbour contrast susceptibility. For the high-tannin food, there was a lower consumption per bucket in the good patch than in the bad patch ($P = 0.02$, Fig. 1), corresponding to neighbour contrast defence.

The analysis of the log consumption from the group experiment led to rather similar conclusions as that of the singleton experiment. Low-tannin food was preferred and there was a higher consumption per low- and high-tannin bucket in the bad patch (Table 1, Fig. 2). Post hoc tests showed that there was again a higher consumption per low-tannin bucket in the bad patch than in the good patch ($P = 0.04$, Fig. 2), but the same kind of comparison for high-tannin food was non-significant. The most striking difference between the experiments was that the deer appeared to be more selective between low- and high-tannin food in the singleton experiment compared to the group experiment (Fig. 2). Since these were performed at different points in time, the statistical comparison must be viewed with

**Table 1** Repeated measures analyses of variance of log consumption per bucket, with low or high concentration of tannin (food type) located in the good or the bad patch, for the experiment with one animal at a time (singleton), or the experiment with a group of 16–17 animals at a time (group). As a data point, either one individual's average consumption over eight trials (singleton experiment), or the average consumption per individual in a trial (group experiment) was used

| Source | *df* | Singleton | | Group | |
|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* |
| Food type | 1,9 | 119.84 | < 0.0001 | 71.52 | < 0.0001 |
| Patch | 1,9 | 15.22 | 0.0036 | 5.97 | 0.037 |
| Patch × food type | 1,9 | 0.800 | 0.39 | 1.66 | 0.23 |

**Fig. 1** The logarithm of the amount of food eaten (g) per low- and high-tannin bucket in the singleton experiment with two patches of overall different quality (data shown as mean ± SE for $n=10$ individuals, where the value for each individual is an average of eight trials; see text and Table 1 for statistical analyses)

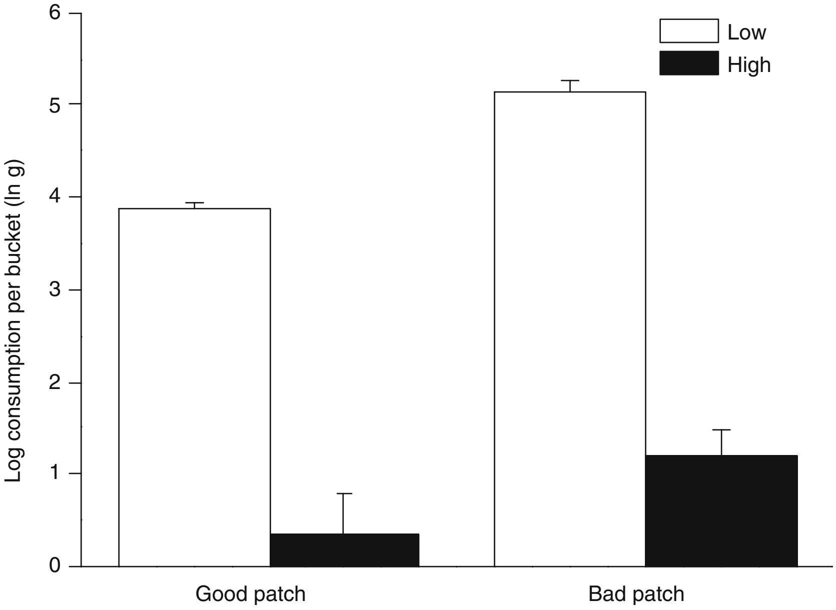
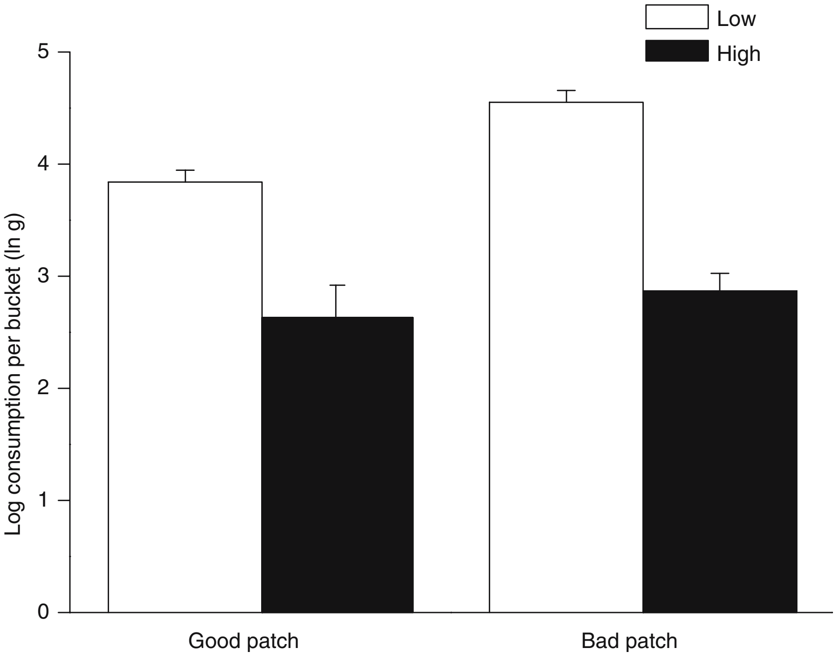


