

# The effect of spatial scale on plant associational defences against mammalian herbivores<sup>1</sup>

Ulrika Alm BERGVALL<sup>2</sup>, Stockholm University, Department of Zoology, S-106 91 Stockholm, Sweden,  
e-mail: Ulrika.Alm-Bergvall@zoologi.su.se

Pasi RAUTIO, Finnish Forest Research Institute, Kaironiementie 54, FI-39700, Parkano, Finland.

Hanna SIRÉN & Juha TUOMI, University of Oulu, Department of Biology, P.O. Box 3000,  
FIN-90014, Finland.

Olof LEIMAR, Stockholm University, Department of Zoology, S-106 91 Stockholm, Sweden.

**Abstract:** Intraspecific variation in plant toxins at different spatial scales can influence foraging decisions by wild herbivores. In order to investigate plant associational defences in relation to spatial scale, we performed an experiment with fallow deer encountering 2 patches of low- and high-tannin hazel branches. One patch was good, consisting of 7 low- and 1 high-tannin branch, and the other bad, with 1 low- and 7 high-tannin branches. We kept the between-patch spatial scale constant and varied the within-patch spatial scale: the branches in a patch were either spread out or close together in a bundle. When the branches were spread out, the deer showed a clear preference for low-tannin branches in both patches and consumed similar amounts from low-tannin branches in the good and the bad patch, which means that there was no associational defence. In contrast, when the branches instead were together in a bundle, within-patch selectivity decreased and between-patch selectivity increased, and the low-tannin branches in the bad patch were less eaten than the low-tannin branches in the good patch, which corresponds to associational defence. We conclude that small inter-plant distances can be crucial for the operation of plant associational defences.

**Keywords:** associational defence, associational susceptibility, fallow deer, selectivity, spatial scale.

**Résumé :** La variation intraspécifique des toxines des plantes à différentes échelles spatiales peut influencer les décisions de quête alimentaire des herbivores sauvages. Pour examiner les défenses associatives des plantes en fonction de l'échelle spatiale, nous avons effectué une expérience dans laquelle des daims avaient l'option de s'alimenter dans 2 types de parcelles contenant des branches de noisetier, un dont le contenu en tanins des branches était élevé et l'autre bas. Une des parcelles était bonne, contenant sept branches à faible contenu en tanins et une seule à fort contenu en tanins. L'autre parcelle était mauvaise, avec une seule branche à faible contenu en tanins et sept autres à fort contenu en tanins. Nous avons maintenu l'échelle spatiale constante entre les parcelles et avons fait varier l'échelle spatiale à l'intérieur des parcelles où les branches étaient soit dispersées, soit rassemblées dans un paquet. Lorsque les branches étaient dispersées, les daims ont démontré une nette préférence pour les branches à faible contenu en tanins dans les 2 types de parcelles et ont consommé des quantités semblables de branches à faible contenu en tanins dans les parcelles bonne et mauvaise, ce qui signifie qu'il n'y avait aucune défense associative des plantes. Au contraire, lorsque les branches étaient rassemblées dans un paquet, les daims ont été moins sélectifs à l'intérieur des parcelles et plus sélectifs entre les parcelles. Les branches à faible contenu en tanins ont été moins mangées dans la mauvaise parcelle que dans la bonne, ce qui correspond à une défense associative des plantes. Nous concluons que de faibles distances entre les plantes peuvent être cruciales pour que les défenses associatives de celles-ci soient fonctionnelles.

