tinction. From the tens of millions that once grazed our central grasslands, a few dozen were held on ranches, and these became the breeding stock from which herds were propagated and distributed to parks, regufes, zoos, and private areas. Today there are some 50,000 American bison alive and doing well on various ranges. This is looked upon as a great success story, as indeed it is. But the common assertion that we have "saced the buffalo" is open to question.

Except for a few introduced animals in Alaska, all of our bison are behind fences and handled like herds of cattle, with annual surpluses removed for sale of butchering. But who, except the wild wolf, knows how to cull a bison herd? Nowhere is the buffalo living free on its native grassland under the primitive husbandry of its natural carnivore custodian. There is little doubt that is speciation is being directed in unnatural and unknown directions. We see the need for a major grassland park, where buffalo bands have space to roam, under inspection by wolves closely related to the now-extinct race that inhabited the central plains in early times. Until that comes about, we will not have saved the buffalo, or any kind of buffalo wolf.

We obviously are "preserving" rare and endangered species under compromising conditions, but we are in a period of our history when compromise is necessary. We may be approaching a time when the last tigers, lions, and other big cats will be in wildlife parks and zoos. The same can be said of the California condor, the red wolf, and perhaps our most endangered American carnivore, the black-footed ferret. We can be thankful for behavioral studies and for the zoos that are getting ready. Such methods could provide our only opportunities to retain breeding stocks, whatever their quality, of many species. Work of this kind could make possible—in 50 ro 100 years—the stocking of restored ranges. However it turns out, even makeshift preservation expedients are better than giving in to failure.

As all of us are well aware, in this attempt to appraise the future, I have not anticipated the worst that could befall our own species and other liv[illegible] things. I ha[illegible] gnored the nuclear threat, and likewise the chances of a drastically changed climate. A climatic disaster could reward our impatience to burn up every carbon deposit in the rock mantle beneath our feet—added to the worldwide oxidation of denuded soils and disturbed biomass. These are possibilities, but we probably can assume that biologists will not do much about them.

I think our particular role is to draw upon what we know of living systems and contribute to public understand of man-environment-wildlife relationships. Humanity is in the biosphere lifeboat, and we do not travel alone. It should be our theme that no species exists in isolation. Plants and animals come packaged for survival in communities, and there is no other way for creature or for man.

As we bring our message to people of other faiths, we will do well to emphasize the population status of our own kind—the rapid increase, the urgency of reducing birth rates. The most authentic and persuasive objective in a population policy is to improve living standards. But that needs some definition if we are to avoid pitfalls. A living standard should be based on omdigenous culture and traditions, and also largely on local resources. It must be for the future as well as the present. Inherently, this involves concern for the quality of air, soil, and water; stabilizing the hills and their protective greenery; sharing space with other animal life.

Surely most of us believe, and are able to convey to others that respect for the earth is respect for ourselves. A moral issue is involved, that of honoring our children by guarding the estate that is both ours and theirs. As individuals we learn that providing for the future is the way to security, and sometimes that involves a wholesome self denial in the present. Perhaps it is the essence of civilization that as a society we must do the same. In using the vast wealth that was so recently ours, we obviously have overdrawn our account, and some frugal saving is now in order.

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Factors Limiting Numbers of Vertebrate Predators in a Predator Prey Community

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Abstract

Dynamics of co-existing vertebrate predators were examined in an open field area in southern Sweden (4500 ha). The predators contained two groups: one feeding mainly on small rodents i.e. long-eared owl, kestrel, stoat, and weasel (the small rodent specialists), and another having a varied diet of rabbits, small rodents, birds, frogs, insectivores and invertebrates (the generalists). This group consisted of the fox, the badger, the domestic cat, the polecat, the common buzzard, and the tawny owl. The generalists consumed much greater quantities of prey than did the specialists; the populations of the generalists were larger than those of the specialists, and the former ones have larger body size and greater food requirements. The main part of small rodents (80% of the yearly consumption) was eaten by the generalists. It was concluded that the small rodent specialists were limited in numbers by shortage of food, primarily due to food competition by the generalists. For the small mustelids (the stoat and the weasel) predation by the larger predators was probably also important. The other predators, the generalists, were primarily regulated by territorial behaviour. The number of breeding individuals in these populations were similar from year to year. The populations of the specialists, on the other hand, varied greatly.

