Food choice in fallow deer –
experimental studies of selectivity

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Abstract:
In this thesis, I experimentally investigate feeding selectivity in fallow deer (Dama dama), with respect to plant secondary compounds, especially tannins, which can decrease the quality of foods. I found that fallow deer avoided foods with higher amounts of tannic acid and Quebracho tannin, even though the deer ate some high-tannin food. The food choice was strongly dependent on the context in which the food was presented, so that the food choice in relation to tannin content was relative rather than absolute. When high-tannin food occurred at low frequency, the deer ate proportionally less from this type of food, at least when the difference in tannin content between the two foods was large. A basic implication is that an unpalatable plant type could benefit from its unpalatability, especially when occurring at low frequency. In experiments with two patches, the finding of a stronger within- than between-patch selectivity was mirrored in associational effects. First, low-tannin, palatable food was more eaten when occurring in a high-tannin patch, which corresponds to neighbour contrast susceptibility. Second, high-tannin, unpalatable food in a less defended patch was less eaten, which corresponds to neighbour contrast defence. A proximate cause of the associational effects can be the presence of a simultaneous negative contrast, which was experimentally demonstrated in an additional study. Individual differences in selectivity were present early in life and were consistent over five years, and selectivity was correlated with foraging exploratory behaviour. The results from this thesis suggest that fallow deer are selective in their food choice with respect to tannins from the beginning, and that the frequency of occurrence of different foods, but also the distance between foods and the complexity of presentation, influence the food choice. It is also suggested that a foraging behavioural syndrome is present in mammalian herbivores.

Keywords: behavioural syndrome, neighbour contrast defence, neighbour contrast susceptibility, plant secondary compounds, simultaneous negative contrast, tannins
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The thesis is based on the following papers, which will be referred to as their roman numbers (I – V).


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Introduction

For a mammalian herbivore, selectivity between foods is fundamental to make adequate choices between food items and in its attempt to adapt to seasonal changes (Hofmann 1989). A majority of all mammalian herbivores are generalists and live in habitats that have seasonal changes (Freeland 1991, Hofmann 1989). A mammalian herbivore normally takes between 10 000 to 40 000 bites from the vegetation on a single day (Milne 1991). The number of different plant secondary compounds in the available food items is enormous (see Harboure 1991 for a review). Nevertheless, it has been suggested that the eaten food contains smaller amounts of toxins and larger amounts of nutrients than the average of the food available (Freeland & Janzen 1974).

Many factors influence food choice in mammalian herbivores, for example protein, carbohydrate and mineral concentrations (Forbes 1995), the amount of fibre and the presence of silica (McNaughton et al. 1985), spines and thorns and the presence of plant secondary compounds (Lindroth 1989). The nutritional value and physical and chemical properties differ greatly between plant species (Freeland & Janzen 1974, Hanley 1997), but a common pattern is that a high content of cellulose and therefore a low digestibility is found in plants containing smaller amount toxins (Lindroth 1989). On the other hand, plant materials containing smaller amounts of cellulose, which are more easily digested, often contain higher amounts of plant secondary compounds (Lindroth 1989). These different challenges require different specializations, and it has been shown that diet choice is related to the morphology (Hofmann 1989).

A prerequisite for selectivity is to recognise the different food items. The taste perception is complex and involves the smell and texture as well as the temperature of the food (Keverne 1982). Major mammalian taste categories are sweet, sour, bitter, salt (Lindemann 1996) and the taste of umami (Chaudhari 2000, Lindemann 1996). Not all mammals respond to all tastes; for example cats do not respond to sweet taste (Björnhag 1989). On the other hand, bitter taste seems to be rather universal, because species from several different phyla respond adversely to compounds that are bitter to humans (Glendinning 1994). A different type of perception or sensation of a food is astringency, which sometimes is defined as the combination of components such as roughness, dryness and puckering (Lawless et al. 1994), and is suggested...
to be a consequence of complex formation of superficial glycoproteins in the mucous (Haslam 1989).

Selectivity is influenced by preference, and learning about food in turn influence preference. In experiments with rats it has been found that they learn about food after ingestion and develop preferences for nutritious food (LeMagnen 1955). Ingestion of food with negative consequences gives the opposite effect that animals form aversion against the food (Garcia & Koelling 1966). This phenomenon, called postingestive learning is an important mechanism for food choice in generalist herbivores (Provenza & Balph 1987), since nothing stays the same, neither the needs for different substances nor the plant contents.

Plant defences

Plant secondary compounds were first mentioned in the literature by Stahl (1888), and after that there are some observations of plant poisoning of domestic animals; for example plant poisoning of camels exported to Australia (Leese 1942). For the plant, the production of plant secondary compounds is costly, since the substances of these compounds are the same as for products in the primary pathways of the plant (Harboure 1991). Plant secondary compounds include a diverse array of phenols, terpenes, acetylenes, alkaloids and other organic compounds (Harboure 1991). Even though the evolutionary origin of different plant defences is not known, many secondary compounds act as defences against mammal herbivores as well as against fungi, bacteria and insects (Lindroth 1989). To protect the plant itself, secondary compounds are often stored in vacuoles or plastids in the cell wall or in the leaves and stem (Lindroth 1989). Animals, in turn, have some protection in form of detoxification pathways, and vertebrates can deal with toxicants such as alkaloids, glycosides, saponins and tannins to some extent (Fowler 1983). Nevertheless, there are several examples in the literature that describe plant poisoning by wild mammalian herbivores (see Fowler 1983 for a review). Acute poisoning seems be a more frequently reported phenomenon than less obvious effects like growth inhibition, interference with reproduction, shorten life span or weight and fur loss etc. (Freeland & Janzen 1974, Fowler 1983). A common feature of examples of acute poisoning is that the ecological balance has been disturbed, as during drought, or when animals forage in totally new areas (reviewed in Fowler 1983).

Among the most widely distributed secondary compounds in the plant kingdom are the tannins (McSweeny et al. 2001). Tannins are
polyphenolic compounds that have an influence on the diet composition in many mammalian herbivores (Palo and Robbins, 1991). They occur in both woody (about 80%) and herbaceous (15%) dicotyledonous plant species, but more rarely in monocotyledonous plants (Bryant et al. 1991). Tannins are divided into two major groups; condensed tannins, which seem to have evolved earlier, and hydrolysable tannins, which only are present in evolutionary younger groups of plants (Meyer and Karasov 1991). It has been found that tannins influence rumen bacteria, protozoa and fungi (Smith et al. 2005). Tannins are able to form stable complexes with macromolecules such as protein, polysaccharides and alkaloids that are not readily degraded by mammalian digestive enzymes, thus negatively affecting the digestibility of plant materials (Haslam 1989, Goel et al. 2005).

There are also reports of beneficial consequences, for instance that tannins in some cases are able to bind to valuable amino acids and in turn protect these from being digested in the rumen by microbes, which can lead to an increased influx of essential amino acids into the small intestine (Min et al. 2003), and increased nutrient uptake (Makkar 2003). Condensed tannins have been shown to limit the presence of gastrointestinal parasites in goats and sheep (reviewed in Min et al. 2003). Therefore, tannins seem to have both negative and beneficial effects on the animals. Nevertheless, since the effects are important for the animal in one way or another, the ability to recognize and judge the amount tannin present, appears to be an important skill.

