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A comparison of the feeding biology of Mink *Mustela vison* and otter *Lutra lutra*

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(With 20 figures in the text)

The feeding habits and prey selectivity of Mink *Mustela vison* and otters *Lutra lutra* were compared in two localities in Devon: a eutrophic lake and a moorland river, in which both species occurred and had access to the same prey populations. The effects of prey availability on the predators' diets were assessed by comparing prey consumed, as revealed by scat analysis, with estimates of prey abundance and size range. Otters specialized in fish at all times of year but showed seasonal variation in species taken. Selection for slow-moving fish and seasonal changes in behaviour of some fish species were the probable causes of this variation. Otters diversified more into non-fish food in summer, when fish availability was reduced. The main alternative prey in the lacustrine habitat was waterfowl, but in the riverine habitat, rabbits. Mink were more generalized carnivores, taking a variety of fish, waterside and terrestrial prey in all seasons. These three prey categories were taken to an almost equal extent in the lake but terrestrial prey dominated in the riverine habitat. Fish were taken most frequently in winter and birds and mammals in summer. Neither predator showed selection in respect of prey size. In each area, about one third of the otter and Mink diets was common to both species. Fish was the principal group of the shared component, and dietary overlap in respect of them was greatest in autumn and winter. In view of the dietary preferences of each predator, the existence of alternative prey items and limited degree of dietary overlap, it is considered unlikely that the two species competed for food to any extent. Other factors must therefore be responsible for the spread of feral Mink and the decline in otter populations in many parts of Britain.

Contents

Introduction

The escape of Mink *Mustela vison* from fur-farms and their ability to establish themselves in the wild (Thompson, 1962, 1968) to such an extent that they can now be considered a

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permanent addition to the British fauna has caused concern on two main counts: the possible impact on their prey and their effect on the native carnivores. Feeding studies on the American Mink in its native country have shown it to be a generalized carnivore, but with aquatic organisms forming a significant component of its diet (Sealander, 1943; Guilday, 1949; Wilson, 1954; Korschgen, 1958; Hamilton, 1959). Its association with watercourses has been demonstrated in every country into which it has been introduced (Westman, 1968; Wildhagen, 1956; Gerell, 1967*a*; Novikov, 1962; Gudmunsson, 1952; Cuthbert, 1973). Previous studies on its diet and habits in Britain have confirmed its association with water and shown that aquatic prey comprised 30–50% of its diet (Akande, 1972; Day & Linn, 1972; Chanin & Linn, 1980). Thus, the native carnivore most likely to be affected by the spread of Mink is the otter *Lutra lutra*.

The possibility that Mink may deleteriously affect otters is of particular concern in view of the recent decline in the otter population in Britain (J.O.G. Report, 1977). Although many factors may have contributed to this decline, the fact that it has occurred simultaneously with the expansion of Mink and that otters have disappeared from areas where Mink had become established has suggested that the events may be causally related (Thompson, 1968, 1971). A similar decline in otters and an inverse correlation between densities of Mink and otter has been noted in Sweden by Erlinge (1972*a*). He suggested (1972*b*) that the reduction in the otter population may have made it easier for Mink to colonize the country, but he also concluded that since the diet of the two predators overlapped by 60–70% (Erlinge, 1969), in severe winters competition between the two species occurred. Studies on the diet of otters in Britain and Sweden have shown that in all instances fish were the major prey and other items, although taken regularly, were of minor importance (Erlinge, 1967; Stephens, 1957; Weir & Banister, 1973, 1977; Chanin, 1976). The only direct comparison of Mink and otter diets in England is that of Chanin (1976), who found that otters fed mainly on fish, whereas Mink had a much more varied diet. He considered that the feeding habits of both species to some extent reflected the availability of prey, a conclusion reached for each species independently in Sweden by Erlinge (1967) and Gerell (1967*b*). All these authors, however, were concerned primarily with the carnivores and were not able to make detailed quantitative estimates of the prey species.

The particular aim of this present study was to make a detailed comparison of the feeding habits of otters and Mink present within the same areas and so having access to the same prey populations. The effects of prey availability on the predators' diets were investigated by comparing the feeding habits of otters and Mink in two areas which differed markedly in nature and faunal composition and by assessing prey availability and comparing it with prey consumed. The results are then discussed with particular reference to the feeding ecology of the two predators, the possibility that they may compete for food and the likelihood of Mink having a deleterious effect upon otters.

Methods

Study areas

Two contrasting areas were selected for the study. Slapton Ley is a small, shallow, eutrophic, freshwater lagoon on the South Coast of Devon, described in detail by Mercer (1966) and Morey (1976). It comprises two basins, the larger of which is open water with a narrow fringe of reed

Phragmites communis, which may locally form a reed swamp. The smaller basin is connected to this, but is almost completely covered by vegetation, with a fringing reed swamp surrounding floating rafts of peat and carr. The Ley is bordered by fields, woodlands, marsh and scrub. It supports a rich and varied fauna. The fish fauna is dominated by Roach *Rutilus rutilus*, perch *Perca fluviatilis*, eels *Anguilla anguilla* and Pike *Esox lucius*. Other species including Brown trout *Salmo trutta* and Rudd *Scardinius erythrophthalmus* are found in the lake but are rare or of local occurrence. A variety of passerines is abundant around the lake, whilst the lake itself is used by several species of resident and migratory waterfowl (Burton & Mercer, 1978). Preliminary studies indicated that the otter population was at a higher density here than anywhere else in Devon, whereas there was only a sparse and localized Mink population.

The River Webburn is a tributary of the River Dart. It rises on Dartmoor and is a typical fast-flowing moorland river. It flows through fields and woods before reaching the study area. This was a stretch of about 4 km, where the river flowed through a gorge-like wooded valley containing mixed deciduous woodland and stands of conifers. There is considerable development of shrub and vegetation along the margins. The rapid flow and seasonal flooding limits the aquatic macrophytes. The fish fauna is dominated by salmonids, comprising Brown trout *Salmo trutta fario*, Sea trout *S. trutta trutta* and salmon *S. salar*. Eels, Bullhead *Cottus gobio* and Stone loach *Noemacheilus barbatulus* are also present. The dominant birds are passerines and pigeons (*Columba* spp.)—waterfowl are scarce. Both Mink and otter were present in the study area throughout the study period. High winter water levels rendered much of the stretch inaccessible, and so a subsidiary area was selected for winter sampling. This was a stretch of the River Dart below its junction with the Webburn. It was essentially similar in character to the main study site.

Determination of predator diets

Predator diets were determined by means of scat collection, identification of contained prey remains and analysis. The advantages in using scats were held to outweigh the disadvantages, and scat analysis has been shown to give an accurate reflection of prey items ingested (Erlinge, 1968; Akande, 1972). Scats were collected from the two study areas over a period of two years from December 1974 to November 1976. Standard collection routes were followed on each visit and all scats removed along the routes on each occasion. Each site was visited at least twice a month and frequently more often. As monthly samples were small, results were grouped according to season as follows: winter, December–February; spring, March–May; summer, June–August; autumn, September–November. The number of scats found in each season at each site is shown in Table I. Otter and Mink scats were distinguished by form and smell (Gerell, 1967*b*). Any which could not be positively identified were rejected. Each scat was placed in a separate tube and details of its identity and locality recorded.

Scats were oven dried at 50°C for 24–48 h, weighed and stored dry before analysis. They were then crumbled gently between finger and thumb, and their contents examined. Invertebrate remains were identified by recourse to a reference collection. Fish were identified using scales, operculae or vertebrae. Wherever possible, the remains, especially vertebrae, were used to estimate the length of the prey fish in the manner described by Wise (1980). Amphibian and reptile remains were identified by recourse to reference skeletons. Birds were identified using Day's (1966) key to downy barbules, and mammal remains by using tooth (Morris, 1966) or guard hair characters (Day, 1966).

No one method of presentation was considered to reflect accurately the relative importance of the wide variety of prey species to the predators. Results were therefore presented in a variety of ways so that the biases of each method could be studied, and to enable comparison of results with other studies. Frequency of occurrence data were used to test for seasonal variation within prey groups and species, using Chi-square. However, as experimental trials using a known diet on captive Mink showed frequency of occurrence to be an unreliable estimate of dietary intake,

over-representing minor items and under-representing major ones, a bulk estimate was developed which, without being any more laborious or time-consuming than the frequency of occurrence method, established a considerably more realistic relationship between major and minor food items. The importance of each prey item was estimated visually and scored on a scale of 1–10, so that the total score for each scat was 10. The score for each item was then multiplied by the scat dry weight, the resulting figures summed for each item in each sample and expressed as a percentage. This bulk estimate is similar in principle to the method used by Lockie (1959); experimental trials showed it to be reliable, consistent and repeatable. Bulk percentages were therefore used to compare seasonal, annual and overall patterns of dietary importance of prey to otters and Mink.

Estimation of prey populations

Previous studies at Slapton Ley (Chanin, 1976) had indicated that plants and invertebrates were unimportant in the Mink and otter diets, and so both were ignored. Fish were caught regularly by seine, gill net, electric fishing and traps as part of an independent research programme (Burrough, 1978; Burrough & Kennedy, 1979; Bregazzi, 1978) and data on their abundance and size were available for each month throughout the sampling period. Both amphibia and reptiles were very scarce, and quantitative estimates of them were neither feasible nor warranted. Waterfowl were assessed by monthly visual counts at selected sites, the results being supplemented by reference to local records. Direct counts were made of other waterbirds but information on terrestrial birds was also obtained from local records. Relative abundance of small mammals was assessed from the results of catches in Longworth traps. Lines of traps were set up in four different types of habitat adjacent to the Ley in each season and an index of relative abundance obtained in the manner described by Linn & Downton (1975, 1976). Live-trapping of rats proved unsuccessful, and an estimate of their activity was eventually obtained by using a footprint detector (Wise, 1978). Initial attempts were made to estimate squirrel densities by monthly transect counts but numbers were so low that quantitative estimation was abandoned. An index of rabbit abundance was initially obtained by dawn and dusk counts along a transect at monthly intervals, but this was later changed to spotlight transect counts at night in two areas adjacent to the Ley.

Estimates of vertebrates only were made on the river site. Data on movements of migratory fish based on commercial seine and rod catches were obtained from the Water Authority. Estimates of population number and size composition of resident fish were obtained from electric fishing operations carried out on two sections of the river in each season. Densities were estimated by the catch depletion method (Zippin, 1956; Seber & Le Cren, 1967). Both amphibia and reptiles were very scarce, and no quantitative estimates of them were attempted. Waterfowl were scarce and not estimated. Indices of woodland bird abundance were obtained from auditory and visual dawn counts carried out along a fixed route each season. Birds were not identified to species but only separated into size groups. Relative abundance of small mammals was estimated as at Slapton from catches in four trap lines set up in four different types of riverside habitat in each season. Estimates of rat activity were obtained using the footprint recorder mentioned earlier. Squirrels were scarce in the woods adjacent to the river and so were not counted. An index of rabbit abundence was obtained by monthly night counts in two areas close to the river.

