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A methodological note on the measurement of the diet specialization of predators

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In recent years, many theoretical studies have been made on the strategies and tactics of prey selection (see ELLIS et al. 1976 for a useful compilation of the theoretical predictions of a great number of authors). It is the purpose of this communication to elaborate briefly certain points made in a Finnish paper (JÄRVINEN 1974). The main ideas have already been discussed by several authors (e.g. COLWELL & FUTUYMA 1971, LEVINS et al. 1973, JUMARS 1974, SCHOENER 1974), but it may be worthwhile to re-examine them in an ornithological context.

The diets of owls have long been a favourite subject for ornithological studies. As a result, abundant information is available, at least in Europe, on the food preferences of different species. Attempts have been made to summarize these exhaustive lists of food items; for example they have been used by HERRERA (1974), HERRERA & HIRALDO (1976) and BEZZEL et al. (1976) to study how theoretical predictions agree with the facts. Using the Shannon function, these authors have calculated the diversity of the diet (or trophic diversity) of many European owl species. For example, in the Barn Owl *Tyto alba* the average diversity of the diet decreases northwards (HERRERA 1974). He attributed this result to the high abundance of voles (Microtinae) in the north, for theoretical models of MACARTHUR & PIANKA (1966) and EMLEN (e.g. 1968) predict that abundance of food results in food specialization.

However, theoretically at least, the concept of feeding specialization is meaningful only with respect to the diversity of the food items available. For example, if rats are the only food available, an owl can either feed on rats or perish. When alternative food sources are lacking, the range of food items taken by a specialist will be identical with that of a generalist (this point was also made by BEZZEL et al. 1976). So, feeding specialization can be measured only if the data on the diet can be considered in relation to the food available.

The monograph by KELLOMÄKI (1977) on the food of breeding Pygmy Owls *Glaucidium passerinum* includes results which substantiate the suggestion that trophic diversity may depend closely on the diversity of the food available. KELLOMÄKI found that the diversity of the bird community around a nest of Pygmy Owls correlated significantly with the diversity of the avian diet of the owls. His results thus show that the availability of food items should not be overlooked in studies of the diet: trophic diversity is not an unequivocal measure of diet specialization, but also depends on food availability.

Further studies should clearly be devoted to the concept of availability. Attention should evidently be paid to the abundance, catchability (measured, perhaps, with the time or amount of energy needed to catch one item) and the energy value of the separate food items. Most Finnish owls feed principally on small rodents and the measurement of the availability of the prey may be a rather difficult task, since the methods for obtaining quantitative estimates of the proportions of coexisting shrews, mice and voles are perhaps not very reliable. However, comparison of data already available reveals rather great differences in diversity between certain habitats. For example, I have calculated the values of the Shannon function (H', corrected for sample size) from the data presented in Table 1 of LAHTI et al. (1976). They snap-trapped small rodents at Kilpisjärvi, northern Lapland, and gave results from four habitats. The diversity values ($H' \pm S.D.$) are as follows:

EMT forest	0.45 ± 0.06
GDrMT forest	1.06 ± 0.09
TrGT forest	1.23 ± 0.07
Bogs etc.	1.16 ± 0.05

As the figures show, appropriately selected study habitats may sometimes differ widely with respect to rodent diversity. Such data can at least tentatively be used in interpreting differences in the

trophic diversity of different raptor populations (or communities).

I shall conclude by quoting from SOUTHWOOD (1976). He was actually writing about the effects of prey populations on the population dynamics of the predator, but, with appropriate deletions, the quotation shows which approach should be favoured by students of trophic diversity: "There are very real difficulties in quantifying bionomic observations (on habitats, feeding habits, and other such parameters); the more the investigator knows of the biology of the organisms in the trophic levels above and below, the sounder will be his judgment in the process . . . But how many students of bird ecology measure changes in available prey . . . ? Certainly some, but are they becoming proportionately rarer or more abundant?"

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Selostus: **Saaliinvalinnan riippuvuus tarjolla olevasta saaliista**

Saaliinvalinnan teoria on viime aikoina kehittynyt nopeasti, mutta teoreettisten ennusteiden testaus ei ole aina ollut sitovaa. Tärkeänä muuttujana on tutkimuksissa ollut saaliin monipuolisuus. Monipuolisuutta voidaan kuitenkin tutkia vain suhteessa tarjolla olevaan ravintoon: jos tarjolla on vain rottia, ei rottien saalistus todista rottiin erikoistumisesta. Tätä periaatteellista näkökohtaa (ks. JÄRVINEN 1974) tukee KELLOMÄEN (1977) tulos, että varpuspöllöjen käyttämän linturavinnon monipuolisuus korreloi merkitsevästi pesän ympäristön lintuyhteisön diversiteetin kanssa. Periaate pätee yleisemminkin ekologisen erikoistumisen mittaukseen.

References

BEZZEL, E., J. OBST & K.-H. WICKI 1976: Zur Ernährung und Nahrungswahl des Uhus (Bubo bubo). — J. Ornithol. 117:210—238.

COLWELL, R. K. & D. J. FUTUYMA 1971: On the measurement of niche breadth and overlap. — Ecology 52:567—576.

ELLIS, J. E., J. A. WIENS, C. F. RODELL & J. C. ANWAY 1976: A conceptual model of diet selection as an ecosystem process. — J. Theor. Biol. 60:93—108.

EMLEN, J. M. 1968: Optimal choice in animals. — Amer. Naturalist 102:385—389.

HERRERA, C. M. 1974: Trophic diversity of the Barn Owl Tyto alba in continental Western Europe. — Ornis Scandinavica 5:181—191.

HERRERA, C. M. & F. HIRALDO 1976: Food niche and trophic relationships among European owls. — Ornis Scandinavica 7:29—41.

JÄRVINEN, O. 1974: Valitsevatko lintumme runsaimpia saalistyyppejä? (Summary: Do our birds choose the most abundant food?). — Lintumies 9:19—24.

JUMARS, P. A. 1974: Two pitfalls in comparing communities of differing diversities. — Amer. Naturalist 108:389—391.

KELLOMÄKI, E. 1977: The food of the Pygmy Owl Glaucidium passerinum in the breeding season. — Ornis Fennica 54:1—29.

LAHTI, S., J. TAST & H. UOTILA 1976: Pikkujyrsijöiden kannanvaihteluista Kilpisjärvellä vuosina 1950—1975 (Summary: Fluctuations in small rodent populations in the Kilpisjärvi area in 1950—1975). — Luonnon Tutkija 80:97—107.

LEVINS, R., M. L. PRESSICK & H. HEATWOLE 1973: Coexistence patterns in insular ants. — Amer. Scientist 61:463—472.

MACARTHUR, R. H. & E. R. PIANKA 1966: On optimal use of a patchy environment. — Amer. Naturalist 100:603—609.

SCHOENER, T. W. 1974: Some methods for calculating competition coefficients from resource-utilization spectra. — Amer. Naturalist 108: 332—340.

SOUTHWOOD, T. R. E. 1976: Continuing in the MacArthur tradition. — Science 192:670—672.