

Food-niche and trophic relationships among European owls

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The study of three western European owl communities revealed the existence of geographical patterns concerning food-niche characteristics of the individual owl species and, consequently, of community composition and structure. Middle and Northern European communities show a close packing of species along the food dimension of the niche; the ways in which the available food resources are exploited are very restricted owing to the abundance of a particular prey type (voles, *Microtinae*). With increasing scarcity of this microtine prey, some species are eliminated in the Mediterranean community, food exploitation methods are diversified, and some substantial dietary shifts occur.

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Introduction

Previous studies on the diet of two owl species in Europe (*Tyto alba* and *Bubo bubo*) have revealed the existence of geographical changes in the diet that could easily be related to changes in diversity and abundance of their prey species (Herrera 1974b, Hiraldo et al. in press). If changes in the food-niche occur in any one of the species, one would expect associated effects on community composition and interspecific relationships. As a way of testing this assumption we analyse in this paper the geographical patterns of community composition, niche breadth of individual species, and niche overlap between coexisting species. We intend to show that the observed geographic food-niche changes were simply manifestations of a process involving the owl community as a whole. Our main aim is to show that owl predation in the Mediterranean area shows very peculiar features in comparison with the remainder of Europe.

Material and methods

Food data were collected for three groups of sympatric owl species (designated as 'communities' below) from western Europe. These three

communities were as follows: 1) the Scandinavian community, represented by data from Finland, Norway, and Sweden; 2) the Middle European community, with data from Germany and northern France; 3) the Mediterranean community, with data from the southern half of Spain. The three communities were not spatially delimited by means of any predetermined, closed boundaries, but rather they were chosen as representative of the three main types of climatically defined communities along a gradient from northeastern to southwestern Europe, namely, tundra and boreal forest, temperate forest, and mediterranean shrub and woodland (Whittaker 1970).

Food data were gathered from the available literature for communities 1 and 2. The data used for the Mediterranean community were mostly from the authors' unpublished material. A complete list of references is shown in Appendix I. Two species (*Asio flammeus* and *Strix aluco*) were excluded from the Scandinavian community in the analysis of niche breadth and overlap owing to the lack of appropriate food data. However, they were considered when dealing with the latitudinal gradient in species diversity. This artificial reduction in the number of species of the northern community was thought to be a conservative one

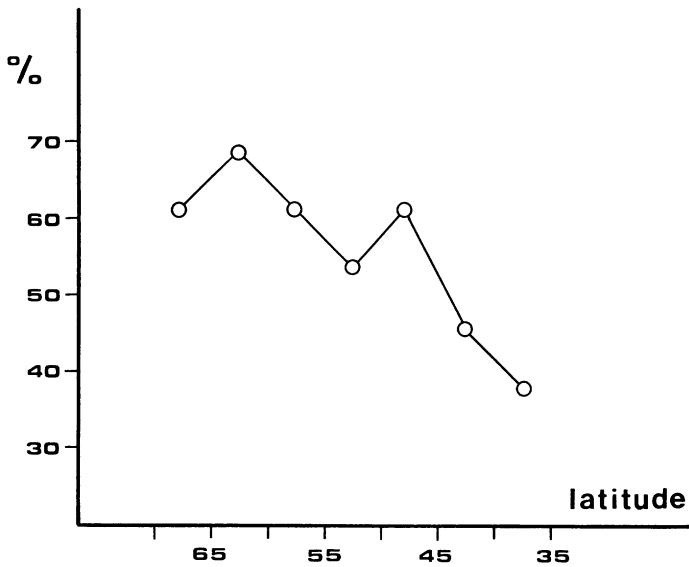


Fig. 1. Latitudinal changes in number of breeding owl species in western Europe, west of a straight line running from eastern Finland through the Balearic Islands. Percentage of the thirteen western European owl species (ordinate) occurring at each latitudinal belt five degrees wide (abscissa). Distributional data from Voous (1960).

and results are not expected to have been substantially affected by this.

Within each community we established a set of taxonomically defined food categories, and we determined for every component owl species the percentage of prey items occurring in each of them. The number of different food categories used varied from eighteen in the Mediterranean community to twenty-one in the Middle European one. Their taxonomic levels oscillate between the genus, in the case of all the small mammals (rodents and shrews), and the class, for amphibians, reptiles, birds, and fishes. The taxonomic level chosen for a given item was always inversely related to its importance in the diet of the owls. The finest partitioning (to genus) of those items which would be expected to be shared most extensively by the various owl species (e.g. voles, mice, shrews) provided a degree of 'resolution' fine enough for the purpose of this study. From these data, values of food niche breadth of individual species and food niche overlap between sympatric species were obtained. The complete list of raw data used may be obtained from the authors upon request and a succinct summary of them is given in Appendix II.

Niche breadth was calculated by means of the expression

$$B_i = \exp \left(- \sum_h p_{ih} \lg_e p_{ih} \right) \quad (1)$$

MacArthur (1964), Levins (1968)

and the values of niche overlap were computed by using the formula

$$\alpha_{ij} = \frac{\sum_h p_{ih} p_{jh}}{\sum_h p_{ih}^2} \quad (2)$$

MacArthur & Levins (1967), Levins (1968)

Symbols are as follows:

$h = 1, 2, \dots, n$ = number of food categories.