For mammalian herbivores tannins seem to influence the palatability (Bernays et al. 1989) and this is probably an effect of the astringent taste they produce in the mouth (Robbins et al. 1987). Tannins are also described to have a bitter taste (Brannan et al. 2001), and the bitterness is related to type of molecule and molecular weight (Peleg et al. 1999). Because astringency correlates with total tannin contents (Mali and Borges 2003) it has been suggested to serve as a sensory cue to foraging animals, to avoid plant substances that are high in tannins (Prinz & Lucas 2000). For species ingesting large amount tannins astringency might acts as a signal to the animal of the amount of tannins a plant contains, and the animal could then make a decision, based upon earlier experiences, how much to eat from the plant.

Associalional effects

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). One important issue is over what temporal and spatial scales the food choice is made. 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 the 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-Meyr 2002). The fact that plants occur in patches, and are not evenly distributed, can influence the outcome of the choice. The situation when a herbivore is selective between patches but unselective within a patch can have two separate effects. First, associational defence occurs when herbivores are leaving the overall better defended patches uneaten, and the less defended plants in these patches achieve protection through their highly 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 smaller scale, the within-patch scale. An example of associational defence involving mammalian herbivores is decreased grazing by cattle on grasses (*Agrostis* and *Festuca*) with increasing presence of avoided buttercup (*Ranunculus bulbosus*) (Phillips & Pfieffer 1958). Second, associational susceptibility occurs when the herbivore decides to forage from the less defended patch and a highly defended plant growing in this patch is more eaten than those in the highly defended patch (Hjältén et al. 1993).

Compared to associational defence and susceptibility, quite different associational effects will come about if the herbivore instead is unselective between patches and selective within a patch. This situation can also have two separate effects. First, a highly defended plant in a patch of less defended plants could be less eaten when the herbivore is selective within the patch, which is referred to as neighbour contrast defence (Bergvall et al. 2006). The effect is the opposite of associational susceptibility, in the sense that a highly defended plant is less attacked instead of more attacked when occurring in a palatable patch. Second, a less defended plant could be eaten more when growing in a patch of mainly highly defended plants, which is referred to as neighbour contrast susceptibility. The less defended plant is more susceptible to herbivory through the contrast between itself and its highly defended neighbours, resulting in a situation that is the opposite of associational defence (Bergvall et al. 2006).
Contrast effects

At small scales herbivores probably discriminate between plants mainly through taste (Robbins et al. 1987) and, as a consequence, the tastes are compared. In several sensory systems, the response to a given stimulus depends on its context (Flaherty 1996). The study of contrast investigates how rewards influence behaviour when animals are exposed to two or more levels of rewards compared to when they experience only a single level. The appearance of an exaggerated response to a shift in reward is referred to as a contrast effect in animal psychology and is an empirically well-established phenomenon (reviewed in Flaherty 1996). It has been suggested that contrast effects could be important in foraging (Flaherty 1996, Waddington & Heinrich 1981). For example, contrast effects can trigger search behaviour, or make an animal wait for a better reward and thus perhaps bias its intake towards higher quality food (Flaherty 1996). For mammalian herbivores, continuously encountering plants containing different amounts of secondary compounds and nutrients, contrast effects could represent important behavioural mechanisms to select proper food, in particular in view of the large number of choices needed.

In simultaneous contrast experiment, a given reward is presented together with a similar reward, making up the control treatment, and with a reward ranked lower or higher, corresponding to tests of positive or negative contrast (Flaherty 1996). This type of contrast seems relevant for mammalian herbivores, in the sense that these animals encounter a range of plants of differing quality and the plants are encountered in different order, perhaps depending on the frequency of occurrence. In a typical consummatory simultaneous contrast experiment, an animal receives two alternating rewards of either equal or different quality, so the animal can compare the two alternatives more or less directly, which means that the procedure does not rely on memory or expectation over longer periods of time. Successive contrast, on the other hand, entails a comparison of a current reward with the memory of a previously experienced reward (Flaherty 1996). A classic study is that by Crespi (1942) on reward-shifted rats in a runway. Rats that were shifted from a larger to a smaller reward ran more slowly to the reward than rats that only experienced the smaller reward, and this is referred to as a successive negative contrast. The procedure presupposes that the animal forms a mental representation of the reward in the memory and thereafter makes an evaluative comparison of the current reward with the memory of past rewards (Flaherty 1982, 1996). From experiments mainly on rats and pigeons both negative and positive contrasts have been found, but negative contrast effects seem to be somewhat stronger (Flaherty 1996).
Behavioural syndromes

Individuals of the same sex, size and from the same population often differ in the way they behave (Bell 2007). Already when Pavlov (1927) made his famous discoveries on classical conditioning, he noticed that the dogs systematically differed in their behaviour, something that Pavlov regarded as empirical data on personality differences, rather than just experimental ‘errors’. This early observation of animal personality has been described as “scientifically courageous” (Corr & Perkins 2006). Nevertheless, individual variation has for a long time been regarded as “the raw material on which natural selection acts, rather than the end product of natural selection” (Wilson 1998), but a more modern view is that even a single population could contain different behavioural types, simply because the environment offers several ways to survive and reproduce (Wilson 1998, Sih et al. 2004). Suites of correlated behaviours that are consistent for individuals in situations and between contexts have been described as personality or behavioural syndromes (Wilson 1998, Sih et al. 2004, Bell 2007). Behavioural syndromes have been studied in a diverse range of species from insects to fish, birds and mammals (reviewed in Gosling 2001). Currently, behavioural syndromes are viewed from an evolutionary perspective in attempts to explain the maintenance of individual variation in behavioural types and limited behavioural plasticity (Wilson 1998, Sih et al. 2004, Wolf et al. 2007).

Within the ruminants, several feeding types have been identified, which differ in their physiological traits such as rumen size, intestine length and the size of the salivary glands (Hoffman 1989). However, intermediate feeders, such as the fallow deer, change the intake of cellulose and toxins with the season and the availability of different foods (Jackson 1977). This gives the opportunity for individual specialization so that one individual perhaps has a higher intake of toxins and nutrients and at the same time a higher cost of detoxification. Another individual can instead have a lower intake of toxins and nutrients, but at the same time also a lower cost of detoxification.
Study specie and experimental set up

Study specie and background

The fallow deer (*Dama dama*, Linnaeus 1758) belong to the genus *Dama*, subfamily, Cervinae (Eurasian deer), family Cervidae (deer family) within the Ruminants, in the order Artiodactyla (even-toed ungulates). Fallow deer are known to live in quite high densities and females from several generations form large groups (Chapman and Chapman 1997). Ruminant feeding niches have been divided into three large groups based on morphology (Hofmann 1989). The fallow deer is classified as an intermediate mixed feeder between the grass and roughage eaters, which ingest lower amount plant secondary compounds, and the concentrate selectors, which ingest larger amounts of plant secondary compounds (Hofmann 1989).

Investigations on food choice in nature in different countries and habitats confirm the fallow deer feeding classification (Jackson 1977, Caldwell et al. 1983, Poli et al. 1996, Moore et al. 2000). The specific plant species eaten differs between countries and habitats, simply because there are different plants available (Borkowski & Obidzinski 2003, but reports from tree damage especially on seedlings are common (see Gill 1992 for a review). The fallow deer is a generalist herbivore with a broad food spectrum (Chapman & Chapman 1997), depending on the season (Moore et al. 2000). In a study by Jackson (1977), the rumen content from more than 300 fallow deer were examined and divided into several foraging types. The study is one of the most all-encompassing studies on rumen content in fallow deer. The deer in the study were primarily from road kills, except those from the hunting season, and food choice from all four seasons was included in the study. It was found that the diet contained over 60% grass during the summer period, while during the autumn and winter the deer ingested fruits and nuts, holly, conifers, fern, bramble and bushes (Jackson 1977). In some cases the rumen content during the autumn consisted of on average 40% acorns, which are known to contain much tannin (Jackson 1977).

