Journal of Mammalogy, 84(4):1341–1355, 2003

THE BURDEN OF CO-OCCUPANCY: INTRASPECIFIC RESOURCE COMPETITION AND SPACING PATTERNS IN AMERICAN MINK, *MUSTELA VISON*

NOBUYUKI YAMAGUCHI AND DAVID W. MACDONALD*

Wildlife Conservation Research Unit, Department of Zoology, South Parks Road, Oxford OX1 3PS, United Kingdom

Live-trapping and radiotracking of American mink (*Mustela vison*) on 24 km of the River Thames, United Kingdom, revealed range sizes (male: 6.8 km, female: 2.7 km), numbers of other mink found in the range of each male (0.98 males, 1.95 females) and each female (1.18 males, 0.32 females), and range overlaps between dyads of males (88.2%), a male and a female (male: 32.6%, female: 69.1%), and females (66.3%). We used these data to estimate the potential energetic burden of conspecifics on each other. As a monthly average, cohabiting males and other females take an estimated 30% and 9%, respectively, of the total energy consumption by mink within the range of each female. Similarly, cohabiting males and females consume an estimated 21% and 40%, respectively, of the energy in each male's range. Intraspecific resource depression may force both sexes, especially males, to maintain larger ranges. We suggest that, in the case of American mink, intraspecific prey-resource competition affects the range sizes of both sexes.

Key words: American mink, home range, intrasexual territoriality, intraspecific competition, lowland England, *Mustela vison*, resource dispersion, spatial organization

The basic mustelid spacing pattern is generally thought to derive from intrasexual territoriality, where individuals maintain territories only with respect to members of the same sex (reviewed in Macdonald 1992; Powell 1979). In principle, the considerable sexual dimorphism in mustelids may allow 2 potentially competing individuals of different sexes to have different diets and thus to cohabit (McDonald 2002; Powell 1994). In practice, few data demonstrate clear resource partitioning between the sexes. Two sexes compete through using the same prey species—resource depletion and, visiting prey patches in each other's home ranges, and thereby, affecting each other's hunting success—resource depression (Charnov et al. 1976; Jedrzejewski and Jedrzejewski 1990; Powell 1994). The American mink (*Mustela vison*) is a solitary, sexually dimorphic, semiaquatic mustelid (Dunstone 1993). Individuals of both sexes defend their territories against other conspecific individuals of the same sex, at least during the nonbreeding season, and there is evidence of intrasexual territoriality (Birks 1981; Dunstone 1993; Dunstone and Birks 1983; Gerell 1970; Ireland 1988). While most females continue to maintain their territories into the breeding season, many males abandon their ranges and roam over larger areas in search of receptive females (Birks 1981; Birks and Dunstone 1991; Dunstone 1993; Ireland 1988).

Among polygynous mammals, it is widely held, although largely untested, that the spatial distributions of females are determined by food resources and those of males are strongly influenced not only by food but also by the dispersion of females (Clutton-Brock 1989; Ims 1988; Krebs and Davies

---

* *Correspondent: david.macdonald@zoo.ox.ac.uk*

1984; Macdonald 1983; Ostfeld 1986; Sandell 1989). In this context, a few studies have tackled the influences of habitat-related productivity on mink spacing patterns (Birks 1981; Birks and Dunstone 1991; Dunstone 1993; Halliwell and Macdonald 1996; Ireland 1988). Also a few reports have been published on resource competition between mink and sympatric competitors (polecats, *Mustela putorius*—Lodé 1993; European mink, *M. lutreola*—Macdonald et al. in litt.; Maran et al. 1998; otters, *Lutra lutra*—Bueno 1996; Clode and Macdonald 1995; Canadian otters, *Lontra Canadensis*—Ben-David et al. 1995; Melquist et al. 1981; southern river otter, *L. provocax*—Medina 1997). However, the role of conspecific competition has remained largely unquantified despite its theoretical importance.

In this article, we test whether the spacing patterns of conspecifics affects the home-range size in mink and the larger home-range size of male mink reflects differences in crucial resources between sexes, based on the demography and spacing patterns of a free-ranging American mink population in the Upper Thames, United Kingdom.

MATERIALS AND METHODS

Study area and trapping.—The study area consisted of approximately 24 km of the River Thames (about 51°40′N, 1°25′W), in a lowland, mixed agriculture landscape to the west of Oxford, United Kingdom. The area's mink population was not harvested, and attempted control was opportunistic and not intense. Potential competitors such as otters, polecats, stoats (*M. erminea*) and weasels (*M. nivalis*) were either absent or uncommon.

Mink were trapped in commercial, single-entry aluminum mink and rat cage traps of approximately 14 by 14 by 76 cm (A. Fenn and Co., Redditch, Worcestershire, United Kingdom). The study area was divided into 4 stretches of river, each consisting of 3–6 km between 2 neighboring locks. Trapping was conducted in each stretch for 1 week, and a trap was set, on average, every 200–300 m of riverbank. We increased trapping effort during the breeding season by increasing the number of traps set. The 4-week cycle of trapping was continued for 28 months from May 1995 and August 1997. A mink was classified as a kit if it was observed or trapped with its mother before dispersal, at approximately 13 weeks old (early August); thereafter, it was classed as a juvenile until the onset of the first breeding season (January), at approximately 8 months old, and thereafter as an adult.

Radiotracking.—Captured animals were fitted with waterproof radiotransmitters (frequency range 173–174 MHz) attached to collars with integral reed switches (Biotrack Ltd., Wareham, Dorset, United Kingdom) and monitored through the use of receivers (M57, Mariner Radar Ltd., Lowestoft, Suffolk, United Kingdom) connected to 3-element Yagi antennas (Biotrack Ltd.). Radiocollars weighed approximately 15 g, $<3\%$ of the lightest adult female mink caught in our study area (about 550 g). During radiotracking, the subject's location was recorded every 15 min; individuals were generally tracked between dusk and dawn. Fixes were taken from within 100 m, and locations recorded as coordinates on the map to the nearest 10 m. Prior to radiotracking, we evaluated triangulation error. The accuracy of triangulation at a 100-m range gave, for antennas with rigid elements, the fixation error of 16 ± 2.87 m (*SE*—$n = 9$), and with flexible elements 10 ± 3.73 m ($n = 9$). However, triangulation was rarely necessary within the configuration of our study area, where mink confined their movements to a narrow ribbon of riparian habitat. In almost all cases, we could confirm the subject's exact location.

Analysis of trapping data.—Individual mink were identified using ventral spot patterns (Chanin 1983; Dunstone 1993). Data were analyzed on the basis of calendar month (facilitating direct comparison with, e.g., Ireland 1988; Smal 1991). Presence of each individual in the study area was assessed by the combination of monthly trapping, radiotracking, and occasional direct observations. Juveniles born in the study area were generally trapped for the first time in July, when they were still closely associated with their mothers. Juveniles were included in analyses only after August, when they started to disperse. Following Hatler (1976) and Ireland (1988), females present for ≥ 3 consecutive months were classified as residents. Because of the reported seasonal change in their spacing patterns (Birks 1981; Dunstone 1993; Ireland 1988), males were classified as residents only if they were in the study area for ≥3 consecutive months in the nonbreeding season (May–December). Other adults were classified as transients.