$i, j = 1, 2, \dots, s$ = number of owl species.

B_i = food niche breadth of species i .

α_{ij} = food niche overlap between species i and j (effect on species i caused by species j).

p_h = proportion of prey items in the h -th food class.

p_{ih}, p_{jh} = proportion of prey items belonging to the h -th food class found in the diets of the species i and j respectively.

Expression (2) leads to alpha-values which can exceed unity and values of α_{ij} differing from the symmetrical α_{ji} .

In addition to the above food-niche measurements, latitudinal changes in number of coexisting owl species were investigated to assess the geographical changes in community composition.

Table I. Food-niche breadth values for the three owl communities studied. Species are arranged according to increasing body weights (data from Dementiev & Gladkov 1966, König 1968). Asterisks denote mainly invertebrate feeder species. See text for meaning of D_r and derived expression

Species	Body weight (g)	Scand.	Mid. Eur.	Medit.
<i>Glaucidium passerinum</i>	65	3.45	—	—
<i>Otus scops</i>	100	—	—	1.33(*)
<i>Aegolius funereus</i>	150	4.32	4.81	—
<i>Athene noctua</i>	170	—	3.18(*)	1.27(*)
<i>Surnia ulula</i>	300	2.85	—	—
<i>Asio otus</i>	300	4.33	2.73	—
<i>Tyto alba</i>	300	—	4.60	5.88
<i>Asio flammeus</i>	400	—	1.45	—
<i>Strix aluco</i>	500	—	5.84	4.30(*)
<i>Strix uralensis</i>	800	4.90	—	—
<i>Strix nebulosa</i>	900	2.32	—	—
<i>Nyctea scandiaca</i>	1,850	2.06	—	—
<i>Bubo bubo</i>	2,500	6.68	2.40	3.30
	\bar{B}	3.86	3.57	3.22
	s.d.	1.52	2.06	1.97
	D_r	5.84	5.06	5.56
	$100 \times \frac{D_r - \bar{B}}{\bar{B}}$	51.29	41.73	72.67

Results and discussion

Latitudinal gradient in number of coexisting owl species

Fig. 1 shows that the number of coexisting owl species in western Europe decreases strongly southwards, reaching its minimal value in the Mediterranean region of southern Spain. Absolute numbers of breeding species fall from 8–9 at the two northernmost areas to 5 at the southernmost one. This gradient in species diversity can presumably be explained by intra-community ecological factors and we think the following paragraphs will largely support this assumption.

Niche breadth

Table I shows the values of food-niche breadth obtained for the individual species in each of the three communities. There are no significant differences between communities regarding B_i values ($P > 0.389$, $P > 0.562$, $P > 0.528$, for the three pairwise comparisons; Mann-Whitney U-test, Siegel 1956). However, some species show changes in their food-niche breadth from one community to another. *Athene noctua*, an almost exclusive invertebrate-feeder, contracts its niche noticeably in passing from Middle Europe to the Mediterranean region. The reverse is true for

Tyto alba. *Bubo bubo*, the largest European species, first contracts its diet when passing from Scandinavia to Middle Europe, but follows an opposite trend when arriving at the Mediterranean area. However, no consistent pattern emerges regarding the niche breadth changes of the individual species.

The constancy of the average food-niche breadth for the three communities (despite their differences in number of coexisting species) deserves further comments. It could be argued that one community holding a lower number of species than another, but with both showing similar average food breadth, might simply reflect the fact that the species-poor community faces a narrower range of exploitable food resources, thus maintaining a constant average food-niche breadth by means of species elimination. In other words, the total range of food resources available to a community would be roughly proportional to the product

\bar{B} (average breadth) · n (number of species)

In order to measure the overall utilization by the community of the food resources, and thus to obtain a value of 'food-niche breadth' of the community as a whole proportional to the range of exploited resources, we have used the following expression:

Table II. Food overlap matrices for the three owl communities studied

	<i>G.p.</i>	<i>A.f.</i>	<i>S.u.</i>	<i>A.o.</i>	<i>S.u.</i>	<i>S.n.</i>	<i>N.s.</i>	<i>B.b.</i>	
<i>G. passerinum</i>	1	0.637	0.946	0.578	0.623	0.689	0.412	0.331	SCANDINAVIAN COMMUNITY Mean 0.654 s.d. 0.295
<i>A. funereus</i>	0.775	1	1.123	1.004	0.931	1.243	0.891	0.171	
<i>S. ulula</i>	0.698	0.680	1	0.672	0.639	0.853	0.577	0.123	
<i>A. otus</i>	0.574	0.818	0.904	1	0.944	1.287	1.005	0.225	
<i>S. uralensis</i>	0.633	0.776	0.880	0.967	1	1.327	1.038	0.304	
<i>S. nebulosa</i>	0.378	0.560	0.634	0.711	0.716	1	0.803	0.128	
<i>N. scandiaca</i>	0.260	0.462	0.494	0.640	0.646	0.925	1	0.113	
<i>B. bubo</i>	0.613	0.261	0.309	0.420	0.553	0.431	0.331	1	