However, we cannot know from these studies what the basis for the choices are, since we do not know between which plants the choices were made or the frequency of occurrence of different foods. In order to get a more detailed picture of the food choice, one needs to make experiments. Traditionally, feeding experiments are made on domesticated species and the driving force is many times the economical interest in production. The advantage of using domesticated species is that they are easy to get individual data from. These types of experiments
have greatly increased our knowledge about food choice (see Provenza 1995 for a review). Another type of experiments, with wild mammalian herbivores, are those where free ranging moose or hares forage from trees (see for example; Danell et al. 1991, Edenius et al. 2002, Hjältén et al. 1993). In these experiments the outcome, for example the associational effect, is the important issue. The number of animals participating is many times unknown. Preferably, in order to get a more detailed picture of food choice of wild mammalian herbivores, one needs to come very close. In one attempt to make direct observations, without disturbing the animals, Beringer and colleges (2004) attached a video camera to the antlers of a white-tailed deer. In this way they could not only identify the chosen plants, but also between which plants the choices were made. This method can perhaps increase the knowledge about food choice in the future. A third type of experiments involves wild species in enclosures, where the number of participating animals is known. This type of experiments can be divided into two types; first, a herd of animals where behaviour and outcome from the herd is known, and second, hand-raised individuals, which can be handled one at a time and for which one can get individual data on behaviour. The benefit of these two methods is that the outcomes can be studied immediately and the number of animals participating are known. In this way both the effects and the behaviour can be studied. In this thesis I use hand-raised fallow deer, which are used to humans and can be observed closely without imposing any stress. Many times they are more easily handled one at a time than mother-raised domesticated animals like horses, cows and sheep.

A very relevant question is how experiments on hand-raised wild ruminants can be regarded as natural and could represent wild animals. In an experiment with tame and wild white-tailed deer preference rankings of 6 browses were performed, and it was shown that the ranking from wild and tame deer were not statistically different when preferences were ranked according to mass consumed or number of bites taken (Spalinger et al. 1997). In another study by Longhurst et al. (1968), artificially fed black-tailed deer showed similar feeding pattern as their free-ranging counterparts when introduced to the same forage as in a feeding experiments. Therefore it is suggested that hand-reared deer are essentially the foraging equivalents of maternal-reared or wild animals (Longhurst et al. 1968, Spalinger et al. 1997).
General methods

Of the 17 hinds used, 16 were hand-raised and they were all kept in a four ha enclosure with forest and meadow, situated at Tovetorp zoological research station in south-central Sweden. Five hinds were born 1996, one was born 1990, the mother-reared hind was born 1993 and ten were born 2000. During the time of the experiments they had ad libitum access to pasture or silage, water, minerals and salt stone. All experiments, except the two-bottle test in Paper V, were performed in a smaller enclosure (Fig. 1) that was placed inside the larger enclosure. The entrance to the experimental enclosure had a small vestibule into which an animal could be led. To start a trial I released a deer from the vestibule, but in the group experiment in Paper III, all deer walked from the large enclosure through the vestibule into the experimental enclosure. The vestibule was used for the two-bottle tests in Paper V. The deer were easy to handle one at a time and were always willing to enter the experiment enclosure and forage from the bowls. In this way, I could get data from each individual separately.

Figure 1. The experimental enclosure placed within the larger enclosure. The start box is about 5 m$^2$ and the experimental area about 100 m$^2$.

During all cafeteria trials, the experimental arrangement consisted of eight or sixteen numbered bowls (1-8, A and B if two patches) that were placed equally spaced along the perimeter of one or two circles. I also recorded the animal’s sequence of visits to the different bowls, together with the duration of each visit, using a hand held computer. When a
group of deer (Paper III) entered the experimental enclosure, I used both a handheld computer and video camera to document the behaviour.

Two types of pellets were used in the experiments; Viltfor which is intended for wild cervids, (made of corn, milling bi-products, sugar beet bi-products, minerals, vitamins, fat and vegetable oils containing 10.5 MJ digestible energy and 120 g crude protein per kg) and Avrens pellets (which is made of rests from milling bi-products containing 9.2 MJ and 10.9 % crude protein), manufacturer Lantmännens, Sweden. I used two types of tannins in the different experiments; Tannic acid and Quebracho tannin. Tannic acid is a type of hydrolysable tannin (tannic acid, Sigma-Aldrich, CAS #: 1401-55-4, EC NO: 215-753-2). Quebracho extract is a type of condensed tannin distributed from Unitan Ato containing 75 – 77 % condensed tannin. Quebracho tannin contains mainly large amounts of profisetinidins (Vivás et al. 2001). In all experiments where pellets treated with tannin were used, the tannin was dissolved in water and sprayed over the pellets, so that the pellets became coated with a thin or thick tannin surface. In a typical experiment, the amount pellets was measured using a scale before and after the trial, and the amount consumed pellets of each type recorded. In almost all experiments the average consumption from several trials was used as a measure as an individual’s choice, so that N in each experiment is equal to the number of participating individuals. It is worth noting that commercial tannin products can differ between and within manufacturer (Rautio et al. 2007). Therefore it has been suggested that the starting point for all advanced tannin experiments should be a two-choice preference test with the tannin used (Rautio et al. 2007).

Specific methods

Food choice (Paper I)

The experiments in paper I took place from February to May 2000 and were performed with 6 adult fallow deer. One part of the experiments consisted of 17 two-choice tests using water or pellets with different compounds added, in order to investigate binary taste preferences. Each animal performed six trials per experiment, which were averaged and treated as one data point. The compounds tested were acetic acid, ascorbic acid, methyl salicylate, monosodium glutamate, saccharine, sucrose and hydrolysable tannin. Since tannin and sucrose were the compounds that had the strongest influence on food intake, I then performed two separate cafeteria experiments, one with tannin and one
with sucrose. For these experiments, each animal performed eight trials per experiment.

**Frequency dependence (Paper II)**

The experiments in paper II took place from June to October 2001 and were performed with ten one-year old fallow deer. Two similar experiments were performed, each with two types of food, but with a large difference in tannin concentration in the first experiment and a smaller difference in the second. In both experiments there were three treatments, in which the low tannin concentration occurred in either one, four or seven of the eight bowls. Each deer went through the treatments in a random order, but performed eight trials in sequence for each treatment. The low concentration food had 0.3% tannin (per weight) in both of the experiments. For the large difference experiment, the high concentration was 1.5% (i.e. five times the low concentration), and for the small difference experiment it was 0.6% (i.e. twice the low concentration). Each deer performed in total 24 trials in each experiment.

![A sketch of hind eating from one bowl of eight in the frequency experiment.](image)

**Patch choice (Paper III)**

The experiment in Paper III consisted of two parts, one part with individual deer data on within and between patch choice, and a similar experiment, but with a group of 16 or 17 deer. 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, placed equally spaced along the perimeter of a circle with a diameter of 3 m. The low concentration food had 0.3% tannin (per weight) and the high
concentration was 1.5% (i.e. five times the low concentration). In one of the two patches (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. Each deer performed in total eight trials. In the group experiment, more individuals were added in order to increase the competition for food during a trial. The buckets (vol. 12 litres) 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. The duration of a trial was 20 minutes and the deer performed two trials per day, in total ten trials. At the start of a trial each bucket contained 2000 g pellets.

