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RESOURCE PARTITIONING AND COEXISTENCE OF SYMPATRIC MINK AND RIVER OTTER POPULATIONS

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ABSTRACT: Resource partitioning by mink and river otter based on utilization along the dimensions of food, space, and time were investigated in west-central Idaho during 1976 - 1979. Twenty-six mink and 37 otter instrumented with transmitters and monitored for 889 and 3,437 hr, respectively, provided data on activity patterns, habitat utilization, and interspecific relations. Foraging strategies were determined by visual observations of otter for 68.8 hr and mink for 2.1 hr. Feeding habits were determined through identification of prey remains from 657 mink and 1,902 otter scats collected on the study area. Differences in body size and morphological adaptations were primarily responsible for niche differences between mink and otter. Niche overlap was evident in the feeding habits, activity patterns, and habitat utilization of both species. The degree of overlap was minimized by different foraging strategies, variability in prey selection and activity patterns, and differential habitat use enhanced by environmental heterogeneity. Resource partitioning was sufficient to permit coexistence of viable mink and otter populations. Theoretical and management implications regarding the mechanics of this coexistence are discussed.

The American mink (*Mustela vison*) and river otter (*Lutra canadensis*) are 2 closely related members of the weasel family, Mustelidae. Although both species are associated with an aquatic habitat, the river otter is more adapted to this type of existence due to several morphological features (e.g., interdigital webbing, short and dense fur, dorso-ventrally flattened tail, smaller ears in proportion to body size). The general shape of both mink and otter is similar: long, slender, and weasel-like. However, in west-central Idaho adult otter weighed 8.5 kg (N=8); and adult mink, 0.72 kg (N=45), a ratio of 12:1. Thus, one can assume differences between the species with regard to bioenergetics, behavior, and general ecology manifested by these differences in morphology and size. The concept that differences in body size promote niche differences is well established (Wilson 1975).

Indeed, mink and otter do coexist and are usually sympatric throughout most of their ranges. Obviously then, they are not complete competitors based on the competitive exclusion principle (Gause's Principle) that complete competitors cannot coexist (Hardin 1960). There is, however, evidence that indicates mink and otter do compete, primarily for food, at certain times of the year and in certain areas.

Following its escape from fur farms in the 1950's, the presence of mink in Britain has been criticized for depressing local populations of otter (Linn and Chanin 1978). In Sweden, mink and otter compete for a limited food resource during the winter, with certain areas dominated by otter and others by mink (Erlinge 1969, 1972). In both Sweden and the USSR, mink appear to have caused a restriction of the otter to optimal habitat (Erlinge 1972, Novikov 1962). In turn, areas of high otter density locally limit mink populations in Sweden. Lack of suitable research techniques, however, has prevented further investigations regarding niche overlap, niche differentiation, and the importance of physical characteristics to the coexistence of mink and otter.

Development of a feasible implant telemetry technique for otter (Melquist and Hornocker 1979a) and its application to mink enabled us to investigate the interrelationship of mink and otter based on utilization along several important dimensions of their respective niches. In this paper we discuss the manner in which partitioning of food, space, and time permit coexistence 1) on a broad scale, and 2) in a limited area intensively used by both species. Basic ecological data, as well as an understanding of the factors that permit coexistence, are a necessary prerequisite to the development of sound and practical management plans for these interesting furbearers.

Data presented in this paper were collected between 1976 and 1979 as part of a detailed investigation into the ecology of mink and otter.

THE STUDY AREA

The study took place on the upper portion of the North Fork Payette River drainage in west-central Idaho. Elevations range from 1,500 m in the valley to 2,800 m on surrounding mountain peaks. Physiographic characteristics, climate, weather, vegetation, and land-use practices have previously been described (Melquist and Hornocker 1979b).

A portion of Lake Fork Creek was chosen as a site to investigate the interspecific relationship of mink and otter because there is a greater amount of simultaneous use by members of both species. Lake Fork Creek flows out of the mountains into a glacial trough up to 13 km wide and enters Cascade Reservoir immediately east of the mouth of the Payette River. The intensive study area comprised about 2 km of Lake Fork Creek as it enters the valley floor, just prior to flowing into Little Payette Lake. The stream in this section is generally 10 - 15 m wide and has frequent shallow riffles interspersed with deep pools. Riparian vegetation, consisting primarily of several species of shrubs and conifers, is well distributed along both banks. A gravel road parallels the Creek for about 500 m and ranges from 5 - 30 m away from the water. The upstream limit of the intensive study area is marked by a narrow, steep gorge with frequent rapids and waterfalls. A massive logjam is located above and on both sides of an island at the lower third of the intensive study area. Resulting from the yearly accumulation of logs and debris transported downstream during spring run-off, this logjam is a unique and important component of the habitat. All streams in the valley remain partially ice-free during winter months and are therefore accessible to mink and otter. Valley lakes freeze completely over and are only accessible at the confluence with streams.

METHODS AND MATERIALS

Otter were captured primarily in Hancock livetraps (Melquist and Hornocker 1979a); mink in baited Tomahawk traps. Captured animals were

Table 1. Summary of telemetry data collected from instrumented mink and otter in the intensive study area along Lake Fork Creek from September through December, 1977 - 1979.

	Mink	Otter
Animals monitored	7	8
Total monitor days	157	257
Total hours monitored	271	515
Total visual observations (min.)	28	169

Foraging Behavior and Feeding Habits

Foraging Behavior. Visual observations of mink and otter revealed differences in their foraging behavior. Otter always foraged from the water for aquatic and semi-aquatic prey. Any terrestrial prey consumed was either scavenged or caught when the animal inadvertently fell into the water. Mink, on the contrary, often foraged among the riparian vegetation or investigated overhanging banks, holes, and crevices while traveling along the shore. When foraging for aquatic prey, a mink would either travel along the shore or on floating logs extending into the stream, pausing frequently to peer into the water for potential food. Once the prey was detected, the mink would quickly dive into the water after it. Logjams were excellent foraging areas for both mink and otter because they provided shelter for several species of fish, as well as security for the predators and a structure from which the mink could forage.

Feeding Habits: General Study Area. Prey remains were identified from 657 mink and 1,902 otter scats collected on the study area between 1976 and 1979 (Table 2). The feeding habits data were a reflection of each predator's foraging behavior. Although fishes occurred more frequently in the diet of both mink (59 percent) and otter (97 percent) than other major prey categories, mink exhibited a more balanced feeding pattern

Table 2. Food of mink and river otter based on 659 mink and 1,902 otter scats collected from the general study area in west-central Idaho, 1976 - 1979.

Food item	No. of occurrences		Frequency (%)[a]	
	mink	otter	mink	otter
FISHES	387	1,844	59	97
Family Catostomidae				
Largescale sucker		551		29
Family Cottidae				
Mottled sculpin	49	722	7	38
Family Cyprinidae	191	506	30	27
Northern squawfish		49		3
Unidentified cyprinid	189	457	29	24
Family Ictaluridae				
Brown bullhead		17		1
Family Percidae				
Yellow perch		169		9
Family Salmonidae	66	1,189	10	63
Mountain whitefish		510		27
Kokanee	19	170	3	9
Unidentified salmonid	45	651	7	34
Kokanee and unidentified salmonid	61	815	9	43
Unidentified fishes	76[b]	25	12	1
MAMMALS	280	49	43	3
Family Cricetidae	241		37	
Meadow mouse	159		24	
Deer mouse	39		6	
Jumping mouse	7		1	
Muskrat	32	38	5	2
Miscellaneous	4		1	
Family Leporidae (snowshoe hare and pika)	7		1	
Family Sciuridae	10		2	
Yellowpine chipmunk	5		1	
Miscellaneous	5		1	
Family Soricidae				
Shrew	11		2	
Unidentified and miscellaneous mammals	8	11	1	1

Table 2. Food of mink and river otter based on 659 mink and 1,902 otter scats collected from the general study area in west-central Idaho, 1976 - 1979.

Food item	No. of occurrences		Frequency (%)[a]	
	mink	otter	mink	otter
BIRDS	127	56	19	3
Unidentified and miscellaneous waterfowl	56	40	9	2
Unidentified bird egg	5		1	
Unidentified and miscellaneous birds	66[c]	16	10	1
INVERTEBRATES	155	159	24	8
Terrestrial beetle (Coleoptera)	82		12	
Aquatic beetle (Coleoptera)	49	18	7	1
Stonefly nymph (Plecoptera)		130		7
Grasshopper	12		2	
Bee	9		1	
Unidentified and miscellaneous invertebrates		12		1
REPTILES				
Garter snake	13		2	

[a] Percentage values rounded to the nearest whole number and those less than 0.5 are omitted.