**Mots-clés :** daim, défense associative, échelle spatiale, sélectivité, sensibilité associative.

**Nomenclature:** Farrar, 1995; Macdonald, 1999.

## Introduction

Intraspecific variation in plant toxins can be found at different spatial scales (Lawler, Foley & Eschler, 2000; Brenes-Arguedas & Coley, 2005; Laitinen *et al.*, 2005) and this can influence foraging decisions by wild herbivores (Farentinos *et al.*, 1981; Brown & Morgan, 1995; Vourc'h *et al.*, 2001; Moore & Foley, 2005), with possible consequences for the operation of plant defences. Browsing and grazing can enhance or reduce defence mechanisms within plant populations and influence species diversity within

communities (Provenza *et al.*, 2003). In recent years there has been increasing interest in spatial heterogeneity and spatially varying processes that act on plants and in turn shape ecological systems (WallisDeVries, Laca & Demment, 1999; Foley & Moore, 2005). One such process is mammalian herbivory, given that food choice is dependent on the spatial scale. There are several studies that deal with the influence of spatial scale on selectivity (Edwards *et al.*, 1994; WallisDeVries, Laca & Demment, 1999; Dumont, Carrère & D'Hour, 2002; Parsons & Dumont, 2003; Pietrzykowski *et al.*, 2003). In 2 experiments with sheep (*Ovis aries*), Edwards *et al.* (1994) showed that selectivity increased with increased size of the food pieces in a mixture, and also with increased scale of aggregation of food patches, in the sense

<sup>1</sup>Rec. 2007-06-07; acc. 2007-12-17.

Associate Editor: André Desrochers.

<sup>2</sup>Author for correspondence.

DOI 10.2980/15-3-3112

that larger numbers of high- or low-quality patches were grouped together. Similarly, in experiments with steer (*Bos taurus*) grazing on patchworks of grass of different nutritional quality, WallisDeVries, Laca, and Demment (1999) found an increase in selectivity when patches of high- and low-quality grass were larger. Here we report on an experiment on the relation between spatial scale and plant associational defences, which is a previously unexplored aspect of the effects of spatial scale on herbivory.

Foraging decisions are taken at several hierarchical levels, where the highest level is the habitat choice and the lowest level is which plant or plant part to eat (Senft *et al.*, 1987). A mammalian herbivore needs to find appropriate food items in sufficient amounts, but the ability to select food items will depend on how well the herbivore can distinguish between these, which in turn can be influenced by both the physiology and the behaviour of herbivores. Studies on food choice in mammalian herbivores have shown that there are species differences in the degree of selectivity (Rook *et al.*, 2004), but within any given species selectivity is likely to depend on the spatial scale and the complexity of the foraging task. The spatial scale of herbivore selectivity can lead to different associational effects in plant defences (Milchunas & Noy-Meyer, 2002). Of these, associational defence has been found in terrestrial as well as marine habitats providing food for fish, insects, and mammalian herbivores (Tahvanainen & Root, 1972; Pfister & Hay, 1988; Hjältén, Danell & Lundberg, 1993). Several mechanisms have been proposed to explain this phenomenon, one of the most frequently mentioned being that certain plants repel herbivores from patches or sites, which is referred to as the repellent plant hypothesis (Tahvanainen & Root, 1972; Atsatt & O'Dowd, 1976; McNaughton, 1978; Pfister & Hay, 1988). This kind of associational protection can be caused by physical characteristics, as when small plants grow close to larger plants having spines, or by chemical characteristics, as when undefended palatable plants grow together with well-defended unpalatable plants. If herbivores are selective between patches, leaving the overall better defended patches uneaten, the undefended plants in these patches achieve protection through their defended neighbours. The mechanism behind associational defence thus lies in greater selectivity at a larger spatial scale, the between-patch scale, and lesser selectivity at a smaller scale, the within-patch scale. An example of associational defence involving mammalian herbivores is the reduction in grazing by cattle on grasses (*Agrostis* and *Festuca*) with increasing presence of avoided buttercup (*Ranunculus bulbosus*) (Phillips & Pfeffer, 1958).

In this work, we have investigated how associational defence, as well as the related phenomenon of associational susceptibility, depends on the spatial scale of food offered in a patch-choice setup, where the between-patch scale was kept constant but the within-spatial scale was varied. We studied these effects using fallow deer (*Dama dama*) foraging on patches of hazel (*Corylus avellana*) branches to which we applied different concentrations of condensed tannins. Tannins make up a large group of defence substances that are eaten to some extent by several mammalian herbivores. Since the sensation of astringency during consumption is correlated with the tannin concentration in a particular

plant (Mali & Borges, 2003), this defence trait has signal value for the herbivore, making it possible to distinguish defended and undefended plants (Tuomi, Augner & Nilsson, 1994). In previous studies on fallow deer exposed to pellets with different concentrations of tannin it has been found that the deer preferred lower concentrations in two-choice or preference tests (Alm, Birgersson & Leimar, 2002; Bergvall & Leimar, 2005).