For full details of methods and exact sites of prey estimates, see Wise (1978).

Results

Slapton Ley

General results

Results for the otter are based on the analysis of 1547 scats containing 2906 prey items, and for Mink 513 scats containing 698 prey items. Sample sizes in each season are shown

in Table I. The average bulk percentages of the main vertebrate groups taken by otter and Mink over the whole period are shown in Fig. 1. It is clear that otters specialized in taking fish (93%), whereas Mink took fish, birds and mammals in approximately equal proportions. The difference in the proportions of all vertebrate groups taken by each species of predator is highly significant ($P < 0{\cdot}001$).

TABLE I

Scat sample-sizes in each season in the two study areas

Locality		Season							
		1975				1976			
		Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
River	Otter	5	29	108	159	72	112	131	59
	Mink	10	27	135	96	12	39	104	25
Slapton	Otter	281	186	186	184	222	208	75	205
	Mink	53	81	59	47	59	62	104	48

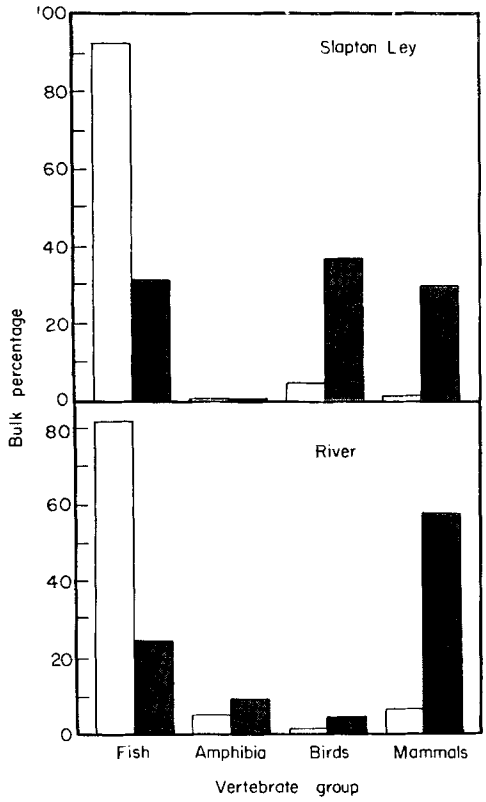

FIG. 1. Average bulk percentages of the vertebrate groups taken by otters and Mink overall at each locality; ■, Mink; □, otter.

Vegetation

Plant matter was of no dietary significance to either predator. It formed less than 0·5% of the diet in both cases, and was probably eaten incidentally.

Invertebrates

Invertebrates occurred in scats sporadically, comprising 1·0% of the otter diet and 1·2% of the Mink diet: the majority of occurrences were traces of aquatic arthropods and molluscs.

Fish

Fish formed 92·7% of the otter's diet, and 31·6% of the Mink's, overall. There was no significant seasonal variation in the frequency of occurrence of fish in the diets of either otters or Mink ($P=0·78$, $P=0·15$ respectively). The seasonal bulk importance of fish is shown in Fig. 2, from which it is evident that they tend to be more important to both predators in winter than in summer. The relative bulk importance of the different species of fish to each predator is shown in Fig. 12. Despite the difference in overall importance of fish, the order of importance of the different species is the same for each predator. All the major fish species were abundant in the Ley throughout the period of study and showed no obvious cycles of seasonal abundance, although they were more difficult to catch in nets in winter when they moved away from the shore line and into deeper waters.

Roach formed the greatest bulk of all fish taken, comprising 45·4% of the otter's diet and 13·2% of the Mink's (note that Roach and Rudd remains cannot be distinguished in scat material, so the cyprinids from scats are classified as Roach since this species is

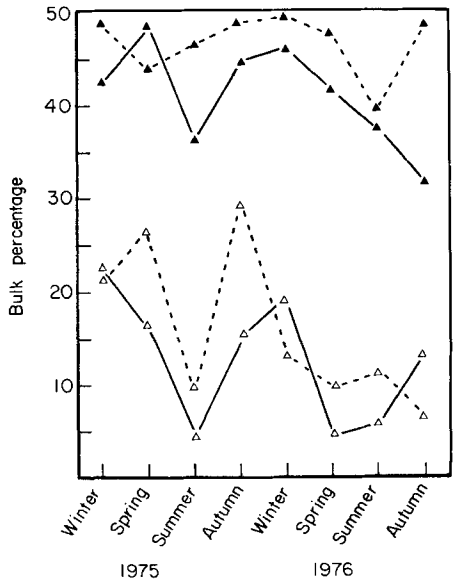

FIG. 2. Comparison of the seasonal dietary importance of fish to otters and Mink in each locality; ▲, otter; △, Mink; – – –, Slapton Ley; ——, river.

numerically vastly superior). The length-frequency distributions of Roach taken by otters and Mink and by netting are shown in Fig. 3, from which it is clear that both predators ate fish of a similar size range and that there was no size selection of fish by either predator species. The size frequency of the fish captured by predators corresponded closely with that caught in the nets. Friedman's test indicated that there were no significant differences between the mean sizes taken by otters, Mink and in nets. Small Roach and fry were underrepresented in the fish net samples, but the larger size groups were considered to be representative of the Roach population. No evidence of seasonal variation in size selection by either predator was found, but seasonal variation in the frequency of occurrence of Roach in the diet was highly significant ($P < 0{\cdot}001$) for both otter and Mink. Roach were more important to both predators in winter than in summer (Fig. 4).

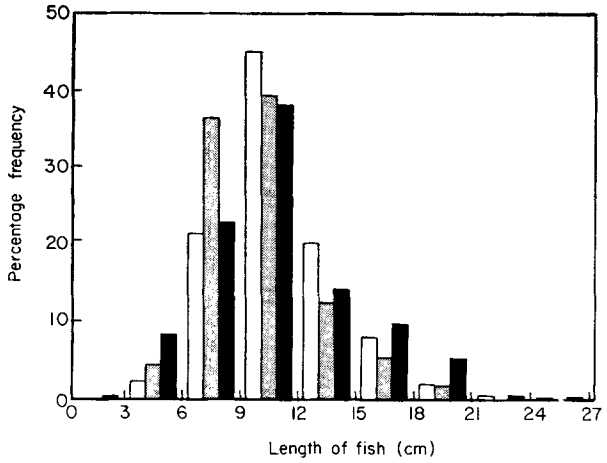

FIG. 3. Comparison of the overall length-frequency distribution of Roach taken by otters, Mink and fishing techniques at Slapton; □, otter ($n = 1567$); □, Mink ($n = 112$); ■ fishing ($n = 4385$).

Eels comprised 26·6% of the diet of otters and 11·0% of that of Mink overall. The length-frequency distributions of eels taken by otters, Mink and by electric fishing are shown in Fig. 5. There was no significant difference in the mean sizes taken by the two predator species, although otters took eels of a greater size range than Mink, indicating that there was no size selection of eels by either Mink or otters. No evidence of seasonal variation in the length-frequency of eels taken by otters was found, although eels as a group were taken to a greater extent in summer than in winter by both predators (Fig. 4).

Perch comprised 10·6% of the diet of otters and 5·4% of the diet of Mink overall. The length-frequency distributions of perch taken by otters, mink and fishing methods are shown in Fig. 6, from which it is clear that there is no size selection of perch by either predator. The small number of Mink scats containing perch remains precluded any statistical comparison of mean size taken by each species. No evidence of seasonal variation in length-frequency of perch taken by otters was found, nor was there any seasonal variation in the frequency of occurrence of perch in the diet of either predator (Fig. 4), despite the fact that the perch population was declining throughout the period.

Pike comprised 9·2% of the diet of otters and 1·5% of that of Mink overall, a greater difference than for any of the other fish species considered. The length-frequency distribution of Pike taken by otters, Mink and nets is shown in Fig. 7. The small number of Mink scats containing Pike precluded any statistical comparisons, but there is no clear evidence of size selection by either predator. Analysis of the seasonal length-frequency distributions of Pike eaten by otters indicated that in winter and spring the mean length of fish taken was significantly ($P < 0{\cdot}05$) greater than in summer and autumn. The seasonal variation in frequency of occurrence of Pike in the diet of otters was also significant ($P = 0{\cdot}006$), and it is clear from Fig. 4 that Pike were most important in spring.

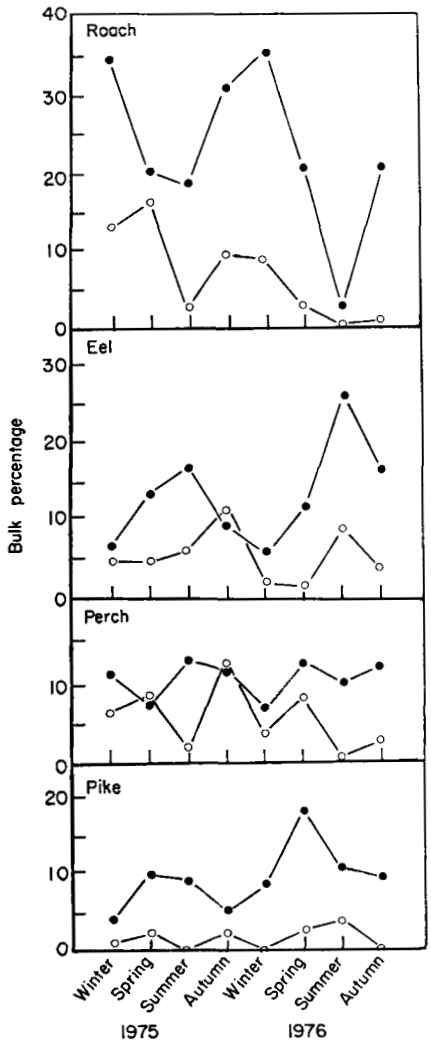

FIG. 4. Comparison of the seasonal dietary importance of four fish species to otters and Mink at Slapton; ●, otter; ○, Mink.