Contrast effect (Paper IV)

In the simultaneous negative contrast experiment I investigated the consumption of a test food containing a certain concentration of tannin (1%) after preloading with comparison food of either lower (0.25%) or equal (1%) concentrations of tannin. The food used was Viltfor treated with Quebracho tannin. The preloading consisted of two bowls; the first preloading bowl was placed within the vestibule and contained 100 g pellets whereas the second was placed within the experimental enclosure and contained 500 g pellets. Each trial was started by offering the first preloading bowl (containing pellets with either 0.25% or 1% tannin) within the vestibule. When this amount was finished, I released the deer from the vestibule into the experimental enclosure having two bowls; the second preloading bowl and the test bowl. Each individual made a total of eight trials, with four trials of each treatment (i.e. 1% and 0.25% tannin preloading). For each deer the preloading treatment was changed in every other trial.

The successive contrast experiments needed a runway, which was put up within the experimental enclosure, beginning at the vestibule entrance. The first and the second passing times were recorded, using two laser beams connected to a computer, and used to compute the walking speed. A familiar bowl containing the reward was placed at the end of the runway. Each deer was trained to walk straight forward to the reward before the test started.

Behavioural syndromes and development of feeding selectivity (Paper V)

This paper is a compilation of data from several experiments performed from 1999 to 2004. Sixteen individuals were used in the different studies
and ten of these were tested both as fawns and as adults. The postigestive experiment on adults was performed in September 1999, the experiments and observations on fawns took place from June to September 2000 and the tannic acid selectivity experiment was performed in June 2001. Complementary experiments on selectivity according to tannic acid content were performed in June 2002, June/July 2003 and February/March 2004. The fawns were captured within 24 hours after birth, and reared by hand following the procedure by Birgersson et al. (1998).

**Two-bottle test**

The fawns were 10 days at the start of the sucrose experiment and between 15 to 26 days old at the start of the tannic acid and ascorbic acid experiments. The experiments took place in a small enclosure (5m$^2$) before the feeding durations in the morning (8.00), midday (13.00) or evening (17.00; only sucrose). The experiment consisted of three separate treatments with two-choice tests between pure water and water with sucrose (3.4%), ascorbic acid (2%) or tannic acid (3.2%) dissolved in water. For the tannic acid and ascorbic acid treatments there were in total eight trials per fawn, so that each compound was tested in four trials. For the sucrose treatment, four fawns made 7 trials, one fawn made 4 trials, two fawns made 3 trials and one only performed one trial. During a trial, a fawn was offered two bottles, one at a time, but the order in which bottles were offered to the fawn differed, so that the water was offered first every second time. Each bottle was offered twice in each trial and the order of treatments was randomized between individuals.

**Behavioural syndromes**

In order to compare the selectivity of individual deer over time, I used data from several experiments over a five-year period. In order for data to be comparable, the relative abundance of low- and high-tannin food in the experiments was 50 % and the difference between low- and high-tannin concentration was five times in all experiments with pellets, but the set-up and concentrations differed slightly. The intake of low- and high-tannin food was recorded for each individual, from which both the proportion low-tannin food and the total intake of tannins could be calculated. The data for the explorative behaviour is the average number of visits to bowls with pellets in the frequency dependence experiment performed 2001 (Paper III). The average number of visits to a bowl was measured for each individual over eight trials in the three treatments, giving 24 trials per deer.
Results and Discussion

Preferences and aversions

Preferences and aversions are best understood as the interplay between nature and nurture. First, many animals show innate aversions and preferences (Glendinning 1994, Lindemann 1996, Rhodes 1979). Second, these preferences and aversions can be changed through learning (Provenza 1995). In general, the value of a certain food is determined by its effect on the animal, and postingestive learning is thought to be an important food choice skill (Provenza 1995). It is not only the poisonous effects that are learned: animals that are deprived and lack a specific compound in the diet develop a preference for the food that gives them this specific compound (Forbes 1995). From experiments on postingestive learning in fallow deer it was found that postingestive learning occurred, since the intake of food of low and high quality did not differ in the first trial, before learning (Mean ± SD, high: 4.6 ± 3.6; low: 4.9 ± 1.7), but after eight presentations of each food type more high quality food than low quality food was eaten (Mean ± SD, high: 10.3 ± 1.5; low: 6.3 ± 1.1, Paper V).

Experiments with guinea pigs (Lichtenstein & Cassini 2001), goats, sheep and cattle (Provenza & Cinotta 1993) indicate that these discriminate between foods containing different amounts of tannin and prefer lower amounts in a two-choice test. This is also true for fallow deer, since in several two-choice test and cafeteria experiments, fallow deer ate less from the food (pellets) containing higher concentrations of tannins (Papers I-V, Rautio et al. manuscript). In a two-choice test between tannin solution and water there was an even stronger aversion against tannin (Paper I) and when the fallow deer foraged from two bundles of hazel branches sprayed with low or high concentrations of tannin, they preferred the low-tannin leaves (Bergvall et al., manuscript). Even though the tannin intake for a certain individual can vary between days, they seem to consistently prefer low-tannin food before high-tannin food over the long term and this has been true for both tannic acid and Quebracho tannin. At the same time, plants containing tannins seem to be an important food source, since whenever tannin-rich foods in the form of leaves and bark were offered to the deer, they ate a lot. Almost all trees in the enclosure were foraged from and no leaves or stems appear further down than a deer can reach while standing on its back legs. In fact, even animals classified as grass eaters like cow, sheep and horse eat leaves, bark and twigs from trees (Ciszuk 1996, Kuiters et al. 2006).
It has been suggested that mammalian herbivores should have a rule of thumb to avoid stronger flavours (Augner et al. 1998). Nevertheless, when fallow deer were offered foods with two concentrations of methyl salicylate (Paper I), cheese, strawberry or banana flavour (Birgersson B unpublished) it was found that the strength of the added flavour did not affect food intake. A possible explanation is that the food used was familiar and that this extra flavour was too weak to produce a neophobic reaction. The umami taste (mono sodium glutamate), which could signal proteins (Chaudhari 2000) produced either positive or negative reactions (Alm et al. 2002), but sour taste (acetic acid and ascorbic acid) often produce negative reactions, but not as reliably as tannin does (Paper I).

Many animals show innate aversion to bitter compounds, including protozoa, birds and mammals, probably since many toxic compounds are bitter (Keverne 1982), although, there is no correlation between bitterness and the toxicity when comparing a broad range of compounds (Glendinning 1994). When fallow deer were offered bitter substances (denatonium benzoate and Quinine) they did not show a preference for lower bitterness (Bergvall U.A. unpublished). The results from other deer species are somewhat contradictory; commercially available preparations containing denatonium benzoate was not shown to reduce intake by mule deer (Andelt et al. 1994), white-tailed deer (Swivhart and Canover 1990) or elk (Andelt et al. 1992) foraging. Nevertheless, in a study of red deer and roe deer, a two-choice test between one food containing denatonium benzoate and one food without it was shown that they avoided denatonium benzoate (Wright & Milne 1996). One reason can be that they were offered this food in four periods of two days, and perhaps did not learn the postingestive consequences, which the free ranging deer species in the previous example probably did. Nonetheless, when the animals were given only food with denatonium benzoate they simply ate it (Wright & Milne 1996).