## Methods

We used 16 adult female fallow deer, freely foraging in a 4-ha enclosure with meadow and forest at Tovetorp zoological field station in south central Sweden. Since the deer were reared by hand they were tame and could be handled individually. During the study they had *ad libitum* access to silage, pasture, water, salt, and mineral stone, and there was no fasting before the trials. The study took place during April and July 2004 and was performed with permission from the Swedish National Board for Laboratory Animals. A small experimental enclosure (100 m<sup>2</sup>) with 1.4-m-high solid walls was placed within the larger enclosure where the deer were kept. The entrance to the enclosure had a small vestibule where a deer could be led and then guided to the experimental enclosure. The deer were tested one at a time in random order.

For the trials we used fresh hazel branches soaked or sprayed with water containing either 0.5% (low) or 15% (high) condensed tannin. Fresh branches were taken from the surrounding woods every morning and kept in water while the tannin solution on the leaves dried, in order to keep them fresh until the trials were conducted. We used Quebracho powder (Unitan Ato) containing 75–77% condensed tannin in the solution. The branches were arranged in the experimental enclosure by tying them to wooden stakes (1.5 m high). The weight of each branch was recorded before and after each trial (the weight difference then corresponds to the amount of leaf biomass eaten). Before the initial two-choice test (see below) the deer were habituated to the setups by tying hazel branches to wooden stakes in the experimental enclosure and letting the deer freely forage there for a couple of days.

### TWO-CHOICE TEST

The two-choice test consisted of a single treatment with 2 bundles of hazel branches (of the same size and appearance) with either low- or high-tannin concentration. The bundles (weighing on average 205 ± 30 g [± SD]) were tied to 2 stakes standing 1 m apart, at a height the deer could easily reach (60–80 cm). All of the 16 deer were subjected to 4 trials. In order to control for place preference, the positions of the low- and high-tannin bundles were switched between the trials. A trial started when a deer was released into the experimental enclosure from the vestibule, and it ended 3 min later. From the 4 trials an average consumption was computed for each deer, giving each individual deer ( $n = 16$ ) 2 values (consumption of low- and high-tannin leaves).

### SPATIAL SCALE EXPERIMENT

The experimental setup consisted of 8 hazel branches arranged in 2 patches of overall different quality (low- or

high-tannin), with 2 treatments: one in which the branches in the patch were spread out on 8 stakes and one in which they were together in a bundle on a single stake. The heights of the edible parts of the branches were between 50 and 100 cm, and they weighed  $15.3 \pm 6.7$  g (mean  $\pm$  SD). Two circles (2 m in diameter), each consisting of 8 stakes, were positioned 6 m apart in the experimental enclosure. The bad (low quality) patch consisted of 7 high-tannin branches and 1 low-tannin branch, and the good (high quality) patch consisted of 7 low-tannin branches and 1 high-tannin branch. In the “spread-out” treatment the 8 branches were tied to separate stakes in the patch, and in the “bundle” treatment the 8 branches were tied in a bundle that was tied to 1 of the 8 stakes in the patch (the other stakes were left empty). For a human observer, the deviating low- or high-tannin branch in a bundle was easily identified, and because in two-choice test (as well as in earlier observations) the deer were noticed to select leaves 1 by 1, we assumed that they would in principle be able to select the low-tannin leaves in a bundle. In the spread-out treatment, the position of the single low- or high-tannin branch along the perimeter of the circle was randomized for each trial and the positions of the good and bad patches were changed between consecutive trials. A trial lasted a maximum of 5 min, but sometimes a deer stopped eating before that time. Each deer ( $n = 16$ ) were subjected to 4 trials in each treatment (spread-out and bundle), giving in total 128 trials. In half of the trials (in both treatments) the deer started from the bad patch and in half from the good patch. This was controlled by gently directing the deer to start with a particular patch by opening one of the doors leading from the vestibule to the experimental enclosure slightly more than the other.