	<i>A.f.</i>	<i>A.n.</i>	<i>A.o.</i>	<i>T.a.</i>	<i>A.f.</i>	<i>S.a.</i>	<i>B.b.</i>	
<i>A. funereus</i>	1	0.327	0.829	0.865	0.878	0.577	0.786	MIDDLE EUROPEAN COMMUNITY Mean 0.713 s.d. 0.399
<i>A. noctua</i>	0.148	1	0.248	0.359	0.275	0.167	0.477	
<i>A. otus</i>	0.322	0.213	1	0.667	1.113	0.567	0.959	
<i>T. alba</i>	0.652	0.599	1.295	1	1.445	0.764	1.243	
<i>A. flammeus</i>	0.271	0.188	0.886	0.592	1	0.485	0.851	
<i>S. aluco</i>	0.601	0.385	1.521	1.057	1.634	1	1.454	
<i>B. bubo</i>	0.331	0.445	1.041	0.695	1.161	0.588	1	

	<i>O.s.</i>	<i>A.n.</i>	<i>T.a.</i>	<i>S.a.</i>	<i>B.b.</i>	
<i>O. scops</i>	1	1.015	0.052	0.607	0.056	MEDITERRANEAN COMMUNITY Mean 0.383 s.d. 0.463
<i>A. noctua</i>	0.983	1	0.051	0.600	0.056	
<i>T. alba</i>	0.183	0.186	1	0.246	0.065	
<i>S. aluco</i>	1.423	1.453	0.166	1	0.173	
<i>B. bubo</i>	0.135	0.137	0.044	0.175	1	

$$D_r = \exp \left[- \sum_h \left(\sum_j \frac{p_{hj}}{s} \lg_e \sum_j \frac{p_{hj}}{s} \right) \right]$$

where

$h = 1, 2, \dots, n =$ number of qualitative food categories,

$j = 1, 2, \dots, s =$ number of owl species,

$p_{hj} =$ frequency of the h -th food class in the diet of the j -th owl species.

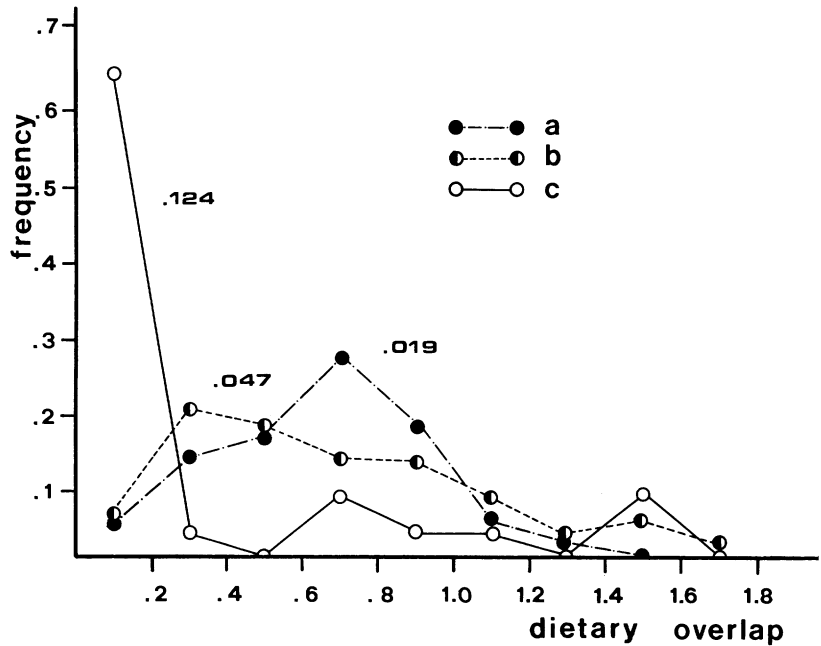
Furthermore, the difference between D_r and \bar{B} (average food-niche breadth), expressed as a percentage of \bar{B} , provides a measure of the different ways in which the food resources are exploited by the owl communities, since such a difference measures the intra-community utilization heterogeneity.

Table I shows that overall resource utilization values (D_r) are approximately equivalent for the three communities, thus indicating that they do not differ in the amplitude of the range of food

resources exploited by the component owl species. Also, the food spectrum is not qualitatively more diverse in the species-rich communities than in the species-poor, southernmost one. There are, however, inter-community differences regarding the intra-community utilization heterogeneity levels ($(D_r - \bar{B}/\bar{B}) \times 100$). The two northernmost communities show the lowest values, indicating a more restricted number of food exploitation methods despite their higher species richness. Paradoxically enough, species richness appears to be inversely correlated with food exploitation methods.

Diet breadth must be regarded as a function both of prey diversity and prey density (MacArthur & Pianka 1966, Emlen 1966, 1968, Schoener 1971, Jumars 1974). In the present instance it has been seen that available prey diversity, via niche breadth adjustments, does not appear to account for species diversity changes from one community to another. Geographical patterns of prey abundance will be mentioned below when dealing with the subject of food-niche overlap.

Fig. 2. Frequency distributions of dietary overlap values for the three communities studied: a, b, and c, Scandinavian, Middle European and Mediterranean communities respectively. Figures beside the curves are skewness measurements obtained by means of the third-order momentum with respect to the mean ($1/n \cdot \sum f_i (x_i - \bar{x})^3$).



