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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,

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