HABITAT PREFERENCES OF FERAL AMERICAN MINK IN THE UPPER THAMES

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Habitat use by members of a wild population of American mink (*Mustela vison*) was evaluated by continuous monitoring of individuals that were live trapped and radiotracked year round in the Upper Thames region, United Kingdom. Spatially lagged autoregressive models were used to investigate the relationship between population abundance and measured habitat variables. Resident mink were found in places characterized by rich tree cover, plenty of scrub, rank grasses, and especially abundant rabbits, and they avoided open habitat characterized by farming activities. These trends were not detected, however, in either transient adults or juveniles. The presence of the opposite sex did not appear to influence the presence of resident mink of the other sex. The single most important feature influencing the presence of resident mink was the size of rabbit warrens. Warrens were, overall, the most important den sites for mink, especially for breeding females. Because the distribution of rabbit warrens seemed to be strongly affected by riverside farmland management, this might eventually determine the distribution and local population growth of feral mink in the Upper Thames region.

Key words: *Arvicola terrestris*, conservation, invasive species, land-use, mink predation, *Mustela vison*, *Oryctolagus cuniculus*, riverside habitat

The American mink (*Mustela vison*), which is native to North America, is the only widely distributed nonindigenous carnivore in the United Kingdom, and the potential negative impact of its predatory habits has led to much debate (Birks and Dunstone 1991; Clark 1991; Linn and Chanin 1978; Macdonald 1995; Macdonald et al. 1999). However, in spite of its reputation as a vicious alien killer, and with exceptions concerning some negative relations with local populations of ground nesting sea birds (Craik 1995) and water voles (*Arvicola terrestris*—Barreto et al. 1998a, 1998b; Jefferies et al. 1989; Strachan and Jeffries 1993; Woodroff et al. 1990), few studies have been able to explore the complicated

relationship between mink predation and other processes in natural habitats (Barreto et al. 1998a, 1998b; Macdonald et al. 1999; Sidorovich et al. 1998). Management of wildlife populations, whether to preserve threatened species or control pests, requires an understanding of the species' habitat requirements. The best measure of habitat quality would be a test of its effects on demographic parameters, such as population growth and carrying capacity (Garshelis 2000). Earlier field studies have related the pattern of space use by mink to vegetation types and to the availability and distribution of food and dens (Birks 1981; Birks and Linn 1982; Clode and Macdonald 1995; Dunstone and Birks 1983; Erlinge 1972; Gerell 1970; Halliwell and Macdonald 1996; Hatler 1976; Melquist et al. 1981).

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More recently, detailed quantitative studies have reported on the habitat preferences of mink in coastal populations in Scotland and in Argentina (Bonesi et al. 2000; Ireland 1988; Previtali et al. 1998). There have been no such analyses, however, for riverine habitats, which are the most frequently used noncoastal habitats.

An analytical complication is that the presence of mink in one area is likely to be dependent not only on the presence of suitable habitat features there but also on the presence of such features (and mink themselves) in adjacent areas. Therefore, the records of mink in nearby areas are not truly independent of each other, and as such, correlations between abundance of mink and measured habitat features of an area may be spurious. This autocorrelation between mink abundance and the lagging of habitat variables in adjacent areas may complicate analyses of species–habitat relationships using simple linear models and correlation. In order to evaluate species–habitat relationships fully, we have specifically modeled the spatial component introduced by habitat in adjacent sections as well as autocorrelation.

In this article, we investigate the habitat preferences of free-ranging American mink in a riparian system in the Upper Thames region, United Kingdom, using data derived from a field survey of habitat characteristics and an intensive study of space use derived from radiotracking of captured mink. We then use the correlation and spatial autoregression approaches to investigate the relationship between mink abundance and habitat features.

MATERIALS AND METHODS

Study area and habitat survey.—The study area consisted of approximately 24 km along the River Thames (about 51°40′N, 1°25′W) to the west of Oxford City, Oxfordshire, United Kingdom. The river was between 15 and 45 m in width and >1 m in depth, providing a heterogeneous habitat fringed with trees such as willow (*Salix fragilis*). Bands of vegetation, such as

common reed (*Phragmites australis*) emerged from the water in summer. Adjacent land was mainly pasture, but arable land and woodland also occurred, where abundant populations of rabbit (*Oryctolagus cuniculus*) were found.

The habitat survey was carried out following the guidelines developed by The Environment Agency (Environment Agency, in litt.). The survey recorded 12 habitat variables concerning proportions of the area covered by tree, scrubgrass, grass, water grass, and open field, and existence of public path, human activities, and other water sources (Appendix I). Because rabbits were the most important food source for mink in the study area (Ferreras and Macdonald 1999), size of rabbit warrens was also included in the survey to assess its effects on mink habitat preferences. The survey was carried out on both sides of the river ≤50 m from the water's edge. This width was chosen because earlier radiotracking of mink in the study area revealed that none of the animals had gone >50 m from the nearest water source. The survey for major permanent features (e.g., tree coverage) was carried out during winter in 1996 and for the complementary seasonal features (e.g., emergent vegetation) during summer in 1996.

Trapping and radiotracking.—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 of which consisted of 3–6 km between 2 neighboring locks. A 4-week cycle of trapping was continued throughout the year between May 1995 and August 1997. Trapping was conducted in each stretch for 1 week, and a trap was set, on average, every 200–300 m of riverbank. A mink was classified as a kit if it was observed or trapped with its mother before dispersal, which is at approximately 13 weeks of age (early August); after that, it was classed as a juvenile until the onset of the 1st breeding season (January), at approximately 8 months of age, and after that as an adult. 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 individuals were classified as transients. Some of the captured animals were fitted with waterproof radiotags attached to collars with integral reed switches (Biotrack Ltd., Wareham, Dorset, United Kingdom), and followed with receivers (M57, Mariner Radar Ltd., Lowestoft, Suffolk, United Kingdom) connected to 3-element Yagi antennas (Biotrack Ltd.).