Niche overlap

Food-niche overlap was calculated for all the species pairs within each community, and three alpha-matrices were obtained (Table II). It can be seen that average dietary overlap is greatest at the two northernmost, species-rich communities. Mean dietary overlap is minimal for the Mediterranean community, decreasing by 43.9 per cent with respect to the average of the other two mean values. Some individual alpha-values are remarkably high in the Scandinavian and Middle European communities, where there exist many species pairs showing alphas greater than unity. It is partially an effect of the expression used to calculate the overlap values, but it reflects also the reality of an almost exact coincidence between the diets of certain pairs of species.

Strong differences between communities appear when comparing the frequency distributions of alpha-values (Fig. 2). Asymmetry of the distributions increase noticeably southwards, leading to a greatly skewed curve for the Mediterranean community, where low values of dietary overlap predominate. Frequency distributions largely illustrate the intercommunity differences in interspecific overlap levels and show how dietary similarity of coexisting species follows a regular, latitudinal trend. Species packing along the food

dimension of the niche is then much tighter at the two communities showing a greater species richness as revealed by the average values of overlap. This was not unexpected since it was seen above that the total range of food resources exploited remains about the same for the three communities; furthermore, an increase in the number of coexisting species should imply a closer packing of them for the average food-niche breadth to remain as constant as observed. However, species packing is neither homogeneous along the food resource gradient nor proportional to the increasing number of coexisting species, but it occurs more intensely in some zones of the food spectrum and affects differentially the various species. Community dendrograms (Cody 1973, 1974) (Fig. 3) show the existence of clusters of species ('guilds', Root 1967) within which interspecific dietary overlap is more extensive, thus indicating the existence of species groupings in certain zones of the food dimension. This clustering effect is strongest in the Middle European community where five of the seven component species form a compact guild at a high level of dietary overlap (over 0.95).

An objective measure of the degree of clustering may be obtained by cutting across the dendrograms at an arbitrarily chosen level of overlap (say 0.70) and then recording the number of species

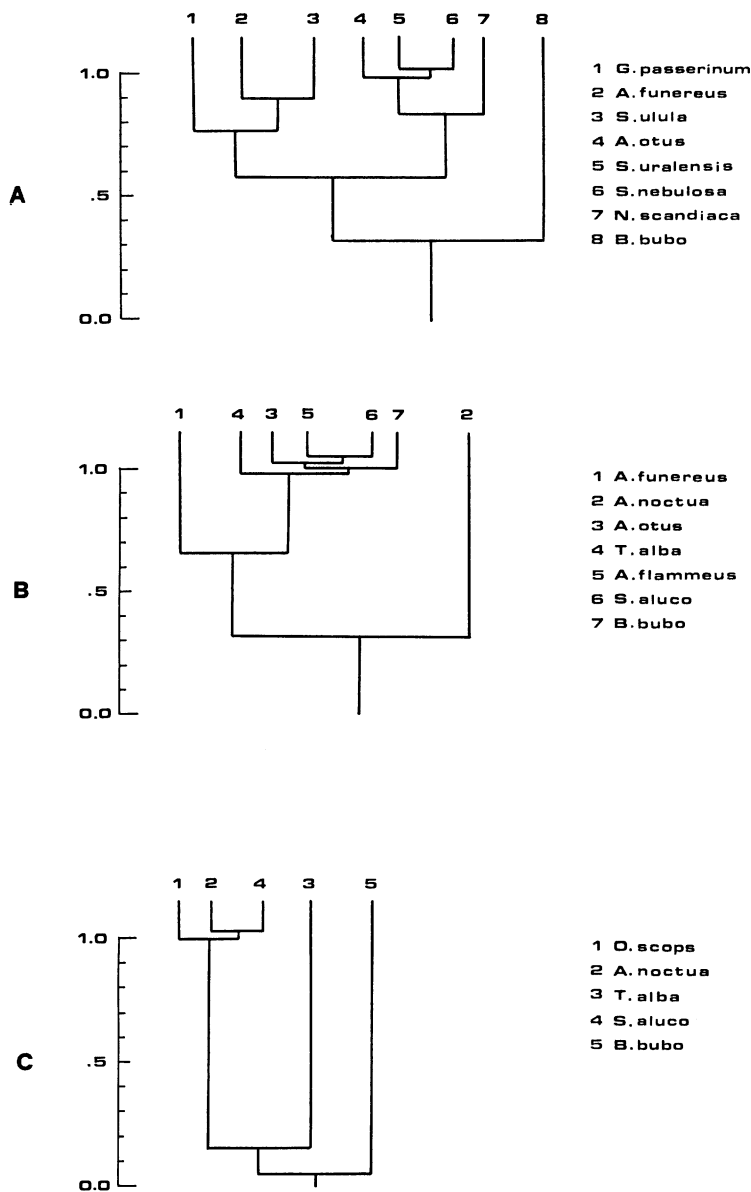
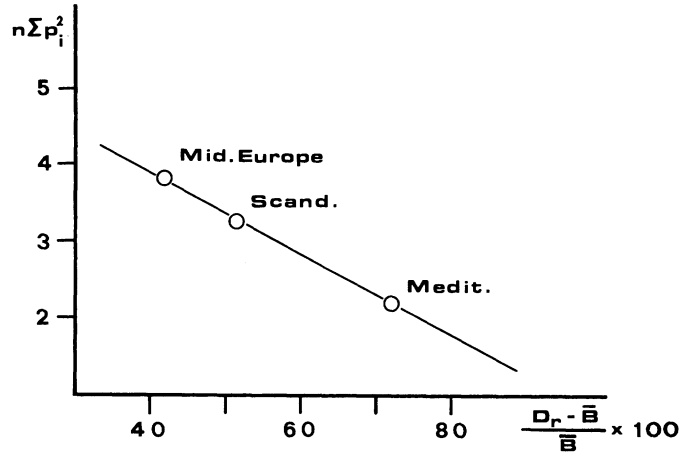