[b] Of this total, 73 were considered small fish (< 15 cm).

[c] Of this total, 59 were considered small birds.

(Figure 1). While mammals, birds, and invertebrates were also important prey to the mink, these groups merely supplemented the otter's fish diet and could only be considered seasonally important at best. Reptiles were unimportant to both mink and otter, occurring in less than 1 percent of the otter scats and 2 percent of the mink scats.

Because fishes were the key prey of otter and occurred most frequently in mink scats, the degree of overlap was important in understanding the mechanics of coexistence. Although mink have adaptations that permit them to exploit mammals, birds, reptiles, amphibians, and invertebrates more successfully, the otter's aquatic adaptations enabled them to effectively forage on a wider variety of fishes (Figure 2). Body size and morphological adaptations influenced the size of fishes preyed on as well. Two of the 3 groups of fishes represented in mink scats were comprised of specimens less than 15 cm in length; the major group, unidentified cyprinids, consisted of fish species ranging from 7 - 12 cm in length (Figure 2). The 3rd group, kokanee plus unidentified salmonids, consisted of larger fishes but these were likely scavenged. Otter, on the other hand, fed heavily on fishes larger than 15 cm.

Largescale suckers (*Catostomus macrocheilus*) were important to otter, but primarily because of their large size (see Figure 2 for size range of fishes), were not utilized by mink.

Mottled sculpins (*Cottus bairdi*) are a small (7 - 10 cm) bottom-dwelling fish widely distributed throughout the study area. Otter, especially younger and consequently smaller individuals, frequently preyed on these fish. As many as 80 sculpins were found in a single otter scat. Although mink occasionally preyed on sculpins (7 percent by frequency of occurrence), sculpins were less available to mink because they live on the stream bottom.

Large numbers of northern squawfish (*Ptychocheilus oregonensis*) occur in the major valley streams of the study area during the spring when they spawn. Squawfish were infrequently preyed on by otter, however, probably due to their quickness and the concurrent availability of large schools of spawning suckers. Squawfish remains did not show up in mink scats because they were likely too large and difficult for the mink to capture.

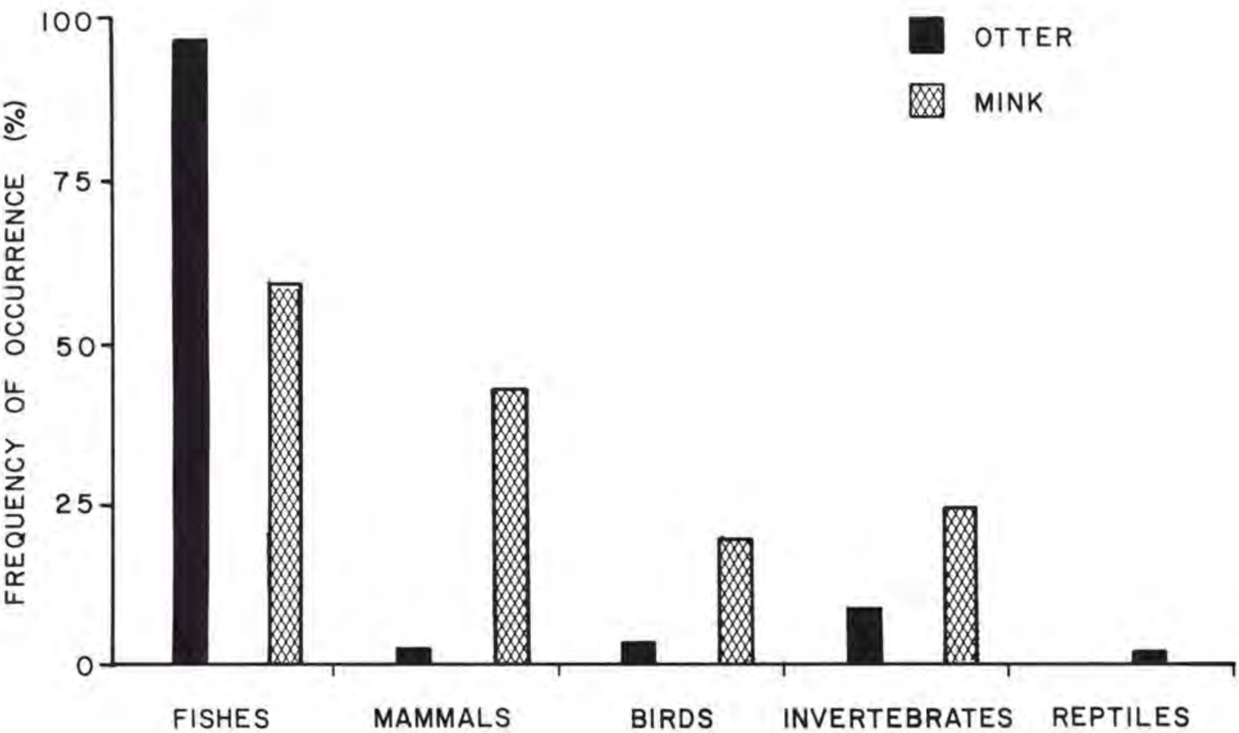

Figure 1. Major prey categories in the diet of mink and otter based on 657 mink and 1,902 otter scats collected from the general study area in west-central Idaho, 1976-1979.

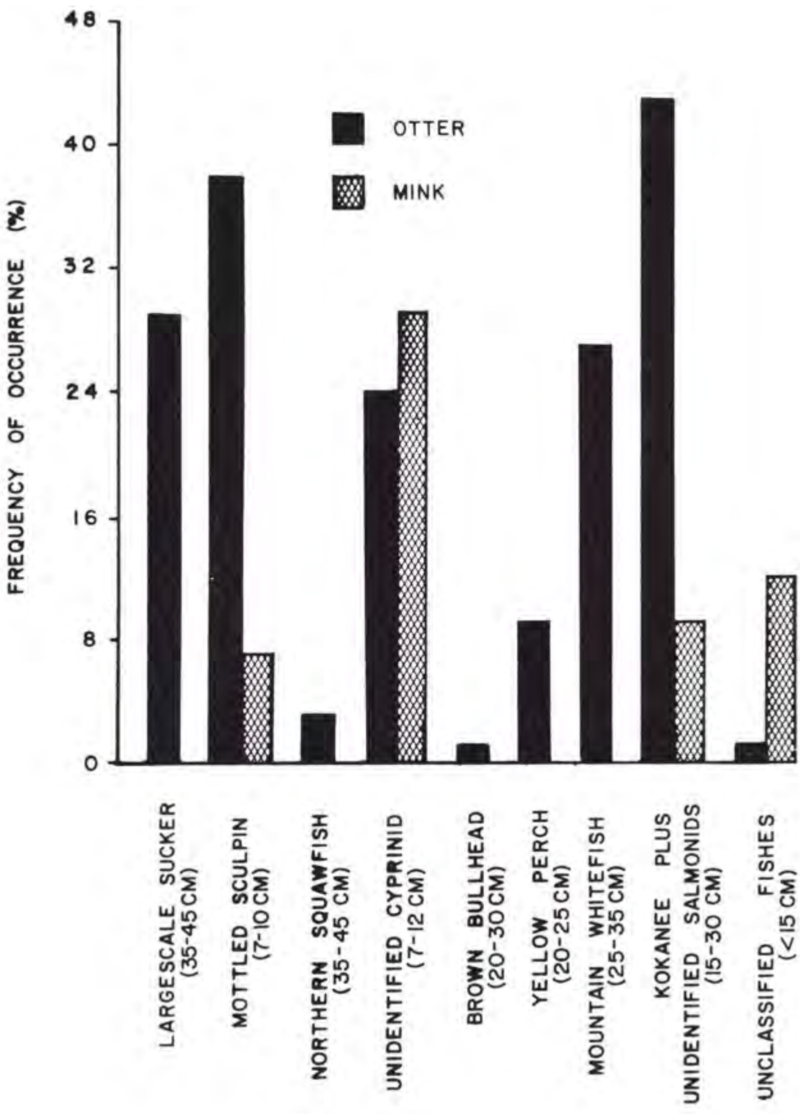

Figure 2. Fish species represented in the diet of mink and otter in westcentral Idaho, 1976 - 1979. (Approximate length of adult fish in parentheses.)