#### STATISTICAL ANALYSIS

For the comparison of consumption from low- and high-tannin branches in the two-choice test we used a paired  $t$ -test. From the 4 trials of each treatment of the spatial scale experiment, an average consumption per branch was computed for each deer ( $n = 16$ ), giving 4 values for each individual deer (amount eaten from low- and high-tannin branches in the good and the bad patch) for each treatment (spread-out and bundle treatment). We analyzed these data with patch (good and bad), tannin concentration (low and high), and treatment (spread-out and bundle) as 3 crossed repeated-measures factors in analysis of variance, using the MIXED Procedure in the SAS 9.1.3 statistical software. We took into account that there might be variation between individual deer in their reaction to treatments, patch types, tannin concentrations, and all

their interactions, corresponding to 7 degrees of freedom, by nesting these as random effects within the subject factor deer. Letting the MIXED Procedure estimate a separate variance component (among deer variation) for each of these 7 effects, we tested each with an  $F$ -ratio with 15 degrees of freedom in the denominator.

We then performed *post hoc* testing to look directly for the presence of associational effects, separately for each treatment, making pair-wise comparisons of Least Squares Means of consumption from low- and high-tannin branches in good and bad patches. The  $P$ -values were corrected based on 6 possible pair-wise comparisons for each treatment, using the sequential Bonferroni procedure (Quinn & Keough, 2002). Unless otherwise specified, we report data as mean  $\pm$  SE.

## Results

In the two-choice test, between a bundle of low-tannin branches and a bundle of high-tannin branches, there was a strong preference for low-tannin food (paired  $t$ -test:  $t = 30.5$ ,  $n = 16$ ,  $P < 0.0001$ ; Low:  $70.45 \pm 1.8$  g; High:  $9.28 \pm 1.6$  g). Nevertheless, the deer also ate from the high-tannin branches to some extent.

For the spatial scale experiment, we found statistically significant interactions between the treatment factor and each of the effects patch quality, tannin concentration, and patch quality  $\times$  tannin concentration, demonstrating that the pattern of consumption differed between spatial scale treatments (Table I). Starting the interpretation of this difference from the highest order interaction, one sees from Figure 1 that the good–bad patch contrast of the low–high tannin consumption was greater in the bundle treatment than in the spread-out treatment. Next, and perhaps of greater interest, the statistically significant effect of treatment  $\times$  tannin concentration implies that, averaged over the 2 patch types, the deer were more selective between low- and high-tannin branches in the spread-out treatment compared to the bundle treatment, corresponding to greater within-patch selectivity in the spread-out treatment (Figure 1). Similarly, the statistically significant effect of treatment  $\times$  patch quality implies that the good–bad patch contrast of the consumption per branch, averaged over the 2 tannin concentrations, was greater in the bundle treatment compared to the spread-out treatment, corresponding to greater between-patch selectivity in the bundle treatment (Figure 1).

The *post hoc* tests showed no difference between patch types in consumption from low-tannin branches in the spread-out treatment (Figure 1a), implying that we did not

TABLE I. Analysis of variance of amount eaten per branch in the spatial scale experiment with low- and high-tannin branches presented in 2 patches of either good or bad overall quality, with 2 spatial scale treatments (spread-out and bundle patch arrangements).

Effect	df	$F$	$P$
Treatment	1	3.7	0.0732
Patch quality	1	11.2	0.0042
Tannin concentration	1	82.6	< 0.0001
Treatment $\times$ patch quality	1	15.7	0.0013
Treatment $\times$ tannin concentration	1	50.0	< 0.0001
Patch quality $\times$ tannin concentration	1	0.03	0.8740
Treatment $\times$ patch quality $\times$ tannin concentration	1	7.9	0.0132

The denominator degrees of freedom are 15 for each effect, corresponding to between-individual random variation ( $n = 16$  deer).