Analysis of radiotracking data.—Birks and Linn (1982) reported that mink radiotracked at least twice a day revealed more than 80% of their total home ranges in <5 days, and the entire home ranges in <10 days. We included only individuals that were radiotracked for either ≥10 days or intensively (followed, on average, for ≥20 h a day) for ≥5 days during the tracking periods (criteria met by 13 animals out of a total of 24 to which radiotransmitters were fitted). Analyses of the movements of semiaquatic mammals often assume that their ranges are linear, aligned along the water course (mink—Birks and Linn 1982; Bonesi 1996; Gerell 1970; Ireland 1988; otter—Durbin 1998; water vole, *Arvicola terrestris*—Macdonald and Strachan in litt.). Indeed, in our study, all radiotracked mink generally stayed <10 m from the nearest water source (88% of fixes for males and 95% for females). Therefore, the entire study area was considered as a river corridor and was divided into 200-m sections on opposite banks, to which each radiolocation was allocated. The home-range size (expressed as length of water course) used by each radiotracked animal was calculated on the basis of the number of sections between the most upstream and the most downstream sections containing either radiolocations or capture points.

Statistics.—Mann–Whitney *U*-tests, corrected for ties, were used to assess the difference between 2 categories under test, and Kruskal–Wallis tests were used when there were >2 categories. The binominal test was used to examine if the sex ratio differed from parity. Significance of correlation was tested by Kendall rank correlation tests. The sexual differences of monthly data were tested using the Wilcoxon signed rank test. All tests were performed using StatView 4.01 (Abacus Concepts, Inc., Berkeley, California). Monthly data were sorted as follows for seasonal analyses: early breeding season, January and February; late breeding season, March and April; kit-rearing season, May, June, and July; kit-dispersal season, August and September; and winter season, October, November, and December.

General linear models (GLM) were used to identify trends in the finer-scale distribution of radiolocations of 2 individuals whose ranges overlapped. Models were of the form (a = pair + b), where a and b represent the number of locations recorded for each member of an overlapping pair, and pair is the blocking factor representing the identity of each of the 13 pairs used. Separate values for a and b were used for each of the 200-m sections in which fixes of ≥1 individual were recorded. We ran the analysis after eliminating sections with <10 and then <20 locations for at least 1 member of the pair, to exclude sections not being intensively used by ≥1 animal. Location numbers were log transformed if necessary to achieve normality. Results are presented as mean ± *SE*.

RESULTS

Population.—Fifty-one mink were captured a total of 184 times (17 animals were caught only once, 7 twice, 6 three times, 7 four times, 6 five times, 4 six times, and 1 animal each for 10, 11, 14, and 18 times) during 4,336 trap-nights between May 1995 and August 1997—an average of 23.6 trap-nights for each capture. The total number of captures in each month was positively correlated with the total number of different individuals captured in the month (Kendall rank correlation test: $n = 23$, $\tau = 0.78$, $P < 0.0001$). The overall monthly trapping success (number of captures per trap-night) did not change seasonally, based on the 5 mink seasons, in both sexes (Kruskal–Wallis tests: for males, $d.f. = 4$, $H = 3.2$, $P = 0.53$; for females, $d.f. = 4$, $H = 2.3$, $P = 0.68$). Trapping success did not differ between sexes (Wilcoxon signed rank test, $n = 23$, $Z = -1.07$, $P = 0.28$). The monthly likelihood of recapturing mink (total number of captures per trapnight divided by the total number of different individuals) did not change seasonally in either sex (Kruskal–Wallis tests: for males, $d.f. = 4$, $H = 1.6$, $P = 0.81$; for females, $d.f. = 4$, $H = 1.8$, $P = 0.77$).

Overall, 27 different males and 24 different females were recorded in the study area and male:female sex ratio was 1:0.86

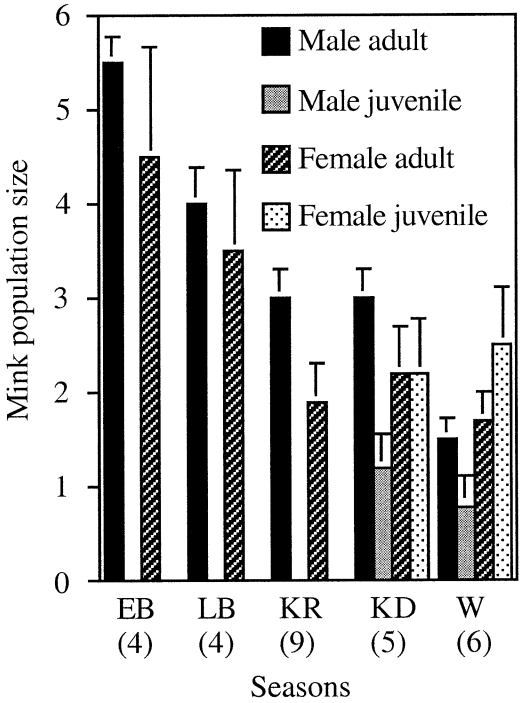

FIG. 1.—Seasonal changes of average monthly population of mink in the Upper Thames study area, United Kingdom. EB (early breeding season: January and February), LB (late breeding season: March and April), KR (kit-rearing season: May–July), KD (kit-dispersal season: August and September), and W (winter season: October–December). Numbers in parentheses indicate sample size.

(1:0.64 among adults, *n* = 41), which does not depart significantly from 1:1 (binominal test, *P* = 0.79 for total population, *P* = 0.21 for adults). Among juveniles, the sex ratio was 1:3 and also not significantly different from 1:1 (binominal test, *P* = 0.08, *n* = 12). The monthly average number of mink along the 24-km river stretch was 7.19 ± 0.58 (1 mink per 3.3 km) with 3.61 ± 0.35 males and 3.58 ± 0.34 females. Among males, the monthly population changed significantly throughout the year (Kruskal–Wallis test: *d.f.* = 4, *H* = 19.66, *P* = 0.0006) with 2 population peaks in early breeding season and kit-dispersal season (Fig. 1). However, among females, there was no significant difference in monthly population size between the 5 seasons (Kruskal–Wallis test: *d.f.* = 4, *H* = 6.57, *P* = 0.16) (Fig. 1).

Recruitment, immigration, emigration, and mink biomass.—The average recorded litter size at about 2 months after birth was 2.5 ± 0.29 (*n* = 4), not significantly biased toward females (1:2.3, binominal test, *P* = 0.34). During kit-dispersal and winter seasons, average monthly adult:juvenile ratio was 1:0.46 for males and 1:1.24 for females, a significant difference between sexes (Wilcoxon signed rank test: *n* = 11, *Z* = −2.4, *P* = 0.018).