During radiotracking, the location of the focal animal was recorded every 15 min, mainly between dusk and dawn. When each radiofix was recorded, the following additional data were also logged. Distance of the focal animal from the nearest water: within 10 m (<10 m), 10–50 m, 50–100 m, and >100 m; and habitat type where the animal was located: rabbit burrow, willow tree, scrub, rank grass, open area, water, others, and unknown.

Den search.—In the United Kingdom, mink in freshwater habitats are predominantly nocturnal and are inactive in the den by day (Birks and Linn 1982; Dunstone 1993). Opportunistic daytime radiotracking (den searching) revealed animals' dens. When the location of a mink was detected by daytime radiotracking, a short block of radiotracking was continued for the following 1 h to confirm that it was stationary. Mink dens were defined as follows: places where mink were found by den searching during daytime, places where mink were stationary for >2 consecutive h leading up to sunrise, and places where mink were located with >20 fixes (5 h) in total during the entire radiotracking period. In each case, the locations and features of dens were confirmed by subsequent field searches and the vegetation type of the location was recorded. Dens were classified as breeding dens if a female and dependent kits were observed together at the den by early July, or a female with developed nipples returned to the den regularly during May—early July. In addition to these, for cases where breeding dens were not confirmed, the dens used regularly from the middle of April onward by pregnant females were classified as potential breeding dens.

Analysis of mink habitat relationships.—Four sets of analyses were undertaken using correlation and regression analysis, investigating the relationships between habitat characteristics and mink abundance based on the trapping success, abundance of resident mink, spatial utilization by radiotracked mink within their ranges, and abundance of mink dens.

The entire study area was considered as a river corridor and was divided into sections, each of which consisted of a 200-m river stretch: 200 m by 50 m areas on both sides of the river. Except for the analyses based entirely on radiotracking, which treated the 2 areas along the same river stretch separately, all analyses were carried out on the bases of these sections. Home-range size was calculated as a length along the river corridor on the basis of the number of the sections between the most downstream and the most upstream sections that contained either capture points or radiofixes of the individual. We assumed that the mink was present in all intervening sections. The number of resident mink in each section was calculated by summing the numbers of all individuals for which the home ranges included the section. The average number of resident mink per month per section was estimated from the residence period of each mink in each section. For example, if there was 1 mink recorded in a section for 10 months and another for 5 months, during the 28-month study period, the average number of resident mink per month for the section is $(10 + 5) \div 28 = 0.54$. For breeding females, the number of females with kits per breeding season per section was used. Associations between habitat variables and levels of preference may be prone to dependence problems because habitat variables are often intercorrelated (Aebischer et al. 1993; Garshelis, 2000). Therefore, we first investigated correlations among habitat variables and used principal component analysis (PCA) to exclude possible redundant variables from further analyses.

We analyzed the relationship between habitat variables and trapping success using the total number of captures per section. The habitat preference of radiotracked mink was analyzed on the basis of the number of radiofixes per section within their home ranges. The relationship between habitat characteristics and the abundance of dens was analyzed based on the number of dens per section within the animals' home ranges. Correlation tests, Mann–Whitney U-tests and chi-squared tests were used for these analyses. To avoid statistical problems concerning simultaneous correlation tests, appropriate probability values were adjusted using the Bonferroni technique (Rice 1989). All these tests were per-

formed using StatView 4.01 (Abacus Concepts, Inc., Berkeley).

The relationships between habitat characteristics and the abundance of resident mink were also analyzed using correlation tests, Mann–Whitney U-tests, and chi-squared tests. However, the relationships were further investigated using regression modeling.

While individual 200-m sections of river provide a convenient unit of sampling for habitat features such as vegetation and space use by mink, this unit does not necessarily relate to the scale of space use by the mink themselves. On this basis, it is unlikely that individual 200-m river sections were used solely by 1 mink; indeed, records in multiple sections may derive from the same mink. This means that recorded space use by mink in any 1 section will reflect a range of processes. The abundance of mink is likely to be determined not only by the presence of suitable habitat features in that section but also by the abundance of mink in other sections (an autoregressive response) as well as by the distribution of such habitat features in other sections (a spatially lagged predictor variable). In order to evaluate the impact of these variables on the presence of mink abundance in adjacent sections and the presence of mink in the focal section, we used spatial autoregression. This model includes both spatially lagged predictor variables as well as an autoregressive component.

The full model is described in its matrix form as follows: $Y = rWY + Xb - WXg + u$, where Y is the response variable, number of mink per section; X is a matrix of predictor variables (habitat features, rabbits); W is a weighting matrix representing the effects of spatial separation of the river sections; u is the vector of errors, and r, b, and g have to be estimated. Note that the response variable Y appears on both sides of the equation and the product rWY (the autoregressive component) effectively quantifies the spatial effects of mink in adjacent sections. When explained in biological terms, Xb reflects the impacts of habitat features in the section where the mink abundance is estimated. The term WXg is the spatially lagged term for independent predictor variables and reflects the effects of habitat variables in all of the other sections surrounding the section where the mink abundance is estimated. The term rWY is the autoregressive predictor and represents the im-

pacts of mink in other sections on records in the focal section. W, in both the spatially lagged habitat features and autoregressive terms, is a matrix that gives the weight of each of the sections in the sample. Setting an entry in this matrix to 0 means that the habitat features and mink records it contains have no effect on the focal section. Variation in the number of nonzero elements in this weighting matrix allows the investigation of the importance of the autoregressive and spatially lagged variables on the response of interest.