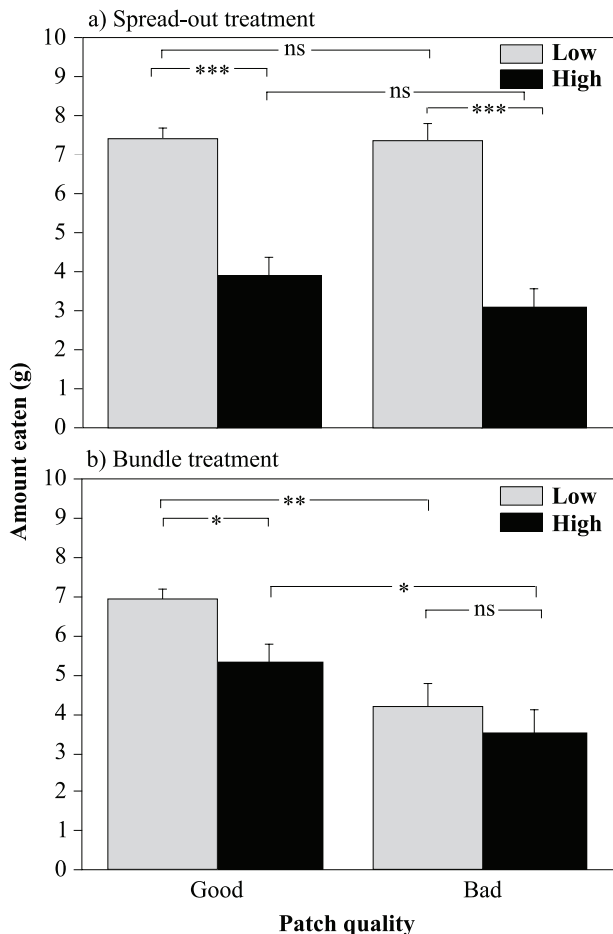


FIGURE 1. Trial-average amount eaten per branch (mean + SE for  $n = 16$  individual deer) in the spatial scale experiment with 1 good patch (7 low-tannin branches and 1 high-tannin branch) and 1 bad patch (7 high-tannin branches and 1 low-tannin branch). (a) The spread-out treatment, where the branches were tied separately to the 8 stakes in a patch. (b) The bundle treatment, where the branches were tied in a bundle to a single stake in each patch. For each treatment, the statistical significance of 4 of the 6 possible pair-wise *post hoc* comparisons is illustrated (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). See Table I for further statistical analysis.

find evidence for associational defence in this treatment. On the other hand, in the bundle treatment the deer ate less from the low-tannin branches in the bad patch compared to the low-tannin branches in the good patch, demonstrating associational defence in the bundle treatment. Further, the similar *post hoc* comparisons of consumption from high-tannin branches showed that the high-tannin branches were eaten more in the good patch than in the bad patch, indicating associational susceptibility, while no such effect was seen in the spread-out treatment. Finally, in the spread-out treatment the deer were selective between low- and high-tannin branches in both the good and the bad patch (Figure 1a), while this within-patch selectivity was less pronounced in the bundle treatment, being statistically significant only in the good patch (Figure 1b). The greater selectivity in the spread-out treatment was mirrored in the pattern of total consumption per trial, which was  $59.42 \pm 2.28$  g low-tannin leaves and  $25.58 \pm 3.95$  g high-tannin leaves in the spread-out treatment and  $52.56 \pm 2.24$  g low-tannin leaves and  $30.33 \pm 4.36$  g high-tannin leaves in the bundle treatment.

## Discussion

We found that fallow deer food selection depended on the spatial distribution of food items, which in turn was mirrored in associational effects of plant defences. When the hazel branches in a patch were spread out, and presumably easier to distinguish, the deer showed a clear preference for low-tannin branches in both patches and they consumed equal amounts from low-tannin branches in the good and the bad patch, implying an absence of associational defence. On the other hand, when the branches in a patch were close together in a bundle and perhaps more difficult to distinguish, within-patch selectivity decreased and between-patch selectivity increased. As a result, the low-tannin branches in the bad patch were less eaten than the low-tannin branches in the good patch, supporting our prediction of more pronounced associational defence in the bundle treatment. At the same time, high-tannin branches were more consumed in the good than in the bad patch, indicating associational susceptibility. While eating, the deer tended to taste leaves 1 by 1, but they typically did not spit out a tasted leaf, even if it was a high-tannin leaf, which suggests that they in principle could be more selective in the bundle treatment.