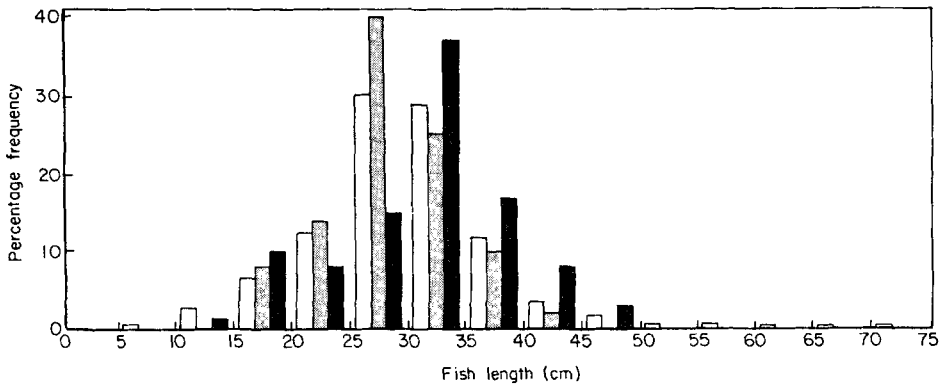

FIG. 5. Comparison of the overall length-frequency distribution of eels taken by otters, Mink and fishing techniques at Slapton; □, otter ($n=876$); ⊡, Mink ($n=99$); ■, fishing ($n=100$).

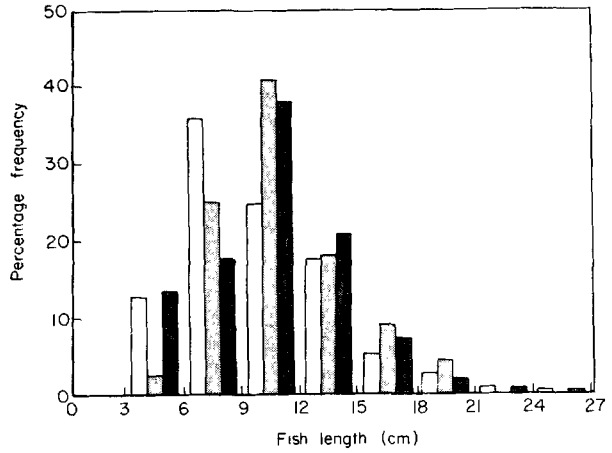

FIG. 6. Comparison of the overall length-frequency distribution of perch taken by otters, Mink and fishing techniques at Slapton; □, otter ($n=497$); ⊡, Mink ($n=44$); ■, fishing ($n=5083$).

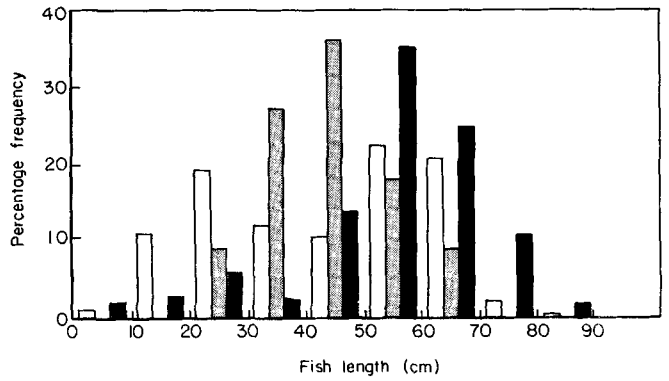

FIG. 7. Comparison of the overall length-frequency distribution of Pike taken by otters, Mink and fishing techniques at Slapton; □, otter ($n=274$); ⊡, Mink ($n=11$); ■, fishing ($n=326$).

Although trout were common in the feeder streams to the Ley, they occurred in the lake itself only sporadically and in very low numbers in summer. They similarly occurred only sporadically in the diet of otters and Mink, and their overall importance was insignificant, comprising $<0{\cdot}3\%$ of their combined diet overall. Sticklebacks were also scarce and local in the lake, and comprised only $0{\cdot}6\%$ of the otter's diet and $0{\cdot}4\%$ of the Mink's.

Amphibia and reptiles

Both groups of vertebrates were scarce in the environs of the Ley and were observed only occasionally and irregularly. The commonest reptile was the adder *Vipera berus*, which was seen during spring and summer in a number of areas around the Ley. Amphibia, however, formed less than $0{\cdot}5\%$ of the overall diets of both otters and Mink at Slapton and were clearly insignificant as prey items. No evidence of predation on reptiles by either predator species was found throughout the study.

Birds

Birds formed the most important prey category for Mink ($36{\cdot}9\%$ of the overall diet) and the second most important group for otters, although only comprising $4{\cdot}6\%$ of their

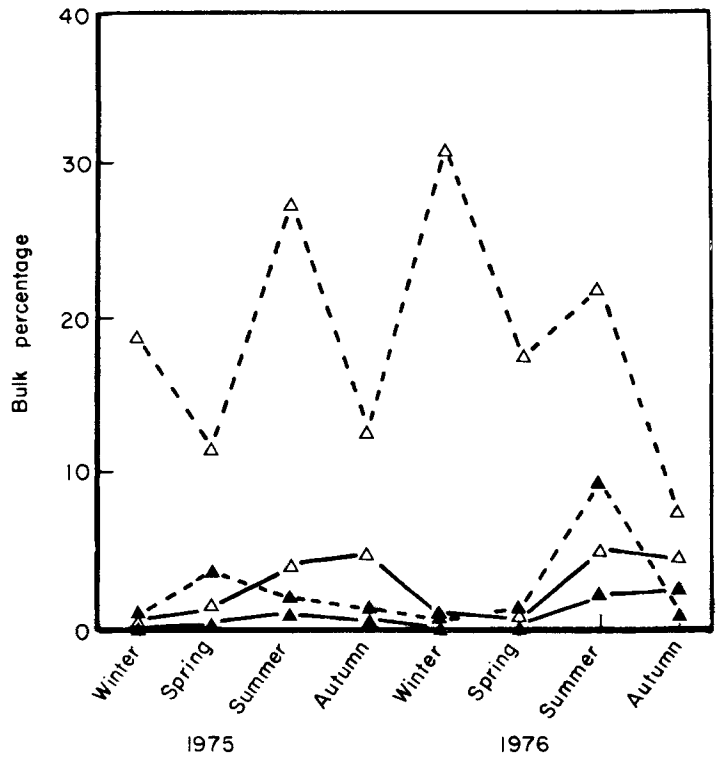

FIG. 8. Comparison of the seasonal dietary importance of birds to otters and Mink in each locality; ▲, otter; △, Mink; – – –, Slapton Ley; ——, river.

diet. Seasonal variation in the frequency of occurrence of birds in the diet was significant for both otters and Mink ($P<0{\cdot}001$ and $P<0{\cdot}002$ respectively). Their importance in the diet of Mink increased in winter and summer and decreased in spring and autumn (Fig. 8). There is no clear seasonal pattern of importance evident for otters, only an increase in the summer of 1976.

The data for otters are scarce, but it was noted that Anseriformes was the most important group taken overall (Table II), being especially important in the summer of 1976; that Ralliformes were taken in small numbers throughout the period with no evident seasonal variation; and that other birds including passerines and galliforms were taken occasionally. The most important group taken by Mink was the Ralliformes. Seasonal variation in their frequency of occurrence in the Mink diet was significant at the 5% level: predation upon them was greater in winter and summer. Seasonal variation in predation on Anseriformes was not significant ($P=0{\cdot}13$). Seasonal comparison of waterfowl densities on the Ley with their importance to Mink (Table II) indicates that there was selection by the predator. Ralliforms were always more important in the diet, despite being less common on the lake, except in autumn, when predation on anseriforms was greater. Passerines formed 4·8% of the Mink diet, and were taken more frequently in winter and summer than at other times, especially in the winter of 1975–6 when they comprised 17·6% of the Mink diet. Galliforms and columbiforms were taken infrequently and spasmodically. Remains of eggs were only found in two scats. No predation on other bird orders was found, although swans, cormorants and gulls were common or abundant on the lake.

Mammals

Mammals comprised only 1·2% of the diet of otters but 29·5% of that of Mink. There was no evidence of seasonal variation in their frequency of occurrence in the diet of otters, but seasonal variation in Mink predation was significant ($P=0{\cdot}005$). They tended to be less important to Mink in the winter period, but more important in 1976 than in 1975 (Fig. 9).

TABLE II

Comparison of the relative proportions of Anseriformes and Ralliformes on the Ley and the relative proportions taken by otters and mink

Season		Visual estimate (%)		% in Mink diet	
		Anseriformes	Ralliformes	Anseriformes	Ralliformes
1975	Winter	86·3	13·7	16·8	83·2
	Spring	88·6	11·4	34·2	65·8
	Summer	70·4	29·6	41·9	58·1
	Autumn	75·8	24·2	82·6	17·4
1976	Winter	85·2	14·8	27·1	72·9
	Spring	81·0	19·0	37·6	62·4
	Summer	65·2	34·8	19·8	80·2
	Autumn	66·0	34·0	59·7	40·3
	Overall mean	76·4	23·6	36·4	63·6
	(Otter predation: mean overall:		Anseriformes	63·8%	
			Ralliformes	36·2%)	

There was little seasonal variation in the numbers of small mammals trapped around the Ley, although the numbers declined in both springs and increased in Autumn 1976. Of the four species trapped most frequently, the Wood mouse *Apodemus sylvaticus* and the Bank vole *Clethrionomys glareolus* were almost equally abundant, and twice as numerous as the Short-tailed field vole *Microtus agrestis* and the Common shrew *Sorex araneus*, although there was some variation in the relative abundance of each species in the different trap lines in relation to habitat. Other species were trapped only occasionally. *A. sylvaticus* numbers increased in autumn of both years and *M. agrestis* in summer and winter (Fig. 10). Insectivores (mainly *Sorex* spp.) comprised only 0·4% of the otter's diet and 3·2% of that of mink. Seasonal variation in Mink predation on shrews is shown in Fig. 10, and there is some indication that the importance of shrews increased in summer and autumn but declined in winter and spring. Small samples prevent full analysis of this trend. Mice and voles comprised only 0·1% of the diet of otters and 7·6% of that of Mink. There was little evidence of seasonal variation in their importance to Mink (Fig. 11), but their overall