Fig. 3. Community dendrograms (Cody 1973, 1974) for dietary similarity obtained from the matrices in Table II previously symmetrized. Within each community, species are ranked and numbered according to increasing body weights: A, B and C, Scandinavian, Middle European and Mediterranean communities respectively. Ordinates are food overlap levels.

included in each of the resulting clusters. Expressing them as frequencies (p_i 's) with respect to the total number of species (n) in the community, a weighted measure of clustering is $n \cdot \sum p_i^2$. The values obtained were 3.248, 3.850, and 2.200 for the Scandinavian, Middle European and Mediterranean communities, respectively. Results agree well with the subjective impression obtained

by simply looking at the dendrograms. Clustering is maximal at the Middle European community and minimal at the Mediterranean one. As expected, the degree of clustering is negatively correlated with the food utilization methods ($D_r - \bar{B}/\bar{B} \times 100$) and correlation appears to be significant despite the extremely low number of pairs ($r = -0.9981$, $P < 0.05$, $n = 3$) (Fig. 4). This

Fig. 4. Plot of 'clustering degree' ($n \cdot \sum p_i^2$) against 'intracommunity utilization heterogeneity' ($(D_r - \bar{B}) / \bar{B} \times 100$) and line fitted by eye showing the inverse relationship between them. See text for further explanations.



demonstrates that, in fact, guilds represent species accumulations along the food co-ordinate of the environment and that utilization methods or 'intracommunity-exploitation-heterogeneity' as defined above has a real significance. Then, species packing is not homogeneous along the food resource continuum. Apparently, predator body weight is the basis on which guilds are formed (Fig. 3) although some exceptions occur. For instance, medium sized species (200–500 grams) tend to form the closest aggregations at the two northernmost communities although some large species may enter the groups. This suggests that intercommunity differences regarding the pattern of clustering may be related to differences in availability of the diverse prey sizes; this will be dealt with below.

Average dietary overlap found at the two northernmost communities appears remarkably high when compared with other predatory communities, and it is much more similar to the dietary overlap of primary consumer communities (Table III). On the other hand, dietary similarity in the Mediterranean community does not differ from the predatory communities' values listed in Table III. Parenthetically, it must be noted that the observed difference between predators and primary consumers regarding average dietary overlap is statistically significant, at least for the data shown in Table III, where predators show lower values than primary consumers ($P = 0.015$, Mann-Whitney U-test, Siegel 1956).

Now we are faced with the theme of the 'limiting similarity' (MacArthur & Levins 1967) or the maximum permissible overlap along a

single dimension of the niche (food in this instance) for coexisting species. May (1973, 1974) and May & MacArthur (1972) established that there is in fact a theoretical upper limit to the similarity between adjacent species which is not dependent on the degree of environmental fluctuations, but their model assumes a community in a saturated environment with all resources being fully used. Also, the model does not take account of resource abundance changes. Other authors (Colwell & Futuyma 1971, Pianka 1972, 1974a, 1974b) postulate that niche overlap in itself need not necessitate competition, and that two organisms can share common resources without detriment to one another if resources are not in short supply. Also, the maximum tolerable niche overlap is set by resource abundance (expressed by means of the demand/supply ratio, Pianka 1972) and extensive niche overlap may actually be correlated with reduced competition. A similar conclusion may be obtained from MacArthur's (1969, 1970) model of species packing: closer packing derives from a greater resource production.

The staple food of birds of prey in Central and Northern Europe is microtine species (cf. Appendix II) which undergo periodic population outbreaks or 'vole plagues' (Elton 1942). Lack (1946) analysed in a qualitative fashion the possible competition for food by Middle European birds of prey, both nocturnal and diurnal species, given the extensive dietary similarity shown. For those species pairs with similar diets but not differing in hunting habitat or time, Lack (op.cit.) postulated that competition did not occur because, for most of

Table III. Average food-niche overlap values for several ecological communities. Except for the data from Pianka (1973), calculated using a similar expression, overlap was calculated by using the formula of Levins (1968) described in the text