On average, each month, 1.64 ± 0.33 new individuals appeared in the study area, of which 0.93 ± 0.24 were males and 0.71 ± 0.21 females. The number of newly recorded adult males peaked in early breeding season (Kruskal–Wallis test: *d.f.* = 4, *H* = 9.69, *P* = 0.046) and newly recorded juvenile males peaked in kit-dispersal season (Kruskal–Wallis test: *d.f.* = 4, *H* = 14.86, *P* = 0.005). However, in females, only the number of newly recorded juveniles peaked in the kit-dispersal season (Kruskal–Wallis test: *d.f.* = 4, *H* = 11.16, *P* = 0.025). On average, 1.61 ± 0.32 individuals disappeared from the study area per month (0.86 ± 0.19 males and 0.75 ± 0.21 females). Among males, the number of individuals that left the study area changed throughout the year (Kruskal–Wallis test: *d.f.* = 4, *H* = 10.32, *P* = 0.035), and the disappearance of adult males peaked in the early breeding season (Kruskal–Wallis test: *d.f.* = 4, *H* = 13.84, *P* = 0.008). However, among females, there was no significant seasonal change in numbers disappearing (Kruskal–Wallis test: *d.f.* = 4, *H* = 4.88, *P* = 0.30). When the new appearances and disappearances were combined, this mobile section of the population changed seasonally significantly in males (Kruskal–Wallis test: *d.f.* = 4, *H* = 12.42, *P* = 0.015), but not in females (Kruskal–Wallis test: *d.f.* = 4, *H* = 5.43, *P* = 0.25). A population instability index (number of appearances and disappearances each month summed, divided by the total population of resident mink in that month) was high in early breeding and late breeding seasons and low in winter and kit-rearing seasons in males (Kruskal–Wallis test: *d.f.* = 4, *H* = 9.84, *P* = 0.043), but again, did not vary seasonally in females (Kruskal–Wallis test: *d.f.* = 4, *H* = 5.93, *P* = 0.205).

The average body weights of males and females were 1,374 ± 43.2 g (*n* = 25) and 707 ± 27.6 g (*n* = 16) respectively for adults, those for juveniles were 1,134 ± 83.2 g (*n* = 3) and 587 ± 22.7 g (*n* = 9), and for nearly independent kits in July were 790 ± 85.4 g (*n* = 3) and 548 ± 31.5 g (*n* = 6). Therefore, for the following modeling, the body weights of a male and a female during kit-dispersal and winter seasons are calculated on the bases of adult: juvenile ratios as 1,298 g and 641 g, respectively, and for the rest of the year they are 1,374 g and 707 g. The total male and female mink biomass (monthly average) in the study area is shown in Fig. 2. The male biomass changed significantly throughout the season (Kruskal–Wallis test: *d.f.* = 3, *H* = 15.25, *P* = 0.002) although that of females did not (Kruskal–Wallis test: *d.f.* = 3, *H* = 1.22, *P* = 0.747–these analyses excluded the kit-rearing season due to unknown biomass of kits).

Home-range size.—The mean home-range size of males encompassed 5.98 ± 0.71 km of water course (Table 1). This was significantly longer than the 2.73 ± 0.52 km used by females (Mann–Whitney *U*-test: *n* = 5 and 8, *U* = 0.5, *P* = 0.004). Males 1 and 2 were transients during the breeding season. Although male 3 traversed the study area for 3 consecutive months, we lost his signal intermittently from the 24-km study area. Therefore, the 4.5 km of the study area he used may have been only a part of his full range. Furthermore, although he was very intensively radiotracked, male 4 had been followed only for 5 days before he was found dead in a moored boat. It may therefore be appropriate to exclude these 2 individuals from analysis. Then the mean range size of the remaining males was 6.80 ± 0.90 km, again significantly longer than that used by females (Mann–Whitney *U*-test: *n* = 3 and 8, *U* = 0, *P* = 0.013).

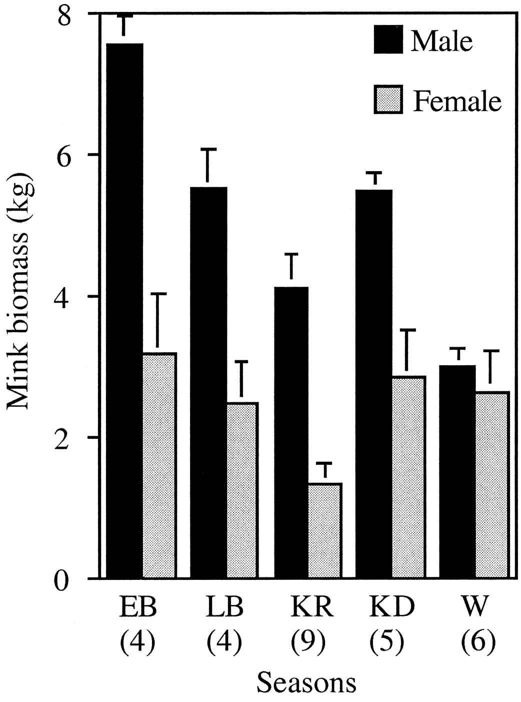

FIG. 2.—Seasonal changes of average monthly biomass of male and female mink in the study area. Abbreviations as in Fig. 1.

During the breeding season, an average home range of a female was 2.80 ± 0.55 km along the water course, not significantly longer than 2.80 ± 0.85 km during the non-breeding season (Mann–Whitney *U*-test: *n* = 6 and 4, *U* = 11.5, *P* = 0.91). Unlike females, all resident males disappeared from their non–breeding-season home range by the end of February and subsequently were not found within the 24-km study area. Radiotracking and trapping indicated that resident male 1, (which had stayed in his home range for the previous 9 months) and male 5 (resident for the previous 11 months) used their non–breeding-season home ranges until their disappearances in February. Therefore, for the following analyses, the breeding-season home range of male 1 until his disappearance was

TABLE 1.—Home-range size of radiotracked individuals either during the breeding season (January–April) or the nonbreeding season (May–December). Female 4 was studied first as a juvenile, later as an adult. Status refers to resident (r) or transient (t).

Individual	Age	Status	Tracked period (number of fixes)	Range (km)
Nonbreeding season				
Male 1	Adult	r	23 May–08 December 1995 (382)	5.9
Male 2	Adult	r	06 July–05 September 1995 (124)	8.6
Female 1[a]	Adult	r	24 July 1995–14 July 1996 (79)	4.1
Female 2[a]	Adult	r	15 June 1995–07 August 1996 (297)	4.3
Female 4[a]	Juv–adult	r	16 October 1995–10 May 1996 (196)	2.0
Female 5[b]	Adult	r	02 September–06 October 1995 (137)	0.8
Breeding season				
Male 3	Adult	r	30 January–19 March 1996 (971)	4.5
Male 4[c]	Adult	t	21 February–25 February 1996 (313)	5.0
Male 5	Adult	r	30 January–22 February 1997 (344)	5.9
Female 1	Adult	r	19 March–26 April 1996 (504)	4.3
Female 3	Adult	r	11 April–02 May 1996 (68)	0.9
Female 4	Adult	r	27 May–30 April 1996 (3010	2.0
Female 6[c]	Adult	r	05 April–23 April 1996 (221)	2.0
Female 7	Adult	r	04 February–17 April 1997 (903)	3.8
Female 8	Adult	t	02 April–17 April 1997 (312)	3.8

[a] ''Tracked period'' does not include breeding season (January–April).