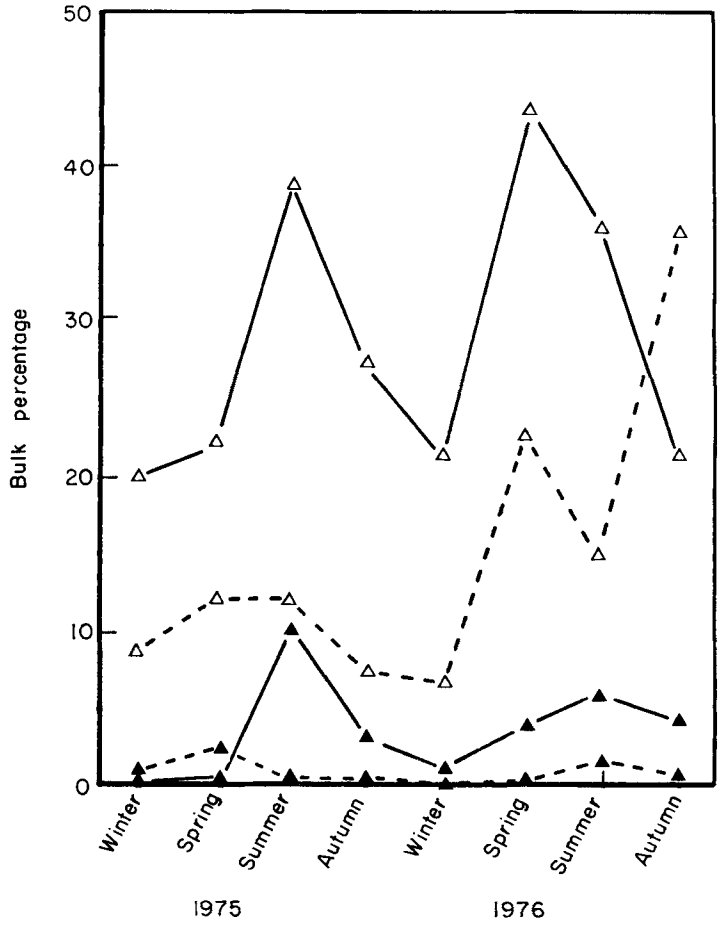

FIG. 9. Comparison of the seasonal dietary importance of mammals to otter and Mink in each locality; ▲, otter; △, Mink; – – –, Slapton Ley; ——, river.

importance increased in Summer and Autumn 1976, when they comprised 27·9% of the diet. This increase was not due to selective predation upon any one species but to increased predation upon all the four common species (Fig. 10), although only *A. sylvaticus* showed a noticeable increase in numbers at this time. Otters took each of the species, but infrequently and sporadically.

Footprint recorders produced no evidence of rat presence around the Ley, suggesting that if rats were present it was only in very small numbers. They comprised only 0·3%

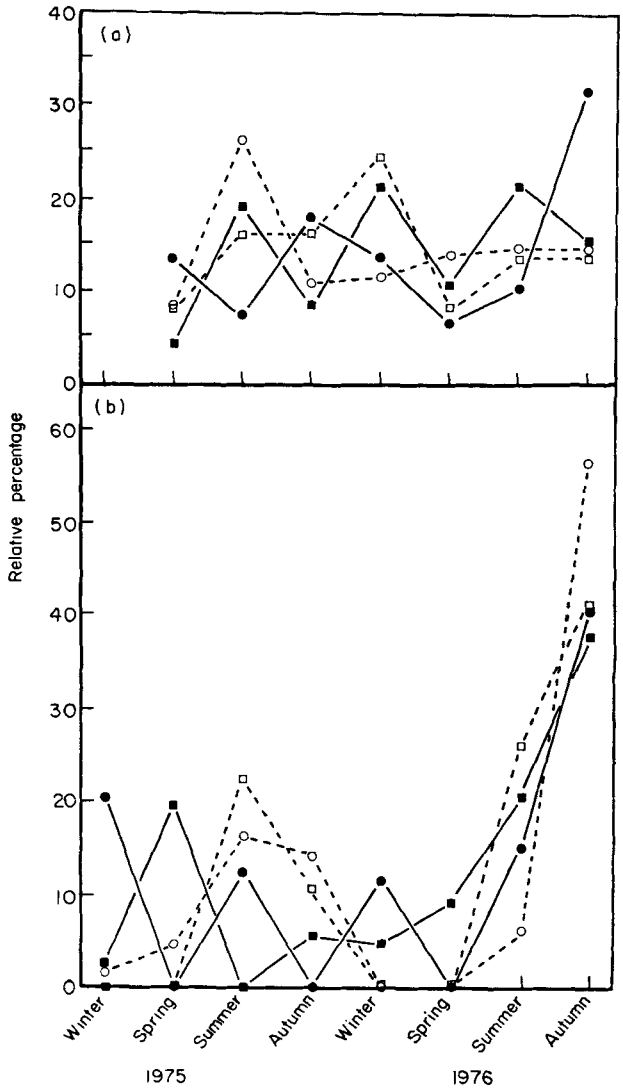

FIG. 10. Comparison of the seasonal abundance of small mammal species as revealed by Longworth trapping (a), with their dietary importance to mink at Slapton (b); ●, *Apodemus sylvaticus*; ○, *Clethrionomys glareolus*; ■, *Microtus agrestis*; □, *Sorex araneus*.

of the diet of otters and 1·3% of that of Mink: predation on them was sporadic, with no indication of seasonal variation.

Squirrels were seen only sporadically in the area and were equally of insignificant dietary importance. They were taken only very occasionally, forming 0·1% of the diet of otters and 0·6% of that of Mink.

Rabbits were present in all seasons but were rather more numerous in summer and autumn. They comprised only 0·3% of the diet of otters but 15·4% of that of Mink. Seasonal variation in the frequency of occurrence of rabbits in the diet of Mink was highly significant ($P < 0{\cdot}001$). Their importance was greatest in spring (Fig. 11) and they formed a greater part of the diet in 1976.

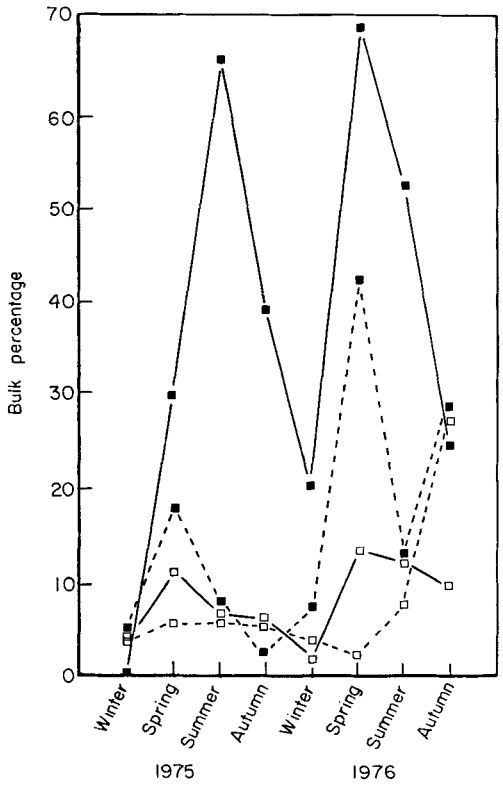

FIG. 11. Comparison of the seasonal variation in Mink predation on small rodents (□) and rabbits (■) in each locality; – – –, Slapton Ley; ——, river.

Other mammals including Dormouse *Muscardinus avellanarius* and Harvest mouse *Micromys minutus* were found in scats on only one or two occasions. Occasionally remains of Mink were found in Mink scats, but there was no evidence of Mink preying upon otters or vice versa.

Comparison of Mink and otter diets

A comparison of the main prey items taken by otter and Mink, expressed as bulk

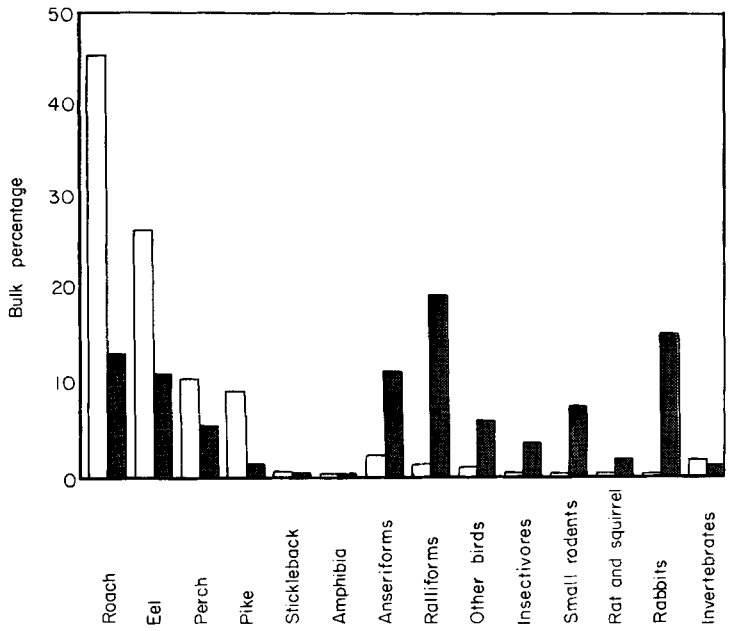

FIG. 12. Bulk percentages of the main prey items taken by otters (□) and Mink (■) at Slapton overall.

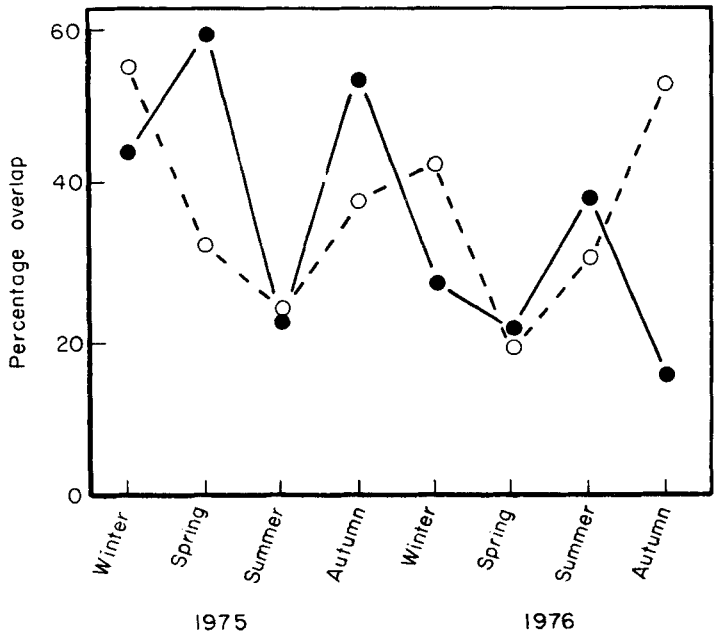

FIG. 13. Percentage overlap in the otter and Mink diets in each season in each locality; ●, Slapton Ley; ○, river.

percentages, is shown in Fig. 12. Application of Spearman's coefficient of rank correlation to these data indicated that there was no significant correlation between the diets of the two predators ($r=0{\cdot}13$). Fish clearly constituted the most important prey for otters, whereas the diet of Mink was more diverse, with fish, birds and mammals being of almost equal importance. The proportion of the diet which was common to both species was calculated on a seasonal basis using bulk percentage estimates. It is clear from Fig. 13 that there is no consistent seasonal pattern of variation in the degree of dietary overlap. The overall average percentage of prey shared by otters and Mink over the whole period was 38·3%. Fish comprised the greater part (82·2%) of this shared portion, and this group formed by far the greatest shared element of their diets in all seasons (Fig. 14). The decline in the importance of fish as the shared group during the summers (especially in 1976) was due to otters taking more birds and mammals at these times.