**Fig. 2** The logarithm of the amount of food eaten (g) per low- and high-tannin bucket and individual during a trial in the group experiment with two patches of overall different quality (mean ± SE for $n=10$ trials; see text and Table 1 for statistical analyses)



some caution, although formally the difference would be statistically significant (overall log ratio low/high tannin consumption—singleton 3.27 ± 0.30, group 1.08 ± 0.11, *t*-test $t=7.01$, $P=0.0002$).

Concerning the total consumption (measured in grams) per individual and patch, the deer ate overall more food from the good patch than from the bad patch in both the singleton and group experiments (singleton—good 349 ± 24.5, bad 213 ± 22.8, paired *t*-test $n=10$, $t=3.96$, $P=0.0050$; group—good 353 ± 24.7, bad 234 ± 21.1, paired *t*-test $n=10$, $t=4.62$, $P=0.0013$). Overall, an individual deer ingested more total tannin (g) per trial in the group experiment compared to when foraging alone (singleton 2.1 ± 0.08; group 3.6 ± 0.32; paired *t*-test $n=8$, $t=4.31$, $P=0.0035$), because of a higher intake of high-tannin food in the group experiment.

In contrast to the consumption, the total time spent on the good and the bad patch in the singleton experiment did not differ, suggesting a lack of between-patch selectivity (mean visiting time (s)—good patch 257.03 ± 37.93; bad patch 334.47 ± 41.47; paired *t*-test $n=10$, $t=1.10$, $P=0.30$). Further, comparing the average numbers of animals visiting each patch type in the group experiment, we found no evidence for between-patch selectivity (mean number of visiting deer—good

6.69 ± 0.58; bad 5.51 ± 0.57; paired *t*-test $n = 10$, $t = 1.14$, $P = 0.28$). For the number of changes between patches, per individual and trial, there were more changes in the group than in the singleton experiment (singleton 0.86 ± 0.14; group 4.78 ± 0.91; paired *t*-test $n = 10$, $t = 4.3$, $P = 0.002$). We also checked for the number of shifts between bowls per individual, within the good and the bad patch. We found no difference in number of shifts either for the singleton experiment or the group experiment (singleton experiment—good patch 9.84 ± 1.22, bad patch 11.11 ± 1.17, paired *t*-test $n = 10$, $t = 0.89$, $P = 0.40$; group experiment—good patch 18.98 ± 1.95, bad patch 23.43 ± 1.50, paired *t*-test $n = 10$, $t = 1.58$, $P = 0.15$), but it is clear that there were many more within-patch shifts than between-patch shifts. Finally comparing the number of within-patch shifts between the singleton and group experiments, there were more shifts per individual in the group experiment, both for good and bad patches (paired *t*-test—good patch, $n = 10$, $t = 4.18$, $P = 0.0024$; bad patch, $n = 10$, $t = 6.68$, $P < 0.0001$).