Fallow deer prefer sweet foods like raisins (Birgersson et al. 2001). The preference for sweet has been found in two-choice tests with sucrose and water solutions and in experiments with sucrose treated pellets, even though the selectivity for sweet does not seem to be as important as the selectivity against tannin (Paper I).
Relative food choice

A conceptual null hypothesis for food choice with respect to secondary compounds could be that individuals have a threshold value of how much of for instance, tannin they accept in their food. Any food with tannin content below this value would be consumed and food that contains higher amounts than the threshold value would be rejected. If that were the case, the food choice would be absolute. Alternatively, individuals could have a threshold of how much tannin they can ingest each day. However, in experiments on food choice with pellets treated with low, medium or high amounts of tannin it was shown that the food choice was relative. In two choice tests with low-, medium- and high-tannin food all individuals consumed more medium-tannin food per bowl when paired with high concentration than when paired with low concentration (fig. 2, Paper I). The difference was fairly large, with on average about twelve times as much medium-tannin food consumed when paired with the high concentration. This implies that the food choice is relative, since the amount of a food type consumed is dependent on which other foods are available.

![Figure 2. Amount eaten food/bowl of low, medium and high concentrations of tannin (0.12, 0.6, 3.0%). Of the eight bowls in the cafeteria experiment, one contained a low, three a medium and four a high concentration (X ±SE for N=6 individuals). Significant differences are given by * (Wilcoxon signed-rank test: P<0.05).](image-url)
In cafeteria experiments with three concentrations of tannins, all individuals consumed more from a low-tannin bowl than from a medium-tannin bowl (Paper I), but also more from a medium-tannin bowl than from a high-tannin bowl. Since the relation between the number of bowls with low, medium, and high concentrations of tannin were 1:3:4, the amounts eaten per bowl differed from the total amounts. The total amounts consumed of low and medium concentration food were about the same, but the high concentration was eaten very little. Thus, the deer seemed to discriminate less between low and medium in the cafeteria test as compared to the two-choice test and the presence of an upper limit in total intake might be one explanation for the low intake of high tannin food.

All deer in the study ingested some food from the high-tannin bowls, even though there was low-tannin food left. Experiments with goats have shown that experienced individuals can consume more tannins than inexperienced (Distel & Provenza 1991) and it has also been shown that the rumen microflora ecosystem can adapt to a tannin-rich diet (Gordon et al. 2002). Therefore, the optimal strategy for a mammalian herbivore is perhaps to adjust the intake to the current distribution of plants, but also to be prepared to eat more tannin if it becomes necessary.

![Figure 3. Amount eaten food from the first and second bowl containing low, medium and high concentrations of Quebracho tannin (0.25%, 1% and 4%).](image)
In an additional study on relative food choice, the exact amounts food eaten from the first and second bowl encountered was measured. From this study it was found that the quality of the first food determined the amount eaten from that bowl. The lower the amounts of tannin it contained, the more was eaten before the deer decided to change to the second bowl (Fig. 3, Bergvall, U. A. unpublished). The consumption from the second bowl was influenced by of the tannin content in that food, but also by the quality of the food in the first bowl (Fig. 3, Bergvall U. A. unpublished). The high tannin food was eaten to a very small extent, both when occurring as first and as second bowl.

**Frequency dependence**

Frequency dependence has been investigated for interactions like predation or herbivory, because of its potential relevance for the coexistence of different prey types (Greenwood & Elton 1979, Allen 1988, Weale et al. 2000). Applied to herbivory, frequency-independent food choice could mean that the consumption from a plant individual of a given type is independent of the relative frequency of that type. One possible deviation from such frequency independence is that the relative consumption per plant individual of a given type increases with the frequency. This pattern of food selection is referred to as positive frequency dependence, and conversely, if the relative consumption per plant individual of a given type is highest for low frequency of that type, there is negative frequency dependence (Allen 1988), which will disfavour rare types and favour common types. It has been suggested that mammalian herbivores choose food on the basis of taste and odour rather than on visual stimuli (Tuomi & Augner 1993) even if they are able to learn a visual discrimination task (Birgersson et al. 2001). The study by Danell & Ericsson (1986) on moose foraging on different species of birch was perhaps the first investigation of frequency-dependent food choice by mammalian herbivores. Danell & Ericsson (1986) found that the proportions of two birch species *Betula pendula* and *B. pubescens*, in the moose (*Alces alces*) diet were only weakly affected by their frequencies of occurrence. In an experiment with sheep grazing on clover and grass, Parsons et al. (1994) found that the sheep did adjust their diet with changes in relative abundance, but they also sustained a mixed diet in a manner corresponding to positive frequency dependency. On the other hand, in a selection experiment with moose feeding on birch (*B. pubescens*) and rowan (*Sorbus aucuparia*), Lundberg et al. (1990) found that the relative preference for birch over rowan did not vary with their frequencies of occurrence, which corresponds to frequency-independent selection (Greenwood & Elton 1979).
In order to experimentally investigate the frequency dependency in western grey kangaroo foraging behaviour, Parsons and colleagues (2006) performed cafeteria tests with food pellets treated with different concentrations of tannins and NaCl. From this study it was found that the food containing higher concentrations were more eaten when occurring at lower frequency (Parsons et al. 2006). Conversely, in a study designed to investigate the effect of frequency of occurrence on fallow deer foraging relative preference the opposite results was found, at least when the difference between foods was large. In this study the relative frequency of different food types was altered and the food types used were low- medium- and high-tannin food (Paper II). With small difference in tannin concentration between foods (low- and medium-tannin foods), there were no significant differences between the three frequency treatments (group I in Fig. 4a), indicating a lack of frequency-dependent food choice for small concentration difference. However, in the experiment with large difference (low- and high-tannin foods) there was frequency-dependent food choice, so that a high-tannin bowl was relatively less utilized when occurring in low frequency (III vs. II in Fig. 4a). The proportion high-tannin food ingested depended rather strongly on the proportion available, so the deer were far from keeping a constant, mixed diet of the presented food types.

Perhaps the most basic implication of the results is that an unpalatable plant type could benefit from its unpalatability also when occurring at low frequency, and perhaps even in particular when occurring at low frequency (Paper II). The findings thus suggest that frequency-dependent food choice by mammalian herbivores could facilitate the evolution of plant defences. The preference for low-tannin food in the experiments ought to be interpreted as an attempt by the deer to limit the intake of tannin, but the deer were also more willing to eat high-tannin food when this kind of food was more common (Paper II). Apart from the concentration difference and the frequency of occurrence, the manner of presentation also seemed to influence relative preference, at least in the experiment with small difference (Paper II). The complementary two-choice tests both had 50% low-tannin food, but the deer showed a stronger preference for low tannin food in the two-choice test with small difference than in the corresponding 4 low of 8 treatment (Fig 4a). When looking at the overall consumption, the proportion low-tannin food eaten by an individual during a trial varied from 27% up to almost 99% over the different frequency treatments and experiments (Paper II). Thus, the frequency of occurrence and the difference in tannin concentration had a rather strong influence on food intake.
Figure 4. (A) The relative preference for low over high tannin food (±SE for N=10 individuals), measured as the log-ratio of the trial average amount eaten per low tannin bowl and the trial average amount eaten per high tannin bowl. A log-ratio equal to zero would mean a lack of preference. There was an even stronger preference for low-tannin food in the large difference. The open symbols correspond to the complementary two-choice tests, and the closed symbols give the results from the main experiments. The symbols I – III indicate homogenous groups in the SNK post-hoc tests. (B) The absolute amounts eaten per bowl, averaged over trials (±SE for N=10 individuals), for the different treatments in the two experiments.
Search strategies