Our observation that herbivore selectivity decreased at small spatial scales is in general agreement with previous studies on sheep feeding on spatial arrangements of pellets (Edwards *et al.*, 1994) and cattle feeding on patchworks of grasses (WallisDeVries, Laca & Demment, 1999). There are several possible explanations for such a decrease, including different behavioural and physiological constraints that may limit a herbivore's ability to recognize, select, or utilize particular food (Illius & Gordon, 1993). For instance, a decreased selectivity of cattle feeding on a patchwork of 4-m<sup>2</sup> patches, compared to one with 25-m<sup>2</sup> patches, was interpreted as a failure to adjust the movement pattern during grazing to the smaller-scale patchwork (WallisDeVries, Laca & Demment, 1999). Other examples of constraints could be the morphology of the mouthparts and incisor dentition and also the size of the mouth opening (Hofmann, 1989; Illius & Gordon, 1993; Van Soest, 1996). Observations of the morphology and feeding style of herbivores living in the savannahs indicate that the larger grazers and the smaller browsers differ in how well they can select plants. The grazers leave areas with a high density of unsuitable plants, while the browsers can stay and select suitable plants (McNaughton, 1978). Fallow deer eat a wide range of food items, including grass, leaves, fruits, and herbs, and they typically take small bites from many plants rather than consuming whole plants 1 by 1 (Chapman & Chapman, 1997). Nevertheless, our observations show that their selectivity decreases when branches with varying levels of defence substances occur close together.

In addition to the effects of small spatial scales seen here, herbivore selectivity might decrease also at larger spatial scales, suggesting that there could be an intermediate spatial scale where selectivity is maximal. This appears to be the case in fallow deer, which have been found to be essentially unselective between patches that are 30 m apart (P. Rautio, unpubl. data). A possible consequence of such an intermediate maximum could be that within-patch selectivity can sometimes be more pronounced than between-patch

selectivity, and this has in fact been observed for fallow deer foraging on pellets (Bergvall *et al.*, 2006), potentially making it unfavourable for an undefended plant to occur among defended plants.

One explanation for a decrease in selectivity with longer distance between patches could be a longer time between the tasting of different foods simply makes it more difficult to remember and compare the foods. In experiments investigating simultaneous negative contrast in food intake (*i.e.*, whether the intake of a certain food depends on the context the food is presented in), less-preferred food tends to be more eaten when the time interval between the 2 foods offered becomes longer (Flaherty, 1996). In addition to the spatial scale, other factors like the magnitude of the difference in palatability between food types and the overall complexity of the foraging situation can influence selectivity. We found greater selectivity in the two-choice test compared to the within-patch selectivity in the spatial scale experiment (Figure 1). Similar phenomena of greater selectivity in two-choice tests compared to more complex foraging situations have also been found in previous experiments with fallow deer (Alm, Birgersson & Leimar, 2002; Bergvall & Leimar, 2005).

If we compare the outcome of the spread out treatment (Figure 1), where no associational effects were found, with the results from a similar experiment with fallow deer foraging from patches of pellets (Bergvall *et al.*, 2006), where on the contrary neighbour contrast defence was found, the food in the current setup might have a higher hedonic value for the deer, since hazel leaves are rare in the enclosure. This could be part of the explanation for the different outcomes from the otherwise quite similar setups. Another possible explanation for why differences in within-patch selectivity were detected in the pellet experiment (Bergvall *et al.*, 2006) but not here (in the spread-out treatment) is the amount of food that the deer ate before eating from the single high-tannin item in the good patch. In the pellet experiment (Bergvall *et al.*, 2006), a larger amount of food was available, and therefore on average more food was eaten before the high-tannin food in the good patch, compared to here where the amount of leaves eaten per branch was usually only a few grams. In an experiment on simultaneous negative contrast (Bergvall *et al.*, 2007), it was found that larger amounts of low-tannin food eaten before the change to high-tannin food resulted in a larger contrast effect and consequently a lower intake of high-tannin food. Hence the strength of associational effects seems to depend not only on the contrast between the high-quality and low-quality food but also on the amount eaten before changing to the other quality.