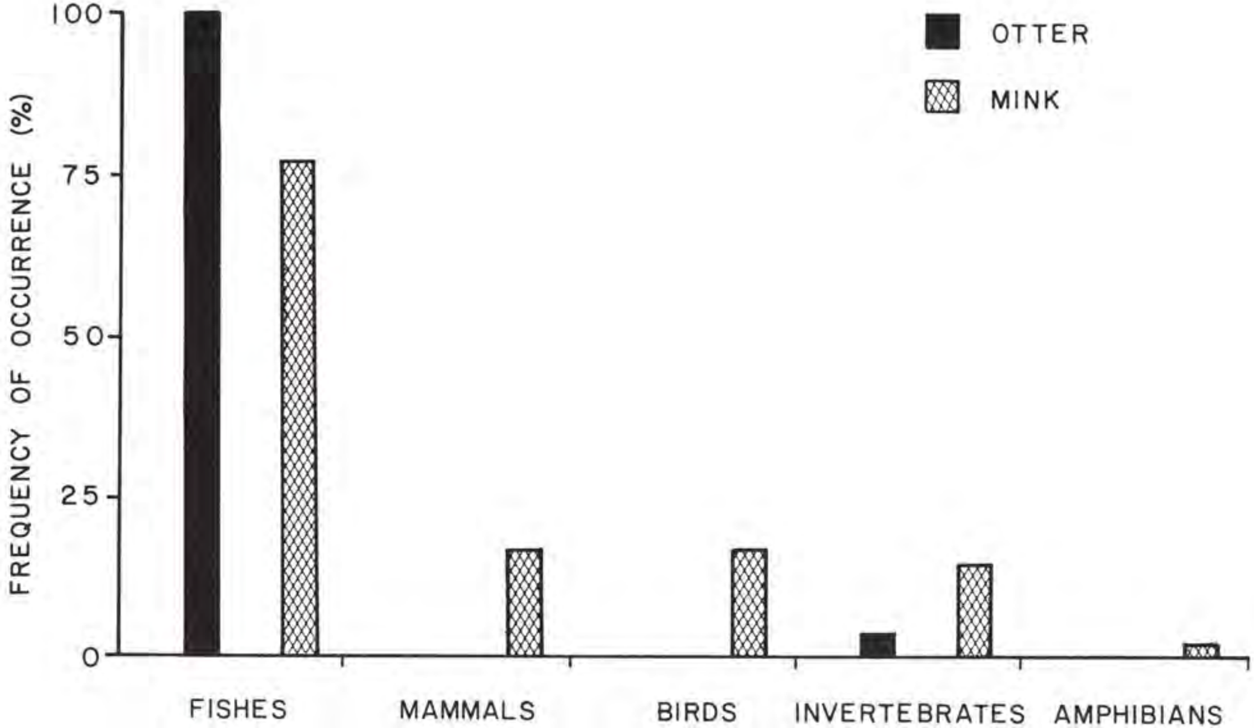

Figure 3. Major prey categories in the diet of mink and otter based on 66 mink and 416 otter scats collected from the intensive study area along Lake Fork Creek during August through November, 1976 - 1979.

The greatest amount of overlap occurred in the utilization of unidentified cyprinids, probably redside shiners (Richardsonius balteatus) and speckled dace (Rhinichthys osculus), which range from 7 - 12 cm in length. Fish sampling by electro-fishing showed that northern squawfish, redside shiners, speckled dace, and a small number of longnose dace (Rhinichthys cataractae) were the only cyprinids occurring in the study area. Large schools of shiners and dace were frequently seen in the shelter of numerous logjams, areas where both mink and otter often foraged.

Brown bullheads (Ictalurus nebulosus) were identified in only 17 otter scats and did not occur in any mink scats. Evidence of predation on bullheads was difficult to detect in the scats because otter generally do not eat the head and pectoral spines of larger specimens and scales are absent. As a result, the importance of bullheads in the food habits of otter was undoubtedly underestimated. On several occasions instrumented otter were observed foraging and feeding on bullheads in small farm ponds and where the major streams enter Cascade Reservoir.

Yellow perch (Perca flavescens) occurred in 9 percent of the otter scats, primarily those collected near Cascade Reservoir where perch were abundant. Perch did not occur in any mink scats, probably because few scats were collected in areas where perch occur and they were not readily available to mink.

As a group salmonids were the most important prey of otter. However, there was a certain amount of bias because a considerable number of scats were collected in areas where otter concentrate on fall spawning runs of kokanee (Oncorhynchus nerka). With the exception of mountain whitefish (Prosopium williamsoni), salmonids could not be accurately distinguished to species in scats. Based on the time and location scats were collected, we felt that 1) most unidentified salmonids were probably kokanee, and 2) predation on other unidentifiable salmonids, such as trout, was likely insignificant. Since kokanee could not be consistently identified by either a red tinge or roe in the scat, kokanee and unidentified salmonids were lumped together. Kokanee plus unidentified salmonids occurred in 9 percent of the mink and 43 percent of the otter scats.

These percentages increased considerably in scats collected from the intensive study area. Mountain whitefish were not utilized by the mink but were important to the otter, especially during late fall and winter. Mammals comprised an insignificant portion of the prey consumed by otter (3 percent), but were an important part of the mink's diet (43 percent). Mink preyed on a variety of terrestrial mammals associated with the riparian habitat. Only the muskrat (Ondatra zibethicus) jointly occurred in the diets of both mink and otter. Muskrat remains were most frequently found in otter scats collected from backwater sloughs and marshy areas where they were fairly common. In general, it appeared that only adult male mink weighing an average of 781 g (N=34) were large enough to consistently prey on muskrats. This relationship was similar to that found by Sealander (1943).

Birds, like mammals, were not considered to be important in the diet of otter. Although less important to mink than fishes and mammals, mink probably preyed on birds when they could be easily caught, such as wounded and young birds and those found dead. Both mink and otter preyed on waterfowl, especially during the spring and early summer when young ducks were more abundant. Mink also preyed on bird eggs, probably ground-nesting shorebirds, and various small birds found in the riparian habitat.

Invertebrates, primarily stonefly nymphs (Plecoptera) and aquatic diving beetles (Coleoptera), that range from 2 - 6 cm in length occurred in 8 percent of the otter scats. From the standpoint of bioenergetics, it is likely that only young otter could afford to actively forage for this type of prey. Visual observations of foraging otter substantiated this relationship. Invertebrates occurred in 24 percent of the mink scats collected. Terrestrial and aquatic beetles were the most frequently consumed. Similar to the situation with otter, invertebrates were probably utilized to a greater extent by juvenile mink.

Reptiles were an insignificant food of both mink and otter in the study area. Reptiles were represented by the garter snake (Thamnophis spp.) in 2 percent of the mink scats and less than 1 percent of the otter scats (not shown in Table 2).

Feeding Habits: Intensive Study Area. In general, otter do not remain long at one specific location; instead, they continue to travel throughout much of their home area visiting preferred foraging sites. This pattern is somewhat different when kokanee spawning runs occur within their home area. Adult kokanee (15 - 25 cm in length) begin migrating up from Little Payette Lake in August and spawn throughout most of the intensive study area. During the spawning run, which lasts through November, otter from Lake Fork Creek below Little Payette Lake moved into the area to utilize the abundant food supply. During the study, at least 2 family groups (2 adult females and 4 - 6 pups) and 2 - 4 other lone otter were concentrated in the area of the large logjam each year. The family group of 1 instrumented juvenile remained at the logjam for 40 continuous days in 1978. In December, when the kokanee disappear, the otter disperse to other parts of their home area.

Several mink, however, are permanent residents of this area. These mink utilize the seasonally abundant food supply as well. We felt that if both intra- and interspecific competition existed, it would be most obvious at this time and in this area, where an unusually large number of both mink and otter were concentrated.

Based on the analysis of 66 mink and 416 otter scats collected from the intensive study area during the time otter were concentrated in the area (August - November), both species foraged heavily on fishes (Figure 3). Fishes occurred in 100 percent of the otter scats, with the other major prey categories comprising an insignificant portion of their diet. Fishes occurred in 77 percent of the mink scats. Mink, however, continued to supplement their diet with mammals, birds, and invertebrates. In comparing these data with the overall feeding habits of each species (Figure 1), it was apparent that both mink and otter exhibit an opportunistic feeding behavior, utilizing an abundant and accessible food source when it was easily available.

