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EFFECTS OF MONOTERPENE ODORS ON FOOD SELECTION BY RED DEER CALVES (*Cervus elaphus*)[1]

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Abstract—The response of red deer calves (*Cervus elaphus*) to the odors of Sitka spruce (*Picea sitchensis*) and lodgepole pine (*Pinus contorta*) needles and five monoterpene constituents of their essential oils was measured by simple two-choice feeding trials. All odors were significantly rejected ($P < 0.05$) except Sitka spruce and lodgepole pine by females and Sitka spruce and alpha-terpineol by males. Females had a stronger dislike of all odors except lodgepole pine than males. Rejection of monoterpene odors weakened slightly with time. A strong logarithmic relationship between the strength of the rejection response and vapor pressure of the compounds tested suggested that the odors were rejected on the basis of concentration rather than quality.

Key Words—*Cervus elaphus*, red deer, terpenoids, monoterpenes, olfaction, *Picea sitchensis*, *Pinus contorta*.

INTRODUCTION

Monoterpenes are a group of secondary metabolites found widely throughout the plant kingdom. They are common constituents of volatile or essential oils, and individual monoterpenes are characterized by highly distinctive odors. Aromatic substances in plants, such as essential oils, may influence food selection by herbivores by acting on the sense of smell. Ruminants such as deer may have good reason to avoid plants rich in essential oils, because some are known

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to inhibit the activity of symbiotic rumen microorganisms, upon which ruminants rely for the digestion of plant material. Essential oils from *Artemisia* spp. (Nagy et al., 1964; Welch et al., 1982), *Pseudotsuga menziesii* (Oh et al., 1967, 1970; Radwan, 1972; Conolly et al., 1980) and *Juniperus* spp. (Painter, 1971; Schwartz et al., 1980a) have all been shown to inhibit rumen microorganisms, Longhurst et al. (1968) reported that black-tailed deer fawns (*Odocoileus hemionus columbianus*) rejected the odor of essential oils from *Ubellularia california*, and Schwartz et al. (1980b) suggested that mule deer (*Odocoileus hemionus hemionus*) used smell to discriminate between feeds contaminated with varying levels of juniper oils. Narjisse (1981) reported that sheep also rejected the odor of essential oils of *Artemisia tridentata*. However, essential oils consist of many monoterpene constituents, and the objective of the experiment reported here was to measure the response of red deer to both whole essential oils from conifers and also to pure monoterpenes.

METHODS AND MATERIALS

Odor trials were carried out on 20 red deer calves (*Cervus elaphus*) using methods adapted from Arnold et al. (1980), in which food is contaminated by the odors of test materials absorbed in pads of cotton wool. The calves were all 3–4 months old and had been reared at Reedie Hill Deer Farm, Fife, Scotland. They had no previous experience of conifers or monoterpenes in their diet. A group of 10 males and another of 10 females were housed in separate rooms. In each room, eight buckets mounted in wall brackets 1 m above the floor were arranged in four pairs. The members of each pair were placed 2.5 m apart. Throughout the experiment, a pelleted ration (Calfrearer Cakelets, 16% protein, 8% fiber) was offered ad libitum in these buckets, which were topped up with pellets twice daily. Water and hay were available ad libitum throughout the experiment. The deer were allowed eight days to become accustomed to the system, while the effect of bucket positioning on the mass of pellets consumed from each bucket was assessed (Table 1). Seven treatment periods, each lasting

TABLE 1. MEANS AND CONFIDENCE LIMITS FOR PERCENTAGE OF TOTAL FOOD CONSUMPTION TAKEN FROM TREATMENT BUCKETS DURING ACCLIMATION PERIOD

	Food Consumption (%)			
	Initial position	Reverse position	SE	99% Cl
Females	45.7	54.3	3.3	50 ± 11.7
Males	50.8	49.2	0.8	50 ± 2.8

72 hr, then followed consecutively. The treatments were three monoterpene hydrocarbons: limonene, α-pinene and terpinolene; two monoterpene alcohols: α-terpineol and borneol (monoterpenes supplied by R.C. Treatt and Co., Bury St. Edmunds); and the crushed foliage from two conifer species: lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*).

The food in one bucket of each pair was contaminated by a monoterpene odor by sprinkling 1 ml of the pure compound onto three pads of cotton wool, two of which were taped to the rim of the bucket and one was loose in the food. The control bucket of each pair received three similar pads of cotton wool but with no monoterpenes applied. Borneol (a solid) and the conifer foliage were placed in bags of nylon gauze which replaced the cotton wool pads. The mass of pellets consumed from all buckets was recorded 3, 6, 12, 24, 48, and 72 hr after starting the treatment. The cotton wool pads were recharged with 1 ml of the test compounds every 24 hr. In order to eliminate the effects of bucket positioning on food consumption from each bucket, the positions of the treatment and control buckets were interchanged at 12, 24, and 48 hr.