Evaluation of spatial autoregressive models relating the abundance of mink to habitat variables, to mink in adjacent river sections, and to habitat variables in adjacent sections was undertaken using the SPACESTATPACK package developed by Pace et al. (1997) using the data set on the basis of the 200-m section. As with all spatially lagged regression models, the user has to define the form of weighting matrix and quantify the relative impacts that adjacent sites contribute to the model. Because there were no specific data available on the extent to which the records of mink and presence of habitat features in adjacent river sections could influence the presence of mink in a section, models were fitted over a range of neighborhoods with 2, 4, 6, or 8 nearest river sections contributing (those having nonzero entries) to the weighting matrix W. The weight given to each section was assumed to be equal among all neighbors. Models were fitted with 3 predictor variables. These were 2 summary habitat variables that were principal component scores derived from a PCA of the habitat features in each river section, and a 3rd ordinal variable quantifying the relative abundance of rabbits in each river section. The data on habitat features were summarized by PCA for 2 reasons: first, to overcome the unit-sum constraint imposed by the use of areas of individual habitat features within a river section, and second, to provide a reduced set of predictor variables for the regression analysis because the use of spatially lagged variables doubles the effective number of predictors in each model leading to model overparameterization. The models were estimated using maximum likelihood. Likelihood ratio tests were used to assess the significance of the parameter estimates of coefficients of individual lagged explanatory variables and the autoregressive parameter between models and the Akaike information criterion was

used to identify the best model among the suite of potential models. Three sets of analyses were undertaken, 1st with the overall abundance of resident mink of both sexes combined in each section and then with the records of single sexes with the incorporation of the abundance of the opposite sex as a predictor and spatially lagged predictor. These last 2 models were investigated in order to assess the extent to which the observed abundance of one sex was influenced by the abundance of the other. Analyses for transient individuals were not undertaken because preliminary spatial analyses indicated that these animals were not distributed in relation to any habitat variables. Models were fitted in a stepwise fashion starting with the simplest, ordinary least squares, followed by models with spatially lagged predictors, and finally with the full model with autoregressive components.

RESULTS

Mink.—Fifty-one mink were captured a total of 184 times during 4,336 trap nights between May 1995 and August 1997—an average of 23.6 trap-nights for each capture—consisting of 27 males (10 residents adults, 11 transient adults, 3 unclassified adults, 4 juveniles, and 2 kits) and 24 females (13 residents adults, 3 transient adults, 1 unclassified adult, 11 juveniles, and 6 kits). Birks and Linn (1982) reported that mink radiotracked at least twice a day revealed more than 80% of their total home ranges within 5 days and their entire home ranges within 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. Out of a total of 24 mink to which radiotransmitters were fitted, these criteria were met by 13 animals: among these was 1 female whose range lay largely outside the study area and was excluded from most analyses.

Habitat features, PCA, and mink trappability.—There were highly significant negative correlations between variables positively related to the existence of open field and most other variables that associated with natural and seminatural vegeta-

tion (Appendix II). In general, total captures of juveniles and transient individuals were not correlated with habitat variables. On the other hand, total captures of resident individuals, both males and females, were significantly correlated with some habitat variables (Table 1). The number of captures of kits was significantly and positively correlated only with the size of rabbit warrens (Table 1). The 1st axis of the PCA was associated with the existence of natural and seminatural vegetation (Fig. 1). The 2nd axis was associated with the existence of features taller than rank grass.

Habitat features and the presence of resident mink.—In general, the number of resident mink was positively correlated with the area covered by trees, scrub, and rank grasses, and negatively with the open area (Table 2). Habitat characteristics along the edge of water alone, including the emergent vegetation, did not strongly influence the presence of resident mink (Table 2). The most important single habitat variable significantly and positively correlated with the number of resident mink was the size of rabbit warrens. This was especially so for females with dependent young. The number of females with kits was negatively associated with the presence of public footpaths (Mann–Whitney U-test; $n = 104$ and 8, $U = 194$, $P = 0.0019$) and positively related to the presence of other water sources nearby (<100 m; Mann–Whitney U-test: $n = 78$ and 34, $U = 922.5$, $P = 0.0016$). The number of resident females was negatively related to the presence of human activities (Mann–Whitney U-test: $n = 91$ and 21, $U = 697$, $P = 0.044$). None of these 3 variables had a significant relationship with the presence of resident males (Mann–Whitney U-test: $P > 0.05$). Also, there was no significant association between any 2 of these 3 variables (chi-squared test, $P > 0.5$). A correlation between the PCA scores for river sections with the number of resident mink was significant for the 1st axis of the PCA only (1st axis: $r = -0.442$, $P < 0.0001$; 2nd axis: $r = -0.148$, $P = 0.11$).

TABLE 1.—Correlation between habitat variables and the number of captures of mink in the section, based on total capture, resident males, resident females, transient males, transient females, juvenile males, juvenile females, and kits (Kendall rank correlation's τ). Statistically significant correlations were detected by Kendall rank correlation tests ($n = 64$ sections) with appropriate probability values adjusted using the Bonferroni technique (Rice 1989).