A closer examination of fishes preyed on by otter and mink in the intensive study area revealed an overlap in the utilization of the families Cottidae, Cyprinidae, and Salmonidae (Table 3). As was expected, salmonids were exploited the most, specifically the kokanee plus unidentified salmonids group. After spawning, spent or spawned out kokanee

Table 3. Food of mink and river otter based on 66 mink and 416 otter scats collected from the intensive study area along Lake Fork Creek during August through November, 1976 - 1979.

Food item	No. of occurrences		Frequency (%)[a]	
	mink	otter	mink	otter
FISHES	51	416	77	100
Largescale sucker		7		2
Mottled sculpin	7	124	11	30
Unidentified cyprinid	6	93	9	22
Mountain whitefish		78		19
Kokanee	24	85	36	20
Unidentified salmonid	2	232	3	56
Kokanee and unidentified salmonid	26	316	39	76
Unidentified (unclassified) fishes	12		18	
MAMMALS	11		17	
Meadow mouse	4		6	
Deer mouse	3		5	
Columbian ground squirrel	1		2	
Snowshoe hare	2		3	
Red squirrel	1		2	
BIRDS	11		17	
Dipper	1		2	
Unidentified waterfowl	6		9	
Unidentified small bird	4		6	
INVERTEBRATES	9	13	14	3
Terrestrial beetle (Coleoptera)	2		3	
Aquatic beetle (Coleoptera)		8		2
Grasshopper	1		2	
Unidentified and miscellaneous invertebrates	1	5	2	1
AMPHIBIANS				
Spotted frog	1		2	

[a] Percentage values rounded to the nearest whole number and those less than 0.5 are omitted.

begin to die and thus become easy prey for the predators.

Otter begin to prey on kokanee as soon as the fish arrive on the spawning beds in August (Figure 4). However, at this time sculpins were an important part of their diet as well. Cyprinids and mountain whitefish occurred in only a small percentage of scats during August. In September, when numerous spent kokanee begin to die, utilization increased to 93 percent. Simultaneously, sculpin occurrence dropped from 86 percent in August to 20 percent in September, as the otter concentrated on the kokanee. Both cyprinid and mountain whitefish utilization remained essentially unchanged. As the spawning run tapered off, and fewer kokanee were available, their occurrence in otter scats dropped to 77 percent in October and 51 percent in November. At the same time, sculpin occurrence remained between 20 percent and 25 percent. However, cyprinids and mountain whitefish increased to 27 percent and 15 percent in October, and 43 percent and 69 percent in November, respectively. The high occurrence of whitefish in scats collected during November was due, in part, to the presence of an increased number of fish that spawn in late October and November. Therefore, the otter compensated for a reduction in kokanee by increased utilization of cyprinids and whitefish.

The situation was somewhat different for mink because of their ability to exploit both aquatic and terrestrial prey. Regarding fishes separately, a marked increase in kokanee utilization by mink did not occur until October, followed by a decrease in November (Figure 4). Kokanee survive for several weeks after spawning and thus were not easy prey for mink until nearly dead and washed up on shore. This probably explains why mink, unlike otter, did not show an increase in kokanee utilization in September. When kokanee were abundant and easily obtained, mink preyed very little on other fishes. Prior to the increased utilization of kokanee in October, sculpins (in August) and both sculpins and cyprinids (in September) supplemented the kokanee diet.

If we examine feeding habits of mink in the intensive study area based on all prey categories, there was a negative relationship between the occurrence of fishes in their diet with the occurrence of birds, mammals, and invertebrates (Figure 5). Fishes increased from August to October, then

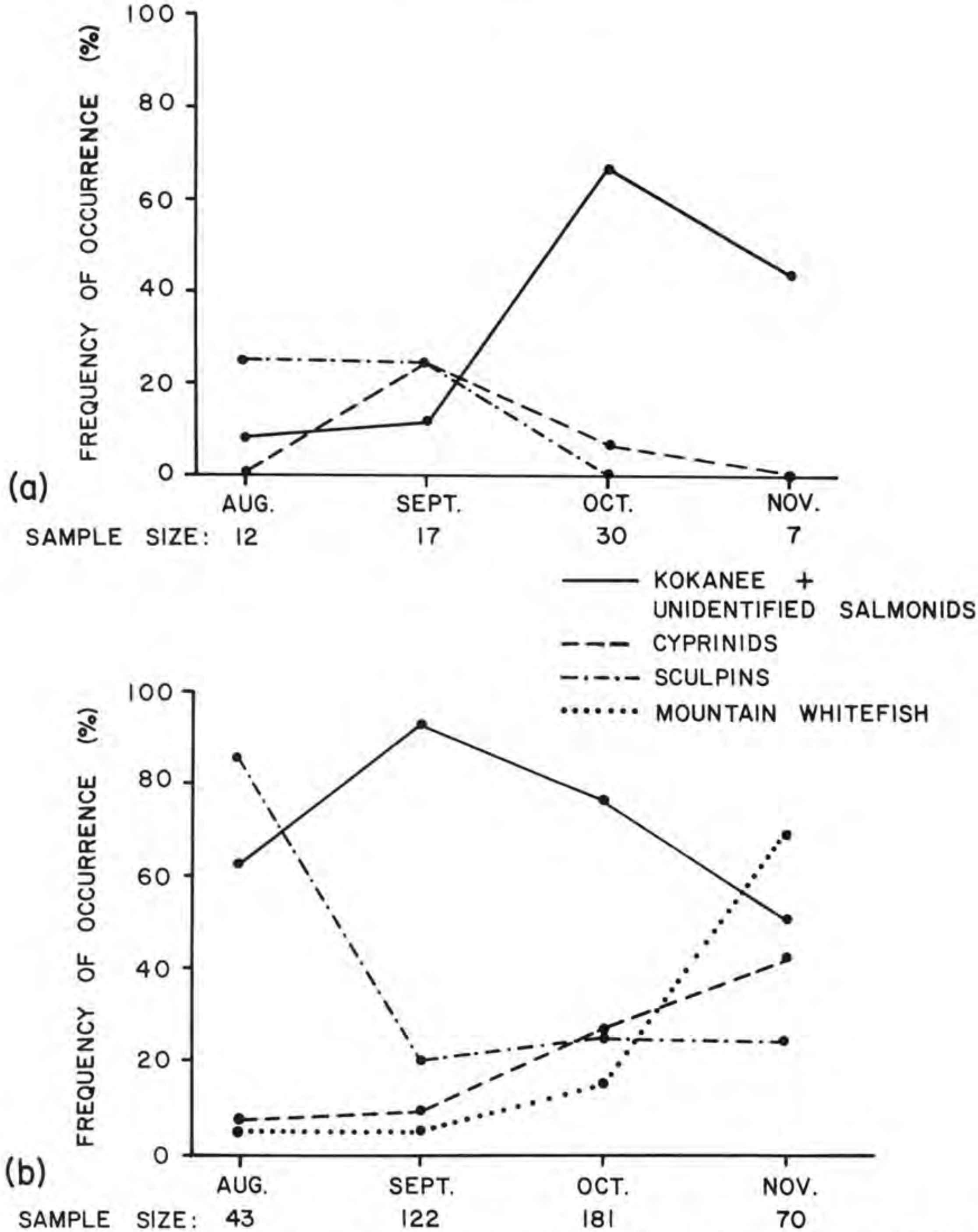

Figure 4. Monthly occurrence of fishes preyed on by mink (a) and river otter (b) based on 416 otter and 66 mink scats collected from the intensive study area along Lake Fork Creek, 1976 - 1979.