The mass of pellets consumed from the treatment buckets was expressed as a percentage of total food consumption for each group of animals. If the deer had shown no discrimination between treatment and control buckets, this figure would have been 50%. Consumption of less than or greater than 50% from the treatment buckets would indicate rejection or preference of the test odor, respectively. During the acclimation period, 99% confidence limits were calculated for the mean mass of pellets consumed from the treatment buckets with no monoterpenes present (Table 1). During the treatment periods, significant rejection was said to have occurred when the percentage of pellets consumed from the treatment buckets was below the appropriate 99% confidence limit for the acclimation period.

RESULTS AND DISCUSSION

Over the experimental period as a whole, total consumption of pellets rose gradually as the calves grew accustomed to an ad libitum diet. Females consistently consumed significantly less than males ($P < 0.001$, 1.19 kg/day per head $\pm$ SE 0.42 for females compared with 1.67 kg/day per head $\pm$ SE 0.38 for males).

The overall responses of the calves to the odors during the 72-hr treatment periods are presented in Table 2. The odors of all pure monoterpenes were significantly rejected ($P < 0.01$) by both males and females (except α-terpineol by males). The only significant response to crushed conifer foliage was the rejection of lodgepole pine needles by males. The weakness of the rejection response to conifer foliage was probably due to weakness of the odor they emitted compared with the pure monoterpenes. Females rejected all treatments more strongly than males (except lodgepole pine).

TABLE 2. EFFECTS OF MONOTERPENE ODORS ON FOOD SELECTION BY RED DEER CALVES—CONSUMPTION FROM ODOR-TREATED BUCKETS OVER 72 HR

	Consumption (kg/head)			
	Females		Males	
Treatment	Total	From treatment (%)	Total	From treatment (%)
Sitka spruce	3.79	1.70 (44.9)	4.67	2.26 (48.4)
Lodgepole pine	3.78	1.65 (43.7)	5.01	2.25*(44.9)
Alpha-terpineol	3.96	1.18*(29.8)	5.59	2.76(49.4)
Borneol	3.86	1.46*(37.9)	5.25	2.35(44.9)
Limonene	4.33	1.20*(27.7)	5.79	2.23(38.6)
Terpinolene	3.83	0.94*(24.6)	5.42	2.30(42.4)
Alpha-pinene	3.80	0.76*(20.0)	5.33	1.96(36.8)
Nondiscrimination zones (99% CL)		(38.3-61.7)		(47.2-52.8)

*Significant rejection of treatment odor ($P < 0.01$).

Evidence of partial adaptation by the deer to some of the odors is presented in Figure 1. Between 24 and 72 hr, both males and females reduced their initially strong rejection of α-pinene, limonene, and terpinolene, and females also reduced their rejection of α-terpineol and borneol. The monoterpene hydrocarbons limonene, terpinolene, and α-pinene were more strongly rejected by both males and females than the monoterpene alcohols. α-terpineol and borneol. There was a strong logarithmic relationship between the vapor pressure of the compounds tested (vapor pressure data from Jordan, 1954) and initial response ($r = 0.95$ for males and 0.98 for females) (Figure 2).

These results suggest that deer may reject monoterpenes on the basis of odor concentration rather than odor quality. It is likely that the rejection of monoterpene odors by deer is an innate response. Since the deer in this experiment had never encountered monoterpenes or conifers in their diet before, their response could not have been based on learning from previous experience. An innate rejection of foods containing monoterpenes may have selective advantages for deer since several authors (Schwartz et al., 1980; Conolly et al., 1980; Welch and Pederson (1981) have demonstrated that monoterpenes inhibit digestion in ruminants, such as deer, by inhibiting the activity of rumen microorganisms.

Olfactory adaptation is the process whereby odors initially perceived as strong, gradually seem to weaken when exposure to them is prolonged. Originally, olfactory adaptation was thought to be due to the inability of the olfactory receptors to respond to prolonged stimulation, but now it is believed that olfactory stimuli may be suppressed at a central level (Ottoson, 1963). In domestic