## Discussion

In the present experiments, the herbivore consumption was influenced both by the palatability of the food and by the spatial positions of food sources, as well as by whether the deer foraged alone or in a group. The deer utilized both patches, spending approximately the same amount of time in the good and the bad patch, but showed a preference for low-tannin food in each of the patches. Our finding of a stronger within- than between-patch selectivity was mirrored in the associational effects we observed. First, the less defended, palatable food was more eaten when occurring in a highly defended (bad) patch, which corresponds to neighbour contrast susceptibility. The reason for this seems to be that a deer arriving at the bad patch often stayed and utilized the palatable low-tannin food, instead of directly leaving the patch. Since there was only one bucket with this type of food in the highly defended patch but seven in the less defended patch, the utilization per low-tannin bucket became greater in the highly defended patch. It seems that the deer used a similar search strategy in both patches since the numbers of shifts between buckets within a patch were similar. Second, the defended, unpalatable food in a less defended (good) patch was less eaten, which corresponds to neighbour contrast defence. The reason may be that a deer arriving at the good patch easily could locate and ingest the abundantly available palatable food.

One possibility for being selective between patches is the use of visual cues to separate wanted patches from unwanted at a distance, and the other is to make the decision to leave a patch if it is not good enough. It has been shown that cattle encountered two patch types, differing in sward density, with the same frequency, perhaps because the quality of the patches was difficult to assess from a distance (Distel et al. 1995). The same could be true for patches with plants containing different amounts of defence substances. In our study, the total time each deer spent on each patch in the singleton experiment did not differ between the less defended (good) and highly defended (bad) patch, suggesting a lack of between-patch selectivity. The same holds good for the group experiment since the average number of deer visiting the two patches did not differ. A possible reason for the lack of between-patch selectivity in the present study could be that there were no visual cues to separate the two patches. Furthermore, the deer did not leave the bad patch immediately, but instead explored a number of buckets in the patch, even if several successively sampled buckets contained high-tannin food. For the singleton experiment, the decision not to leave the patch could simply be that there was enough food of the preferred type in the bad patch. In the group experiment, however, the behavioural mechanisms behind the food selection were more complex.

Living and foraging in a group has both benefits such as better predator avoidance, alloparental care and social learning of foods, and costs such as increased parasite pressure and competition for food (Krebs and Davies 1999). For group living animals, foraging decisions are probably taken in hierarchical levels. At a higher level, there is a decision for the entire group about where to forage, but at a lower level, the individual animal makes detailed decisions about what to eat. Nevertheless, an individual in a group will not be free to forage wherever it wants. We found that the deer were less selective between low- and high-tannin food in the group experiment compared to the singleton experiment. As a consequence, an individual ingested more tannin per trial in a group than when foraging alone, so the deer consumed food of lower average quality when foraging in a group. This was most likely due to competition for food: when foraging in a group most of the low-tannin buckets were more crowded and, hence, the deer were less free to choose buckets. There may have been differences between individual deer in the group in how much and in what kind of pellets they ingested, but we could not determine each individual's consumption in the group experiment. Our results agree with an investigation of Molvar and Bowyer (1994) on American moose, where the foraging efficiency and the quality of the food eaten decreased with increasing group size. In large groups, the moose were less selective and ate from a greater variety of trees, instead of choosing the better ones, as when feeding alone or in smaller groups. Although there are not many studies on the effect of group size on herbivore food choice, a decreased within-patch selectivity for large groups might well be a common pattern.