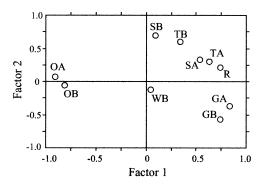| Habitat variable	Mink category							
	Total capture	Resident male	Resident female	Transient male	Transient female	Juvenile male	Juvenile female	Kit
Vegetation area								
Trees	0.337**	0.242*	0.258*	0.046	0.120	0.048	0.241*	−0.016
Scrub	0.259*	0.105	0.278**	−0.051	0.059	−0.037	−0.002	0.182
Rank grass	0.179	0.163	0.271**	−0.031	−0.079	0.048	0.057	0.103
Open	−0.266**	−0.250*	−0.246*	−0.001	−0.048	−0.032	−0.184	−0.016
Vegetation along the edge of water								
Trees	0.330**	0.232*	0.175	0.100	0.240*	0.169	0.112	−0.148
Scrub	0.109	0.027	−0.038	0.188	0.205	0.014	0.136	−0.052
Other variables								
Emergent vegetation	−0.037	0.083	−0.051	−0.089	0.028	−0.033	−0.150	−0.080
Rabbit warrens	0.213*	0.260*	0.328**	−0.052	−0.058	−0.062	−0.095	0.237*

* $P < 0.05$, ** $P < 0.01$.

FIG. 1.—Factor plot of habitat variables along the first 2 factors, which explain 52.7% of the original variance, of a principal component analysis (200-m section). The shorter the distance between 2 variables, the more closely correlated they are. Abbreviations indicate habitat variables described in Appendix I: A = area; B = length along edge of water; T = trees; S = scrub-grass; G = grass; O = open; and R = rabbits.

Spatially lagged and autoregressive models.—An ordinary least squares analysis relating the abundance of mink in river sections to the 1st and 2nd axes of the principal components scores, size of rabbit warrens, and the spatially lagged habitat variables showed that only 2 variables, the 1st PCA axis scores and size of rabbit warrens, were significant predictors of mink (Appendix III). Comparison of the log likelihoods for the ordinary least squares analysis mod-els based on the PCA scores and size of rabbit warrens with no spatial lagging showed that inclusion of the 2nd axis of the habitat PCA did not decrease the log like-lihood significantly (Appendix IV). This is in agreement with the preliminary linear analyses of mink resident numbers with both PCA habitat variables. In general, in-clusion of spatially lagged variables, both axes scores from the PCA, or an autore-gressive component for mink in neighbor-ing sections decreased the log likelihood significantly (Appendix IV). Also, likeli-hood ratio tests comparing the autoregres-sive models with the equivalent ordinary least squares analysis models with spatially lagged and simple nonspatial models were significant for all neighborhood ranges (Ap-pendix IV). The Akaike information crite-rion was smallest for the models fitted for 4 nearest neighbors with both the PCA axes, size of rabbit warrens, the spatial lag for these variables, and the autoregressive component for neighboring resident mink indicating that this (400 m on each side of the focal section) was the spatial range over which the spatially lagged variables had in-fluence on the mink abundance in any one river section (Appendix V). Analyses com-paring the full autoregressive model includ-ing spatially lagged habitat variables with

TABLE 2.—Correlation between habitat variables and the number of mink present in the section. Statistically significant correlations were detected by ANOVA ($n = 112$ sections) with appropriate probability values adjusted using the Bonferroni technique (Rice 1989).

Habitat variable	Resident males	Resident females	Females with kits
Vegetation area			
Trees	0.441**	0.409**	−0.016
Scrub	0.103	0.159	0.174
Rank grass	0.450**	0.377*	−0.001
Open	−0.519**	−0.479**	−0.053
Vegetation along the edge of water			
Trees	0.214	0.187	0.132
Scrub	−0.071	−0.089	0.207
Other variables			
Emergent vegetation	0.225	0.229	0.178
Rabbit warrens	0.469**	0.462**	0.273*

* $P < 0.05$, ** $P < 0.01$.

TABLE 3.—Correlation between habitat variables and the numbers of radiofixes in the section of 12 radiotracked individuals (correlation coefficient or Kendall rank correlation's τ). ''Length variables'' means vegetation along the edge of water. ''All'' means all individuals combined. Animals 01, 02, 03, 04, and 05 are males, and 06, 07, 08, 09, 10, 11, and 12 are females. Sample size is numbers of 200-m river section within each animal's home range.

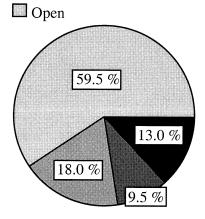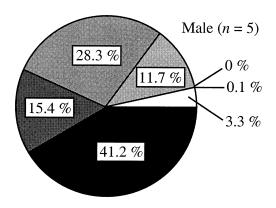| | | Habitat variable | | | | | | | |
| | | Vegetation area | | | | Length variables | | Other variables | |
Mink ID	Sample size	Tree	Scrub	Rank grass	Open	Tree	Scrub	Emergent vegetation	Rabbit warrens
01	56	0.38*	0.30*	0.25*	−0.36*	0.39*	0.20	−0.10	0.22*
02	76	0.06	0.27*	0.21	−0.18	−0.03	−0.00	0.13	0.25*
03	40	0.21	0.20	0.04	−0.14	0.20	0.04	−0.13	0.41*
04	46	0.48*	0.36*	0.31*	−0.43*	0.38*	0.24	−0.16	0.33*
05	52	0.19	0.10	−0.00	−0.12	0.20	0.12	0.04	0.13
06	40	0.20	0.37*	0.08	−0.15	0.14	0.06	−0.29	0.47*
07	37	0.21	0.18	0.16	−0.19	0.22	0.27	0.03	0.25
08	8	0.00	−0.51	−0.47	0.53	0.00	−0.64	−0.12	0.20
09	20	0.51*	0.12	0.26	−0.42	0.45*	−0.17	−0.24	0.19
10	21	0.49*	0.34	0.03	−0.37	0.19	0.13	−0.33	0.11
11	37	0.29	0.46*	0.18	−0.34*	0.41*	0.22	−0.19	0.39*
12	36	−0.02	−0.00	−0.31	0.04	0.24	0.19	−0.11	0.05
All	173	0.05	0.24*	0.19*	−0.22*	0.25*	0.03	0.01	0.46*