[b] Lived outside main study area.

[c] Died during the tracking period.

substituted by his non–breeding-season range and male 5's non–breeding-season range by his breeding-season range (see Table 1).

Home-range overlap.—A mink home range was not completely exclusive, and other mink of both sexes were present within it. As a monthly average, within the home range of each of the 5 radiotracked males, 0.98 ± 0.31 other males and 1.95 ± 0.24 females were found. Within the home range of each radiotracked female ($n = 7$; female 5 excluded because she lived outside the main study area), 1.18 ± 0.17 males and 0.32 ± 0.08 other females were found. Females had a large number of males in their home ranges during the breeding season compared with the rest of the year, and the seasonal difference was statistically significant (Kruskal–Wallis test; $d.f. = 4$, $H = 14.81$, $P = 0.005$—Fig. 3). Although females may also tend to have more females in their home ranges during the breeding season (Fig. 3), any such trend was not statistically significant (Kruskal–Wallis test: $d.f. = 4$, $H = 8.13$, $P = 0.09$) nor was it for males (Kruskal–Wallis tests: other males, $d.f. = 4$, $H = 4.22$, $P = 0.38$; females, $d.f. = 4$, $H = 4.32$, $P = 0.36$—Fig. 3). The extent of range overlap was analyzed on the bases of radiotracked individuals (Table 2). When 2 home ranges overlapped, on average 66.3% ± 15.6% ($n = 4$) of the home range of a female was overlapped by that of the other female, and 69.1% ± 9.4% ($n = 10$) of the home range of a female was overlapped by that of the overlapping male. Similarly, on average 88.2% ± 7.4% ($n = 2$) of the home range of a male was overlapped by that of the other male and 32.6% ± 5.1% ($n = 10$) of the home range of a male was overlapped by that of the overlapping female.

On the bases of radiolocations, on average, 78.1% ± 10.8% ($n = 4$) of radiolocations of a female were found in the area overlapped by the home range of the other female and 68.8% ± 10.5% ($n = 10$) of the locations of a female were found in the area used by the overlapping male. Similarly, on

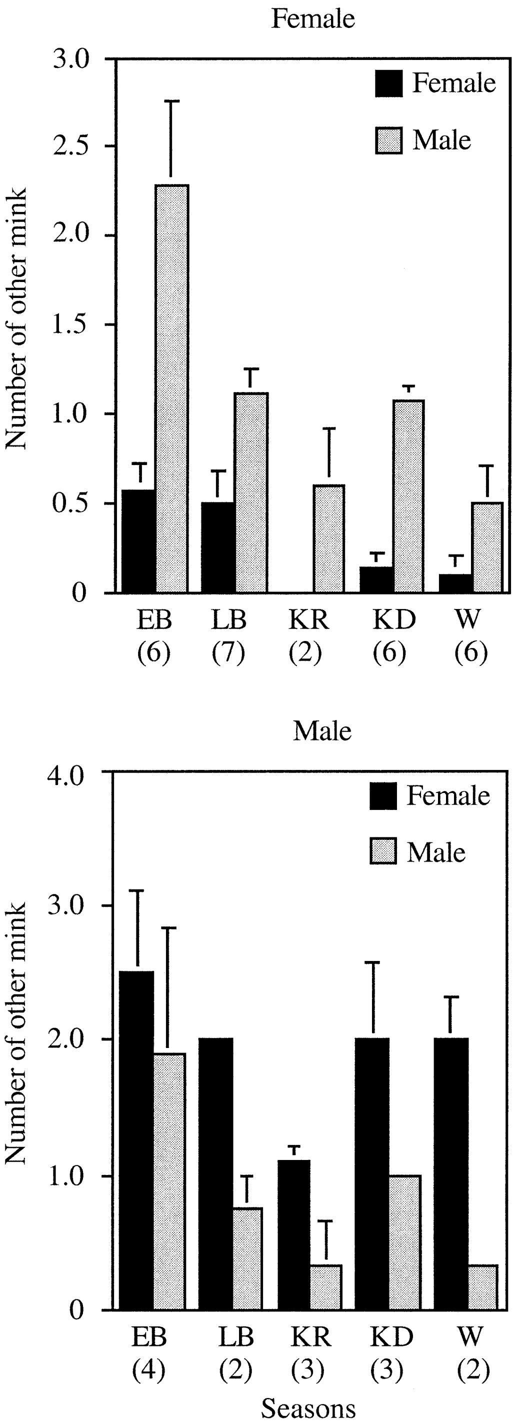

FIG. 3.—Seasonal changes of average monthly number of other females and males accessing the home ranges of radiotracked females and males. Abbreviations as in Fig. 1.

average, 84.6% ± 3.7% ($n = 2$) of the locations of a male were in the area overlapped by the home range of the other male and 36.2% ± 7.9% ($n = 10$) of the locations of a male were in the area used by the overlapping female. The overlapped area and the numbers of radiolocations in it were significantly positively correlated (Kendall rank correlation tests: $n = 26$, $\tau = 0.838$, $P < 0.0001$).

Spacing patterns inside home ranges.—A male home range contained, on average, 34.0 ± 8.79 sections with no radiolocations, significantly more than the 12.5 ± 2.60 sections of a female (Mann–Whitney *U*-test: $n = 5$ and 8, $U = 3$, $P = 0.012$). However, the average male home range did not contain significantly more sections with radiolocations of either >0, ≥ 10, or ≥ 20 than did a female home range (Mann–Whitney *U*-tests: $n = 5$ and 8; for >0, $U = 12$, $P = 0.24$; for ≥ 10, $U = 18.5$, $P = 0.83$; for ≥ 20, $U = 17.5$, $P = 0.71$). Using only sections with ≥ 10 radiolocations from ≥ 1 animal, the GLM detected a significantly negative relationship between the number of locations of each member of the pair recorded in sections ($n = 13$ pairs, 99 sections: $F = 4.84$, *d.f.* = 1, 85, $P = 0.035$). Including sections with ≥ 20 locations for ≥ 1 of the pair improved the relationship considerably ($n = 13$, 75: $F = 40.57$, *d.f.* = 1, 61, $P < 0.0001$). Post hoc analysis revealed that this relationship held within male–male ($n = 1$, 8: $F = 7.91$, *d.f.* = 1, 6, $P = 0.031$) and male–female ($n = 10$, 52: $F = 35.3$, *d.f.* = 1, 41, $P < 0.001$) pairs, but not female–female pairs ($n = 2$, 15: $F = 2.20$, *d.f.* = 1, 12, $P = 0.163$).