Comparing with the patch use strategies assumed by Brown and Morgan (1995), their 'fixed amount' strategy where a forager exploits a patch until it reaches satiation, could give rise to associational effects similar to those we found. However, the deer in our study did not stop eating and leave a patch after a fixed amount as a result of satiation; instead they continued to eat from the next patch. This behaviour to continue to sample other patches and plants may correspond to information collection during foraging (Dall et al. 2005).

Our results on associational effects differ from a number of earlier observations. Several studies have found associational defence and associational susceptibility caused by herbivores that are selective between patches and unselective within a patch. In one of the few studies on mammals, Hjältén et al. (1993) found both associational defence and associational susceptibility caused by voles and hares. There are also reports of associational defence or associational susceptibility caused by insects or herbivorous aquatic animals (Pfister and Hay 1988; Hambäck et al. 2000; White and Whitham 2000). For these associational effects to occur, herbivores should be selective between patches but unselective within a patch, whereas we found the opposite in the form of greater within- than between-patch selectivity, leading to neighbour contrast defence and neighbour contrast susceptibility. This latter option, that an herbivore can be unselective between but selective within patches, has been mentioned in the literature (Milchunas and Noy-Meir 2002), and it has been studied using the special perspective of attractant decoy plants. The attractant decoy hypothesis suggests that insects can be ‘deceived’ to attack certain plants within a patch (Atsatt and O’Dowd 1976). Furthermore, the attractant decoy effect has been used by planting a trap crop within a field, to save the principal crop from insect damage (Hokkanen 1991). Our reason for introducing the terminology of neighbour contrast defence and neighbour contrast susceptibility is to provide general labels for phenomena that might be of equal importance in plant–herbivore interactions as associational defence and associational susceptibility.

On the basis of the present results, it seems likely that associational effects produced by herbivore food choice behaviour could have an influence on the spatial distribution and coexistence of palatable and unpalatable plant types, as well as on the investment in defence by members of a plant population (Tuomi and Augner 1993; Leimar and Tuomi 1998). According to our results, in situations where herbivores are unselective between, but selective within patches, less defended plants would benefit by growing together, thus avoiding the cost of neighbour contrast susceptibility, whereas more defended plants would benefit by growing dispersed among less defended plants, and in this way gaining from neighbour contrast defence. The combination of associational defence and associational susceptibility, corresponding to selectivity between but not within patches, would instead lead to the opposite situation, where more defended plants benefit from growing together, and less defended plants benefit from being dispersed among more defended plants. Concerning coexistence of undefended and defended plant species, the most favourable situation would be a combination of associational and neighbour contrast defences, ensuring that rare undefended plants profit by growing among defended plants, and that rare defended plants profit by growing among undefended plants, thus in this way stabilizing coexistence. Such a combination of associational effects could occur if herbivores quickly abandon patches with mainly defended plants, but stay and display within-patch selectivity in patches with mainly less defended plants, which seems to be a realistic possibility. On the other hand, the combination of associational susceptibility and neighbour contrast susceptibility would make coexistence less likely, by disfavouring rare defended as well as rare undefended plant types.

For the evolution of the level of investment in defence in a plant population, neighbour contrast defence would increase the advantage of reduced herbivory for a mutant with higher investment, and neighbour contrast susceptibility would increase the cost of herbivory for a mutant with lower investment; thus these effects both select for a higher level of investment. It has also been shown that the magnitude of the contrast in defence levels influences herbivore selectivity, so that a larger difference between low- and high-tannin food increases the intake of low-tannin food (Alm Bergvall and Leimar 2005).

Associational defence and associational susceptibility would instead select for lower level of investment, compared to a situation without any associational effects. It thus seems possible that within-patch herbivore selectivity could have played an important role for the evolution of costly plant defences, by causing neighbouring plants to compete with each other in reducing the risk of herbivory.

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