* $P < 0.05$.

an autoregressive model without spatially lagged habitat features are also shown in Appendix IV. The models shown are for both PCA habitat axes and the rabbit variable and for the 1st PCA axis and rabbit variables for each of the 4 neighborhood distances. For the analyses with 2 PCA habitat variables, there was a significant difference between the simple autoregressive model without spatially lagged variables and the models that included lagging, with models including lagged variables having a smaller maximum likelihood than those based on an autoregressive predictor alone. For the single PCA model, only the 2- and 4-neighbor models were different. The analyses show that inclusion of spatially lagged habitat variables with an autoregressive model explained more of the variation in the mink abundance data than did the autoregressive component alone. In other words, habitats in river sections were an important predictor in their own right (i.e., over and above an autoregressive component for adjacent mink). When the analyses

were repeated for the individual sexes, using the abundance of the opposite sex as a predictor (both lagged and nonlagged), abundance of the opposite sex was not a significant predictor in the models. This suggests that the presence of male and female mink did not impact on the abundance of animals of the opposite sex in river sections.

Habitat use inside the home range.— There were individual differences in habitat use; however, in general, mink used the sections that had larger scrub–grass-covered area, had larger rank-grass area, had bank with more tree cover, and had bigger rabbit warrens (Table 3). They tended to avoid open areas. Radiotracked mink, both males and females, stayed within 10 m of the nearest water source most of the time (88% for males and 95% for females); however, compared with females, males tended to be found further from the water (more than 10 m from the nearest water source) on more occasions, and significantly so (chi-squared test: $d.f. = 1$, $\chi^2 = 265.6$, $P < 0.0001$).

Average vegetation cover
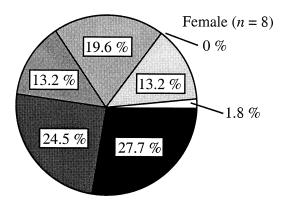### (*n* = 13 home ranges)

■ Tree ■ Scrub-grass ■ Grass

□ Open

59.5 %

13.0 %

18.0 %

9.5 %

■ Rabbit warren ■ Willow tree

▨ Scrub-grass ▨ Grass ▨ Open habitat

□ Others □ Unknown

Male (*n* = 5)

28.3 %

11.7 %

0 %

0.1 %

3.3 %

15.4 %

41.2 %

Female (*n* = 8)

19.6 %

0 %

13.2 %

13.2 %

1.8 %

24.5 %

27.7 %

Although, on average, nearly 60% of their home ranges were covered by open areas, radiotracked animals were never found in these areas (Fig. 2). Males were more often found in rabbit warrens and females more often in willow trees and in rank grass (rabbit burrow, willow tree, scrub, grass, and the rest combined; chi-squared test: $d.f. = 4$, $\chi^2 = 550.7$, $P < 0.0001$)

Habitat features and dens.—Altogether, 119 dens of 13 radiotracked individuals were found in the study area. The presence of a den was significantly and positively correlated with the size of rabbit warrens (Table 4). Dens of radiotracked individuals were exclusively found <50 m from water and most of them were found <10 m from it (84% for males and 98% for females). Females had their dens closer to water than did males (for <10 m category; Mann–Whitney U-test: $n = 5$ and 8, $U = 7$, $P = 0.039$). In total, there were 8 dens recorded in the area >10 m from the water. Among them, 5 were in rabbit warrens, 2 were in scrub, and 1 was under a bridge. The radiotracked animals had no den in open habitat (Fig. 3). Rabbit warrens were the favorite den site for both sexes (Fig. 3). Male dens were more often found in rabbit warrens and scrub areas, female dens in rank grass (rabbit burrow, willow tree, scrub, grass, and the rest combined; chi-squared test: $d.f. = 4$, $\chi^2 = 9.64$, $P = 0.047$). Out of the total of 77 dens detected in the home ranges of 10 females (8 females successfully radiotracked and 2 other females that were radiotracked only briefly), 5 dens were confirmed to be used when they had dependent kits. Females significantly preferred rabbit warrens for kit-rearing dens (chi-squared test: $d.f. = 1$, $\chi^2 = 12.60$, $P = 0.0004$).

←

FIG. 2.—(top pie chart) Vegetative cover in home ranges of radiotracked mink, and (middle and bottom pie charts) habitat types where radiotracked mink were found.