Biomass within an adult female's home range.—If B is the mink biomass to be supported within the home range of an adult female that successfully reproduces in the study area, then

$$B = x + y, \qquad (1)$$

where x represents the body weight of the home-range occupant and her offspring and

TABLE 2.—Home-range overlap between radiotracked individuals calculated both as overlapped home-range length divided by total home-range length of the animal (area) and as proportion of radio locations within the area of overlap (radiofixes). For example, 38.5% of the home range of male 1 is overlapped by that of female 2, and the overlapped area contains 32.7% of all radiofixes of male 1. Juv-Adult=Studied 1st as juvenile, then as adult.

1st individual				2nd individual			
		Overlap (%)				Overlap (%)	
No.	Age	Area	Radiofixes	No.	Age	Area	Radiofixes
Male–male overlap							
Male 1	Adult	80.8	80.9	Male 4	Adult	95.5	88.3
Male–female overlap							
Male 1	Adult	38.5	32.7	Female 2	Adult	52.6	42.1
Male 1	Adult	34.6	28.0	Female 4	Juv–Adult	100	100
Male 1	Adult	7.7	12.3	Female 6	Adult	22.2	13.1
Male 2	Adult	34.2	37.1	Female 1	Adult	65.0	79.2
Male 3	Adult	65.0	95.6	Female 1	Adult	65.0	79.2
Male 3	Adult	20.0	0.01	Female 3	Adult	100	100
Male 4	Adult	27.3	31.0	Female 2	Adult	31.6	26.3
Male 4	Adult	40.9	46.0	Female 4	Juv–Adult	100	100
Male 5	Adult	42.3	37.2	Female 1	Adult	55.0	79.2
Male 5	Adult	15.4	37.5	Female 3	Adult	100	100
Female–female overlap							
Female 2	Adult	47.4	62.0	Female 6	Adult	100	100
Female 7	Adult	58.8	93.2	Female 8	Adult	58.8	57.2

y is the aggregated body mass of other mink using her home range. For simplicity, we assume

$$y = \sum w_i p_i \qquad (0 \le i \le n), \qquad (2)$$

where n is the number of mink for which the home ranges overlap with the female's home range, w_i is the body weight of animal i, and p_i is the proportion of the number of animal i's radiolocations within the occupant's home range compared with the total number of radiolocations of animal i. Substituting from our results, equation 2 can be written as

$$y = \sum 0.362 n_m w_m + \sum 0.781 n_f w_f \qquad (n_m + n_f = n), \qquad (3)$$

where n_m and n_f are, respectively, the number of males and females for which home ranges overlap with the female's home range, and w_m and w_f are the average body weights of males and females, respectively. Now, by substituting equation 3 into equation 1, we have

$$B = x + \sum 0.362 n_m w_m + \sum 0.781 n_f w_f, \qquad (4)$$

From Dunstone (1993) and our results, we assume that the female bears 6 kits (3 males and 3 females) at the beginning of May, and 3 of them (1 male and 2 females) survive until July. We assume 4 kits (2 males and 2 females) still survive in June. From Dunstone (1993), we fix the average body weight of kits in May at about 10% of July's body weight for males (79 g) and about 13% of July's body weight for females (55 g). Similarly, the average body weight of kits in June is about 45% of July's body weight for both males (356 g) and females (247 g). This gives the estimated monthly average biomass of the primary occupant's kits during the kit-rearing

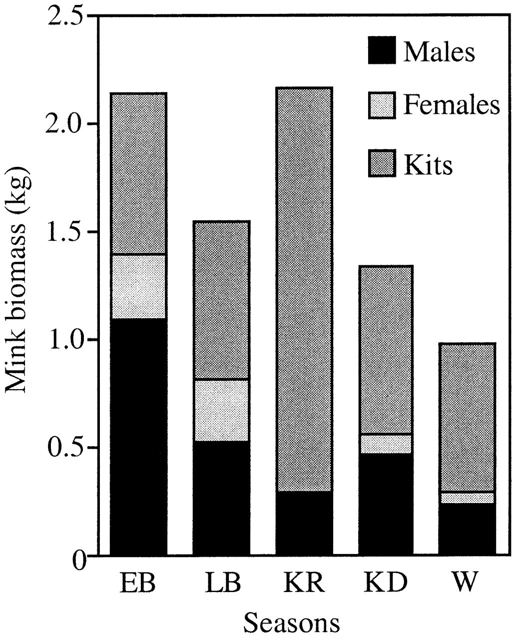

FIG. 4.—Seasonal changes of the estimated average monthly biomass of mink supported by a female's home range. "Males" means males whose home ranges are at least partially overlapped with her home range, "Females" means other females whose home ranges are at least partially overlapped with hers, and "Kits" means the home-range owner and her offspring.

season as 1,165 g. The average numbers of males and females found in a female's home range in each season is given above. The estimated mink biomass to be supported within the home range of an adult female peaked in early breeding and kit-rearing seasons (Fig. 4).

The weight-specific energy requirement of mink is estimated to decrease proportionally to $(\text{weight}_1/\text{weight}_2)^{0.25}$ as weight increases (Dunstone 1993). Therefore, the energy requirements per unit body weight of an average adult male (1,374 g), an average male during kit-dispersal and winter seasons (1,298 g), and an average female during kit dispersal and winter seasons (641 g) are estimated about 85%, 86%, and 102% of that of an average adult female (707 g), respectively. Therefore, based on energy requirements, they are 1,168-, 1,116-, and 654-g equivalents of an average adult female, respectively. A similar calculation gives the monthly average energy requirements of the primary occupant's kits during the kit-rearing season as the same as that of an adult female of 1,383.5 g body weight. On this basis, as a monthly average, male mink take about 30% of the energy consumed by all mink accessing the primary female's home range. Where both sexes hunt the same prey species and the prey are homogeneously distributed, in the absence of males, a female might have needed a smaller home range. Similarly, other females in her home range make up a monthly average of about 9% of the energy consumed by all mink accessing the home range. On an annual basis, it is estimated that dependent kits consume about 33% of all energy taken by a female in her home range. Considering this, a 707-g female, rearing kits hypothesized as above, needs to obtain, by hunting, about 90% of all energy consumed by a 1,374-g male annually.