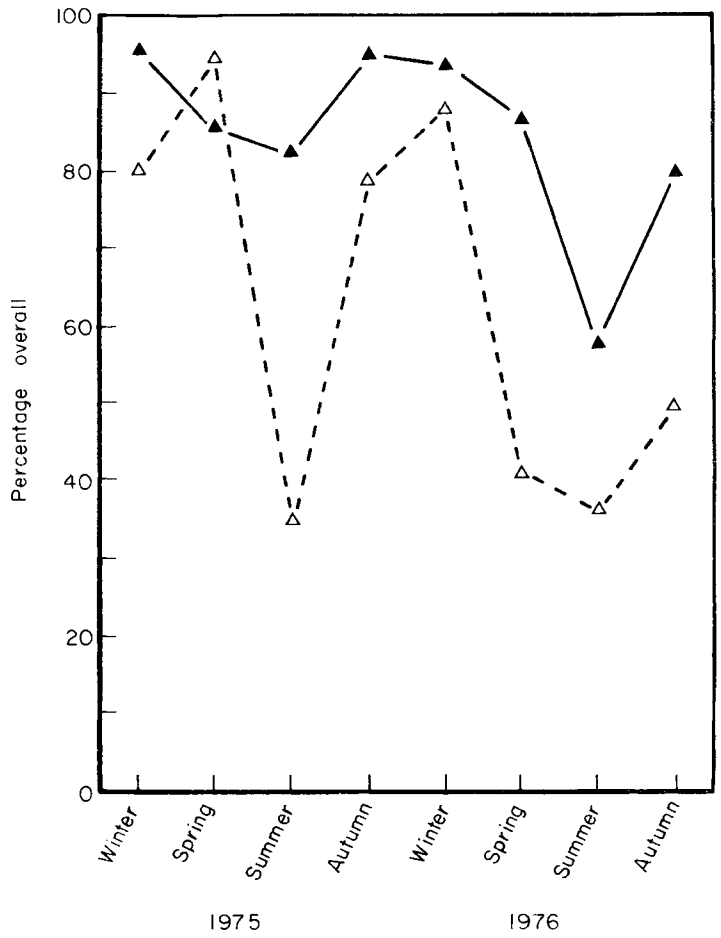

FIG. 14. Percentage overlap in the otter and Mink diets in each season at each locality which was formed by fish; ▲, Slapton Ley; △, river.

Rivers Webburn and Dart

General results

Results for the otter are based on the analysis of 675 scats containing 1248 prey items and for Mink, 448 scats containing 571 prey items. Sample sizes in each season are shown in Table I. A higher proportion of otter scats were found on the River Dart and Mink scats on the River Webburn. The relative proportions of the scats showed seasonal variation, more otter and Mink scats being collected from the Dart in winter. The average bulk percentages of the main vertebrate groups taken by otter and Mink over the whole period are shown in Fig. 1. It is clear that otters specialized in taking fish (81·7%), whilst Mink took more terrestrial prey, especially mammals which formed 57·0% of their diets. The difference in the proportions of all vertebrate groups taken by each species of predator is highly significant ($P < 0{\cdot}001$).

Vegetation

Plant remains, principally grass, were found more frequently in Mink scats (forming 2·0% bulk) than in those of otters (0·2%). They were probably ingested incidentally when feeding, and their greater importance to Mink probably reflects the greater tendency of Mink to feed on terrestrial prey.

Invertebrates

Invertebrates comprised 4·4% of the diet of otters and 1·8% of that of Mink. They were generally found associated with fish remains and this may explain their greater frequency in otter scats. They were often present in small numbers in scats throughout the period, and although some may have been genuine prey, there is the possibility that they may in fact have formed part of the diet of the fish predated upon.

Fish

Fish were of much greater dietary importance to otters (81·7%) than to Mink (24·8%) overall. There was no significant seasonal variation in the frequency of occurrence of fish in the diet of otters ($P = 0{\cdot}82$), but there was in the diet of Mink ($P = 0{\cdot}006$). The seasonal bulk importance of fish to Mink declined each summer and increased each winter (Fig. 2). The relative bulk importance of the different species of fish to each predator is shown in Fig. 20. Despite the difference in overall importance of fish, the order of importance of the different species is the same for each predator.

The most abundant fish present in the River Dart system were salmonids, both resident and migratory. Sea trout feature most in estuarine catches in April–May and salmon in June–July. They move up the river with the summer spates, but do not move into the tributaries until close to the time of spawning. When water levels are low, as in the summer of 1976, the majority of migratory fish remain in the estuaries rather than in the river. Resident Brown trout are present in the river system throughout the year. Population estimates of salmonids in two stretches of the River Webburn are shown in Table III. The high values for Autumn 1975 are considered to reflect the fact that a number of migratory fish were passing through the section at that time and the low values in Autumn 1976, the fact that the migratory fish were still present in the estuary because water levels were unusually low. Winter values are probably under-estimates due to difficulties of fishing in high water conditions, so the apparent seasonal variation may be due in part to

sampling deficiencies. Eels are widely distributed through the river system at all times of year. Captures suggested a ratio of salmonids to eels of 1 : 0·08, but since many eels escape capture, the true abundance of eels relative to salmonids is probably slightly higher. Bullheads are known to occur throughout the whole river but were captured infrequently in the course of the surveys.

TABLE III

Seasonal population density estimates of salmonids in the River Webburn study area

Location	Season 1975 Autumn	1975 Winter	1976 Spring	1976 Summer	1976 Autumn
Section 1					
No. of fish caught	62	UF	UF	110	UF
No. of fish/100 m²	22	UF	UF	27	UF
Section 2					
No. of fish caught	131	78	135	222	46
No. of fish/100 m²	100	25	33	86	27

(UF = River unfishable due to high water levels)

Salmonids comprised 59·1% of the overall diet of the otter and 22·0% of that of the Mink. Seasonal variation in the frequency of occurrence of salmonids in the diets of both otters and Mink was highly significant ($P=0·02$, $P=0·01$, respectively) and they formed a more important part of the diet of both predators in autumn and winter (Fig. 15). The correlation between the seasonal patterns of otter and Mink predation upon salmonids was significant at the 5% level (Spearman coefficient $r=0·73$). The length–frequency distributions of salmonids taken by otters, Mink and electric fishing are shown in Fig. 16. The size frequency of the fish captured by the predators corresponded closely with that caught by electric fishing, and no significant differences in the mean lengths of fish and in the size ranges of fish taken by otters and Mink were found.

Eels comprised 16·2% of the overall diet of the otter but only 1·9% of that of the Mink. The sample sizes for Mink were too small to test for seasonal variation in frequency of occurrence, but seasonal variation of eels in the diet of otters was highly significant ($P=0·01$). Eels clearly formed a more important part of the diet of otters in spring and summer (Fig. 15), at the time when salmonids formed the least important part. This negative correlation between the pattern of seasonal predation on eels and on salmonids by otters is significant ($r=-0·74$). The length–frequency distributions of eels taken by otters, Mink and electric fishing are shown in Fig. 17. The size frequency of the fish captured by the predators agreed quite well with that of fish caught by electric fishing. The size ranges of the fish caught by the two predators is similar, and there is no evidence of size selection by either otters or Mink.

Bullheads comprised 5·8% of the diet of otters and 0·9% of that of Mink. The bulk estimate method underemphasizes the difference in their occurrence in the diets of the two predators since Bullheads, being of a small size, rarely formed the bulk of a scat. In

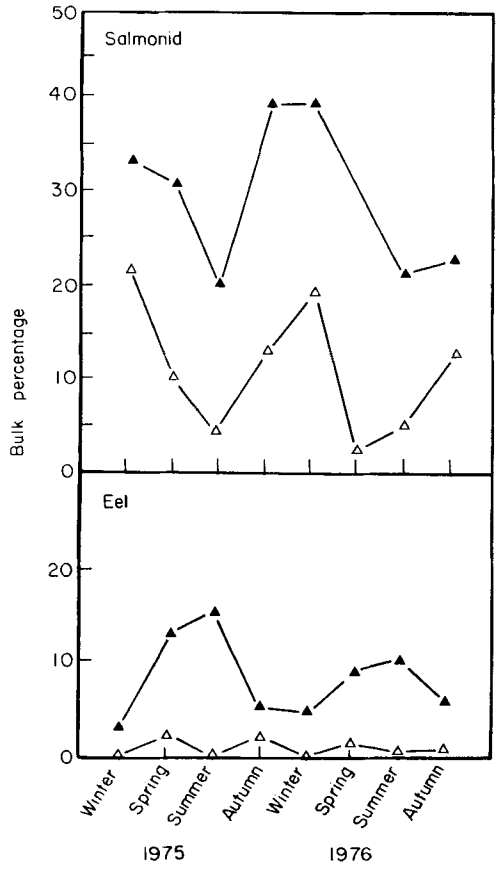

FIG. 15. Comparison of the seasonal bulk importance of salmonids and eels to otters (▲) and Mink (△) in the river area.

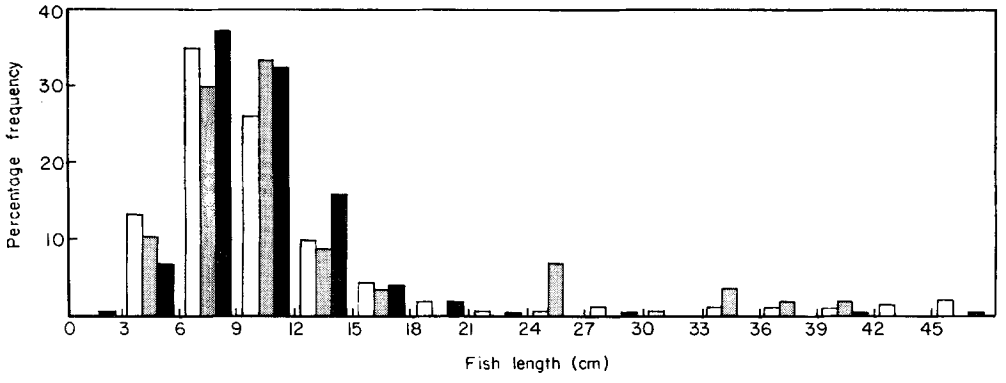

FIG. 16. Comparison of the length-frequency distribution of salmonids taken by otters (□), Mink (▨) and electric fishing (■) during the period Dec 1975–Nov 1976 inclusive in the river area.

terms of actual occurrences, they were found in 117 otters scats and only five Mink scats. They were most important in the winter and spring of 1975, when most scats were collected from the River Dart, and throughout the whole period of the study they were commoner in scats from the Dart. Only one Stone loach was found in the survey of the river: no loach remains were ever found in the Mink scats, and they only formed a minor and insignificant part of the diet of otters (0·1%).

