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The role of energy and resin contents in the selective feeding of pine needles by the Capercaillie

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The Capercaillie *Tetrao urogallus* L. prefers pine needles with high energy and low resin (the ether-extractable fraction of needles) contents, as shown by a comparison of 32 feeding trees with 32 unbrowsed control trees. In addition, 209 trees chosen randomly were examined in order to determine the dependence of energy and resin contents on age and growth rate. There is a slight but significant correlation between the energy content of the needles and the age of the pine, which means that the lowered age structure of managed Finnish forests may prove to be a harmful environmental alteration. No predictable differences in the resin contents of the needles in fast and slow growing pines in two different habitats were found. The male Capercaillie forages mainly in the upper branches of the tree, while the female forages in the schelter of middle branches. The energy and resin contents of needles could not explain this sex-related foraging site difference.

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1. Introduction

The extremely large caeca is the most typical feature of the tetraonid gut. Grouse species are able to digest cellulose and lignin; digestion in the caeca is aided by micro-organisms (e.g. Gasaway 1976, Moss & Hanssen 1980). The Capercaillie *Tetrao urogallus* L. is nearly monophagous in the winter (Seiskari 1962, Pulliainen 1979) after the snow cover reaches the 20 cm level (Pulliainen 1979). The winter diet only comprises the needles, shoots, buds and cones of the Scots pine *Pinus silvestris* L.

The subarctic winter with low temperature and short daylength puts the Capercaillie through a severe test. Usually birds have their highest energy requirements during the winter (e.g. Kendeigh et al. 1977), but this is not the case in the Capercaillie, which has its highest energy requirements in the middle of the summer during the moult and lowest in the winter (Lindén 1984). The most striking winter adaption is roosting in snow burrows (e.g. Marjakangas et al. 1983; see also Lindén 1981).

In this study the nutritional adaptations to harsh winter conditions are studied. Pulliainen (1970) observed the Capercaillie to select pine needles with the highest nitrogen content, which correlates highly with the energy content. Lindroth & Lindgren (1950) observed that Capercaillie prefer pines which often are fire scarred or otherwise injured. This suggests a preference for carbon-stressed tissue (Bryant & Kuropat 1980).

In this study the following aspects are considered in particular:

1. Does the Capercaillie select pine needles on the basis of energy and/or resin content? Resins (ether-extractable fraction of needles) are plant secondary constituents with antiherbivory effect (see Bryant & Kuropat 1980 and references therein).
2. Does age and/or growth rate of the pine tree affect the energy and/or resin content? The growth rate of subarctic plants reflects their carbon/nitrogen balance determining the amount of carbon to be allocated to growth or to chemical defence against herbivores (Bryant et al. 1983).
3. The male Capercaillie feeds in the upper sun crown of the pine, while the female feeds in the middle branches (Seiskari 1962, this study). Is there any differences between the energy and resin contents of the needles in different parts of the pine tree?

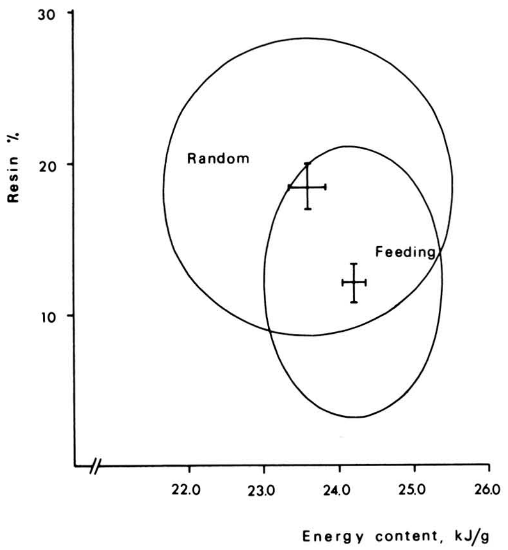

Fig. 1. The energy (abscissa) and resin (ordinate) contents in the needles of feeding trees and randomly sampled trees in study area II. 95 % confidence limit ellipses are drawn. The variables are treated as statistically independent (variance shared about 3 %).

2. Material and methods

This study was carried out in the neighbourhood of the Meltaus Game Research Station (66° 55′ N, 25° 20′ E) during the winters 1978–82.

Feeding trees of the Capercaillie were searched for in March-April by snowscooters. Altogether 32 recently browsed pine were found. Needle samples for analyses were collected with a shotgun from tree tops. The needles were pulled from the tips of upper branches to simulate the browsing of the Capercaillie. Needles were frozen in plastic bags before analysis.

An unbrowsed control tree of similar age, habitat and appearance as the feeding tree was selected for each feeding tree as near it as possible. The energy and resin contents in the needles of the feeding and control trees were compared with paired *t*-test.