Resource depression within an adult female's home range.—In addition to the foregoing biomass effect, the cost to a female of fulfilling her energy requirements is expected to increase as the number of other individuals (either males or females) using her home range increases. This is because such extra individuals cause resource depression (Charnov et al. 1976), forcing her to spend more energy to hunt for her minimum energy requirement (Powell 1994). From Powell (1994), prey availability (A) to a home-range owner can be written as

$$A = a^n \qquad (0 \le a \le 1), \qquad (5)$$

where a is the possibility with which the owner can access an undisturbed food patch when she shares the home range with another individual and n is the number of other individuals accessing her home range. Powell (1994) proposed

$$a = 1 - dc, \qquad (6)$$

where d is a coefficient describing patch depression after it is visited by another individual and c is the proportion of all the patches in an individual's home range that is visited by an individual per unit time. As d increases, it becomes more difficult to catch the prey after the patch has been disturbed. If a mink visits 10 patches a day and there are 20 patches in its home range, then c is 0.5. Adapting equation 6 to the spacing patterns of female mink, we get

$$a = 1 - dcp_i. \qquad (7)$$

With this equation, and incorporating our results, equation 5 can be written as

$$\begin{aligned} A = {} & b_1(1 - d_1c_{m1}p_m)^{nm}(1 - d_1c_{f1}p_f)^{nf} \\ & + b_2(1 - d_2c_{m2}p_m)^{nm}(1 - d_2c_{f2}p_f)^{nf} \\ & + \cdots, \end{aligned} \qquad (8)$$

where b_1 is the proportion of prey species 1 in mink diet in terms of capture. If a mink captures 200 animals per unit time including 50 of species 1, then b_1 is 0.25. The coefficient concerning patch depression with reference to prey species 1 is d_1, c_{m1} and p_m are male-specific values for c concerning prey species 1, and p concerning home range overlap; similarly c_{f1} and p_f are for females. For the sake of simplicity, we fix all values for c_m and c_f as C. Then, from the results, equation 8 can be written as

$$\begin{aligned} A = {} & b_1(1 - 0.362d_1C)^{nm}(1 - 0.781d_1C)^{nf} \\ & + b_2(1 - 0.362d_2C)^{nm}(1 - 0.781d_2C)^{nf} \\ & + \cdots \end{aligned} \qquad (9)$$

This equation describes the availability (monthly average) of prey, on the basis of the number of individual prey animals, to a home-range owner that partially shares her home range with n_m individuals of males and n_f individuals of females. Ferreras and Macdonald (1999) reported the most important prey for mink in the Upper Thames region is rabbits, which form an estimated 43% of ingested energy, much higher than the 2nd most important prey, which is fish (27%). Also, Yamaguchi et al. (2003) suggested that rabbit warrens are the most important single habitat feature concerning the habitat preferences of mink of both sexes in the Upper Thames. These findings suggest that the availability of rabbits is crucial for mink survival, and both sexes are likely competing for this prey. If we concentrate on rabbit availability only, then equation 9 is written as

$$A = b_1(1 - 0.362d_1C)^{nm}(1 - 0.781d_1C)^{nf}. \qquad (10)$$

When the primary occupant does not share her home range with any other mink, then $A = A_0 = b_1$. Now we fix d_1C as 0.05—i.e., if a mink visits 25% (= 0.25) of all warrens in its home range per unit time (say 24 h) and another hunt would be ineffective in the warrens for the following 4.8 h after each visit (4.8 ÷ 24 = 0.2, then 0.25 × 0.2 = 0.05) − 0.1 and 0.2. Based on equation 9, the availability of rabbit A, relative to A_0 (= b_1 = 1), to a female in the Upper Thames region is estimated smaller during the early breeding season (Fig. 5).

As a monthly average, other male mink and female mink (with their kits) respectively claim 25% and 38% of the energy consumed by all mink in a male's home range. However, our only instance of 84.6% (88.2% in terms of area overlapped) overlap between 2 males during the breeding season departs from general findings of male territoriality. Intrasexual home-range overlap among males is generally minimal during most of the nonbreeding season, with the possible exception of kit-dispersal season when dispersing male juveniles may be found in resident males' home ranges (Birks 1981; Dunstone 1993; Dunstone and Birks 1983; Gerell 1970; Ireland 1988). Now, if we fix the overlap between males

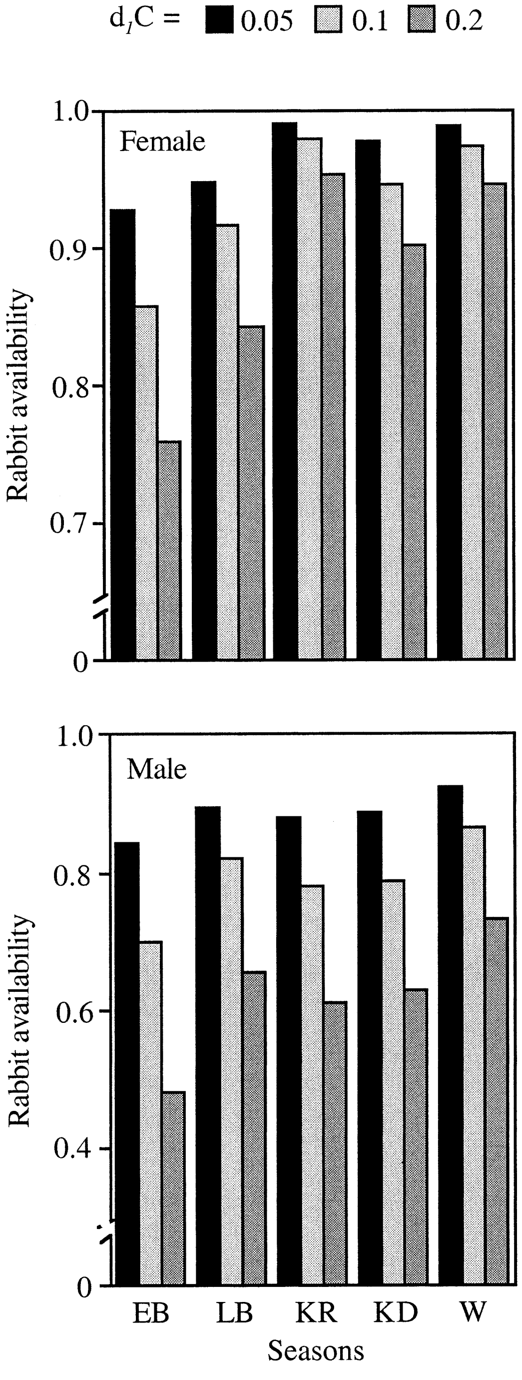

FIG. 5.—Seasonal changes of the estimated relative availability of rabbits (monthly average of A defined by equation 9) to a female and a male with three fixed values of d_1C of 0.05, 0.1, and 0.2.

as 20% during kit-rearing and winter seasons, then, as a monthly average, other male and female mink (and dependent kits), respectively, use 21% and 40% of the energy consumed within his home range by all mink. The estimated effect of resource (rabbit) depression to a male, relative to that where there is no other mink in the home range, with fixed d_1C values of 0.05, 0.1, and 0.2, is larger in the early breeding season (Fig. 5).

DISCUSSION

Trapping success and demography.—Live trapping is likely to underestimate population densities. Some mink evade trapping; Hatler (1976) estimated that untrapped mink comprised <20% of the total population along an 8.5-km shoreline where he made 137 captures with 3,911 trap-nights (28.5 trap-nights per capture) over 5 years. In comparison, we trapped 24 km of river, accumulating 184 captures in 4,336 trap-nights (23.6 trap-nights per capture) in 28 months. The average range of radio-tracked adult females in our study area was about 2.8 km along the watercourse, and within this range we set, on average, 13 or 14 traps, all year round. In addition to the considerable intensity of our trapping, we have no evidence of biases resulting from seasonal differences in the rate of trapping success, seasonal differences of recapture rate, or sexual differences of trappability. We judge, therefore, that while our population estimates must be considered as minima, they are probably close to reality.