PREDATORS	
<i>Anolis</i> , Bimini, 4 sp. (Schoener 1968)	0.598
Lizards, Australia, 59 sp. (Pianka 1973)	0.320
Lizards, Kalahari, 21 sp. (Pianka 1973)	0.640
Lizards, North America, 11 sp. (Pianka 1973)	0.460
Owls, Colorado, 4 sp. (Marti 1974)	0.432
Owls, Iowa, 3 sp. (Weller et al. 1963)	0.384
Skinks, Senegal, 5 sp. (Barbault 1973)	0.510
PRIMARY CONSUMERS	
<i>Drosophila</i> , Puerto Rico, 5 sp. (Pico et al. in Pianka 1969)	0.800
Heteromyidae, Texas, 2 sp. (Alcoze & Zimmerman 1973)	0.698
Desert rodents, North America, 7 sp. (Brown & Lieberman 1973)	0.590
Invertebrate and vertebrate phytophagous, Colorado, 8 sp. (Hansen & Ueckert 1970)	0.495
Rodents, Colorado, 4 sp. (Flake 1973)	0.883
EUROPEAN OWLS	
Scandinavian community	0.654
Middle European community	0.713
Mediterranean community	0.382

the time, food (that is, microtines) is superabundant. Lack also argued that many of Uttendörfer's (1939) analyses he studied were made during times of *Microtus* superabundance, so results were obviously biased. The data we have used for the present study are from many different localities and years; they extend over a considerable period of time for the majority, and thus must be taken as representative of prevailing conditions. A strong dietary similarity appears as well in the Scandinavian and Middle European communities and it suggests that the dietary overlap values obtained correspond to average population levels of prey species. Also, it is not necessary to suppose superabundance (or 'vole plague') conditions to account for the high degree of food-niche overlap observed. It is rather that prevailing conditions lead per se to high overlap values because prey are not in short supply even in years which are not peaks. This is supported by the fact that in local conditions of extreme vole peaks, food overlap between locally coexisting species is even higher than that obtained from the rather general data we have treated throughout. Mean overlap for a group of four sympatric owl species (*Asio otus*, *A. flammeus*, *Tyto alba* and *Athene noctua*)

in a northern French locality in conditions of *Microtus* superabundance was 0.977, calculated from data given by Thiollay (1968).

Cyclic food resources fluctuate regularly between high densities and extreme scarcity; we are well aware that serious objections can be raised to the replacement of this pattern by average values. Community conditions change substantially with time depending on food availability; for instance, many owl species breed in low numbers or not at all in years of rodent scarcity, thus affecting community composition. Furthermore, species packing may be seen as the result of adjustments taking place during times of food scarcity, so average conditions would not be of relevance in studying it. In a broad sense, both the biotic and abiotic parameters of any ecological community are time-dependent, and experience various temporal rhythms. In studying them, a decision must be made involving the strategy to follow. Precision can be sacrificed to generality or, on the other hand, generality can be sacrificed to precision and reality (Levins 1966). 'Precision' strategy would involve a study of a quasi-continuum of states throughout many years and analysis of derivatives and rates rather than integrals over a time interval. We have chosen the 'generality' alternative all through this paper. This was primarily conditioned by the quality of the available information, but also by the fact that it was intended to elucidate geographical trends on a continental scale rather than the analysis of particular conditions in detail. We think that, although open to criticism, this 'long-term average' approach has been able to yield some valuable results.

Point measurements of microtine densities in the field, such as those found in the literature, are not of relevance for testing the above assumptions but indirect evidence may be more useful. If microtine species are in fact the key prey of owls in Central and Northern Europe, availability of such a resource must affect differentially the diversely sized predators, taking account of the well known relationships between predator and prey sizes (e.g. Storer 1966, Hespeneheide 1971, 1973, Beusekom 1972). Food preferences should have evolved in such a way that food items with high 'food values' will be favoured, that is, the predator will choose those items which give it the most 'food value' in return for its efforts; in its simplest form, 'food value' would be simply the calories assimilable in a given food item divided by the time required to find, capture, and devour the item (Valverde 1964, Emlen 1968). Further,

the 'food value' of a given item must be seen in connection with the energy requirements of the predator which are, in turn, dependent on its weight. A given food item is not expected to yield the same relative 'food value' to two differently sized predators. Then, microtine prey, although actually consumed by all the owl species in Central and Northern Europe, must show a different food value for every one of them. In other words, it can be theoretically expected that microtine prey will be optimal only for a given range of predator size. This may be easily tested by correlating food-niche breadth with the percentage of microtines in the diet, taking account of the theoretically known relationships between food-niche breadth and resource availability (Emlen 1966, 1968, MacArthur & Pianka 1966, Rapport 1971, Schoener 1971). Classifying predators according to their weights into three size classes (< 200 g, 200–500 g, > 500 g), results showed that the percentage of microtines in the diet is significantly correlated with food-niche breadth only in the case of those predators weighing between 200 and 500 grams ($r_s = -1.00$, $P < 0.01$, $n = 6$), that is, medium sized predators. It is particularly illuminating to find that the largest guild (five species) in the Middle European community dendrogram (Fig. 3) is mainly formed of species weighing 200–500 grams (four out of five). As microtine abundance produces a concentration of medium-sized predatory species at the two northernmost communities, it may be expected that microtine disappearance in the Mediterranean area must imply substantial changes in owl community organization. These changes do in fact occur: the total number of coexisting owl species decreases and medium-sized species are under-represented in comparison with the other two, northern, communities. This is clearly shown by the community dendrogram in Fig. 3. The only cluster is formed of invertebrate-feeder species (cf. Appendix II) and the remaining two, small mammal eating, species are sharply separated at low food overlap values (under 0.20).