Based on our results, one can conclude that associational defences are more likely to deter a broad range of mammalian herbivore species when defended and undefended plants grow in close proximity to each other. As the nearest-neighbour distances between defended and undefended plants increase, only larger or more unselective herbivores are likely to treat a mixture of plants in a patch as a single food type. Thus, spatial scale could have a number of distinct effects on the distribution of herbivore pressure over the plant community. Furthermore, as we used

the same plant species as unpalatable and palatable food, our results suggest that associational effects work also at the within-population level. This has consequences not only for population structure but possibly also for the evolution of plant defences.

### Acknowledgements

Thanks to S. Meijer for collecting data in the two-choice test. This work was supported by grants from the Swedish Research Council to O. Leimar and the Academy of Finland (project no. 80486) to P. Rautio.

### Literature cited

- Alm, U., B. Birgersson & O. Leimar, 2002. The effect of food quality and relative abundance on food choice in fallow deer. *Animal Behaviour*, 64: 439–445.
- Atsatt, P. R. & D. J. O'Dowd, 1976. Plant defense guilds. *Science*, 193: 24–29.
- Bergvall, U. A. & O. Leimar, 2005. Plant secondary compounds and the frequency of food types affect food choice by mammalian herbivores. *Ecology*, 86: 2450–2460.
- Bergvall, U. A., P. Rautio, K. Kesti, J. Tuomi & O. Leimar, 2006. Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: Neighbour contrast susceptibility and defence. *Oecologia*, 147: 253–260.
- Bergvall, U. A., P. Rautio, T. Loutola & O. Leimar, 2007. A test of simultaneous and successive negative contrast in fallow deer foraging behaviour. *Animal Behaviour*, 74: 395–402.
- Brenes-Arguedas, T. & P. D. Coley, 2005. Phenotypic variation and spatial structure of secondary chemistry in a natural population of a tropical tree species. *Oikos*, 108: 410–420.
- Brown, J. S. & R. A. Morgan, 1995. Effects of foraging behavior and spatial scale on diet selectivity: A test with fox squirrels. *Oikos*, 74: 122–136.
- Chapman, D. & N. Chapman, 1997. *Fallow Deer: Their History, Distribution and Biology*. Coch-y-bonddu-Books, Machynlleth.
- Dumont, B., P. Carrère & P. D'Hour, 2002. Foraging in patchy grasslands: Diet selection by sheep and cattle is affected by the abundance and spatial distribution of preferred species. *Animal Research*, 51: 367–381.
- Edwards, G. R., J. A. Newman, A. J. Parsons & J. R. Krebs, 1994. Effects of the scale and spatial distribution of the food resource, and animal state on diet selection: An example with sheep. *Journal of Animal Ecology*, 63: 816–826.
- Farentinos, R. C., P. J. Capretta, R. E. Kepner & V. M. Littlefield, 1981. Selective herbivory in tassel-eared squirrels: Role of monoterpenes in ponderosa pines chosen as feeding trees. *Science*, 213: 1273–1275.
- Farrar, J. L., 1995. *Trees of the Northern United States and Canada*. Iowa State University Press, Ames, Iowa.
- Flaherty, C. F., 1996. *Incentive Relativity*. Cambridge University Press, Cambridge.
- Foley, W. J. & B. D. Moore, 2005. Plant secondary metabolites and vertebrate herbivores: From physiological regulation to ecosystem function. *Current Opinion in Plant Science*, 8: 430–435.
- Hjältén, J., K. Danell & P. Lundberg, 1993. Herbivore avoidance by association: Vole and hare utilization of woody plants. *Oikos*, 68: 125–131.