As the above data may refer to a very biased sample of pinetrees, I also examined a random sample of 209 pines in order to determine dependence of energy and resin contents on age and growth rate, two virgin, unfertilized study areas (I and II) were selected. Area I is more productive than area II, which may be seen in the higher growth rate of pines in area I. From area I 110 and from area II 99 random needle samples were collected from pines in a transect line. Each random pine (diameter at breast height at least 10 cm) was 30 m apart from the preceding one.

The energy and resin contents of the needles in the upper, middle and lower branches were analysed from six pines to determine the possible differences between the parts of pinetrees.

Almost all the trees were measured; the age was determined from annual rings at breast height with an increment borer, the tree height was measured with an altimeter and the trunk diameters were measured at breast and six metres height with a caliper stick. The height and diameter measures may be converted into solid volumes of cubic metres (Ilvessalo 1969).

The energy contents of the needles were determined from the beginning of the study, but the resins were analysed from only 9 feeding and 9 control trees and 99 random trees from area II. The needles were cut into one centimetre pieces and dried in an oven (60° C) for three days and weighed. The resin content was determined with a Soxhlet apparatus using a solvent mixture of ether-ethanol 3:1 with the solvent completing 20 cycles through the apparatus. The needles were redried and reweighed after the extraction and the resin content was calculated as the percentage of weight loss. The energy content of the dried and carefully homogenized needle samples was analyzed with a Gallenkamp adiabatic bomb calorimeter. 4–6 pellets (0.8–1.0 g) were pressed and burned from each needle sample.

In the winter of 1981/82 the observer network of the Finnish Game and Fisheries Research Institute was asked to observe the feeding sites (upper, middle or lower branches of the pine) of male and female Capercaillies. Altogether 304 observers from the whole country sent feeding site information of 1752 male and 1348 female Capercaillie.

3. Results

3.1. Energy and resin contents in the needles of feeding and nonfeeding trees

Unbrowsed trees include both control trees and randomly chosen trees. Because the majority of feeding (browsed) trees and their control trees are situated outside the study areas I and II, where the random samples were taken, it is best to compare the energy contents of feeding trees (23.78 ± 0.92 kJ/g; *SD*, $N = 32$) only to those of their control trees (23.19 ± 0.83 kJ/g). The difference is only about 2.5 % but it is highly significant (paired $t = 4.70$, $df = 31$, $P < 0.001$). The respective comparison of the resin contents gave: feeding trees (12.1 ± 4.7 %; *SD*, $N = 9$) and their control trees (15.9 ± 6.2 %), the difference being, however, not significant (paired $t = 1.13$, $df = 8$, NS).

In study area II both energy and resin content analyses have been made from 9 feeding trees and 99 random trees which allows us to make a two-variable comparison (Fig. 1). Even though resins tend to be energy-rich compounds, there is no significant correlation ($r = 0.16$, $df = 95$, NS) between energy and resin contents. The 95 % confidence limit ellipse of feeding trees covers 35–40 % of the area of the 95 % confidence limit ellipse of random trees

Table 1. The energy and resin contents (mean ± *SD*) of the pine needles in fast and slow growing trees of the study areas I and II. *N* = number of samples.

Growth type	*N*	Energy (kJ/g dry matter)	Resin (% of dry matter)
Area I fast	47	23.49 ± 0.80	-
Area I slow	57	23.66 ± 1.09	-
Area II fast	40	23.87 ± 1.08	18.0 ± 5.2
Area II slow	55	23.53 ± 1.00	18.7 ± 4.8

and so strongly suggests that the Capercaillie selects needles with high energy and low resin contents. The resin content of the feeding trees is significantly lower ($t = 3.82$, $df = 104$, $P<0.001$), and the energy content higher ($t = 2.18$, $df = 106$, $P<0.05$), than those of random trees.

3.2. Dependence of energy and resin contents on the age and growth rate of the tree

In the random sample areas I and II the dependence of the energy content of the pine needles on the tree age are given by the regression equations:

Area I: $y = 0.0126x + 22.36$, $r = 0.402$, $df = 102$, $P<0.001$,

Area II: $y = 0.0037x + 23.15$, $r = 0.180$, $df = 96$, $P< 0.10$,

where x = age of the tree in years, and y = energy content of the needles, kJ/g dry matter. There is no correlation ($r = 0.09$, $df = 95$, NS) between the tree age and the resin content.

Both the study areas I and II were situated in virgin, unfertilized forests. The growth rate of trees was much faster in area I than in area II due to the differences in forest site types. The tree volume of 0.5 m^3 was reached in area I at the age of 110 years, while the respective age in area II was 175 years. With the aid of power curves I distinguished four arbitrary growth types: fast growth in productive forest (area I fast), slow growth in productive forest (area I slow), fast growth in barren forest (area II fast) and slow growth in barren forest (area II slow). The slow and fast types within each study area clearly belong to the same statistical distribution, and therefore no "dimorphism" is implied. It is nevertheless obvious that the individual histories of the "fast" trees do differ from the "slow" ones, and this could have an effect on the energy or resin contents.