From observations of ruminant foraging behaviour, it has been shown that they tend to eat from a variety of locations and, over the short term, typically ingest small quantities of a variety of foods and sample novel foods rather than making an immediate decision to either eat large amounts or to reject the food (Freeland & Janzen 1974, Vavra & Ganskopp 1998). Even familiar foods in familiar environments are often sampled, probably because the nutrient content and the toxicity of plants change frequently and vary, for example, with time in the season or over different parts of the plant (Provenza et al. 1992). Thus, diet choice through constant sampling and evaluation of food appears to be an important aspect of ruminant foraging. When impalas were foraging from two different types of acacia trees that varied in thorniness and content of secondary compounds, the impalas tasted both options and showed a preference for the less thorny acacia tree (Illius & Gordon 1990). In spite of this, they switched every few minutes to taste some more from the previously abandoned acacia tree (Illius & Gordon 1990). Similarly, in experiments where fallow deer were foraging from several bowls containing pellets, the deer made many shifts between bowls, although the willingness to search seem to be a product of the overall quality. From two separate cafeteria experiments with food treated with sucrose or tannin, it was found that each bowl in the tannin experiment was visited more often than the bowls in the sucrose experiment (Alm et al. 2002). This pattern was also seen in two separate cafeteria experiment where the deer foraged from bowls containing low- and medium-tannin food in one experiment and low- and high-tannin food in another experiment. The deer searched through more bowls in the experiment with low- and high-tannin concentrations (Paper II). One explanation for the difference in search pattern is the time spent on a certain food type. It has been shown that the amount food eaten from a bowl is dependent on the quality of the food and of the quality of the bowl eaten before that, (Bergvall, U. A., unpublished). An outcome of an overall lower quality should then result in more shifts per time unit.

Complexity and distance

Based on simultaneous contrast theory, one would expect the discrimination between two different foods to decrease with the distance between them (Flaherty 1996). Experiments on simultaneous contrast have shown that the size of the decline in intake of a less preferred food, when compared with a more preferred food, depends on the time interval
between the ingestion of the two foods (Flaherty 1996). Studies on mammalian herbivores have shown that they are most selective over intermediate and relatively small spatial scales and are less selective over large scales (Dumont et al. 2002). From experiments with a wild fenced population, it has been shown that a longer distance between patches decreases the selectivity (Rautio et al. submitted manuscript). Similarly, in experiments with individual fallow deer a longer distance between the good and the bad patch, decreased the selectivity in the sense that the ingestion of tannin intake increased (Bergvall, U. unpublished data).

Nevertheless, if the distance between foods decreases so that the complexity increases to a level where it becomes difficult for the animal to select preferable food pieces, the selectivity will decrease. This has been shown in an experiment with hazel leaves and in an experiment with pellets (Bergvall et al. manuscript).

**Associational effects**

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 & Whitham 2000). For these associational effects to occur, herbivores should be selective between patches but unselective within a patch. In experiments with fallow deer the opposite outcome was found, in the form of greater within than between patch selectivity (Paper III). Hence, in the experiment where a single individual foraged from two patches 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, giving support to neighbour contrast susceptibility (Paper III). For the high-tannin food, there was a lower consumption per bucket in the good patch than in the bad patch, corresponding to neighbour contrast defence (Paper III).

Associational effects might act on different scales (Milchunas & Noy-Meyer 2002). In an experiment investigating the selectivity at different scales, fallow deer were foraging from low- and high-tannin branches in a patch choice setup. In order to keep the between-patch spatial scale constant and varying the within-patch spatial scale the set-up consisted of one good (7 low and 1 high) and one bad (1 low and 7 high) patch, which
were spread out or in a bundle (Bergvall et al. manuscript). When the branches were spread out, the deer showed a clear preference for low-tannin branches in both the good and the bad patch. When branches instead where close together, the selectivity within a patch was decreased and the high-tannin branches in the good patch were more eaten than the high-tannin branches in the bad patch, which corresponds to associational susceptibility (Bergvall et al. manuscript). Additionally, the deer consumed less from the bad patch, and consequently, the low-tannin branches in the bad patch were less eaten than low-tannin branches in the good patch, which corresponds to associational defence (Bergvall et al. manuscript). In the pellets experiment, the deer could choose between low or high tannin foods. In one treatment, the food was presented in two buckets, placed close to each other, but in the other treatment the food was instead mixed in one bucket. The total tannin intake was higher in the mixed treatment than in the separate treatment so that an individual on average ate 9.14 ± 2.06 g tannin/trial when the food pellets were mixed in one bucket mixed and 6.17 ± 1.85 g tannin/trial in treatment where the foods was presented in two buckets (\( \bar{x} \pm SD \)).

Contrast effects

From experiments on associational effects it has been suggested that the contrast between perceived foods caused these effects (Paper III). In complex foraging situations with many stimuli, preingestive cues like taste could be of importance (Robbins et al. 1987, Tuomi & Augner 1993, Ginane et al. 2005). Overall, the mechanism ought to be beneficial for the animal, but it will have the side effect that foraging behaviour becomes guided by the perceived strength of a contrast and this perception might not reflect the true difference in quality of food types. In an experiment on simultaneous negative contrast in fallow deer, it was found that the consumption of 1% tannin food from the test bowl depended on the context in which the bowl was presented. If the deer first experienced the better quality (pellets containing 0.25% tannin), they ate less from the second 1% tannin bowl than when they had experienced the same quality (Paper IV).

The amount preloading food consumed had an influence on the strength of the simultaneous negative contrast effect (Paper IV). When less preloading food was consumed, the contrast effect became weak, whereas the effect was quite strong when more preloading food was consumed (see Fig. 5; at the highest levels of preloading, there was a fourfold difference in intake of test food between the 0.25% and 1% treatments). The variation between trials in the amount of preloading
food consumed was most likely an expression of natural variability in foraging behaviour of the fallow deer.

![Figure 6](image)

Figure 6. The amount of pellets eaten (g) from the test bowl with 1% tannin concentration, for the two treatments (0.25% and 1% preloading tannin concentration) in the simultaneous contrast experiment, plotted as a function of the total amount of pellets eaten from the two preloading bowls. The data points represent individual trials, with 4 trials per treatment per individual and 16 individuals. The lines are simple regressions based on these points, fitted separately for two treatments.