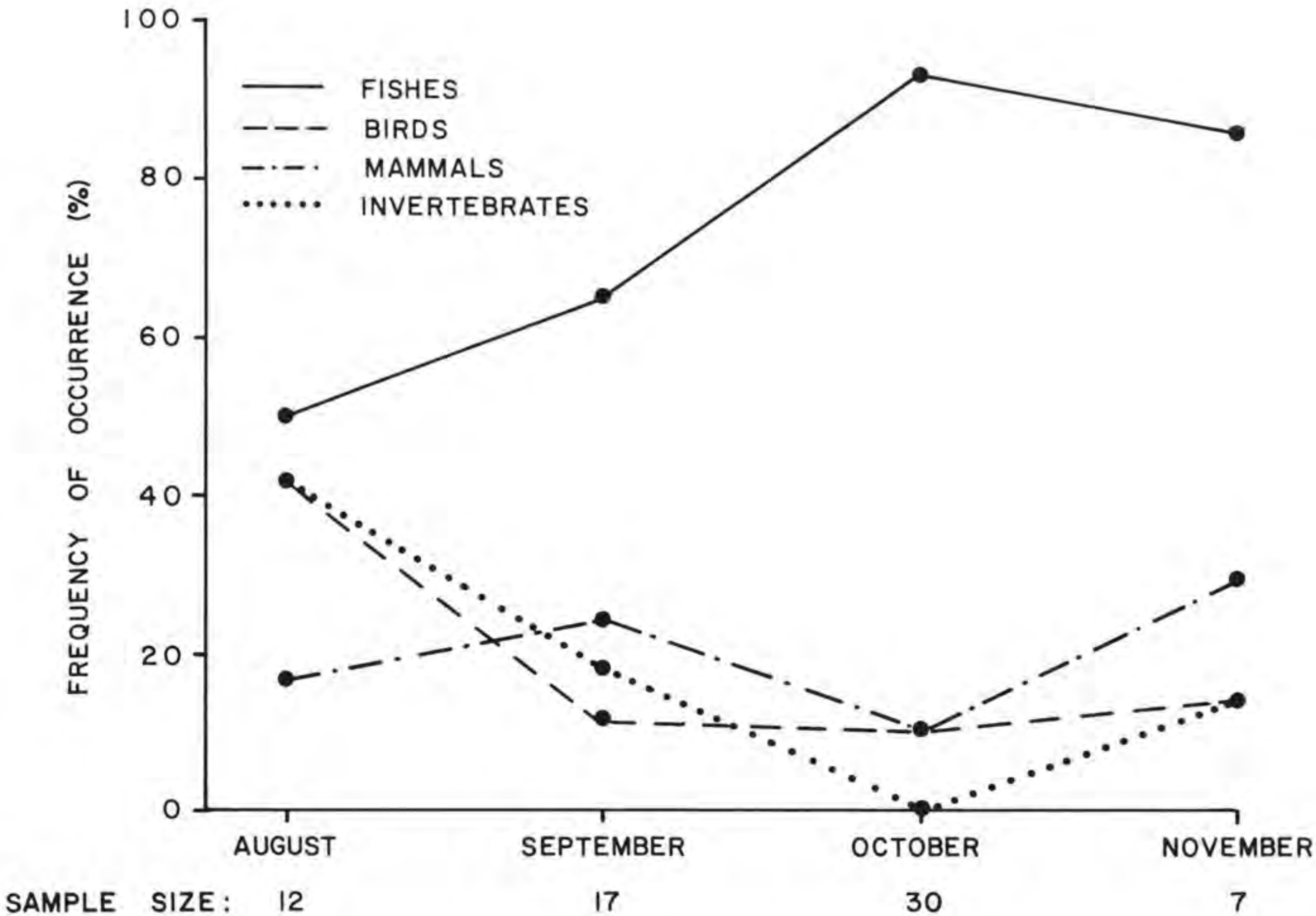

Figure 5. Monthly occurrence of major prey categories in 66 mink scats collected from the intensive study area along Lake Fork Creek, 1976 - 1979.

decreased in November. At the same time, there was a corresponding decrease in occurrence of other prey categories through October, then an increase in November. Therefore, mink were able to adjust their feeding habits to accommodate prey density, distribution, and availability.

Activity Patterns

Activity patterns were based on 416 mink and 974 otter activity fixes (5 min minimum per fix; maximum of 1 fix per hourly period). Mink were significantly more nocturnal (60 percent; N=108) than diurnal (46 percent; N=308) in activity (X^2=6.35, ldf, $P < 0.025$). There was no significant difference between nocturnal (47 percent; N=157) and diurnal (43 percent; N=817) activity of otter (X^2=0.82, ldf, $P > 0.05$). During the time both instrumented mink and otter occupied the intensive study area mink were significantly more nocturnal than otter (X^2=4.37, ldf, $P < 0.05$). Additionally, mink were significantly more active (50 percent; N=416) than otter (44 percent; N=974) in the intensive study area (X^2=4.12, ldf, $P < 0.05$).

Hourly activity patterns of instrumented mink and otter in the intensive study area during September through December, 1977 - 1979, are illustrated in Figure 6. Hours with less than 16 activity fixes for otter and 12 activity fixes for mink were omitted. No telemetry data were available for either mink or otter during August.

Otter exhibited their greatest amount of activity during early morning hours, prior to and shortly after dawn. Activity dropped significantly during the 0900 - 1000 hrs period (X^2=9.81, ldf, $P < 0.005$), and reached a low of 32 percent active at 1000 - 1100 hrs. This low was followed by a gradual increase in the percent of active fixes, although activity remained below 50 percent through 2200 hr. Figure 6 shows a sharp drop in activity between 1900 - 2000 hr; however, this change was not significant (X^2=2.58, ldf, $P > 0.05$). Otter did not exhibit an increase in activity after dusk. Limited data suggest that activity did not increase until about midnight.

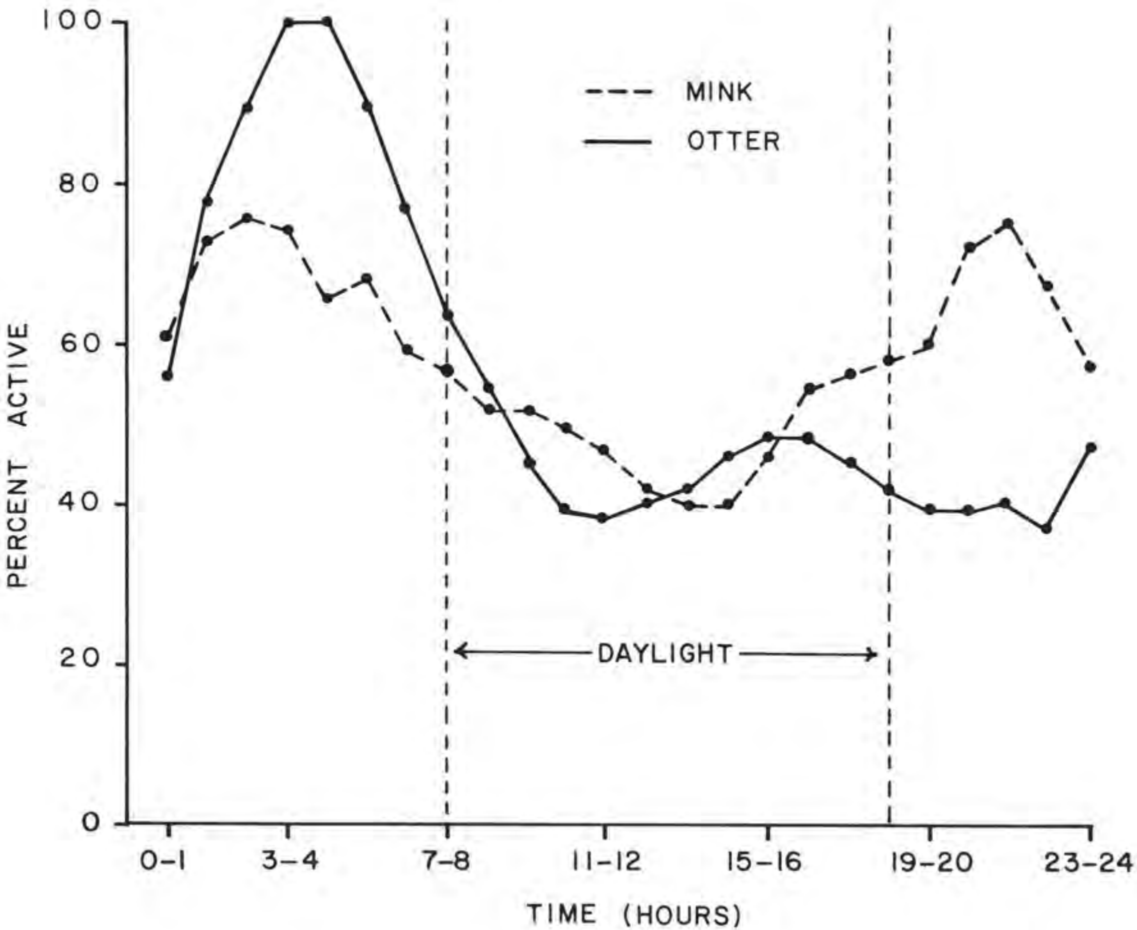

Figure 6. Activity patterns of 6 mink and 8 river otter monitored in the intensive study area during September through December, 1977 - 1979. Data are based on 416 mink and 974 otter activity fixes. Minimum hourly samples for mink and otter were 12 and 16, respectively.

