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SPATIAL AND TEMPORAL RELATIONSHIPS BETWEEN INVASIVE AMERICAN MINK AND NATIVE EUROPEAN POLECATS IN THE SOUTHERN UNITED KINGDOM

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The spatial organization of a species on a landscape is influenced, at least in part, by the presence of sympatric competitors. Interspecific relationships can thus have direct effects on the carrying capacity of the landscape and have important implications for conservation. We investigated the spatial relationships and activity patterns of 2 similarly sized mustelids: the invasive American mink (*Neovison vison*) and the native European polecat (*Mustela putorius*) in lowlands in the United Kingdom. By radiotracking mink ($n = 11$) and polecats ($n = 7$) in autumn when individuals of both species hold stable home ranges, we found that individuals tended to have overlapping home ranges, both within and between species; and the size of overlap areas was similar, but generally small, within and between species (mean approximately 20%, although overlaps were higher among mink of opposite sexes). Mink shared their home ranges with 0.3–1.17 other mink (of both sexes) and 0.83–1.3 polecats; polecats shared their home ranges with 0.6–1.0 polecats (of the opposite sex) and 1.6–2.0 mink. Neighbors avoided simultaneous use of overlap areas; polecats were nocturnal and mink were predominantly diurnal. Our results are consistent with interspecific territoriality although we cannot distinguish between interspecific territoriality and niche differentiation. We suggest that there is habitat partitioning between the 2 species, but that this is incomplete and that temporal partitioning enables avoidance of interspecific neighbors within overlap areas. Niche partitioning by distance from water and time of day when active probably facilitates coexistence in the short term, but it is unclear whether coexistence is stable year-round or in the long term.

Key words: coexistence, home range, interspecific territoriality, *Mustela*, *Neovison*, resource depression, resource partitioning

An individual's home range is classically defined as "that area traversed by an individual in its normal activities of food gathering, mating, and caring for the young" (Burt 1943:351). Although analytically not quite so simple (Powell 2000), the general assumption is that the home range contains all the resources required to satisfy an animal's life requisites (Mitchell and Powell 2004). At a population or community level, the spatial arrangement of home ranges on the landscape is determined not only by social organization of a species (e.g., Powell 1979), but also by the proximity of, and relationships with, sympatric competitors (e.g., Robinson and Terborgh 1995; St-Pierre et al. 2006). Thus, interspecific relationships can have direct effects on the carrying capacity of the landscape and may have important implications for conservation (Linnell and Strand 2000).

The American mink (*Neovison vison*) is an invasive species in the United Kingdom (Macdonald and Harrington 2003) that colonized most of the countryside at a time when the European polecat (*Mustela putorius*) was largely absent because of the lasting effects of intense persecution in the 19th century (Birks and Kitchener 1999). The 2 species are similar in size, weighing approximately 1 kg, and both are adaptable generalist predators occurring in a wide variety of habitats (Birks and Kitchener 1999; Dunstone 1993). In fact, Dayan and Simberloff (1994) suggested that the American mink in the United Kingdom moved into the vacated polecat niche. However, the European polecat is recovering nationally (Birks and Kitchener 1999) and the question arises: what will happen as polecats recolonize areas now occupied by mink?

The effect of 1 species on the other is difficult to predict. Although competition theory suggests that similar species should not coexist (Hardin 1960), the aquatic preference of mink (Dunstone 1993) and the more terrestrial habits of polecats in the United Kingdom (Birks and Kitchener 1999) could provide sufficient resource partitioning along an

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"aquatic–terrestrial" habitat niche axis to enable coexistence (cf. Hutchinson 1959; MacArthur 1958). However, the simultaneous recovery of another native mustelid, the Eurasian otter (*Lutra lutra*), which is competitively dominant to the mink (Bonesi and Macdonald 2004a), may result in greater dependence on the terrestrial environment by mink (Bonesi and Macdonald 2004b), potentially pushing mink into greater contact with polecats. In fact, mink still use the aquatic environment in the presence of otters (Hays et al. 2007) but may depend upon a more terrestrial diet found along the river banks (Harrington 2007). Polecats in mainland Europe are strongly associated with riparian areas (e.g., Rondinini et al. 2006) and it remains unknown to what extent they will use aquatic habitats in the United Kingdom, to what extent they will come into contact with mink, and what the outcome of such contact is likely to be. This study attempts to answer the first 2 of these questions. Keddy (2001) suggested that, in contrast to the hypothesis that competition is most intense between similar species, competition is most symmetrical between similar-sized species. Thus, similar-sized species may be more likely to coexist than dissimilar species precisely because neither has a clear advantage over the other. However, evidence from eastern Europe suggests that female polecats, at least, are ousted from the best habitat there by mink (Sidorovich and Macdonald 2001).