A community of vertebrate predators and their animal prey is being studied in an open field area of about 45km^2 in southern Sweden. Three types of habitats are involved: wet meadows inhabited by voles, primarily the field vole Microtus agrestis L. and the water vole Arvicola terrestris L; dry areas, some covered by pine plantations; and open fields grazed by cattle. The dry areas with adjoining fields are populated by rabbits Oryctolagus cuniculus L. Field mice (Apodemus sylvaticus L.) are found in the grazed fields. Copses of deciduous trees interspersed over the area and the pine plantations provide suitable nesting sites for birds of prey.

The most important prey were rabbits (Fig. 1). During 1975 and 1976, they formed about half of the estimated biomass eaten by the predators. Small rodents were next (about 20% of the total consumption). Others were frogs, birds, insectivores, and invertebrates (insects and earthworms). Important predators are the red fox (Vulpes vulpes L.), the badger (Meles meles L.), the common buzzard (Buteo buteo L.), the domestic cat (Felis catus L.), the polecat (Mustela putorius L.), the tawny owl (Strix aluco L.), the kestrel (Falco tinnunculus L.),

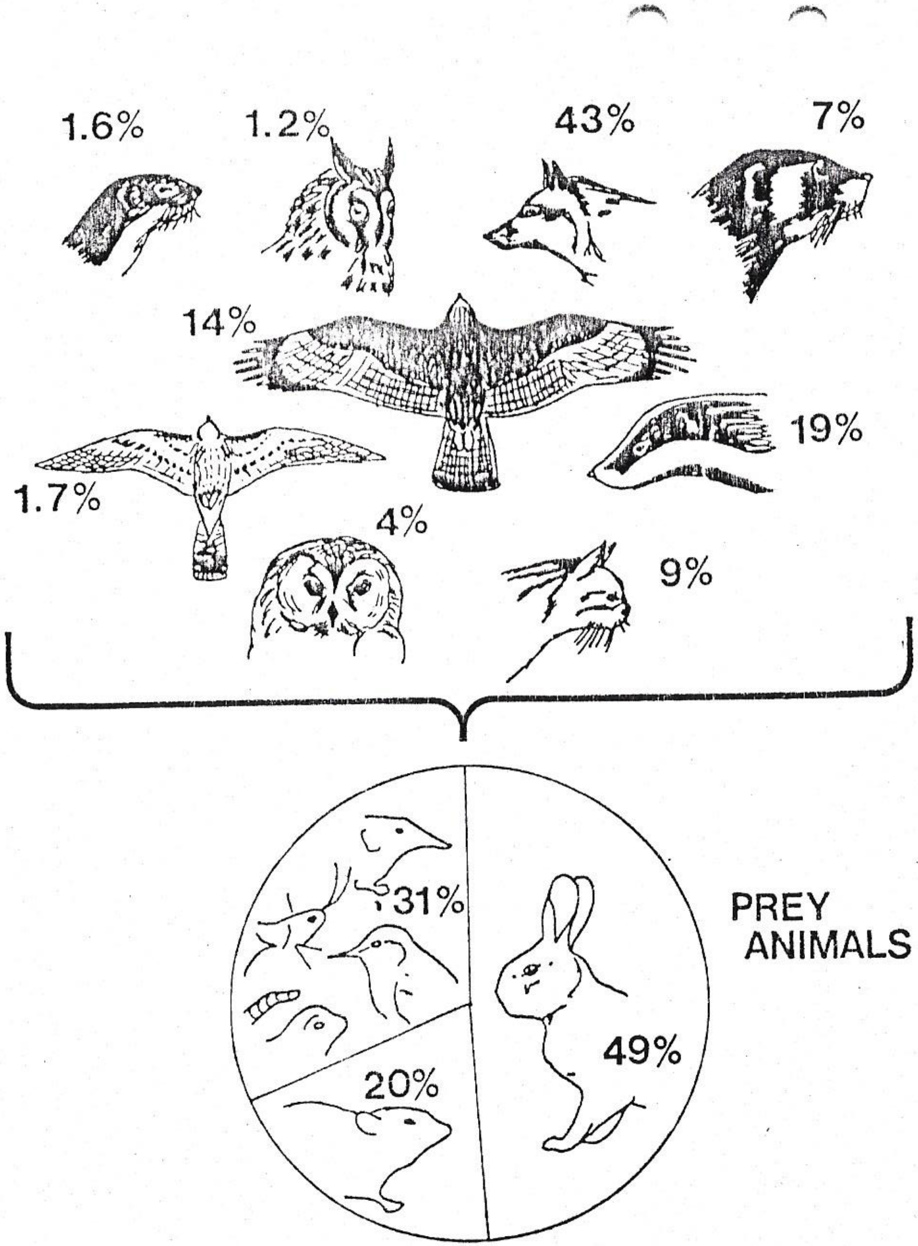