- Hofmann, R. R., 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: A comparative view of their digestive system. *Oecologia*, 78: 443–457.
- Illius, A. W. & I. J. Gordon, 1993. Diet selection in mammalian herbivores: Constraints and tactics. Pages 157–181 in R. N. Hughes (ed.), *Diet Selection*. Blackwell, Oxford.
- Laitinen, M.- J., R. Julkunen-Tiitto, J. Tahvanainen, J. Heinonen & M. Rousi, 2005. Variation in birch (*Betula pendula*) shoot secondary chemistry due to genotype, environment, and ontogeny. *Journal of Chemical Ecology*, 31: 697–717.
- Lawler, I. R., W. J. Foley & B. M. Eschler, 2000. Foliar concentration of a single toxin creates habitat patchiness for a marsupial folivore. *Ecology*, 81: 1327–1338.
- Macdonald, D. (ed.), 1999. *The Encyclopaedia of Mammals*. Greenwich Editions, London.
- Mali, S. & R. M. Borges, 2003. Phenolics, fibre, alkaloids, saponins, and cyanogenic glycosides in a seasonal cloud forest in India. *Biochemical Systematics and Ecology*, 31: 1221–1246.
- McNaughton, S. J., 1978. Serengeti ungulates: Feeding selectivity influences the effectiveness of plant defense guilds. *Science*, 199: 806–807.
- Milchunas, D. G. & I. Noy-Meir, 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, 99: 113–130.
- Moore, B. D. & W. J. Foley, 2005. Tree use of koalas in a chemically complex landscape. *Nature*, 435: 488–490.
- Parsons, A. J. & B. Dumont, 2003. Spatial heterogeneity and grazing processes. *Animal Research*, 52: 161–179.
- Pfister, C. A. & M. E. Hay, 1988. Associational plant refuges: Convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia*, 77: 118–129.
- Phillips, J. D. & R. K. Pfeiffer, 1958. In *Proceedings of the 4<sup>th</sup> British Weed Control Conference*, Brighton, UK, 4-6 November 1958. Society of Chemical Industry, London.
- Pietrzykowski, E., C. McArthur, H. Fitzgerald & A. N. Goodwin, 2003. Influence of patch characteristics on browsing of tree seedlings by mammalian herbivores. *Journal of Applied Ecology*, 40: 458–469.
- Provenza, F. D., J. J. Villalba, L. E. Dziba, S. B. Atwood & R. E. Banner, 2003. Linking herbivore experience, varied diets, and biochemical diversity. *Small Ruminant Research*, 49: 257–274.
- Quinn, G. P. & M. J. Keough, 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Rook, A. J., A. Harvey, A. J. Parsons, R. J. Orr & S. M. Rutter, 2004. Bite dimensions and grazing movements by sheep and cattle grazing homogenous perennial ryegrass swards. *Applied Animal Behaviour Science*, 88: 227–242.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala & D. M. Swift, 1987. Large herbivore foraging and ecological hierarchies: Landscape ecology can enhance traditional foraging theory. *BioScience*, 37: 789–799.
- Tahvanainen, J. O. & R. B. Root, 1972. The influence of vegetational diversity on the population ecology and a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Crysomelidae). *Oecologia*, 10: 321–346.
- Tuomi, J., M. Augner & P. Nilsson, 1994. A dilemma of plant defenses: Is it really worth killing the herbivore? *Journal of Theoretical Biology*, 170: 427–430.
- Van Soest, P. J., 1996. Allometry and ecology of feeding behaviour and digestive capacity in herbivores: A review. *Zoo Biology*, 15: 455–479.
- Vourc'h, G., J. L. Martin, P. Duncan, J. Escarre & T. P. Clausen, 2001. Defensive adaptations of *Thuja plicata* to ungulate browsing: A comparative study between mainland and island populations. *Oecologia*, 126: 84–93.
- WallisDeVries, M. F., E. A. Laca & M. W. Demment, 1999. The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia*, 121: 335–363.