Gerell (1971) reported that sex ratio in an exploited mink population was female biased (1:1.5), and that, in another, initially exploited, population, it swung from 1:1.2 to 1:0.71 following a protection from harvesting. Previous studies also indicate a higher proportion of juveniles to adults in harvested (4.5:1) versus unharvested (0.3:1) populations (Dunstone 1993). In our study, the overall juvenile:adult ratio was 0.4:1, and the sex ratio was male-biased (overall 1:0.86, in adults 1:0.64)—parameter values characteristic of an undisturbed, stable population. Furthermore, American mink in the Thames catchment may have reached carrying capacity, having settled there >25 years previously (Macdonald and Strachan in litt.). In summary, we assume that our study population is a saturated mink population along a lowland watercourse with little direct human-caused mortality.

Overall, our results are in accord with earlier evidence that mink spatial organization is based on intrasexual territoriality. The local mink population increased twice annually. During the breeding season (late winter—early spring), roaming transient males caused one increase, and in autumn, dispersing juveniles caused another. Although resident males may abandon their home ranges and start to roam during the breeding season, females tend to remain in their home ranges throughout the year.

Biomass within an adult female's home range.—The results suggest that the home range of a reproductively successful female may need to support, as a monthly average, 3 times her own energy requirements during the kit-rearing season. She needs to support almost as much during the early breeding season, however, because of the impact of transient males. As a monthly average, males take almost 50% of the energy estimated to be consumed by all the mink accessing an average female's home range during the early breeding season. Males move longer distances during the breeding season (Birks 1981; Ireland 1988); thus, they may use food resources less intensively and their impact per unit area is likely to be diminished. On the other hand, the raised activity level of those males during the breeding season (Ireland 1988) may be interpreted that males need more energy, compensating for the lower intensity at which they use the area. Under the assumptions of our model, had neither males nor other females cohabited in her home range, a female in our study area might have needed only about 60% of her observed range.

Resource depression within an adult female's home range.—The results suggest that a female has access to a lower monthly availability of rabbits during the early breeding season (Fig. 5) as a result of the large numbers of transient males accessing her home range. Interestingly, the primary occupant of a female's home range enjoys the highest rabbit availability during the kit-rearing season. This is not only because the model assumes that dependent kits are unlikely to hunt for themselves but also because, at this time, there is a relatively low biomass of other cohabiting mink in her home range (Fig. 3). Indeed, the results indicate there will be no other females in her home range during the entire kit-rearing season (Fig. 3). Breeding females in the Upper Thames region are very strongly associated with rabbit warrens (Yamaguchi et al. 2003), and excluding competing females from these resources may be energetically worthwhile. By comparison, it may be physically impossible for a female to exclude a much larger male from her home range (Macdonald 1992; Powell 1994). Indeed, males are present in her home range even during the kit-rearing season (Fig. 3). On the basis of the number of radiolocations in each 200-m section, however, the dyads within 10 overlapping male–female pairs showed a significantly negative relationship, suggesting that males and females may avoid each other within areas of overlap.

Males may hunt rabbits more than do females (Birks 1981; Ireland 1988). However, possible sexual differences in favored rabbit size (McDonald 2002) may have little impact on the extent of resource depression. As Macdonald (1992) suggested, where small rodents are a crucial food for mink, the female's capacity to fit into burrows too narrow for males may offer opportunities for niche partitioning. In the Upper Thames region, however, small mammals form only about 10% of ingested energy of mink (Ferreras and Macdonald 1999). Therefore, the combination of increased predator biomass and resource (rabbit) depression due to cohabitation with males may force a female to maintain a large home range in the breeding season. These pressures are not diminished during the subsequent, energy-consumptive, kit-rearing season or during the kit-dispersal season when her range must accommodate dispersing juveniles. Thus, intraspecific forces exert inflationary pressures on female home-range size all year round.

We estimated the rabbit availability (A) assuming, for simplicity, that the resource level (number of rabbits) does not change throughout the year. However, in England generally, the number of rabbits is lowest in early spring (March–April, coinciding with the late breeding season) and highest in late summer (September–October, coinciding with the kit-dispersal season—Thompson and King 1994). The extent of these seasonal variations is wildly variable and hence hard to generalize, but the peaks may be twice as high as the troughs (Thompson and King 1994). Therefore, during the breeding season, home-range occupants may suffer even lower rabbit availability than we estimate. On the other hand, the rabbit availability during the kit-dispersal season may not be higher than our estimate.

Male home range.—Assuming that male home-range sizes were determined by food abundance, Sandell (1989) predicted male home-range size on the basis of size and energy allometry as

$$\begin{aligned}&\text{male home range size}\\&\quad= [\text{female home range size}\\&\qquad\times (\text{male weight})^{0.75}]\\&\qquad\div (\text{female weight})^{0.75}\end{aligned}\tag{11}$$

This assumes that resources used by females and males have the same pattern of availability and that the sexes are not cohabiting or, if they are, that they are not depleting each other's resources. The first assumption may not be plausible everywhere and the second is definitely not. Also, this allometry does not take into consideration dependent kits, which consume one-third of all energy annually obtained by a mother. Considering the energy requirements of kits, following equation 11, the predicted size of a male's home range would be only 1.1 times as long as a female's range. This would predict male home ranges of 3.03 km along the water course of our study area, less than half the average of 6.80 km revealed by radiotracking. To circumvent the second assumption above, we propose the following modification of Sandell's allometry:

$$\begin{aligned}&\text{male home range size}\\&\quad= [\text{female home range size} \times E_f\\&\qquad\times (\text{male weight})^{0.75}]\\&\qquad\div [E_m \times (\text{modified female weight})^{0.75}],\end{aligned}\tag{12}$$

where E_f and E_m are the proportions of energy consumption by female and male range occupants, respectively, compared with the total energy consumption by all mink (in general, all competing predators) accessing the home range. For example, if a female home-range occupant takes only 30% of the total consumption, E_f is 0.3. Modified female weight is obtained as a combined average weight of a female and her dependent kits, standardized for energy requirements per unit body weight. From the results, equation 12 predicts the size of a male's home range as 1.73 times longer than that of a female (about 4.7 km). This still ignores resource depression and assumes that the resources used by females and males have the same pattern of availability. Fig. 5 suggests that males are more susceptible to resource depression than are females. With a value of d_1C of 0.2, a female still has nearly 90% of rabbit availability compared with that without resource depression. However, a male had only about

60% of such availability. This alone may force males to maintain large home ranges solely on the grounds of their energy requirements. If we assume that range size increases inversely to these availability values, then a male's home range is predicted as 5.09 km when the value of d_1C is 0.05. Similarly, home-range size of 5.55 km and 6.72 km would correspond to the values of d_1C of 0.1 and 0.2, respectively. All these figures are much larger than estimates based on the traditional formula for calculating energy requirements (equation 11). These results may suggest that energy requirements alone explain why male American mink home ranges are much larger than those of females although the total annual energy requirements of an adult male and a reproductively successful adult female do not differ greatly. Indeed, there is evidence that male mink are not linked reproductively to the females whose home ranges they overlap (Yamaguchi et al. 2003), and this casts further doubt on the proposition that male American mink maintain large home ranges for reproduction. Currently, it is widely believed that, in many species of Carnivora, and particularly in the Mustelidae, the differential in size between the home ranges of males and females is explicable by the greater energetic demands resulting from the male's larger body size as well as the sexual differences of the spacing patterns concerning reproduction (Sandell 1989). This may indeed be part of the explanation, but our analyses show that such calculations should also take account of the extent of home-range overlap with other conspecifics and, often, other sympatric carnivores.