Figure 1. Important prey animals and predators of the examined community. The proportion of important prey categories (% of the total prey consumption, i.e. 35,000 Kg per year) and the proportion eaten by the various predators (the average for 1976 and 1977) is shown. The figures are based on data on numbers of predators, their food requirements, and food spectra for the whole year.

	M.e	F.t	A.o	S.a	M.p	V.v	F.c	B.b	M.m	x̄
Mustela erminea		0.82	0.62	0.45	0.12	0.10	0.41	0.56	0.10	0.40
Falco tinnunculus	0.82		0.76	0.38	0.11	0.10	0.34	0.54	0.08	0.39
Asio otus	0.62	0.76		0.38	0.10	0.08	0.38	0.48	0.06	0.36
Strix aluco	0.45	0.38	0.38		0.28	0.12	0.32	0.38	0.10	0.30
Mustela putorius	0.12	0.11	0.10	0.28		0.50	0.42	0.44	0.09	0.26
Vulpes vulpes	0.10	0.10	0.08	0.12	0.50		0.66	0.44	0.08	0.26
Felis catus	0.41	0.34	0.38	0.32	0.42	0.66		0.71	0.08	0.41
Buteo buteo	0.56	0.54	0.48	0.38	0.44	0.44	0.71		0.08	0.45
Meles meles	0.10	0.08	0.06	0.10	0.09	0.08	0.08	0.08		0.08

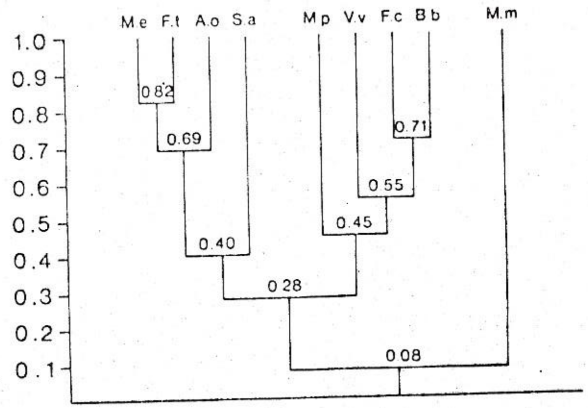

Figure 2. Food overlap in the assemblage of predators in late autumn (October to December). The diet of the predators was compared in pairs and food overlap was calculated according to the formula $1 - ½\Sigma(P_i - P_j)$, where i and j denote the relative importance of the various prey categories in the two compared predators (Colwell and Futuyma 1971). The dendrogram was constructed according to Cody (1974).

the stoat (Mustela erminea L.), and the long-eared owl (Asio otus L.).