The frequency of activity of mink was not as high as for otter during early morning hours. However, cessation of activity after dawn was more gradual for mink. The pattern of inactivity during mid-day was similar for both mink and otter. Mink appeared to respond more quickly to the onset of darkness, with a frequency of 67 percent active during the 2000 - 2100 hr period, as compared to 44 percent for otter. Although data are limited from 2100 - 0600 hr, it appears that the nocturnal activity of mink peaked earlier than otter. Nonetheless, individuals of both species tended to be more active during nocturnal hours.

Habitat Utilization

Den Site Selection. Den site selection by otter in the intensive study area was related to food availability; that is, otter used suitable den sites in close proximity to foraging areas. Therefore, habitat utilization was almost entirely based on foraging and resting areas. Similarly, mink selected den sites close to preferred foraging areas. However, because mink were not as dependent on the aquatic environment, den site locations were occasionally some distance from the stream.

Instrumented otter used 10 different dens that were either in the large logjam (6), or in the stream bank (4) with underwater entrances (Figure 7 and 8). The logjam dens were located in the north channel of the stream within a 15 m radius of each other (Figure 8). Specific den use appeared to be dependent on the number and group composition of otter occupying the logjam at any one time. During the fall when the north channel was dry the mass of twisted logs provided shelter for resting otter, as well as a direct route to the south channel and east end of the logjam where the animals foraged for kokanee.

The logjam dens were used primarily during the height of the kokanee run. Most otter left the area in early December, when available kokanee became more difficult to find. Otter that remained in the area after the spawning run (3 juveniles in 1977) concentrated on other prey and also used bank dens located near the new foraging areas about 300 m upstream from the logjam (Figure 8). Instrumented otter were often observed foraging for small prey, such as sculpins, in the vicinity of these dens during

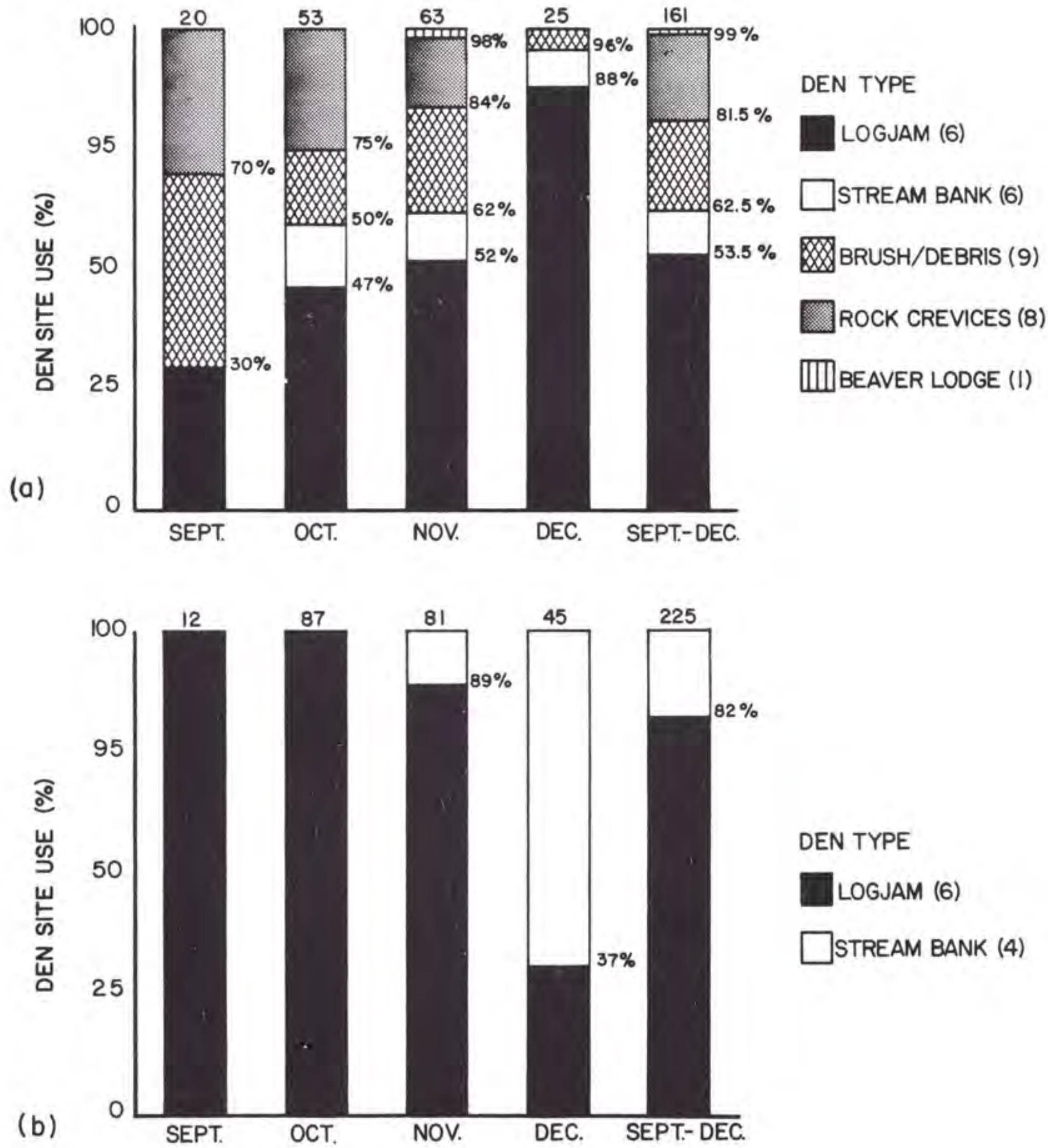

Figure 7. Major den sites used by mink (a) and river otter (b) in the intensive study area along Lake Fork Creek, 1977 - 1979. (Number above each bar indicates sample size. Total number of the major den types used are in parentheses. Fifth bar represents a composite of the monthly percentages.)

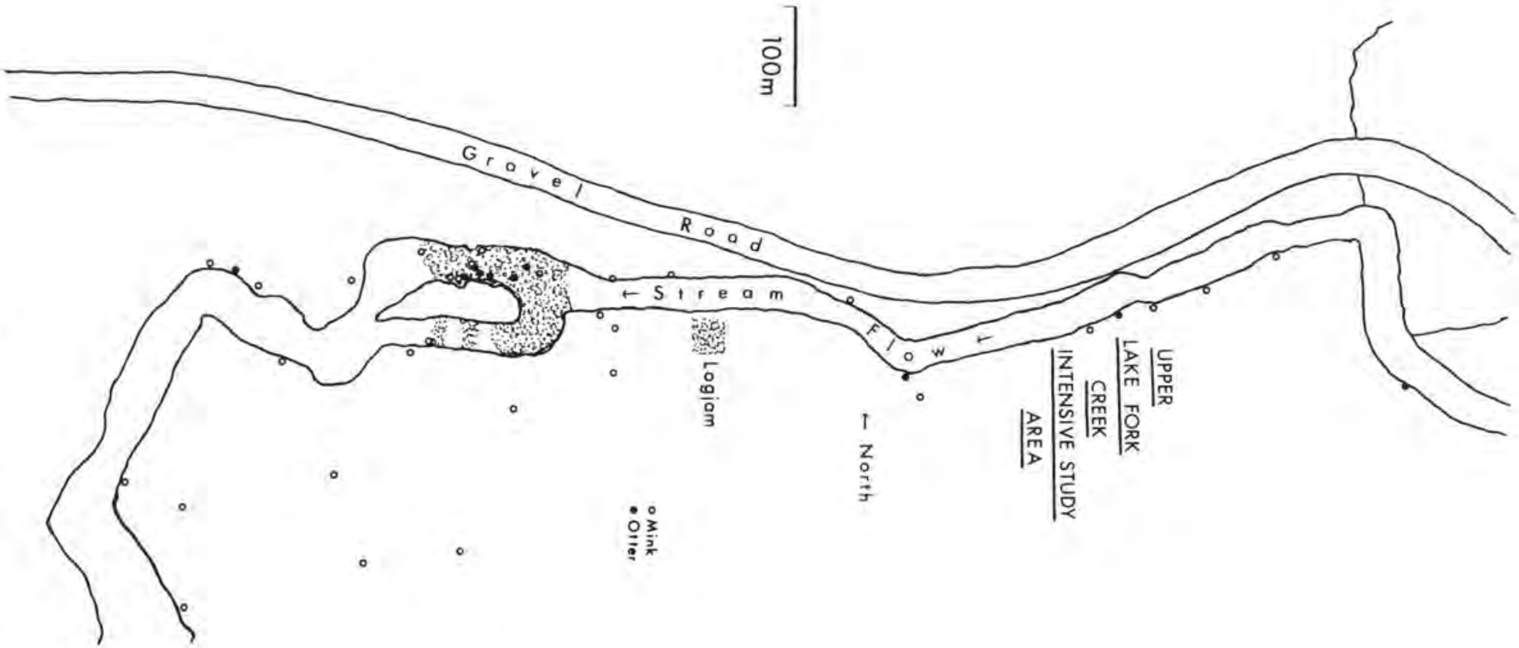

Figure 8. Location of den sites used by instrumented mink and otter in the intensive study area along Lake Fork Creek, 1977 - 1979.