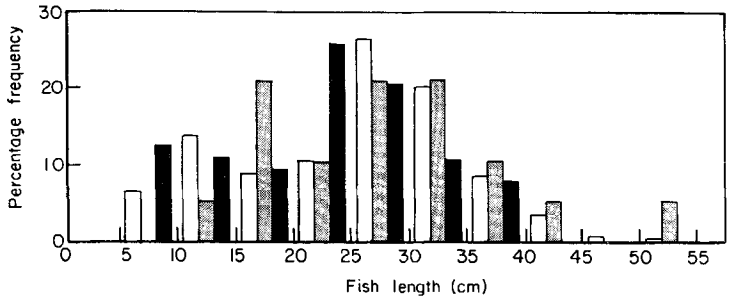

FIG. 17. Comparison of the overall length-frequency distribution of eels taken by otters (□), Mink (□) and electric fishing (■) in the river area.

Amphibia

Amphibia comprised 5·4% of the diet of otters and 9·6% of the diet of Mink. There is no clear pattern of seasonal variation in their importance to either predator, although their importance to both species increased in the summer and autumn of 1976. This may be only a reflection of sample bias; amphibia were never common in the river, but the largest breeding colony of the Common frog *Rana temporaria* was found near the River Webburn from where the summer and autumn scat samples were taken in 1976.

Reptiles

Reptiles were uncommon along the banks of the river, the most commonly observed species being *Lacerta vivipera*, which was only seen occasionally and in small numbers. There was no evidence, however, of predation upon reptiles by either otters or Mink.

Birds

The seasonal pattern of bird counts, both auditory and visual, is shown in Fig. 18. Small passerines were the most important group of birds along the river system, and counts tended to be higher in winter than in summer. In contrast with Slapton Ley, waterbirds, including Ralliformes and Anseriformes, were rare, occasional temporary visitors, or completely absent. Birds were correspondingly relatively unimportant dietary items in the river area, comprising only 1·6% of the diet of otters and 4·8% of that of Mink. Passerines were the most frequent prey, with very few occurrences of predation on birds of other groups. Very little predation took place on birds in winter and spring, but their importance, especially for Mink, increased in summer and autumn (Fig. 8). There was no evidence of predation on bird eggs.

Mammals

Mammals were of far greater dietary importance to Mink than to otters. They comprised 57·0% of the overall diet of Mink, but although the second most important group to otters, they formed only 6·8% of their diet. There was no evidence of seasonal variation in the frequency of occurrence of mammals in the diet of Mink, but seasonal variation in frequency in that of otters was significant; they were more important in summer than in winter (Fig. 9).

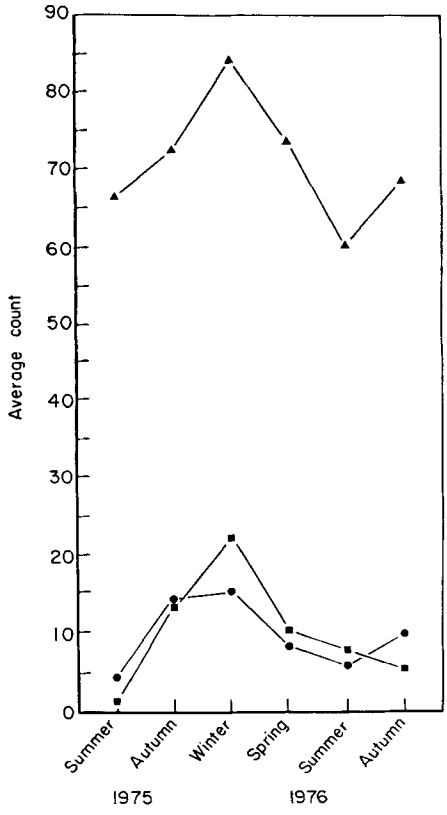

FIG. 18. Seasonal bird counts (visual plus auditory counts averaged) in the river area; ▲, small; ■, medium; ●, large.

There was little seasonal variation in the numbers of small mammals trapped in the river area, apart from a delcine in Spring 1976. Of the four species trapped most frequently, *C. glareolus* was twice as abundant as *A. sylvaticus*, whilst both *S. araneus* and *M. agrestis* were present in small numbers only. Slight differences in the relative abundance of each species were found in the results from the different trap lines in the different habitats. Other species occurred only occasionally and in small numbers. Numbers of *A. sylvaticus* increased in autumn and decreased in spring, whereas numbers of *C. glareolus* remained

more even, apart from a slight increase during the summer months (Fig. 19). *M. agrestis* was commoner in the winter of 1975 than at any other time, whereas *S. araneus* was most abundant in Autumn 1976. Insectivores comprised only 1·4% of the diet of otters and 6·2% of the diet of Mink. Approximately half these occurrences were of Moles *Talpa europaea*. These occurred sporadically in scats in most seasons but their abundance could not be estimated as they are not susceptible to live-trapping by the methods employed. Seasonal variation in Mink predation on shrews is shown in Fig. 19. There was no evidence of predation during winter or spring but the importance of shrews increased during summer to reach a peak in autumn, especially in 1976 when they formed 9·9% of the diet of Mink. Mice and voles comprised only 1·0% of the diet of otters but 8·0% of that of

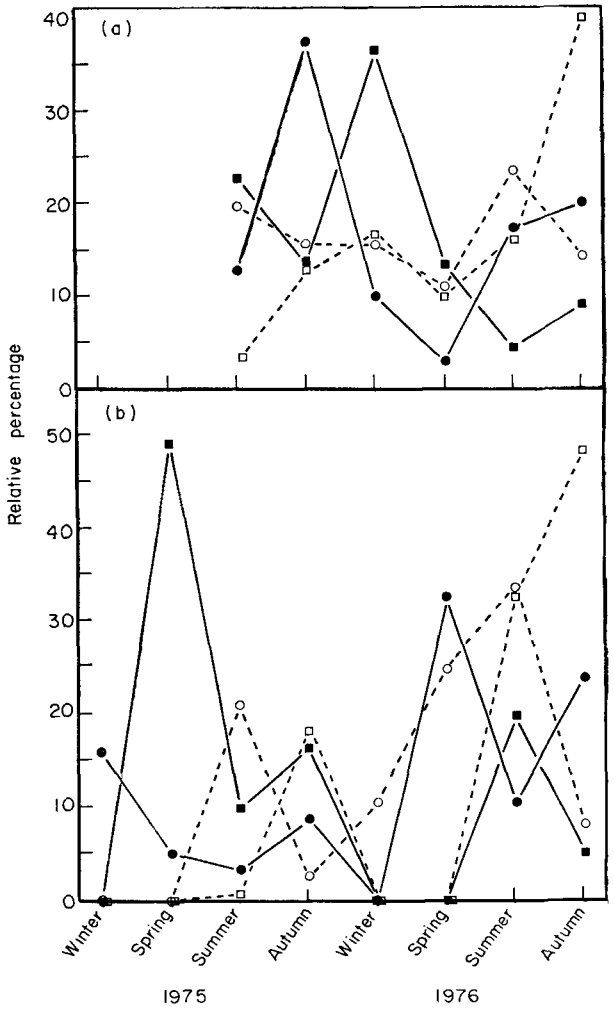

FIG. 19. Comparison of the seasonal abundance of small mammal species as revealed by Longworth trapping (a), with their dietary importance to Mink in the river area (b); ●, *Apodemus sylvaticus*; ○, *Clethrionomys glareolus*; ■, *Microtus agrestis*; □, *Sorex araneus*.

Mink. They tended to be more important in the Mink diet in spring and summer than at other times of year (Fig. 11). *A. sylvaticus* was the most important prey species of Mink (33·3%), followed by *M. agrestis* and *S. araneus* (23·8% each) and *C. glareolus* (19·0%). Seasonal variation in Mink predation on each of these species is shown in Fig. 19. There are no clear patterns evident, although *M. agrestis* was more important in 1975 and the other species in 1976.

No evidence of the presence of rats in the river area was obtained by the footprint recorder or by any other method. They nevertheless comprised 4·3% of the diet of Mink, although they only occurred in one otter scat. This value for Mink is due to the occurrence of rat remains in one scat in a small scat sample in winter and to two other occurrences only, and is clearly an overestimate of their dietary importance.

Squirrels were occasionally observed at all seasons in areas of woodland in the valley of the River Webburn but only occurred in a single otter scat and are clearly insignificant dietary items.

Rabbits were present in all seasons but were less abundant in winter and spring. Their density was believed to be low in the river area. Rabbits were the most important prey of Mink, comprising 37·8% of the diet of Mink but only 3·7% of that of otters. Seasonal variation in the frequency of occurrence of rabbits in the diet of Mink was highly significant ($P < 0{\cdot}001$). Their importance was greatest in spring and summer (Fig. 11) and least in winter.

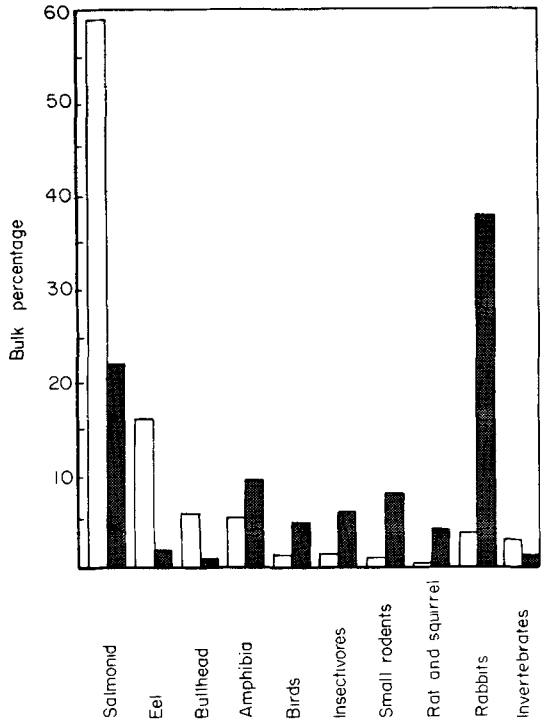

FIG. 20. Bulk percentages of the main prey items taken by otters (□) and Mink (■) in the river area overall.

The only other mammal prey recorded was Mink, remains of which were found in three Mink scats.