ACKNOWLEDGMENTS

We thank the Environment Agency and the People's Trust for Endangered Species for financial support. This work was also funded in part by the Overseas Research Student Award and the New Century Scholarship to N. Yamaguchi. We thank J. Gittleman, C. King, R. Powell, S. Rushton, and M. Thom for their helpful comments, P. Johnson for his statistical advice, and M. Thom for performing general linear models.

LITERATURE CITED

BEN-DAVID, M., R. T. BOWYER, AND J. B. FARO. 1995. Niche separation by mink and river otters: coexistence in a marine environment. Oikos 75:41–48.

BIRKS, J. D. S. 1981. Home range and territorial behaviour of the feral mink (*Mustela vison* Schreber) in Devon. Ph.D. dissertation, Exeter University, Exeter, United Kingdom.

BIRKS, J. D. S., AND N. DUNSTONE. 1991. Mink. Pp. 406–415 in The handbook of British mammals. 3rd ed. (G. B. Corbet and S. Harris, eds.). Blackwell Scientific Publications, Oxford, United Kingdom.

BIRKS, J. D. S., AND I. J. LINN. 1982. Studies on the home range of feral mink (*Mustela vison*). Symposia of Zoological Society of London 49:231–257.

BONESI, L. 1996. Spatial organisation and feeding ecology of the American mink (*Mustela vison*) in a coastal habitat. M.Sc. thesis, University of Durham, Durham, United Kingdom.

BUENO, F. 1996. Competition between American mink *Mustela vison* and otter *Lutra lutra* during winter. Acta Theriologica 41:149–154.

CHANIN, P. R. F. 1983. Observations on two populations of feral mink in Devon. Mammalia 47:463–476.

CHARNOV, E. L., G. H. ORIANS, AND K. HYATT. 1976. Ecological implications of resource depression. American Naturalist 110:247–259.

CLODE, D., AND D. W. MACDONALD. 1995. Evidence for food competition between mink (*Mustela vison*) and otter (*Lutra lutra*) on Scottish island. Journal of Zoology London 237:435–444.

CLUTTON-BROCK, T. H. 1989. Mammalian mating systems. Proceedings for the Royal Society London Series B. Biological Sciences 236:339–372.

DUNSTONE, N. 1993. The mink. T. and A. D. Poyser, Ltd., London, United Kingdom.

DUNSTONE, N., AND J. D. S. BIRKS. 1983. Activity budget and habitat usage by coast-living mink (*Mustela vison*). Acta Zoologici Fennica 174:189–191.

DURBIN, L. S. 1998. Habitat selection by five otters *Lutra lutra* in rivers of northern Scotland. Journal of Zoology London 245:85–92.

FERRERAS, P., AND D. W. MACDONALD. 1999. The impact of American mink *Mustela vison* on water birds in the upper Thames. Journal of Applied Ecology 36:701–709.

GERELL, R. 1970. Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. Oikos 21:160–173.

GERELL, R. 1971. Population studies on mink *Mustela vison* Schreber in southern Sweden. Viltrevy 8:83–114.

HALLIWELL, E. C., AND D. W. MACDONALD. 1996. American mink *Mustela vison* in the Upper Thames catchment: relationship with selected prey species and den availability. Biological Conservation 76:51–56.

HATLER, D. F. 1976. The coastal mink on Vancouver Island, British Columbia. Ph.D. dissertation, University of British Columbia, Vancouver, British Columbia, Canada.

IMS, R. A. 1988. Spatial clumping of sexually receptive females induces space sharing among male voles. Nature 335:541–543.

IRELAND, M. C. 1988. The behaviour and ecology of the American mink (*Mustela vison* Schreber) in a coastal habitat. Ph.D. dissertation, Durham University, Durham, United Kingdom.

JEDRZEJEWSKI, W., AND B. JEDRZEJEWSKA. 1990. Effect of a predator's visit on the spatial distribution of bank voles: experiments with weasels. Canadian Journal of Zoology London 68:660–666.

KREBS, J. R., AND N. B. DAVIES. 1984. Behavioural ecology: an evolutionary approach. 2nd ed. Blackwell, Oxford, United Kingdom.

LODÉ, T. 1993. Diet composition and habitat use of sympatric polecat and American mink in western France. Acta Theriologica 38:161–166.

MACDONALD, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379–384.

MACDONALD, D. W. 1992. The velvet claw: a natural history of the carnivores. BBC Books, London, United Kingdom.

MARAN, T., H. KRUUK, D. W. MACDONALD, AND M. POLMA. 1998. Diet of two species of mink in Estonia: displacement of *Mustela lutreola* by *M. vison*. Journal of Zoology (London) 245:218–222.

MCDONALD, R. A. 2002. Resource partitioning among British and Irish mustelids. Journal of Animal Ecology 71:185–200.

MEDINA, G. 1997. A comparison of the diet and distribution of southern river otter (*Lutra provocax*) and mink (*Mustela vison*) in southern Chile. Journal of Zoology (London) 242:291–297.

MELQUIST, W. E., J. S. WHITMAN, AND M. G. HORNOCKER. 1981. Resource partitioning and co-existence of sympatric mink and river otter populations. Proceedings of the Worldwide Furbearer Conference 1:187–220.

OSTFELD, R. S. 1986. Territoriality and mating system of California voles. Journal of Animal Ecology 55: 691–706.

POWELL, R. A. 1979. Mustelid spacing patterns: variations on a theme by *Mustela*. Zeitschrift für Tierpsychologie 50:153–165.

POWELL, R. A. 1994. Structure and spacing of *Martes* populations. Pp. 101–121 in Martens, sables, and fishers; biology and conservation (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.

SANDELL, M. 1989. The mating tactics and spacing patterns of solitary carnivores. Pp. 164–182 in Carnivore behaviour, ecology, and evolution (J. L. Gittleman, ed.). Chapman & Hall, London, United Kingdom.

SMAL, C. M. 1991. Population studies on feral American mink *Mustela vison* in Ireland. Journal of Zoology (London) 224:233–249.

THOMPSON, H. V., AND C. M. KING (EDS.). 1994. The European rabbit. Oxford University Press, Oxford, United Kingdom.

YAMAGUCHI, N., S. RUSHTON, AND D. W. MACDONALD. 2003. Habitat preferences of feral American mink in the Upper Thames. Journal of Mammalogy 84: 1356–1373.

Submitted 3 May 2002. Accepted 27 November 2002.

Associate Editor was John G. Kie.