Table 2. The frequency of foraging in different parts of the tree by the male and female Capercaillie and the energy and resin contents (mean ± *SD*) in different parts of the tree. The foraging site data consists of 1752 male and 1348 female Capercaillie observations. Energy and resin analyses have been made using 18 samples from 6 different trees.

Part of tree	Foraging site (%)		Energy (kJ/g dry matter)	Resin (% of dry matter)
	Males	Females		
Upper branches	58.7	18.5	23.20 ± 0.83	12.2 ± 3.0
Middle branches	33.7	65.2	23.16 ± 0.67	11.3 ± 3.0
Lower branches	7.6	16.2	23.12 ± 0.38	10.1 ± 2.8

Theoretically we would expect differences in the resin contents of needles of different growth types because fast growth requires a lot of carbon, which is then not available for chemical defence (Bryant et al. 1983). However, no differences in resin or energy contents of trees of the four different growth types were found (Table 1).

3.3. Foraging in different parts of the tree

The male Capercaillie prefers foraging in the upper sun crown of the pines, while the female forages among the middle branches (Table 2, Seiskari 1962: fig. 23). The sex-related difference in the usage of different parts of the tree was obvious and statistically highly significant ($\chi^2 = 506.9$, $df = 2$, $P<0.001$). The resin and energy contents of the needles from different heights of the tree were, however, almost identical to each other (Table 2).

4. Discussion

4.1. The energy content

There is a lot of discussion about whether browse nutritional quality (e.g. energy) or the avoidance of plant secondary constituents (resins) are of greater importance in forage selection by herbivores (e.g. Bryant & Kuropat 1980). As shown here, the Capercaillie balances between the two pressures, for it prefers pine needles with high energy and low resin content (Fig. 1), both variables contributing significantly to the selection of browsing trees.

Pulliainen (1970) observed the Capercaillie, and Gurchinoff & Robinson (1972) the Spruce Grouse *Canachites canadensis*, to select the needles with highest nitrogen or protein content. There is a strong positive correlation between the energy and protein contents. In this study observed differences in energy contents between browsed and unbrowsed trees were rather slight, only 2.5 %, but, during the winter, with a diet of low palatability and short daylight even small differences may be important. The digestive efficiency of the Capercaillie on a pine needle diet is only some 40 % (Andreev 1979, Lindén, unpubl.). During the short winter-day the Capercaillie fills its crop only once a day (Seiskari 1962). On the other hand, the Capercaillie is energetically extremely well adapted to the "shortage" of food during the winter (Lindén 1984).

Mature trees have a slightly but significantly higher energy content in the needles than younger trees. The general trend in forestry towards younger stands may prove to be an environmental factor which has also had an influence on the continuous decrease of Capercaillie populations (Lindén & Rajala 1981). There is an urgent need to study the effects of modern forestry practices on the winter forage of the Capercaillie and to find out the possibilities of repairing the disturbances already produced.

4.2. The resin content

The winter diets of the Capercaillie, Spruce Grouse and Blue Grouse *Dendragapus obscurus* consist almost solely of conifer needles which are rich in resins or phenols. Tetraonids are, however, probably able to detoxify resins in the caeca, where they are concentrated and excreted as energy-rich caecal droppings (Pendergast & Boag 1971, Moss 1973). Red Grouse *Lagopus lagopus scoticus* excretes ornithuric acid, which results from detoxification of prolignin and polyphenols (Moss & Parkinson 1972). However, the detoxification process is energetically costly (Freeland & Janzen 1974) and, in spite of their ability to use a resin-rich diet, the tetraonids tend to avoid high resin contents (Bryant & Kuropat 1980). In this study the avoidance of high resin contents by the Capercaillie was observed. Gurchinoff & Robinson (1972) made similar observations on the Spruce Grouse but they did not connect the result with the plant chemical defence against herbivores.

In this study the expected differences between the energy or resin contents of fast and slow growing trees in productive and barren forests were not found and neither were differences observed between the different parts of the tree (cf. Bryant 1982, Bryant et al. 1983). Tetraonids usually seem to prefer physiologically carbon-stressed tissues in physiologically stressed trees, which are often poorly defended by resins (Bryant & Kuropat 1980). This idea is thus not supported by this study. However, it has to be admitted, that my results concerning resins are still preliminary and a more intensive study on the role of resins in different habitats and in fertilized and unfertilized foreşts is badly needed. Also the possible positive effects of fertilization (Pulliainen 1970, Andersson et al. 1970) should be carefully studied for the development of a management method.

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