Comparison of Mink and otter diets

A comparison of the main prey items taken by otters and Mink, expressed as bulk percentages, is shown in Fig. 20. Application of Spearman's coefficient of rank correlation to these data gave a value of $r = -0{\cdot}25$, indicating that there is no significant correlation between the diets of the two predators and suggesting a tendency towards a negative correlation. Salmonids clearly constituted the most important prey for otters, whereas the diet of Mink was far more diverse but with rabbits being the most important single group. The proportion of the diet which was common to both species was calculated on a seasonal basis (Fig. 13). Dietary overlap was greatest in autumn and winter and least in spring and summer. The overall average percentage of prey shared by otters and Mink over the whole period was 39·3%, a value very similar to that of 38·3% obtained for Slapton Ley. Fish comprised the greater part (63·1%) of this shared portion but its importance as the shared group varied seasonally, being greater in winter and spring and lowest in summer (Fig. 14). This decline is correlated with the increased importance of mammalian prey, especially rabbits, to Mink in summer.

Discussion

The diets of otters and Mink

The choice of the two areas for this study was determined by the desirability of comparing the feeding habits of otters and Mink when they were present in the same area and having access to the same prey population and by comparing feeding habits in two areas which differed in faunal composition. The two localities differed considerably: Slapton Ley was dominated by cyprinid fish and harboured a large population of water birds, whereas the river was dominated by salmonids and harboured no resident population of water birds. Nevertheless, the overall feeding habits of each predator were remarkably similar in the two sites. Fish, whether cyprinid or salmonid, was the major dietary item for otters, whereas Mink had more varied diets, with fish forming a similar proportion of their diet in each site but with either mammals and/or birds forming the major item.

In Slapton Ley, fish was the most important single item for otters and the most important dietary item shared by otters and Mink. Although fish were three times more important to otters, the order of importance for each fish species was the same for both predators, suggesting that the same factors governed their relative availability. This was not due simply to the relative abundance of each species of fish in the Ley. The importance of Roach to otters was approximately four times that of perch. No absolute figures for the abundance of either species of fish in the lake are available but based on the findings of Bregazzi (1978) and Burrough (1978), we would estimate a relative abundance of at most two Roach to one perch. This estimate therefore implies a selection by otters in favour of Roach. Erlinge (1968) has suggested that otters catch fish in inverse proportion to their ability to escape but Bainbridge (1958*a*) found no evidence to suggest that perch could swim faster than Roach of the same length. The selection in favour of Roach may therefore simply be a measure of their greater abundance, their greater conspicuousness or their greater palatability when compared to perch. There was also a marked increase in predation

on Roach but not perch, in winter, which contrasted with the pattern of peak predation on eels in summer. Eels become torpid in winter and probably bury themselves in the mud. They are active in summer but even then are still more slow-moving than the other species of fish (Bainbridge, 1958*b*). They are therefore more susceptible to predation and because of this were preyed upon selectively, whereas in winter their relative inactivity rendered them less attractive to otters and Mink which both prefer to hunt moving prey (Erlinge, 1968; Poole & Dunstone, 1976) and so Roach became the preferred prey species. The absence of any size-selection of Roach, perch or eels by either predator suggests that they were taken simply in relation to their abundance in the population at all seasons. By contrast, the peak of predation upon Pike occurred in spring, when a greater proportion of large Pike were taken. This may well be correlated with the fact that large Pike spawn at this time, become spent and weaker after spawning (Bregazzi & Kennedy, 1980) and so are easier to catch. The relatively greater importance of eels to Mink than to otters may be explicable in terms of the eel being easier to catch by the less well-adapted underwater predator. The lower proportion of Roach, perch and Pike in the diet of Mink could be due not only to their faster swimming speed but also to the readiness of Mink to take alternative terrestrial prey. However, the hunting behaviour of the predator may also have influenced the availability of prey. Mink prefer to locate the prey from above the water and dive in pursuit (Dunstone, 1972) and can only stay under water a short time (Poole & Dunstone, 1976), whereas otters locate prey after diving (Erlinge, 1968) and can stay under water longer. In the conditions of the Ley, this should tend to confine Mink hunting to the margins, whereas otters could hunt more easily in the open water. All the fish species are common near the margins in summer, but in winter Roach and perch move to the more open and deeper waters where they are more accessible to otters than to Mink.

The scarcity of amphibia in the diets of the predators closely parallels the scarcity of the group in the Ley, as does the scarcity of reptiles. Birds, however, were clearly an important prey group to Mink. Despite the wide variety and high density of many bird species around and on the Ley, the great majority of the prey species were waterfowl associated with the lake itself. Abundant aquatic birds such as gulls were not preyed upon at all. This selection for waterfowl, especially ralliforms, appears to be related to their greater vulnerability to predation arising from their habit of roosting on the water or at ground level nearby, their habit of nesting close to the water at ground level and their habit of moulting all their flight feathers at once. The strong selection exercised by Mink for ralliforms is probably due, in addition, to the smaller size of the ralliforms and their lesser ability to escape by flying away and to their greater concentrations on the margins of the lake. Otters were rather less selective and took more anseriforms, since the larger size of the birds made them more susceptible to the larger predator, as did their habit of roosting on the open water. Otters preyed upon waterfowl more in spring and summer, when the prey were more vulnerable and hence available because of their breeding and moult behaviour and when conditions for fish predation were least favourable, whereas the more terrestrial and marginal feeding mink took birds more evenly throughout the year.

Both predators took a wide variety of mammals, ranging from shrews to rabbits in size. There was no evidence of selection against shrews: the absence of predation upon them in winter is probably due to their higher mortality at this time (Southern, 1964). Predation upon other small mammals related closely to their abundance: it increased in summer

and autumn when they were more numerous and there was a greater proportion of more vulnerable juveniles in the population. The increase in the number of small mammals caught in Autumn 1976 was also paralleled by an increase in predation on them. There was no evidence of species selection by Mink: rather, the relative proportions of the species preyed upon indicated that Mink hunted in a variety of habitat types. The apparent selection for *M. agrestis* is probably due to sampling deficiencies and unequal representation of habitat types in the sampling programme. The lack of predation upon rats probably reflects their scarcity around the Ley, whereas lack of predation upon squirrels probably reflects their agility and ability to avoid capture. Rabbits were the most important mammalian prey but predation upon them was not directly related to their abundance. Maximum predation occurred in spring, when counts were low, and to a lesser extent in autumn, when counts were high. The pattern of predation upon rabbits appears instead to relate to the presence of young rabbits in the population. These are considered to be more vulnerable to predation due to their smaller size, slower escape and habit of feeding more in daylight. The period of maximum predation on rabbits also co-incided with the period of litter production by Mink (Chanin, 1976), when female Mink became more diurnal and active (Gerell, 1969).

At Slapton, therefore, there were significant differences between the diets of otters and Mink. These were related in part to species preference, with otters concentrating on aquatic prey and Mink more on waterside and terrestrial prey and in part to species availability. Both predators, but especially Mink, were able to turn to alternative prey when these became more available, either relatively or because of some change in their behaviour that rendered them more succeptible to predation. It would seem that, in a situation where sufficient fish were available to support the otter population, the predator's larger size, superior aquatic adaptations enabling it to hunt more efficiently, especially in the open water and its greater ability to exploit aquatic prey, would render it superior to Mink in any food-based interspecific interaction.

The contrast between the preference for fish shown by otters and the preference for mammals shown by mink was even more apparent in the river area, where it was also seasonally accentuated. Salmonids were the major prey of otters in winter and rabbits of Mink in summer, but when these items became less available at other seasons, the diets of both predators became more diverse. Thus otters took a larger proportion of terrestrial prey in summer and Mink of salmonids in winter. Overlap in diet between the two predators was thus greatest in autumn and winter when fish was the major item.

Salmonids were the most important prey of otters, occurring in a bulk ratio of 2 : 1 to eels in their diet. This ratio is considered to be much lower than the numerical ratio of salmonids to eels present in the river (see p. 000). It seems probable, therefore, that eels were again being preyed upon selectively, because of their slower swimming speed (Bainbridge, 1958*b*). Both the sustained swimming speed and acceleration of salmonids is greater even than those of cyprinids (Bainbridge, 1958*a*) and eels are consequently more vulnerable to capture. There was a clear negative correlation between predation upon eels in summer and salmonids in winter by both predators. This seasonal pattern does not appear to bear any relation to the relative population densities of the two groups, but to be related to the behaviour and availability of each group. The warmer water temperatures in summer would permit salmonids to attain their fast swimming speeds, which would have the effect of reducing their vulnerability to capture when compared with eels. In

winter, salmonids could achieve only much slower speeds at the colder temperatures and so would be more vulnerable to capture, whereas the eels, being more inert and remaining immobile in areas under stones, would not elicit hunting behaviour by either Mink or otters (Erlinge, 1968; Poole & Dunstone, 1976). Increased predation on salmonids in winter by Mink is probably also associated with the reduced availability and vulnerability of rabbits, their other major prey item, at this time and by the slower speed of salmonids making them more available to the less aquatically adapted Mink, especially if their hunting was restricted to the margins of the river or the slower pools where they did not have to combat the fast winter currents. The smaller sample sizes of Mink scats in winter may not be due to a decrease in feeding activity or Mink density, but may merely be a reflection of the sampling programme and the difficulty of collecting scats at this time. Neither Mink nor otters selected fish of a particular size range apart from avoiding very small fry or small eels and they appear to have taken fish in relation to their relative abundance within the population. The main period of predation upon large salmonids thus co-incided with the times of the runs of salmon and Sea trout up the river. The preference shown for Bullheads by otters, particularly in winter, appears to reflect their greater abundance in the River Dart, where most of the winter samples were taken.

The greater importance of amphibia to Mink is probably related to the more terrestrial feeding habits of Mink in general. The increased importance of amphibians as prey in spring is probably related to their spawning aggregations at particular sites, and in Autumn 1976, to the very dry conditions causing local aggregations. The absence of reptiles as prey items relates to their scarcity in the area.

Birds comprised only a small part of the diets of otters and Mink in the river area and this appears to be associated with the virtual absence of the more vulnerable anseriforms and ralliforms. Passerines, which were the most abundant bird group along the river, accordingly were the most important prey group of birds. Predation upon them increased in summer and autumn, when the population contained a greater proportion of juvenile and more vulnerable individuals. They were clearly more important to the more terrestrial Mink.

Both predators took a variety of mammals, of which rabbits were undoubtedly the item of greatest dietary importance. There was again no evidence of selection against insectivores, although their importance declined in winter. In contrast to Slapton, Mink did show selection against a particular species of small mammal, *C. glareolus*. This suggests that although Mink hunted in a variety of habitats, they preferred the open woodland areas beside the river and the rough grassland where Bank voles were less common than in the dense undergrowth. Seasonal increases in the importance of small mammals appear to be correlated with the increase in prey abundance due to reproduction and the presence of the more vulnerable juveniles. Small mammals were taken less frequently by otters, reflecting their more aquatic habitat and food preference for rabbits compared with other terrestrial prey.