In conclusion, when animals rely on sensory cues for selecting a suitable diet, simultaneous negative contrast effects could be a consequence of behavioural mechanisms that enhance selectivity in a manner that is on average adaptive. A basic prediction from such an idea is that there should be stronger selectivity when food types are limited in number, occur in relative proximity of each other and are characterized by distinct tastes or other cues used for food selection. The perspective of contrast effects could thus be quite helpful for the understanding of foraging behaviour (Paper IV).
Group living

Living and foraging in a group has both benefits such as allosuckling (Ekvall 1998), better predator avoidance and social learning of foods, and costs such as increased parasite pressure and competition for food (Krebs and Davies 1993). For group living animals, foraging decisions are probably taken at 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. Thus, an individual in a group will not be free to forage wherever it wants. In an investigation on free-ranging American moose (Molvar & Bowyer 1994), the foraging efficiency and the quality of the eaten food 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 not many studies investigate the effect of group size on herbivore food choice, decreased within-patch selectivity for large groups might well be a common pattern. In an attempt to experimentally test this, a comparison was made between two different situations where fallow deer forage from two patches with bowls containing low- and high-tannin food (Paper III). In the first treatment, one individual deer foraged from two patches and in the second treatment the deer foraged in a group of 16 to 17 individuals. From this study it was found that when fallow deer foraged in a group, they were less selective between low- and high-tannin foods (Paper III). 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 no such data was recorded from this experiment.

Development of feeding selectivity

Studies on how fawns of mammalian herbivores choose food are rare. But in a study on the impala, which is classified as an intermediate feeder, the diet contained less plant secondary compounds in the beginning (Frost 1981), which is similarly to that by fallow deer (Paper V). In a comparison with two concentrate selectors (Hofmann 1989), the roe deer (Tixier et al. 1998) and the white-tailed deer (Spalinger et al. 1997) it was shown that they instead ate several plants in the beginning that were ignored as food plants later in life. Studies on fallow deer
fawns, supported the idea that ruminants show feeding selectivity from the beginning (Paper V). In a two-bottle test fawns showed a preference for sucrose and an aversion towards tannic acid and ascorbic acid, although in no case was there an absolute discrimination against one of the choices (Paper V). However, fallow deer fawns seem to select foods containing less plant secondary compounds early in life, and thereafter increase the intake of plants containing secondary compounds with age (Paper V). From the different studies on mammalian herbivores it seems like the general pattern is that the feeding type affects the development of feeding selectivity and that species with larger grass consumption in the adult diet, consume less plant secondary compound in the beginning and that concentrate selectors ingest higher amounts of plant secondary compounds from the beginning and later in life.

**Behavioural syndromes**

Behavioural syndromes have been described as suites of correlated behaviours that are expressed across different contexts. As a consequence, the individual behavioural rankings among individuals stay constant over time and contexts (Wilson 1998, Sih et al. 2004). Studies on mammalian herbivores have included cow (*Bos Taurus*), (Grandin 1993), goat (*Capra hircus*), (Lyons et al. 1988), horse (*Equus caballus*) (Wolff et al. 1997) and deer (*Cervus elaphus* and *Cervus elaphus x Elaphusus davidianus* hybrids). (Pollard et al. 1994). Some syndromes that have been repeatedly investigated are aggression (reviewed in Sih et al. 2004), the shyness-boldness continuum (Wilson et al. 1994), and fearfulness (Boissy 1995).

In several studies on food choice in fallow deer, the selectivity towards tannin differed between individuals, but was consistent for an individual deer over time (Paper V). Further, for a specific individual, the selectivity was correlated to the degree of exploration, so that the more selective individuals showed more search behaviour, indicating the presence of a behavioural syndrome. The exploration was measured as the numbers of visits to bowls in a cafeteria experiment with eight bowls (Paper II). The selectivity also differed between years, perhaps dependent on the presentation and the absolute tannin concentration, but there was no interaction between individual and year, indicating that the ranking between individuals did not differ between years, which supports the idea of the presence of a behavioural syndrome (Paper V).

From the study on fallow deer, it is impossible to know the proximate causes of the differences in tannin selectivity, but other studies have
shown that even closely related individuals can differ in morphology and physiology, which in turn can affect intake of nutrients (Scott & Provenza 1999). Since fallow deer use different foraging strategies during different times of the year, perhaps some individuals do better in one season than another, which could explain the maintenance of both behavioral types. An alternative explanation could be that the deer in the study have experienced some flavors in the uterus (Hill & Przekop 1988), or in the very first milk, since their mothers had access to plants containing tannin. How much tannin they ingest could therefore be regarded as a learned behavior.

![Normalized intake of tannin in food or water in a number of experiments over five years (2000 to 2004) for the ten individuals (mean + SE).](image)

**Figure 7.** Normalized intake of tannin in food or water in a number of experiments over five years (2000 to 2004) for the ten individuals (mean + SE).

**Conclusions**

In this thesis, some of the causes and consequences of selectivity in mammalian herbivores have been investigated. I have used hand-reared fallow deer hinds, but the results might apply to many free-ranging mammalian herbivores, even though preferences for certain concentrations of secondary compounds probably differ between species. The message, however, is that selectivity is influenced by preferences, by how easy it is to discriminate between foods and by the availability of different foods. The consequence of selectivity is the food choice, and long-term food choice results in diet choice. I found that deer avoided foods with higher amounts of tannic acid and Quebracho tannin, even though they ate some high-tannin food. The food choice was rather
strongly dependent on the context in which food was presented, so that food choice in relation to tannin content was relative rather than absolute. Psychological effects, such as simultaneous contrast effects, enhanced the selectivity. The food choice was affected by the order of encounter, which in turn was a result of the frequency of occurrence. The animals’ selectivity, or in some cases lack of selectivity, can give rise to several associational effects. Individual differences in selectivity were present from the beginning and were consistent over five years, and selectivity was correlated with foraging exploratory behaviour. The results in this thesis thus suggest that a foraging behavioural syndrome occurs in mammalian herbivores.

References


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Swedish summary –

Svensk sammanfattning för lekmän

Betande däggdjur kan ju vid en första anblick antas ha ett helt oändligt matförråd i allt grönt, men i verkligheten står de inför en komplicerad uppgift att få i sig tillräckligt med näring, samtidigt som de skall minimera intaget av växternas försvarssubstanser. Dovhjorten tillhör Cervidae, hjortdjuren, inom idisslarna, och är klassificerad som en intermediär opportunist mellan den gräsätande kon, och det löv- och skottätande rådjuret. Kon har en stor våm och en lång tarm, och är mästare på att tillgodogöra sig svårsmälta fibrer som finns i gräs. Rådjuret har förhållandevis en liten våm och kort tarm och måste på så vis äta föda av högre näringskvalitet än de rena gräsätarna. Men eftersom löv och skott i regel har högre halter av försvarssubstanser än gräs, har rådjuret större lever och salivkörtlar än de gräsätande idisslarna och exempelvis saknar k och får den typ av tanninbindande saliv som finns hos hjortdjuren. Även här finns en gradskillnad, så dovhjorten har en lägre halt tanninbindande ämnen i saliven än rådjuret. Under sommarhalvåret äter dovhjorten så mycket som 60% gräs, men även löv från träd och buskar (20%), bark och örter (10%). Under hösten erbjuder naturen frukt, bär, mossor och både färska och vissna löv, men även ekollen äts i stora mängder. Under vintern åter den hänvisad till bark, grenar, barr och andelen gräs sjunker till 20%. De angivna siffrorna är ungefärliga och kommer från en studie från New Forest, Storbritannien.