TABLE 4.—Correlation between habitat variables and the numbers of dens of 12 radiotracked individuals (correlation coefficient or Kendall rank correlation's τ). Details concerning column headings are presented in Table 3.
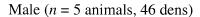
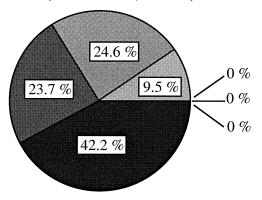| Mink ID	Sample size	Habitat variable							
		Vegetation area				Length variables		Other variables	
		Tree	Scrub	Rank grass	Open	Tree	Scrub	Emergent vegetation	Rabbit warrens
01	56	0.44*	0.25*	0.26*	−0.38*	0.55*	0.09	−0.14	0.25*
02	76	0.15	0.26*	0.20	−0.20	0.00	−0.09	0.07	0.30*
03	40	0.09	0.24	0.08	0.00	0.21	−0.06	0.12	0.39*
04	46	0.09	0.12	0.16	−0.12	−0.00	0.22	−0.08	0.34*
05	52	−0.06	0.07	0.18	−0.16	0.08	0.03	−0.09	0.30*
06	40	0.12	0.37*	0.19	−0.15	0.20	−0.01	−0.23	0.60*
07	37	0.27	0.16	0.03	−0.14	0.25	0.15	0.10	0.36*
08	8	−0.41	−0.45	0.00	0.29	−0.33	−0.32	−0.07	0.09
09	20	0.31	0.01	0.30	−0.26	0.27	−0.24	−0.24	−0.12
10	21	0.36	0.43	0.16	−0.38	0.17	0.13	−0.30	0.30
11	37	0.16	0.23	−0.08	−0.12	0.29	−0.07	−0.35*	0.35*
12	36	−0.22	−0.02	−0.40*	0.17	−0.05	0.31	−0.20	−0.01
All	173	0.12	0.24*	0.13	−0.23*	0.38*	−0.01	−0.09	0.44*

Furthermore, there were 3 other dens that were almost certainly used for rearing dependent kits. They were also all in rabbit warrens. If these 3 dens are included as breeding dens, females' preference of rabbit warrens as breeding dens becomes more significant (chi-squared test: *d.f.* = 1, $\chi^2 = 21.00$, $P < 0.0001$).

DISCUSSION

The presence of mink and habitat features.—The trapping results suggest the presence of resident adult mink was strongly associated with habitat features: positively with the size of rabbit warrens and the areas covered by trees, scrub, and rank grass and negatively with the area covered by open habitat. Resident individuals, which are considered to defend territories (Birks 1981; Gerell 1969, 1970; Ireland 1988), occupy their ranges for a prolonged period. They may need particular habitat features to survive and, in the case of breeding females, to breed, whereas transient individuals, which stay in one area for a short period, may have less demanding requirements. Indeed, the trapping results suggest that the distribution of transient

adults and juveniles in the study area is not influenced by the habitat features as strongly as is that of residents. Alternatively, transients may move on because suitable habitat is unavailable, being occupied already by residents. Most transient adult males recorded, however, were passing through the study area during the breeding season, and there is no evidence that resident males are dominant over transients at that time. On the contrary, reproductively successful males may abandon their territories and travel in search of females (Birks 1981; Ireland 1988). Under such circumstance, the habitat requirement of transient adult males may be different from those of resident males.

Radiotracking revealed that, in general, within their ranges, mink prefer the sections with more tree cover, more scrub-grass, more rank grass, and bigger rabbit warrens and they avoid the sections with more open areas (Table 3). Not a single radiofix out of the total of 5,152 fixes was recorded in the open areas that, on average, comprised nearly 60% of the home ranges of the radiotracked individuals (see Fig. 3). Radiotracking indicates that, on average, com-

Male (*n* = 5 animals, 46 dens)

■ Rabbit warren ▨ Willow tree

▥ Scrub-grass ▦ Grass ▨ Open habitat

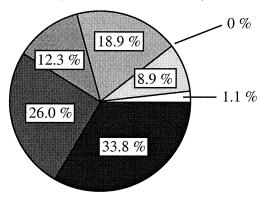▨ Others ☐ Unknown

Female (*n* = 8 animals, 73 dens)

FIG. 3.—Habitat types where dens of radio-tracked mink were found.

pared with females, males spent more time in rabbit warrens and in scrub (see Fig. 2). The size of a rabbit warren had a significant positive relationship with the area covered by scrub-grass, and furthermore, these two variables were very closely associated in the factor plot of habitat variables on the basis of the PCA (see Fig. 1). Male minks' strong associations with rabbit warrens and scrub may be related to their prey selection, as males are reported to hunt rabbits more

than do females (Birks 1981; Birks and Dunstone 1985; Ireland 1988).

Mink den and habitat features.—In our study area, most mink dens were found <10 m from the water and, on average, males had a significantly greater proportion of dens further from the water than did females. Ireland (1988) made similar observations on coastal feral mink in Scotland and argued that this difference between the sexes indicated the greater importance of rabbits as prey for males than females. Birks (1981) also found that mink moved to a rabbit-rich area, away from the river, when aquatic prey became scarce. In our Thames study area, although some rabbit warrens were <10 m from the water, the other main potential den sites (all in hollow willow trees) were at the water's edge. Five out of 8 dens recorded in the areas >10 m from the water were in rabbit warrens. We argue, therefore, that their preference for rabbit as a prey results in the males' tendency to use dens further from the water than do females. Inside their ranges, radio-tracked individuals denned preferentially in some sections (Table 4). The strongest corollary of den site was the presence of rabbit warrens, which comprised 42% of all recorded males' dens and 34% of females' (see Fig. 3). Ireland (1988) reported the same trend in a coastal habitat in Scotland (65% for males' dens in warrens and 43% for females). Hollow willow trees on the river bank were also important den sites for mink in the Upper Thames region (Fig 3; Halliwell and Macdonald 1996), as elsewhere (Birks 1981; Gerell 1970).