Mink exhibit intrasexual territoriality (Dunstone 1993), as do many other mustelid species (Powell 1979), although there is some overlap even between same-sex neighbors (Yamaguchi and Macdonald 2003). It is assumed that polecats follow a similar pattern, although detailed ecological studies are lacking (but see Lodé 1996). Our objectives were to describe the space use of *N. vison* and *M. putorius* with respect to interspecific neighbors, to quantify inter- and intraspecific home-range overlap, and to compare activity patterns of the 2 species. The population of polecats in the United Kingdom is of particular importance because it is the only population that is currently increasing. The decline of populations of polecats throughout mainland Europe is a focus of conservation concern (Birks and Kitchener 1999).

Materials and Methods

Study area.—We undertook the study on a 20-km stretch of the River Thames, in a rural area approximately 5 km west of Oxford, United Kingdom (51°42′N, 1°28′W). Our study site consisted of this stretch of river and an approximately 1-km border on either side of the river. The river was slow-flowing (5–20 m wide, up to 3 m deep); fringed with trees (e.g., willow [*Salix fragilis*]) and vegetation (e.g., nettles [*Urtica dioica*], bramble [*Rubus fruticosus*], blackthorn [*Prunus spinosa*], and hawthorn [*Crataegus monogyna*]); and bordered on either side by a lowland, mixed agricultural landscape. Agricultural land use was mainly grazed pasture, subdivided by an extensive system of interconnecting hedgerows, streams, and irrigation ditches; some arable land and deciduous woodland (predominantly in patches <20 ha) also occurred. Agricultural buildings, houses, and villages occurred intermittently throughout the site.

Mink are estimated to have been resident in the area for approximately 25–30 years (Yamaguchi and Macdonald 2003). During this time, attempted lethal control of mink in the area has been opportunistic and not intense, and no such trapping to control mink was carried out over the duration of our study. Polecats were first rerecorded in Oxfordshire in 1993 (Birks and Kitchener 1999) and first trapped in the River Thames study site in 1996 (A. Grogan, Wildlife Conservation Research Unit, pers. comm.), although they were not observed on the river itself before 2004. Otters, foxes (*Vulpes vulpes*), and stoats (*M. ermine*) also were present in the area. Rabbits (*Oryctolagus cuniculus*) were patchily distributed; other potential prey items included small mammals, birds, and fish.

Autumn–winter temperatures over the period of the study varied between 1.8°C and 17.1°C (data collated per month: lowest mean minimum–highest mean maximum; Oxford weather station: www.metoffice.gov.uk/climate/uk/stationdata). Average monthly rainfall was 57.6 mm. Frost occurred on between 1 and 11 days per month in November and December.

Animal capture.—We captured mink and polecats in the autumn of 2004 and 2005. Wire mesh cage traps (Solway Feeders Ltd., Kirkcudbright, Scotland, United Kingdom) were set on the river on floating rafts (Reynolds et al. 2004), and in hedgerows and other suitable trap sites up to 1 km from the river (details of trapping methods are given by Harrington et al. [2008] and Yamaguchi et al. [2002]). Trapping effort for mink was concentrated on stretches of the river adjacent to areas where polecats were captured to increase the likelihood that study animals shared the same area.

We sedated captured animals (Harrington et al. 2008), then marked animals with subcutaneous passive integrated transponder tags (MID Fingerprint, Weymouth, Dorset, United Kingdom) and fitted them with waterproof radiotransmitters with integral activity switches (frequency range 173–174 MHz) attached to collars (Wildlife Materials, Inc., Murphysboro, Illinois). Standard body measurements were taken and animals were transferred to a plastic holding box for recovery before being released at the site of capture. Radiocollars weighed 10 g, <2% of the body mass of the smallest individual (690 g) in the study. Procedures were usually completed within 10–30 min and animals recovered from anesthesia within 10–25 min.