December. All instrumented otter left the intensive study area by 4 January.

Resting mink used 30 different den sites consisting of 5 basic types (Figure 7). A relationship between the use of logjam dens by mink and the occurrence of kokanee was not as apparent as it was with otter. Increased use of logjam dens was probably due to the availability of kokanee and other prey, as well as the result of increased snow depths that made access to other den types difficult. Logjam den use by mink peaked in December when use by otter was at its low. This did not appear to be a response by mink to the absence of otter, however, since logjam den use by mink increased during peak use by otter. Fallen branches, brush, and other debris that provided sufficient shelter were frequently used prior to December. These sites ranged from 5 - 100 m away from the stream. Cracks or crevices in exposed granite, both adjacent to the stream and up to about 200 m south of the logjam, were often used by instrumented mink. Rock crevices with small openings provided excellent security for mink by limiting entry to animals no larger than the mink itself. Holes in the stream bank, an unoccupied beaver lodge, and other dens infrequently used by mink probably provided shelter for animals temporarily resting between hunting forays.

The logjam was important in terms of providing security for foraging and resting mink and otter. Logjam dens were selected by mink and otter 53 percent and 82 percent of the time, respectively. The 2 logjam dens most frequently used by mink and otter were within 3 m of each other. Even though otter in this area do not have any natural enemies, they are often quite wary. The logjam provided security in the sense that animals could forage among the logs without interruption or concern for possible danger. The logjam provided shelter and minimized exposure of foraging mink to potential aerial, terrestrial, and aquatic predators.

Foraging Areas. Locations of instrumented animals during periods of activity were considered to be foraging areas, since most active animals were either foraging or feeding.

Habitat utilization of otter in the intensive study area was based on 127 active fixes either in the confines of the logjam or in open areas of the stream (Figure 9). Active instrumented otter were located in the logjam 69 percent of the time. However, monthly use varied in accordance with prey availability. Logjam use increased from 75 percent to 92 percent between September and November, when large numbers of kokanee were available. In December, when kokanee numbers dwindled, utilization of the logjam decreased to 30 percent as otter moved into the open stream to forage.

Evaluation of habitat utilization by mink was based on their occurrence in 3 basic habitat types: 1) the logjam, 2) stream bank between the shoreline and high water line (1 - 3 m), and 3) riparian and upland vegetation beyond the high water line. We obtained 129 active fixes from 5 instrumented mink monitored at the intensive study area between September and December 1978 - 1979. Similar to otter, mink selected den sites close to foraging areas, thus reducing unnecessary movement. During the entire period, active mink were located in the logjam 56 percent of the time (Figure 9), indicating the importance of the logjam to mink as well as otter. Utilization of the logjam habitat varied from one month to the next, however. Logjam use increased steadily from September to November, then decreased slightly in December. Use of the shoreline or stream bank habitat above and below the logjam showed little variation throughout the monitor period. Use of riparian vegetation decreased from a high of 64 percent in September to a low of 10 percent in December, when snow depths made access to areas away from the stream more difficult. Instrumented mink were never located more than about 200 m away from the stream. No mink were located in the open stream habitat used extensively by otter in December. Likewise, no otter were located in riparian vegetation away from the stream. Tracks and remains of fish found at various places along the shoreline indicated otter occasionally used the stream bank habitat for rolling, grooming, feeding, and defecating. The stream bank habitat was used by mink 20 percent of the time between September and December.

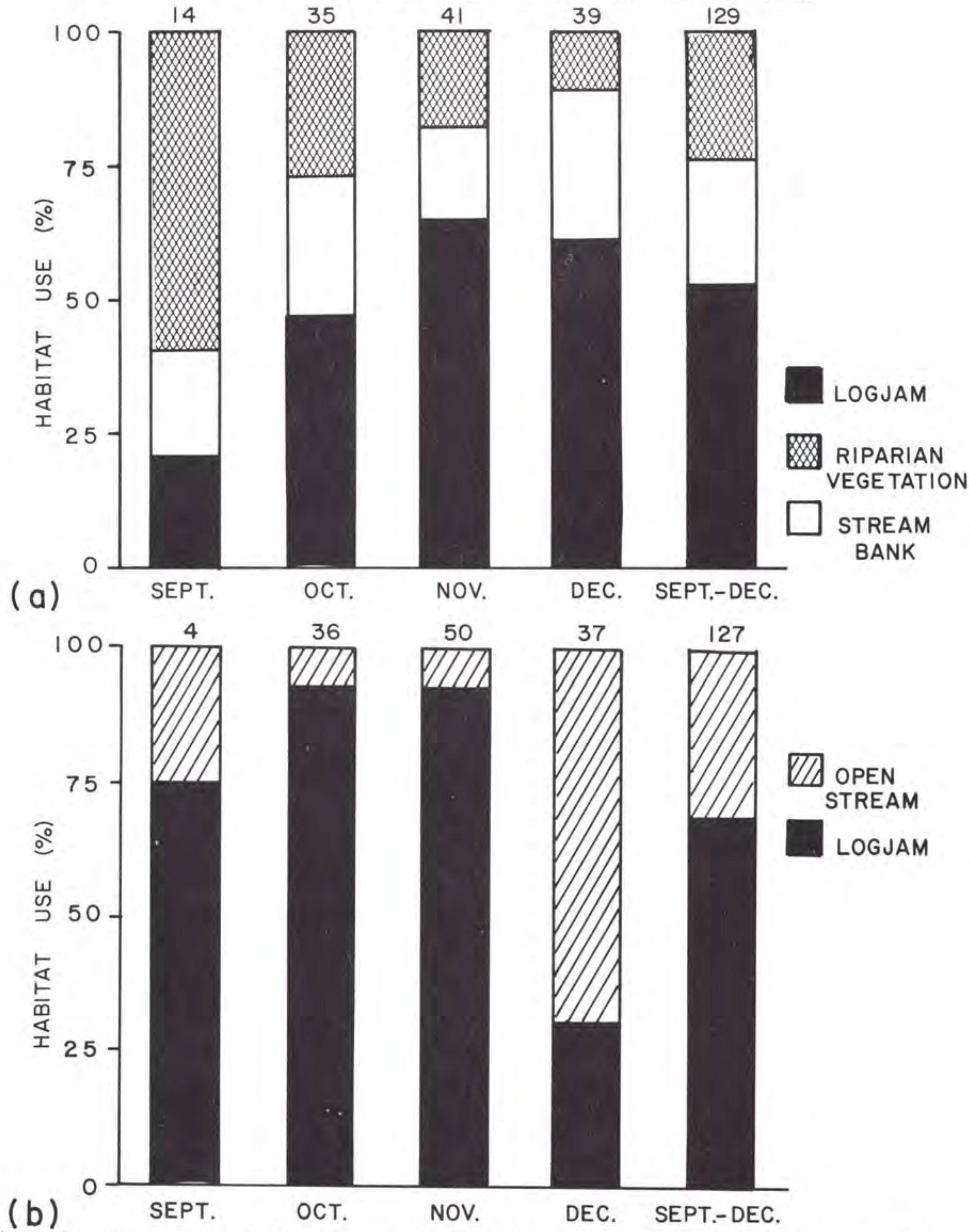

Figure 9. Importance of habitats used by 5 mink (a) and 8 river otter (b) in the intensive study area during September through December 1977-1979. Data are based on transmitter fixes when the animals were active. Number above each bar indicates sample size. Fifth bar represents a composite of the monthly percentages.