It has been suggested that mink restrict their foraging to the vicinity of dens and hence select dens that are close to preferred foraging areas or concentrations of prey items (Birks 1981; Birks and Linn 1982; Dunstone 1993; Ireland 1988). In the Upper Thames study area, rabbits comprise 43% of the estimated ingested energy for mink, much higher than the second-most-important prey, fish, which comprises 27% (Ferreras and Macdonald, 1999). The use of

warrens as dens obviously fits well with the predominance of rabbits in mink diet, especially for breeding females. Breeding dens may be used for up to 40 days and the female mink's prey requirement might rise 5-fold while she is rearing young (Dunstone 1993). Furthermore, the time taken to tend kits and the need to guard them may detract from foraging opportunities and further concentrate the mother's hunting activities close to the den. The opportunity to hunt abundant rabbits in a large warren close to her den therefore fulfills important requirements for breeding female mink. The number of kits captured was strongly influenced only by the size of rabbit warrens, suggesting they are kept close to big rabbit warrens, which are used as dens by the mothers. The size and distribution of rabbit warrens may be one of the most important habitat factors affecting long-term mink population changes in the Upper Thames region.

Modeling the relationship between mink abundance and habitat features.—Spatial models with autoregressive components are computationally difficult because suitable algorithms for analyzing data sets have not been widely available. Furthermore, the need for information describing the abundance of species and their habitats and their relative juxtaposition means that the data sets for such models are usually larger than those used in simple spatial linear modeling approaches. In addition, there are considerable problems with using autoregressive models predictively, so their application in an applied setting is restricted. While Augustin et al. (1996) developed an autologistic approach for modeling the incidence of species in whole landscapes using incomplete census data based on the Gibbs sampler, autoregressive approaches have not been used extensively in modeling species habitat relationships. Our rationale for using the spatial autoregressive approach here was less to quantify the role of space and autocorrelation in determining the abundance of mink but rather was to assess to

what extent the relationships between species and habitat characteristics were evident, after allowing for the effects of any spatial lagging in habitat variables and autocorrelation in the abundance data. To that end, inclusion of spatially lagged predictor variables and an autoregressive component greatly increased the variation in mink abundance on river sections explained by the models. The results suggest that the number of resident mink in a river section is dependent on extent of natural vegetation in the section, rabbit abundance in the section, natural vegetation, and rabbits in adjacent sections up to 400 m away, and also number of mink present in adjacent sections. Considering the autoregressive factor first, positive autoregressive responses could be explained in terms of the attraction of conspecifics, but we reject this hypothesis because there has been no reported evidence suggesting that mink are attracted to each other in this way (Dunstone 1993). Second, the spatial disposition of animal ranges is often dependent on the sex and sexual status of individuals, with male animals often forming ranges encompassing those of females (Sandell 1989). This explanation does not seem feasible given that, in the single-sex models, the number of resident mink in a section was not dependent on numbers of other mink of either the same or opposite sex. The explanation for the significant autoregressive response is simpler, in that mink are likely to range over more than the 200 m representing a river section we used for analyses (Birks 1981; Ireland 1988). We might expect the resident mink in any one section to comprise part of the measured response of mink abundance in other sections, having resulted in the inclusion of mink in adjacent sections as an autoregressive predictor reflects this (i.e., the record in a section comprises part of the record of an adjacent section). The fact that the best model was derived when 4 neighbors were used suggests that the impact of space and the presence of mink declines above 400 m from each sec-

tion. This would suggest that the abundance of mink in any 1 section is determined to some extent by the habitat features 400 m on either side. The most obvious biological explanation for this is that mink have home ranges of the order of 1 km, but this is considerably less than that recorded in the river system, where animals had ranges in excess of 2 km (and up to about 8 km; Yamaguchi and Macdonald 2003). However, it may be worth mentioning that the smallest mink range in the study site was about 1 km, suggesting that, to determine the minimum range for a mink in our study site, this order may have an important meaning. It is possible that other factors besides home-range size influence the models; what these are is difficult to hypothesize. One possible explanation is that mink ranges overlap, as described above. Alternatively, it may be related to the fact that different predictor variables had effects on mink abundance at different spatial lags, the best fit model with 400-m influence then representing an averaging of the effects of the individual variables, or that a more coarse scale, greater than 200 m, was appropriate for studying these relationships. Nonetheless, the fact that inclusion of habitat variables in neighboring sections increased the variation in abundance of mink explained over and above a model with no spatial lagging but including an autoregressive component, suggests that the there was indeed a spatial habitat effect. Unfortunately, the algorithm used in the present study assumed that all variables would have influence over the same spatial lag, and this may be biologically unrealistic. Disentangling these different scaling issues with these sorts of models is difficult because the solution of spatial models with different spatial lags is probably mathematically intractable.

The results suggest that the use of the autoregressive components in the models effectively allows us to identify at what spatial scale mink abundance in adjacent sections have influence and may hence suggest the spatial scale at which habitat mink relationships should be studied. Therefore, although the results also suggest that simpler univariate analyses, after all, may be useful for investigating species' habitat preferences in this case, the autoregressive models contribute greatly to understanding the spatial organization of the species in riparian systems.

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APPENDIX I.

Habitat variables recorded.

Variable	Description
Vegetation area	As percentage of the area covered by the following vegetation in the section
Trees	Area covered by trees > about 10 m in height
Scrub-grass	Area covered by scrub (including trees <10 m in height) and rank grass
Grass	Area covered by rank grass only
Open	Pasture, agricultural field, or bare soil
Vegetation along the edge of water	As percentage of the length covered by the following vegetation along the water edge (within 5 m from the water) in the section
Trees	Length covered by trees > about 10 m in height
Scrub-grass	Length covered by scrub (including trees <10 m in height) and rank grass
Grass	Length covered by rank grass only
Open	Length covered by pasture, agricultural field, or bare soil
Water grass	Length covered by emergent vegetation
Other variables	Variables assessed as present, absent, or scored
Public path	Present or absent in the section
Human activities	Regular human presence (e.g., houses) present or absent in the section
Other water sources	Presence of any permanent water source outside of the section <100 m from any edge of the section
Rabbits	Rabbit abundance estimated by warren size: scored between 0 (no warren) and 3 (largest warren) in the section

APPENDIX II.