Många växter innehåller försvarssubstanser som har till främsta uppgift att skydda växten mot diverse angripare i form av mikroorganismer, svampar, insekter och betande däggdjur. En typ av växtförvar är garvämnen, som känns igen från exempelvis rött vin, te och omogna frukter. Garvämnen har en adstringerande effekt i munhålan och typiskt är att många djur undviker garvämnen i alltför hög grad och i en enkel valsituation väljer de den föda som innehåller den lägsta koncentrationen. Bortsett från att garvämnen kan vara direkt giftiga i höga koncentrationer, har det visat sig att de binder till viktiga näringsämnen och på så sätt minskar födans näringsinnehåll. I vissa fall har de även positiva effekter, både för idisslare och för oss människor. Man kan då fråga sig varför djur äter föda som innehåller garvämne över huvud taget? För det första så kan de inte undvika att äta löv, bark, örter och annat som innehåller garvämnen, för det utgör en viktig del i dieten. För det andra så förekommer ofta garvämnen i den födan som även innehåller höga halter av näringsämnen.
Många idisslare lever i habitat med säsongsvariationer, vilket innebär att tillgången på föda är tillfällig. Vidare så varierar innehållet av försvarssubstanser över årstiderna, mellan växtdelar och i extrema fall även över dagen. En idisslare kan ta mellan 10 000 och 40 000 tuggor från vegetationen per dygn, vilket ger en enorm möjlighet att vara selektiv, och det har visat sig att djur väljer föda som har ett högre näringsvärde och en lägre mängd växtförsvar, än medelvärdet på den tillgängliga födan. Men litteraturen vittnar också om fall då vida djur blivit förgiftade och dött av att ha ätit fel föda. Det kan vara till exempel när extrema väderförhållande som torka, eller då djur blivit förflyttade långa sträckor till främmande miljöer. Det finns också uppgifter som tyder på att vida djur kan bli måttligt förgiftade, vilket kan påverka tillväxt, reproduktion och på längre sikt överlevnad. Detta är dock svårare att upptäcka.

I den här avhandlingen har jag försökt att svara på frågan hur betande däggdjur går tillväga när de väljer föda. Till en början handlade det om att finnas vilka ämnen som hade betydelse alls, och vilka ämnen som verkade vara oviktiga. Till exempel så visade det sig att garvämnen var viktiga, och att dovhjorten väljer den svagaste koncentrationen i ett preferenstest där den kan välja mellan en sorts pellets med högt innehåll an garvämne och en annan typ som innehåller lägre halter. Smaker som surt och bittert verkade vara av mindre betydelse även om sura ämnen undveks till viss grad. Dovhjorten visade sig ha en preferens för söta saker, något som kan vara en följd av inlärning från mjölken.

Nästa fundering handlade om hur betande däggdjur väljer föda när födan förekommer i olika frekvens. Bakgrunden är att man tänker sig att valet i sin tur kan påverka växtligheten och förekomsten av olika växter eller förekomsten av växter som bildat olika halter av försvarssubstanser. I det här experimentet fick dovhjortarna äta från åtta skålar som innehöll pellets med olika garvämnesinnehåll. I en serie experiment fanns en, fyra eller sju skålar av föredragen typ, d.v.s. som innehåller låg (0,3%) halt garvämne. De övriga skålarna innehöll pellets med hög (1,5%) halt garvämne, alltså fem ggr så mycket som den låga. I det andra experimentet användes i stort sett samma uppställning, men de höga byttes ut mot en sort som innehöll 0,6% garvämne, bara dubbelt så mycket som den låga. I det andra experimentet visade det sig att hjortarna valde den lägre halten garvämne, men att de åt mer av den höga ju mer det fanns av den. Dock fann jag en viktig skillnad, när den höga (1,5%) var ovanlig (1 av 8), åt hjortarna mindre än om den var vanligare, även om man tog hänsyn till att den just var mer ovanlig. Om man översätter detta till riktiga växter skulle en välförsvarad växt som är ovanlig klara sig förhållandevis bättre än både en lite mindre försvarad ovanlig och en mer vanlig välförsvarad.
I ett annat experiment undersöktes inom- och mellanpatchval. Här åt hjortarna från två patcher (cirklar) med åtta skålar med pellets i varje patch. Då användes en god patch, men undantaget att en skål av åtta innehöll mindre god pellets (höga halter garvämne). Likaså i den mindre goda patcher så fanns en udda skål som innehöll ”godare” pellets och då blev den goda mer åten än en god i den goda patchen. Det här kallade vi för ”grannkontrastförsvar” (då den välförsvarade i den goda patchen blev mindre åten än den goda i den goda patchen) respektive ”grannkontrastsårbarhet” (då den goda maten i den välförsvarade patchen blev mer åten än en god i den goda patchen). Frågan är då om det verkliga berodde på kontrasten mellan de olika koncentrationerna?


När hjortarna var små testade jag deras reaktion då de fick välja mellan vatten och en vattenlösning som antingen innehöll garvämne,
askorbinsyra eller socker. Det visade sig att redan innan hjo rtkalvarna
hunnit lära sig från att ha åtit växter som innehåller garvämnen så hade
de en aversion mot garvämne. När jag nu samlat så mycket data om deras
val av föda ville jag se om det fanns några mönster? Kunde det vara så
att individer är olika sparsmakade? För att undersöka detta hade jag data
från tvåval mellan föda med olika halter garvämnen från fem år.
Dessutom hade jag data på hur många skålar de besökte i experimentet
med åtta skålar. På så sätt kunde jag undersöka både hur sparsmakade de
var och hur mycket de bemödade sig att leta. Det visade sig att en del
individer genomgående valde mer god mat, alltså födan som innehöll
lägre halter garvämne. Dessa individer letade dessutom mer, medan
andra individer nöjde sig med lite sämre mat och dessutom letade i
mindre utsträckning. Sådana skillnader i beteende mellan individer som
är konstanta över tid brukar benämnas personlighet.

De stora dragen i denna avhandling är menad att kunna appliceras på
stora betande däggdjur i allmänhet, såsom hur de väljer när det finns föda
av olika kvalitet i olika frekvens och hur de gör inom- och
mellanpatchval. Likaså förekomsten av en simultan negativ kontrast
förmodas förekomma hos betande däggdjur i allmänhet. Andra resultat,
såsom exakta mångder av garvämnen och vilka ämnen som är viktiga,
kanske är mer specifika för hjortdjur med liknande nisch eller rent av
specifika för dovhjorten.

En vanligt förekommande fråga är: Vad skall det vara bra för? Förutom
att vi knappast kan veta vilken kunskap som kommer att hjälpa oss att
övervinna problem i framtiden, så kan det ge en pusselbit till förståelsen
för hur betande däggdjur går tillväga när de hittar föda, vilket i sin tur
kanske kan vara bra att veta om man har för avsikt att spara vissa växter.
Det är alltså lätt att hitta en tillämpad aspekt då man exempelvis planerar
träd eller om man oroar sig för den biologiska mångfalden. Ett uttryck
för det är de förfrågningar på artikel I vi fått från främst amerikanska
viltvårdsmyndigheter, men även andra länder som Pakistan och Mexico
och ställen som inte har tillgång till universitetsbibliotek eller just den
tidskriften som vi publicerade i. En annan kunskap är den om hur
evolutionen av växtförsvar fungerar och hur de betande däggjurens
födoval påverkar förekomsten och halterna av växtförsvarssubstanser.
Vidare så är kunskapen om att olika individer beter sig olika,
personlighet, värdefull om man t.ex. har för avsikt att återinföra hotade
djur eller om man inom animalieproduktionen har för avsikt att utnyttja
betet maximalt. Det finns också en vetgirig allmänhet som efterfrågar
kunskap om djur och natur.
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**Olle Leïmar is probably the best supervisor in the world…**

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