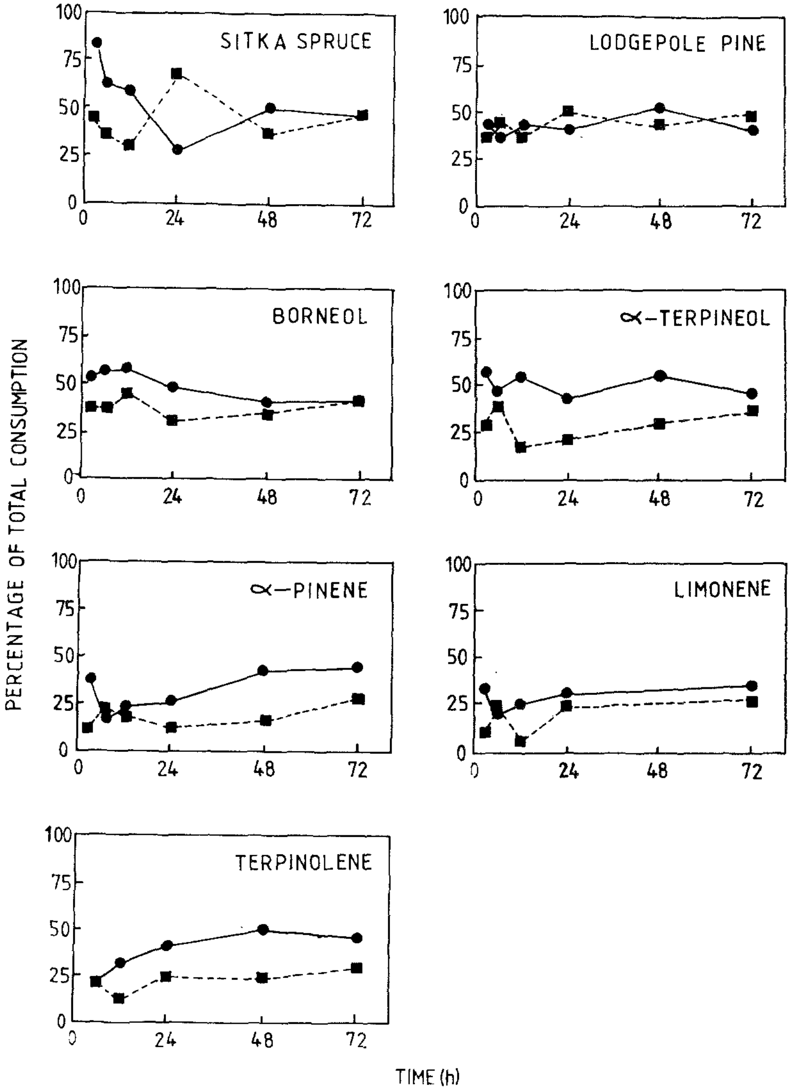

FIG. 1. Variations in response of red deer calves to odors over time. —●—, males; --■--, females.

ruminants, olfactory adaptation has been demonstrated to occur rapidly. Arnold and Hill (1972) and Arnold et al. (1980) showed that olfactory adaptation in sheep could occur within 6–24 hr, and Tribe (1949) found that sheep could adapt in less than an hour to several odors, including two which contained monoterpenes (eucalyptus and cedar wood oils). Figure 1 shows that for red deer calves, olfactory adaptation either did not occur or occurred only partially

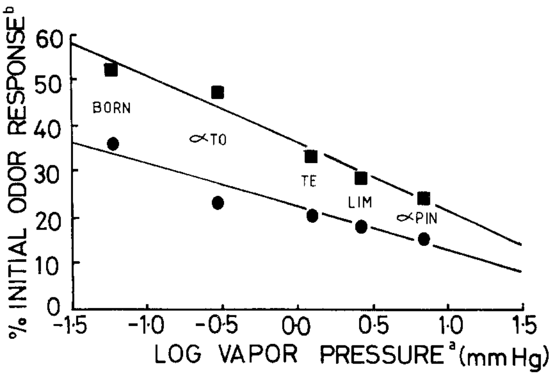

FIG. 2. Relationship between strength of rejection response and vapor pressure for five monoterpene odors: borneol (BORN), alpha-terpineol (αTO), terpinolene (TE), limonene (LIM), and alpha-pinene (αPIN). ■, males, $r = 0.95$; ●, females, $r = 0.98$. [a]Based on data of Jordan (1954) at 30°C. [b]Percentage of total consumption taken from odor-treated buckets 0–24 hr.

over 72 hr. The slowness with which olfactory adaptation occurred in deer compared with published data for sheep suggests that wild ruminants may rely more heavily on their sense of smell when feeding then domestic ruminants. The effect of domestication on olfaction has been demonstrated by Kruska and Stephan (1973), who found that olfactory structures in the forebrain of domestic pigs were about 30% smaller than in wild pigs. Stoddart (1980) suggested that "reductions in the olfactory part of the brain are related to the obvious behavioral changes wrought by domestication." It may be that domestication, in selecting for high productivity, has selected against those animals which reduce consumption in response to adverse olfactory stimuli.

The higher degree of rejection of food contaminated by monoterpene odors by females compared with males may have been due to bullying behavior which was common between males and may have reduced the opportunity for smaller males to select food from the preferred odorless buckets. Bullying between females was rarely observed. Alternatively, this result may reflect a genuine difference between males and females in their ability to detect and respond to olfactory stimuli. Sex differences in olfactory sensitivity have also been demonstrated in several mammals including humans (Doty et al., 1984) and black-tailed deer (*Odocoileus hemionus*) (Rice and Church, 1974). Male and female black-tailed deer differ markedly in their responses to butyric acid and putrefied fish extract.

This clear demonstration of the effects of monoterpene odors on the feeding behavior of deer may be of ecological significance in determining food selection in the wild. It is therefore important to extend these observations to feeding trials under natural conditions.

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