Matrix of correlation coefficients for habitat variables. Statistically significant correlations were detected using ANOVA ($n = 115$ sections) with appropriate probability values adjusted using the Bonferroni technique (Rice 1989).

	Vegetation area				Vegetation along the edge of water				Other variables	
	Tree	Scrub	Rank grass	Open	Tree	Scrub	Rank grass	Open	Emergent vegetation	Rabbit warrens
Vegetation area										
Trees		0.119	0.264*	−0.688**	0.399**	0.024	0.266*	−0.444**	−0.204	0.324**
Scrub			0.264*	−0.526**	0.203	0.181	0.170	−0.361**	−0.004	0.425**
Rank grass				−0.819**	0.022	−0.111	0.648**	−0.569**	0.095	0.471**
Open					−0.271*	−0.000	−0.578**	0.676**	0.047	−0.581**
Vegetation along the edge of water										
Trees						0.091	−0.164	−0.340**	0.063	0.231
Scrub							−0.305**	−0.322**	−0.039	0.146
Rank grass								−0.693**	0.051	0.352**
Open									−0.067	−0.524**
Other variables										
Emergent vegetation										0.067

APPENDIX III.

Log maximum likelihood estimates for full autoregressive and spatially lagged models, ordinary least squares analysis models with and without spatial lagging for 4 neighborhood ranges ($n = 112$). Principal component analysis axis-1 (PCA 1) and PCA 1 and 2 represent the variables including PCA 1, rabbit and other mink, and PCA 1 and 2, rabbit and other mink, respectively, and number of neighbors; 2, 4, 6, and 8 represent the nearest 2, 4, 6, and 8 river sections to the focal section.

Numbers of neighbors	Autoregressive models				Ordinary least-squares analysis			
	PCA 1 and 2		PCA 1		PCA 1 and 2	PCA 1	PCA 1 and 2	PCA 1
	Lagged	No lag	Lagged	No lag	Lagged	Lagged	No lag	No lag
2	−222.7	−235.8	−231.9	−235.6	−292.2	−295.8	−306.6	−307.4
4	−212.0	−223.4	−216.7	−223.8	−282.3	−285.8	−306.6	−307.4
6	−222.4	−227.7	−227.1	−230.0	−282.3	−288.0	−306.6	−307.4
8	−226.2	−230.8	−227.9	−229.3	−276.2	−282.9	−306.6	−307.4

APPENDIX IV.

Results of likelihood ratio tests comparing autoregressive models with ordinary least squares analysis (OLS) models with and without spatial lags for predictor variables. Values approximate to chi squared.

Full autoregressive model with spatially lagged predictors compared with OLS with spatially lagged predictors (PCA 1, 2, rabbit and other mink)

Number of neighbors	2	4	6	8
Likelihood	129.0	140.6	119.6	100.0
P-value	<0.001	<0.001	<0.001	<0.001

Full autoregressive model with spatially lagged predictors compared with OLS with spatially lagged predictors (PCA 1, rabbit, and other mink)

Number of neighbors	2	4	6	8
Likelihood	127.8	138.2	121.8	110.0
P-value	<0.001	<0.001	<0.001	<0.001

Comparison of full autoregressive models with spatially lagged predictors between PCA 1, 2, rabbit, and other mink and PCA 1, rabbit, and other mink

Number of neighbors	2	4	6	8
Likelihood	8.4	9.4	9.4	3.4
P-value	<0.05	<0.01	<0.01	NS

OLS spatially lagged predictors compared with OLS with predictors of no spatial lags (PCA 1, 2, rabbit, and other mink)

Number of neighbors	2	4	6	8
Likelihood	28.8	48.6	48.8	60.8
P-value	<0.001	<0.001	<0.001	<0.001

OLS spatially lagged predictors compared with OLS with predictors of no spatial lags (PCA 1, rabbit, and other mink)

Number of neighbors	2	4	6	8
Likelihood	23.2	43.2	38.8	49.0
P-value	<0.001	<0.001	<0.001	<0.001

OLS (nonspatially lagged model with PCA1, 2, rabbit, and other mink) compared with OLS (nonspatially lagged model with (PCA 1, rabbit, and other mink)

Likelihood	1.2
P-value	NS

APPENDIX IV.—Continued.

Full autoregressive model with spatially lagged variables compared with autoregressive model without lagged habitat variables (PCA1, 2, and rabbit)

Number of neighbors	2	4	6	8
Likelihood	26.2	22.8	10.6	9.2
P-value	<0.001	<0.001	<0.05	<0.05

Full autoregressive model with spatially lagged variables compared with autoregressive model without lagged habitat variables (PCA1 and rabbit)

Number of neighbors	2	4	6	8
Likelihood	7.4	14.2	4.6	2.8
P-value	<0.02	<0.001	>0.05	>0.05

TABLE V.

Akaike's Information Criterion (AIC) for all models. AIC calculated as $2^{(\log \text{likelihood})} + 2^p$, where p is the number of parameters in model. The model with the smallest AIC is the best.

Model	Autoregressive model		Ordinary least squares analysis			
			Spatial lags		No spatial lags	
Number of neighbors	PCA 1 and 2	PCA 1	PCA 1 and 2	PCA 1	PCA 1 and 2	PCA 1
2	469.4	473.8	596.4	599.6	620.8	617.2
4	438.0	443.4	576.6	579.6	620.8	617.2
6	458.8	464.2	576.4	584.0	620.8	617.2
8	466.2	465.8	564.4	573.8	620.8	617.2