The predators' diet overlapped in various degrees. This was examined for different seasons of the year. The dendrogram (Fig. 2) concerns late autumn (October to December). The performance during that period was basically representative for the whole year. Three predators–the stoat, the kestrel, and the long-eared owl–showed a high degree of food overlap. They fed mainly on small rodents (about 85% of their diet) and are referred to in the following as the small rodent specialists. Associated with them, but with a more varied diet and considerably less overlap, was the tawny owl. The common buzzard, the domestic cat, the fox, and the polecat formed another group with much food in common. The badger's food differed from that of the others. The predators, apart from the small rodent specialists, generally had a varied diet of rabbits, birds, frogs (im-

Table 1. Body weight and food requirement of the various predators

	Meles meles	Vulpes vulpes	Felis catus	Mustela putorius	Buteo buteo	Strix aluxo	Asio otus	Falco tinnunculus	Mustela erminea
Body weight (kg;g)	10 8	8 7	4.5 3	1.4 0.9	0.8 1.0	0.55 0.45	240 300	190 210	230 130
Food requirement (g day $^{-1}$)	500	450	350	175	150	100	60	60	65 40

portant especially for the polecat), invertebrates such as earthworms (a specialty of the badger), and small rodents. These predators are referred to as the generalists or the facultative small rodent predators.

The factors limited the number of the various predator populations are examined. We have accepted as a working hypothesis that the predators are primarily limited by food and competition for food. We also examine territorial behaviour as a factor regulating the numbers in the individual populations.

Partitioning of food resources and competition for food

The total prey biomass eaten by the predators was estimated from data on number of individuals in the various populations and their food requirement. Food spectra obtained from the analysis of scats and pellets showed the relative importance of the various prey categories. Used methods, including those for the evaluation of food remains, will be presented elsewhere. One method used for counting two of the predator populations (the red fox and the domestic cat) will be given in another paper at this congress by v. Schantz and Liberg.

The main part (95%) of the total prey biomass eaten by the predators went to the generalists (Fig. 1). Only a small part (5%) was taken by the small rodent specialists. Compared with the specialists the generalists

Table 2. Numbers of individuals in the various predator populations at breeding times in 1975 to 1978. The degree of variation in numbers is shown by the coefficient of variation values. The figures for Mustela erminea are from the calendar of capture and are considered to be minimum numbers.

	Generalists						Specialists		
Year	Meles meles	Vulpes vulpes	Felis catus	Mustela putorius	Buteo buteo	Strix aluco	Asio otus	Falco tinnunculus	Mustela erminea
1975	30	?	72	24	44	28	22	21	19
1976	42	36	55	27	36	32	6	10	19
1977	33	32	66	24	38	32	6	8	14
1978	?	36	75	?	40	32	10	12	8
$\bar{X} = \pm SD$	35.0±6.2	35.2±2.1	67.0±8.8	25.0±1.7	39.5±3.4	31.0±2.0	11.0±7.6	12.8±5.7	15.0±5.2
$CV = (\frac{SD}{\bar{X}} \times 100)$	17.7	5.9	13.1	6.8	8.6	6.4	69.1	44.5	34.7

are large-sized and their food requirements are large (Table 1). Also the populations of the generalists were usually larger than those of the specialists (Tab. 2). These things explain the dominance of the generalists.

Important prey categories, constituting about three-fourths of the total prey consumption were exploited almost exclusively by the generalists, whereas all the prey categories taken by the small rodent specialists were also taken by the generalists. Thus, taking the year as a whole, all the food resources of the small rodent specialists were exploited also by the generalists. The main part of prey used in common consisted of small rodents (Fig. 3). Most of them (i.e. 80% of the yearly small rodent consumption) were eaten by the generalists or the facultative small rodent predators, only a small part being eaten by the specialists.

Available data on numbers and production of small rodents (the field vole and the field mouse) showed in rough terms that the biomass of small rodents eaten by the predators equalled the yearly production of the rodents (Hansson, unpubl., Erlinge et al. unpubl.). Therefore, taken year round, the small rodents were considered to be in short supply for the predators. This and the fact that the main part of the small rodents was taken by the generalists support the conclusion that the small rodent specialists were limited in numbers by food competition, mainly by the facultative small rodent predators. On the other hand, the negative influence by the small rodent specialists on the generalists was probably very slight.