Interspecific Relations

Instrumented mink and otter were monitored simultaneously in the intensive study area on 65 different days during 1978 - 1979. Both mink and otter were active, probably foraging, in the logjam at the same time on 18 of those days. Although it was often difficult to determine the exact location of active animals without disturbing them, mink appeared to use drier portions of the logjam, while otter foraged among the logs in the main channel. However, foraging mink and otter frequently moved through common sections of the logjam and were recorded as close as 5 m of each other.

On 21 days of monitor, either mink or otter were active in the logjam, while the other rested in one of the logjam dens. This difference did not appear to be the result of mink adjusting their activity to that of the otter, since both were frequently active at the same time. Active mink often traveled on logs directly above resting otter. Likewise, active otter moved beneath logs that sheltered resting mink without disturbing them.

Mink and otter were both recorded inactive (resting) in the logjam on 19 days of monitor. Most of the logjam dens were surprisingly close together (see Figure 8). As previously mentioned, the 2 dens most frequently used by mink and otter were about 3 m apart.

On 24 days of monitor, instrumented mink and otter were in different locations within the intensive study area. However, no interspecific implications could be attributed to these differences.

DISCUSSION

Food Habits

Rosenzweig (1968) has shown the importance of dissimilar body size in the maintenance of coexistence between closely related carnivores. Differences in body size resulting in different foraging strategies were important in the coexistence of ? sympatric weasles (Mustela nivalis and M.

erminea), according to King and Moors (1979). Clem (1977) showed that fisher (Martes pennanti) utilized larger prey than marten (M. americana), which are smaller although nothing was mentioned about whether or not body size was important in coexistence. In Sweden, Erlinge (1969) concluded that the differences in food habits in mink and European otter (Lutra lutra) was primarily due to different adaptations. We found that body size was important in allowing otter to exploit larger fish than mink. In general, mink and otter selected a different proportion of the various species and sizes of fish available to both. Overlap was likely greatest between adult male mink (maximum weight of 1.01 kg; N=34) and juvenile female otter (minimum weight of 2.27 kg in early August; N=15), because they come closest to being similar in size and weight. In Sweden, where there is only a 1:2 ratio in body size between mink and European otter, feeding habits overlap as much as 60 - 70 percent, with competition occurring during winter months (Erlinge 1972).

We did not investigate the adaptive significance of sexual dimorphism in either mink or otter, although Erlinge (1979) has shown that size difference in male and female weasels (Mustela erminea) permits the sexes to exploit different sized food and promote habitat segregation. Otter do not exhibit the degree of sexual dimorphism that mink do. However, young (and therefore smaller) otter often foraged for smaller prey thus permitting a family group to exploit a wider range of prey species and sizes. Based on weight, adult male mink in the study area were 48 percent larger than females. This size difference, in addition to the mink being a smaller carnivore, probably resulted in a substantial amount of differential prey selection.

The work of King and Moors (1979) on weasels indicates that Mustela erminea, the larger species, is more of a generalist than M. nivalis. However, the consensus, according to Simms (1979), is that the smaller species are more efficient than larger forms because of their ability to pursue small rodents into their tunnels. In comparing mink and otter, we considered otter to be specialists, and mink generalists. Otter, because of their aquatic adaptations, exploited primarily aquatic prey while mink exploited a variety of both aquatic and terrestrial prey. In terms of efficiency, otter were more efficient fish predators, utilizing a greater number of fish species and a broader size spectrum. Mink were more efficient at exploiting a variety of different prey (e.g., birds, mammals, and fishes). Therefore, if there was a drastic decline in fishes, the mink would be least affected. Likewise, if bird, or especially mammal, numbers were reduced to the point where mink had to depend primarily on fishes, they would be at a competitive disadvantage. However, at present mink and otter population levels and prey diversity and density, competition for food does not appear to exist.

Activity Patterns

Mink displayed a greater nocturnal activity pattern than otter, although both were frequently active at the same time. The reason or reasons for this are only speculative. The data do not indicate that this was a result of competitive interference, however. It is reasonable to assume that the innate physiological cycle of these predators is influenced by external factors such as prey availability. As such, the predator's activity would tend to be synchronized with that of its prey. From the standpoint of predator-prey relationships, otter would not be required to adhere to a nocturnal schedule, since their principal prey (fish) is available at any time. A tendency to be nocturnal may occur primarily as a consequence of human activity and disturbance. In contrast, the tendency for mink to be nocturnal may be a reflection of the mammalian segment of their diet. Small rodents, primarily meadow voles (Microtus spp.) and deer mice (Peromyscus spp.), were an important part of their diet. These rodents tend to be most active at night and during crepuscular hours (Calhoun 1945, pers. observ.), which corresponds with mink activity. Apparent synchrony between predator and prey activity patterns was found in feral mink in Sweden by Gerell (1969), and red fox (Vulpes vulpes) in Wisconsin by Ables (1969).

Habitat Utilization

Otter were confined primarily to aquatic habitats whereas mink utilized aquatic, riparian, and upland habitats. The greatest amount of overlap occurred in the use of logjams as foraging areas and den sites. The presence of otter at logjams did not preclude their use by mink. In fact, utilization of logjams by both species increased when food became abundant.

Energy demands and prey density and distribution generally required otter to frequently move between foraging sites within a home area encompassing 10 - 20 km of stream. This pattern was abandoned, however, when seasonally abundant food existed in localized areas. Mink were able to sustain themselves in a 1 - 2 km section of stream because of their small size and utilization of the aquatic and adjacent riparian habitats. This observation that larger animals meet their requirements by increasing home area size is certainly not new (McNab 1963). The frequent movements of otter helped to insure that a mutual food supply did not become limited, a situation more critical to otter than mink. We have shown, however, that when ample food was available, mink and otter were able to coexist even during simultaneous exploitation of a common food source and a common area.

Coexistence of Mink and Otter: A Synthesis

The existence of niche overlap was evident in the food habits, habitat utilization, and diel activity patterns of both species. However, the degree of overlap was minimized by different foraging strategies, variability in prey selection and activity patterns, and differential habitat use enhanced by environmental heterogeneity. Obvious differences in body size and morphological adaptations were, in turn, largely responsible for these ecological differences.

The following is a synthesis of the important factors which permit coexistence of mink and otter:

1. A considerable amount of overlap in the utilization of certain fishes was not critical because the food supply did not appear to be limited.

2. The likelihood of interspecific interactions was reduced through differences in the foraging strategies of mink and otter.

3. Excessive depletion of available prey, primarily fishes, was avoided because otter frequently moved from one foraging site to another, or dispersed from an area when abundant food supplies diminished.

4. Fishes could be exploited to a greater extent by both species because the resource was partitioned in general accordance with the predator's body size; i.e., mink preyed on smaller fishes, while otter selected larger fishes as well.

5. Excessive overlap in feeding habits was avoided because morphological differences permitted mink to exploit both aquatic and terrestrial prey and otter to exploit a wider variety of fishes.

6. Partitioning of time was not necessary because different foraging strategies minimized the possibility of aggressive interactions.

7. Differences in the activity patterns were probably influenced by external factors, such as prey activity and availability, rather than competitive interference.

8. Morphological differences promoted habitat segregation, confining otter primarily to aquatic habitats, while mink exploited both aquatic and terrestrial habitats.

9. Simultaneous use of a specific habitat type (e.g., the logjam) was permitted because mink could forage and den in portions of the habitat that were inaccessible to otter.

Implications

From a theoretical standpoint, the results of this study help emphasize the importance of dissimilar body size in promoting coexistence between related species through resource partitioning. Morphological variations, although not always obvious and frequently not considered, are evolutionary adaptations developed through natural selection for the purpose of increasing a species ability to compete. Morphological differences between mink and otter provide each species with a competitive advantage.

The otter is a more efficient competitor in an aquatic environment; the mink in a terrestrial environment. Thus, both species are able to live in close association without either being excluded.

The conservation of animals considered important to man depends increasingly on our ability to intelligently manage and preserve existing populations. The economic and aesthetic values of mink and otter make them important to both consumptive and nonconsumptive users. Proper management involves more than just considering the requirements of each species as a separate entity. It requires an understanding of the interrelationship of mink and otter to each other, as well as to other components of the environment.

Environmental heterogeneity is vitally important to the coexistence of mink and otter. This has been demonstrated for other predators in numerous studies (King and Moors 1979). One of the well established dogmas of community ecology is that diversity causes stability (Krebs 1972). This is an important principle to consider in the management of mink and otter. Habitat diversity promotes species diversity, which allows mink and otter to exploit different resources at different levels thus reducing the likelihood that a resource vital to both will be in short supply.

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