The absence of the abundant microtine species (*Microtus*, *Clethrionomys*) affects the Mediterranean community in several ways. a) *Species elimination*. This is the case with *Asio otus* and *A. flammeus* which show the largest percentage of microtines in the diet (Appendix II); they have among the narrowest food niches of the Middle European community and show high dietary overlap values with regard to the neighbouring species (Table II). b) *Substantial dietary shift*. The case of

Strix aluco and *Bubo bubo*. In the Mediterranean community the former preys more often on invertebrate prey (Appendix II) and the latter largely replaces microtine suboptimal prey by rabbits (*Oryctolagus cuniculus*) (Hiraldo et al. in press). c) *Niche breadth adjustments*. The case of *Tyto alba*, which although remaining a small mammal predator (the only true one of the community), more frequently includes in its diet various other prey types (Herrera 1974b). Another community process seemingly characteristic of the Mediterranean community and to some extent balancing microtine disappearance is the emergence of a compact guild of invertebrate consumer species (*Otus scops*, *Athene noctua*, *Strix aluco*) which is absent altogether from the other two communities (Fig. 3). This agrees well with the fact (seen above) that overall community utilization of food resources does not show appreciable intercommunity differences; this suggests that in some manner the owl community finds in the invertebrate prey a new resource sufficiently widespread as to produce a species aggregation (cluster) on its basis. Dietary overlap values among the species constituting the Mediterranean insectivorous guild are as high as those observed among the microtine eating guilds of the two northern communities, thus revealing that dietary overlap values do not have an apparent upper limit but rather depend on resource availability in each spatial and temporal circumstance.

Conclusions

It has been seen above that large geographical changes affect owl community composition and structure; such changes may be easily explained by solely taking account of prey availability, although it may be presumed that in reality this situation must be much more complex than this. High population levels of a particular prey type (microtines) in Central and Northern Europe produce a close packing of species which consume this common resource and then overlap extensively in their diets. Food exploitation methods are there very restricted, and microtine abundance favours a given predator size. Consequently, species packing occurs discontinuously along the food gradient, as revealed by the great degree of clustering shown by the community dendrograms. The cluster of microtine-eating species breaks down in the Mediterranean community as a result of the scarcity of microtine prey. The disappear-

Table IV. Lower left half, recorded number of instances in which an owl species (row) has fed upon another species (column). Upper right half, species pairs which occur together in at least one food analysis. Data from Hagen (1965), Thiollay (1968), Janosy & Schmidt (1970), Mikkola & Sulkava (1970), Schaefer (1971), Choussy (1971), Glue (1972), and Hiraldo et al. (in press)

	<i>G. passerinum</i>	<i>O. scops</i>	<i>A. funereus</i>	<i>A. noctua</i>	<i>S. ulula</i>	<i>A. otus</i>	<i>T. alba</i>	<i>A. flammeus</i>	<i>S. aluco</i>	<i>S. uralensis</i>	<i>S. nebulosa</i>	<i>N. scandiaca</i>	<i>B. bubo</i>
<i>G. passerinum</i>			X	X		X		X					
<i>O. scops</i>			X	X		X			X				
<i>A. funereus</i>				X	X	X	X	X	X	X	X		
<i>A. noctua</i>						X	X	X	X				
<i>S. ulula</i>						X		X		X			
<i>A. otus</i>			1	1			X	X	X	X			
<i>T. alba</i>					1			X	X				
<i>A. flammeus</i>									X	X			
<i>S. aluco</i>													
<i>S. uralensis</i>													
<i>S. nebulosa</i>				1									
<i>N. scandiaca</i>													
<i>B. bubo</i>	2	1	19	11	14	63	11	15	45	1			

ance of the abundant microtines is followed by the elimination of some owl species, and niche breadth adjustments of the remaining ones take place in order to avoid an excessive dietary overlap which would not be tolerated by the limited small mammal supply. Food utilization methods are diversified in the Mediterranean community by means of the emergence of a tight guild of insectivorous species which follows the widespread occurrence of insects, a prey type rarely exploited by the two northern communities. This new exploitation strategy makes the qualitative diversity of resources harvested by the owls comparable with that at the remaining two, northern, communities despite microtine disappearance. Finally, it may be concluded that community average dietary overlap appears to be inversely correlated with prey supply, at least as deduced from the data presented here.

A critique

The preceding reasoning does not take account of an obvious aspect. Two species can share common resources if they do not utilize space or time in the same manner. As may be deduced from Schoener's (1974) recent review, spatial segrega-

tion appears as the more commonly used method of resource partitioning in ecological communities. As far as we know, no detailed, quantified account of habitat selection among European owls has ever been published, and the sparse data found in the literature are either of a general or anecdotal nature. The strongest evidence of species coincidence in the same habitats is the presence of an owl species in the diet of another species, and we have looked for this information in the available literature. Results, although obviously biased towards the larger, powerful species (*B. bubo*), demonstrate that spatial coincidence between species is a common fact and horizontal segregation is far from complete (Table IV). Against this are the theoretical considerations predicting interspecific territoriality for those species showing dietary similarity values as high as those observed among owls, having in mind the large feeding territories of these large birds (Cody 1973, 1974, Schoener 1968); several instances of interspecific territories have been reported from North American owls (Orlans & Willson 1964), but similar information is lacking for the European owl species. On the other hand, taxonomically defined food categories such as those we have used incorporate in themselves an indeterminate amount of informa-

tion about the spatial component of the owl niches because of the differences between prey species and/or genera regarding habitat selection and/or way of life. Also, qualitative food overlap values obtained are not quite independent of spatial overlap values. So, although the very scarce available evidence tends to show that spatial separation in Central and Northern European owl communities is not too obvious, our results must be taken as incomplete ones and they must await the completion of future investigations on owl habitat selection.