Rabbits were important prey for many of the generalists. Contrary to the condition for the small rodents, only a small part of the rabbit production in 1975 and 1976 was eaten by the predators, and the rabbit population increased markedly during these years (Jansson, unpub.). During the winter of 1976/77, the rabbit population markedly decreased due to hard weather; in 1977 and 1978, the density was only about one-third of that in 1976. However, the spring density of the rabbit-feeding predators remained at the same level throughout the period (Table 2). These data indicate that at least in years of high rabbit density, the generalists did not fully exploit available food resources; therefore, their populations were possibly limited by factor(s) other than food.

The influence of territorial behaviour

The social organisation of the examined predators varies. The kestrel and the long-eared owl are mainly non-territorial; they defend only a small area around their nest site, and several individuals sometimes hunt in the same area (Hogstedt unpubl., I. Nilsson, unpubl.). This was also found in kestrels and long-eared owls studied in Holland (Cave

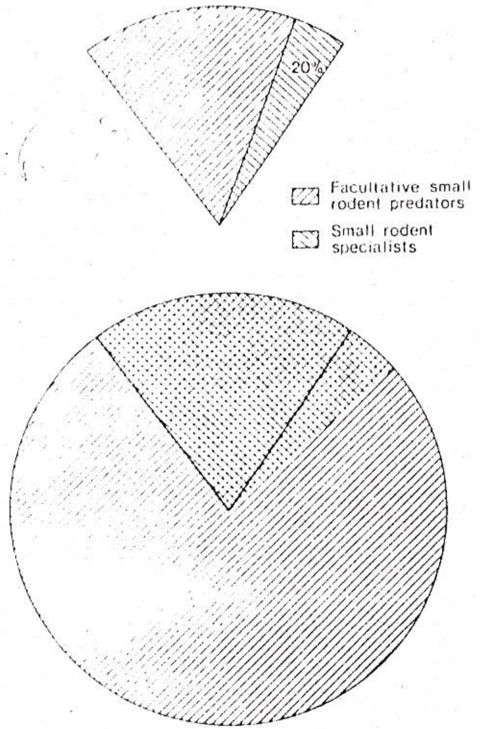

Figure 3. Prey used exclusively by the facultative small rodent predators and in common with the small rodent specialists. The circle denotes the total prey biomass consumed by the predators during a year. The part of overlapping food which consists of small rodents is indicated (the deliniated sector). The proportion of small rodents eaten by the two categories of predators is shown on the upper diagram. The figures are based on data from 1975 and 1976 as in Figure 1.

1968, H. Wijrandts pers. comm.) Other predators are strictly territorial throughout the year, and individual pairs or groups of individuals defend areas with little or no overlap. This concerns the common buzzard (Sylven, unpubl.; also reported in Britain, Dare, 1961), the tawny owl (Southern, 1970, I. Nilsson, unpubl.), the red fox (Macdonald, 1978, v. Schantz, unpubl.), and the badger (Kruuk, 1978, Goransson, unpubl.). In the stoat, breeding females occupy small areas exclusive to other females and situated within the males' home ranges, which are extensive and with overlapping boundaries at mating time (Erlinge, 1977). The spatial organisation of the polecat is probably similar to that of the stoat (T. Nilsson, unpubl.). The number and the distribution of the domestic cat were strongly influenced by the distribution of the households and the behaviour of the householders. Therefore, the social behaviour of the cats had a slight influence on the number although territoriality was found to occur also in cats (Liberg, in press).

To summarise: All the examined generalist predators are territorial, and apart from the domestic cat, whose number was largely due to some special circumstances, territorial behaviour probably limited the number of breeding individuals or pairs in these populations. This was also indicated by the fact that a surplus of non-breeding, but sexually mature, individuals was found in some of the populations.

Populations being regulated by social behaviour typically show a high degree of stability from year to year. This was also found in the examined generalist populations (Table 2). The populations of the small rodent specialists, on the other hand, showed great variations, especially the long-eared owl and the kestrel (Table 2). The number of stoats markedly decreased in 1977 and 1978, and only a few of their preferred habitats were then occupied. Besides being limited by shortage of food, the number of stoats and also weasels (Mustela nivalis L.), which were very scarce in the area, was probably limited by predation. The small mustelids were preyed on by the domestic cat, the polecat, the common buzzard, and the tawny owl as was evidenced from the analysis of food remains. They are probably also killed but not eaten by the fox. Remains of the weasel were also found in scats of stoats and pellets of long-eared owls.