The scarcity of both rats and squirrels in the diets of both predators can be related to their scarcity in the area. By contrast, rabbits were a major item in the diet of Mink and both predators selected for them at the times when they were most abundant and their population contained a greater proportion of the more vulnerable juveniles.

A comparison of the diets of Mink and otters in these two sites thus shows an overall similarity in that otters are clearly the more specialized aquatic predator for whom fish

are their most important prey, whereas Mink are less specialized for aquatic predation and prey more extensively and intensively upon birds and mammals. The actual composition of their diets, however, varied according to habitat and in relation to the abundance and availability of potential prey items. In Slapton Ley, where fish were more available due to their being coarse fish, more abundant and slower swimmers than the salmonids in the river, they were more important in the diet of both predators. In both habitats, however, there was a seasonal change in the importance of particular fish species. Eels were taken to a greater extent by both predators in summer, when they were more vulnerable, although Mink tended to take more terrestrial prey in this season. In winter, however, roach became the most important fish prey at Slapton and salmonids in the river. There was no selection for fish size as such by either predator but when fish of a particular size group became more available or abundant, they were preyed upon proportionately more intensively. Thus large salmonids were taken when they ran up the river and large Pike when they were spent after spawning. Amphibia were relatively unimportant dietary items at both sites but were taken more often in the river area where they were more available due to their seasonal aggregations. The most pronounced difference between the prey in the two sites related to the birds. Passerines were taken to a similar extent at both sites. At Slapton waterfowl were abundant and they formed an important prey item; each predator demonstrated a preference for a particular group in relation to their relative availability to the species in question. The absence of waterfowl from the river was responsible for the far lower importance of birds in the diets of both predators at that site. Instead, in their absence, mammals and especially rabbits, formed the most important terrestrial prey, probably reflecting the reduced number of alternative prey rather than any greater abundance of rabbits. Small mammals were hunted for in a variety of habitats at both sites. They became more important as prey at times of their greatest population density and vulnerability. Differences in the relative proportions of the species taken at the two sites appear to reflect preferences for hunting in particular habitat types, rather than any selective species predation as such. Seasonal and other changes in the availability of prey at both sites appear to have affected both predators equally, despite the differences in importance of the particular prey items to each. Equally, despite the differences in species composition and availability between the two sites, the degree of overlap in diets was remarkably similar.

The dietary habits of Mink and otter in Devon agree closely with what is known of their feeding habits elsewhere. Mink in their native America are regarded as generalist carnivores, associated particularly with water courses, which take prey in relation to their availability and abundance (Errington, 1943, 1954; Hamilton, 1959). Lutrines, by contrast, appear to exploit a far narrower range of prey. In all habitats, fish are consistently of major importance to otters, whereas their importance to Mink varies seasonally and, as at Slapton and the river area, increases in winter (Gerell, 1967*b*; Akande, 1972; Erlinge, 1972*a*; Chanin & Linn, 1980). Increased predation by both otters and Mink upon salmonids in winter and on eels, crayfish or crabs in summer has been reported also by Gerell (1967*b*), Erlinge (1967) and Rowe-Rowe (1977). Both Erlinge (1967) and Jenkins, Walker & McCowan (1979) also found that, as at Slapton, Pike were taken most frequently in spring. Where both salmonids and coarse fish are present in the same body of water, there appears to be selection in favour of the latter group (Sheldon & Toll, 1964; Knudson & Hale, 1968; Erlinge, 1969; Chanin, 1976) due to their greater vulnerability and slower

speed. Selection for fish of a particular size has been reported for both species of predators under experimental conditions (Erlinge, 1968; Poole & Dunstone, 1976) but in field situations there appears, as here, to be no difference in the size of fish taken by otters and Mink (Gerell, 1968; Chanin, 1976). This might suggest that Mink are not after all at such a great disadvantage when hunting under water since they did not select against the larger and faster fish, in which case their lesser dependence upon fish when compared with otters could be due rather to their greater ability to exploit a wider variety of mainly terrestrial prey.

Amphibia always appear to form only a small proportion of the diets of both species and both Gerell (1968) and Erlinge (1967) regard them as buffer prey: items taken when the principal food of the predator becomes scarce. The scarcity of waterfowl in riverine localities and the corresponding decrease in the importance of birds to the diet of Mink have been noted on several occasions (Gerell, 1968; Akande, 1972; Day & Linn, 1972; Sargeant, Swanson & Doty, 1972; Chanin & Linn, 1980). It is generally agreed by these authors that waterfowl are particularly vulnerable to predation because of their semi-aquatic habits and that ralliforms in particular are selectively preyed upon by Mink, especially in summer (Gerell, 1968). By contrast, otters take far fewer waterfowl, despite their abundance in an area and then, as here, generally in summer (Weir & Banister, 1973; Webb, 1975). Chanin (1976) found that mammals only formed a relatively minor part of the diet of otters, although they were of more frequent occurrence in summer. The proportion of the diet of Mink formed by mammals appears to relate to the availability of alternative prey, especially birds, rather than to their abundance and so differs from habitat to habitat. Chanin (1976) also found that their importance increased on the River Teign, a river similar to the Webburn, when compared with Slapton. In agreement with the findings of Gerell (1968) and Chanin (1976), neither predator selected against insectivores, a pattern of feeding behaviour in market contrast to that found in many other small carnivores (Day, 1968; Lockie, 1961). Similarly, most small carnivores and, in other localities, Mink, have been found to prey selectively upon *M. agrestis*, but no such selective predation was apparent in the present study. Instead Mink preyed on mice and voles throughout the year, including the winter period when mortality of small rodents is highest (Southern, 1964). The importance of rabbits in riverine areas where waterfowl are scarce was also noted by Chanin (1976) and increased predation upon them at their times of greatest vulnerability by Moors (1975) and Erlinge (1975).

Inter-relationships between Mink and otters in Britain

It was impossible to determine from the present study whether the introduction of Mink into both sites had caused any change in the diets of the otters. If the species compete for food, such a change might have been expected (Colwell & Futuyama, 1971). The similarity between the diets of otters at Slapton and in the river area and in localities elsewhere where Mink are absent, suggests that there is unlikely to have been any such change. Erlinge (1972*a*) studied the diet of otters in a Swedish lake both before and after the introduction there of Mink but failed to find any change in the feeding habits of otters despite the fact that 30–40% of their diet overlapped with that of Mink. In severe winter conditions when only small stretches of water were ice free, Erlinge (1969) considered that fish, the major item of dietary overlap, was a limiting resource, causing competition between otters and Mink. Otters, as the more specialized fish predators,

should here have the competitive advantage over Mink. However, the greater flexibility in Mink diet should enable them to survive in a wider range of habitats, including those that were suboptimal for otters.

It is concluded that, although competition for food between Mink and otters could take place at the times of the year when food resources are shared and limiting, the present study provided no evidence of such competition. There were large differences between the diets of the two predators at both sites; the greatest degree of overlap was for fish and there was no evidence that fish was ever a limiting resource. Indeed, despite the dissimilar sizes of Mink and otters, there was no evidence of size selection of fish, as might have been expected if they were limiting and each predator was having to compete with the other and specialize.

When animals invade a new area, they frequently disrupt the ecological balance that existed before their arrival (Elton, 1958). There is some evidence that this may have happened when Mink were introduced into Newfoundland (Northcott, Payne, & Mercer 1974), but there is little indication that this has happened in other places to which Mink have been introduced. Although they are reputed to have caused a reduction of wildfowl in some areas (Gudmunsson, 1952; Thompson, 1971), their identification as the causal agent is dubious (Bengtson, 1972) and their wide-ranging diet suggests that they are less likely to be as severe in their effect on any one prey group as those species that are more specialized. Waterfowl are the group most likely to be affected by their predation but there was no indication in the present study, or that of Chanin (1976), that the waterfowl population at Slapton had declined as a result of their activities. There is equally no evidence that the ecology of the mink has changed following its introduction into a new area, or that it has competed with any other species of native mammal. Indeed all the evidence suggests that introduced Mink are exploiting a niche that was either previously unoccupied or was not fully occupied by such a successful species. Their wide diet, ability to feed in terrestrial and aquatic habitats and generalized carnivorous habit would serve to reduce competition with any specialized carnivore. The success with which Mink have occupied this niche is evidenced by their very rapid spread. The decline in the otter population in both Britain and Sweden appears to have occurred before the rapid spread of Mink in both countries (Erlinge, 1972*b*; Anon., 1969; Chanin & Jefferies, 1978) and so seems unlikely to have been caused by the Mink, although it may have allowed them to colonize the countries more easily. Both Erlinge (1972*b*) and Chanin (1976) believe that Mink may have caused a restriction of otters to their optimal habitats, but the decline of the otters in optimal areas and in the absence of Mink (Wert, 1975; Macdonald & Mason, 1976) suggests that factors other than Mink must be primarily responsible. A number of factors including habitat destruction, disturbance and pollution have been suggested as being likely to affect a specialized carnivore such as the otter, far more than they would a generalized carnivore such as Mink. The greater adaptability of Mink and their greater ability to utilize a variety of food resources, would enable them to colonize areas that are sub-optimal for otters but in habitats that are optimal for otters, Mink would correspondingly be at a disadvantage. It is not inter-specific competition for food that is responsible for the present status of otters and Mink but the advantages possessed by a generalized carnivore over a specialized one.

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Addendum

Since this paper was written, Jenkins & Harper (1980) have published their analyses of otter and Mink faecal samples from north-east Scotland. Like us, they found that otters were mainly fish eaters, while Mink took a wider range of prey. Results on otters from the River Dee clearly paralleled our results from the Dartmoor rivers, with salmonid fish dominating and eels an important secondary prey. The seasonal variation in the incidence of these fish in scats, with salmonids commoner in winter and eels commoner in summer, also agrees with our findings. On both the River Dee and the Dinnet Lochs, the sizes of fish eaten were much the same as those recorded by us at both our sites in Devon. The Mink prey picture from Scotland was slightly different from that at either of our two sites, particularly in the lesser importance of fish in the diet. Similarities are the importance of rabbits among mammal prey and the summer high in rabbit predation. This is compatible with what is known of the opportunistic feeding strategy of Mink. We would disagree with the conclusion of Jenkins & Harper that the otter is an opportunist; compared with the Mink, it is very much a fish specialist with bird and mammal prey always of minor importance. Also, we do not think that their variation of the bulk estimate method is an improvement on ours, since ours is just as easy to apply as theirs, and gives an integrated value which is easier to display.

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