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Appendix I. Owl food analyses used throughout this paper and references. Figures are total numbers of prey items in the analysis.

SCANDINAVIAN COMMUNITY

<i>Glaucidium passerinum</i>	Mikkola (1970)	802
<i>Aegolius funereus</i>	Lindhe (1966), Fredga (1964)	1,770
<i>Surnia ulula</i>	Mikkola (1972b)	1,451
<i>Asio otus</i>	Hagen (1965)	3,645
<i>Strix uralensis</i>	Mikkola (1972b)	1,306
<i>Strix nebulosa</i>	Mikkola & Sulkava (1970)	4,026
<i>Nyctea scandiaca</i>	Andersson & Persson (1971)	1,887
<i>Bubo bubo</i>	Höglund (1966)	1,214

MIDDLE EUROPEAN COMMUNITY

<i>Aegolius funereus</i>	König (1969)	280
<i>Athene noctua</i>	Uttendörfer (1939), Thiollay (1968)	6,105
<i>Asio otus</i>	Uttendörfer (1939)	50,698
<i>Tyto alba</i>	Uttendörfer (1939)	36,911
<i>Asio flammeus</i>	Uttendörfer (1939)	4,991
<i>Strix aluco</i>	Uttendörfer (1939)	4,752
<i>Bubo bubo</i>	März (1954)	1,659

MEDITERRANEAN COMMUNITY

<i>Otus scops</i>	Hiraldo & Herrera (unpublished)	159
<i>Athene noctua</i>	Hiraldo (unpublished)	5,018
<i>Tyto alba</i>	Herrera (1974a)	14,806
<i>Strix aluco</i>	Hiraldo & Herrera (unpublished)	1,033
<i>Bubo bubo</i>	Hiraldo et al. (in press)	3,392

Appendix II. Summary of the food data used throughout this paper. Percentages are based on number of prey items. Symbols are as follows: *A.f.*, *Aegolius funereus*; *A.fl.*, *Asio flammeus*; *A.n.*, *Athene noctua*; *A.o.*, *Asio otus*; *B.b.*, *Bubo bubo*; *G.p.*, *Glaucidium passerinum*; *N.s.*, *Nyctea scandiaca*; *O.s.*, *Otus scops*; *S.a.*, *Strix aluco*; *S.n.*, *Strix nebulosa*; *S.ul.*, *Surnia ulula*; *S.ur.*, *Strix uralensis*; *T.a.*, *Tyto alba*. Taxonomic categories listed are not those actually used in the analysis of niche breadth and overlap, but are a summary of them.

SCANDINAVIAN COMMUNITY	<i>G.p.</i>	<i>A.f.</i>	<i>S.ul.</i>	<i>A.o.</i>	<i>S.ur.</i>	<i>S.n.</i>	<i>N.s.</i>	<i>B.b.</i>	Average
Mammals	65.7	97.7	98.6	96.4	83.4	98.5	63.1	56.7	82.5
(Microtinae)	(62.2)	(66.0)	(93.4)	(76.6)	(72.4)	(90.8)	(62.3)	(35.6)	(70.0)
Birds	33.5	2.2	1.2	2.5	10.6	1.1	1.2	23.6	9.5
Amphibians, Reptilians and Fishes	–	–	0.2	–	2.5	0.3	0.0	18.2	2.6
Invertebrate prey	–	–	0.0	0.4	2.6	–	–	0.3	0.4

MIDDLE EUROPEAN COMMUNITY	<i>A.f.</i>	<i>A.n.</i>	<i>A.o.</i>	<i>T.a.</i>	<i>A.fl.</i>	<i>S.a.</i>	<i>B.b.</i>	Average
Mammals	82.8	22.8	91.2	95.2	98.7	72.8	90.6	79.2
(Microtinae)	(24.8)	(17.8)	(82.2)	(55.3)	(91.8)	(50.1)	(78.2)	(57.1)
Birds	12.5	2.3	9.8	3.2	0.9	16.5	7.8	7.6
Amphibians, Reptilians and Fishes	–	1.0	0.0	0.6	0.0	8.7	0.9	1.6
Invertebrate prey	5.0	73.8	0.3	1.0	0.3	1.9	0.3	11.8

MEDITERRANEAN COMMUNITY	<i>O.s.</i>	<i>A.n.</i>	<i>T.a.</i>	<i>S.a.</i>	<i>B.b.</i>	Average
Mammals	1.2	2.8	86.1	28.5	65.1	36.7
(Microtinae)	–	(0.2)	(12.0)	(0.7)	(2.7)	(3.1)
(Murinae)	(1.2)	(2.3)	(56.6)	(22.5)	(3.5)	(17.2)
Birds	0.6	0.4	4.3	8.9	25.9	8.0
Amphibians	1.2	0.2	3.6	4.0	0.3	1.9
Reptilians	2.5	0.5	0.8	1.3	0.7	1.1
Fishes	–	–	–	–	2.7	0.5
Invertebrate prey	94.3	95.9	4.3	57.2	5.1	51.4