To summarise: Extensive field data provide circumstantial evidence for the following conclusions: In the assemblage of predators examined, some of them, i.e. the small rodent specialists, were limited in numbers by shortage of food, primarily due to food competition by the facultative small rodent predators. For the small mustelids (the stoat and the weasel) predation by the larger predators was probably also important. The other predators, the generalists, were primarily regulated by territorial behaviour. The number of breeding individuals in these populations were similar from year to year.

Acknowledgements

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References

Cave, A.J. 1968. The breeding of the Kestrel Falco tinnunculus L. in the reclaimed area Oostelijk Flevoland.–Netherl. J. Zoo. 18 (3) : 313-407.

Cody, M.L. 1974. Competition and the structure of bird communities.

Colwell, R.K., and F.J. Futuyma, 1971. On the measurement of niche breadth and overlap.–Ecology 52:567-576.

Dare, P.J. 1961. Ecological observations on a breeding population of the Common Buzzard Buteo buteo, with particular reference to the diet and feeding habits.–Ph. D. Thesis; Exeter Univ.

Erlinge, S. 1977. Spacing strategy in stoat Mustela erminea.–Oikos 28: 32-42.

Kruuk, H. 1978. Spatial organisation and territorial behaviour of the European badger Meles meles.–J. Zool., Lond., 184: 1-19.

Liberg, O. In press. Spacing patterns in a population of free-roaming domestic cats Felis catus L. – Oikos.

Macdonald, D.W. 1979. Rabies and Wildlife: a biologist's perspective. Oxford Univ. Press.

Southern, H.N. 1970. The natural control of

a population of Tawny owls (Strix aluco). – J. Zool. Lond. 162: 197-285.
Sylven, M. 1978. Interspecific relations between sympatrically wintering Common Buzzards Buteo buteo and Rough-legged Buzzards Buteo lagopus.–Ornis Scand. 9: 197-206.

Hunting Efficiency and Prey Impact by a Free-Roaming House Cat Population

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Abstract

Hunting in free-roaming house cats Felis catus L., was studied by visual observations. A total of 104 hours of observations of cat activity in the terrain were recorded. Cats concentrated on rodent hunting in autumn and spirng, while rabbit hunting dominated in summer. Rodents were taken in about five times as short time as rabbits, but the time input per rodent taken increased from about 40 minutes in autumn, when rodent populations had their highest density, to about 70 minutes in early summer, when rodent populations were at their bottom values. Differences between domestic femals and feral male cats in hunting efficiency and prey selection are discussed in terms of social behaviour and optimal foraging. Cat occurrence in the terrain was measured through counts in sample plots in both daytime and nighttime. Number of rodents taken by cats in the whole area per autumn and spring periods was computed. These figures are compared with corresponding figures based on analysis of faeces, and the discrepancy between the estimates in one of the seasons is discussed. It is shown that cat predation corresponds to 20-40% of the winter loss in Microtus agrestis.

Free roaming domestic cats Felic catus L. are important predators on small vertebrate prey, especially rodents (Pearsson 1964, Ryszkowski et al 1973). In a joint study of predator-prey relationships in Southern Sweden (Erlinge et al, in press) several aspects of house cat predation were studied. The major data on prey selection and numerical exploitation of prey populations are based on faeces analysis, but in this talk I will report on a study of predatory behaviour of house cats based on visual observations. This method yields information on the time budget of the hunting cats, which then can be used to calculate numerical exploitation of the prey. This gives a check on the corresponding data received from faeces analysis, which is especially valuable since exploitation figures based on either method were impossible to evaluate statistically in my case.

I wish to thank S. Erlinge and my colleagues in the Wildlife Research Group in Lund for valuable help and criticism, and to all the cat owners in the study area, without whose cooperation and assistance this study would have been impossible.

Methods

Study area

The study was performed in the Revinge military training area in southernmost Swe-