Polecats were trapped under English Nature license 20052467, and mink were rereleased for monitoring under Department for Environment, Food, and Rural Affairs license WCA/06/4. All procedures were carried out under United Kingdom Home Office licenses PPL30/1826, PIL30/6530, and PIL30/6917; were approved by Oxford University Zoology Department Ethical Review Committee; and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Radiotracking procedures.—Animals were tracked on foot using dedicated radiotracking receivers (TRX-1,000S; Wildlife Materials, Inc.) or scanners (R-1000; Communications Specialist, Orange, California) with 3-element yagi antennae from October to January 2004–2005 and 2005–2006. Each individual was tracked in only 1 year. Radiolocations were obtained by triangulation by 2 people simultaneously taking bearings from a mean distance of approximately 100 m, coordinated via walkie-talkies. Handheld global positioning system units were used to record locations of observers within 5- to 6-m accuracy for each bearing taken. Radiotracking was carried out in discontinuous 8-h shifts over 24 h with fixes taken at 15-min intervals when 1 animal was followed continuously or at hourly intervals if several animals were followed simultaneously. Our goal was to track animals occurring in close proximity to one another simultaneously; thus, while 1 animal was being tracked, observers were intermittently scanning for other individuals that were likely to be within range (approximately 1 km). Bearings recorded in the field were converted to Ordnance Survey grid reference locations using LOAS (1999 Ecological Software Solutions: www.ecostats.com); a standard declination of $-3°$ was used to convert magnetic bearings recorded in the field to grid bearings (British Geological Survey: www.geomag.bgs.ac.uk/gofs/gma_calc.html). For each location, the focal animal was recorded as actively moving or inactive. Den sites were determined when possible by precisely locating inactive animals, in which case, locations were recorded directly as grid references using global positioning system units.

We tested the bias and the precision (White and Garrott 1990) of our radiotracking system by placing transmitters at 19 locations and taking 7–20 replicate bearings from variable distances and angles at each location ($n = 291$ bearings total—Harrington 2007). Transmitters were placed at the river's edge, in the river, in hedgerows, in open fields, among tree roots, and in rabbit burrows. We found no evidence of bias in the system (mean bearing error ± *SE*: 0.29° ± 0.67°, $t = 0.43$, $P = 0.673$, $n = 19$). Precision was estimated as 8.5° (mean *SD* of bearing error, $n = 19$). Linear errors (distance between estimated locations and actual locations, $n = 81$) ranged between 0.9 and 61.4 m. The median linear error was 15.5 m (95% confidence interval [95% *CI*] = 13.3, 17.5 m); we used the upper *CI* of the median to define the tracking resolution in home-range analyses (cf. Withey et al. 2001).

Home-range characteristics.—Various methods have recently been proposed for estimating home ranges in linear habitats (e.g., Blundell et al. 2001; Sauer et al. 1999). However, our choice of method was constrained not only by the linear habitats used by mink (Dunstone 1993), but also by the need to compare home-range size and overlaps with polecats, which typically use a more 2-dimensional area, although polecats tend to restrict their activities to linear habitats within that area (e.g., Rondinini et al. 2006). Because estimation techniques for 1 aspect of home-range analysis are not necessarily the best for another (Worton 1995), we used different methods for different purposes. To allow interspecific comparison of home-range size, and to estimate total home-range overlaps, we calculated restricted edge (concave) polygons using a restriction distance at 75% of range span—the lowest value that did not result in the fragmentation of individual home ranges. Restricted edge (concave) polygons better described use of the river by mink, and included fewer unused terrestrial areas in places where the river meandered, than did minimum convex polygons, which have previously been used to measure home ranges of polecats (e.g., Birks and Kitchener 1999). For comparability with previous studies, we also calculated 100% minimum convex polygons for polecats and length of waterway used for mink (Dunstone 1993). To investigate core-area overlaps, we used 50% core areas estimated by fixed kernel contours with $h_{ref} = 1$. All home-range analyses were performed in Ranges 7 (Kenward et al. 2003; www.anatrack.com). The length of waterway used was the distance between the furthest upstream and downstream locations, measured in ArcMap in ArcGIS 9 (www.esri.com). In all cases, estimates of home ranges represent monthly home ranges in autumn–winter.

For all analyses of home ranges, we included only individuals that had been tracked on ≥ 5 ($\bar{X} = 13.9$, $SD = 5.5$) days and for which we had ≥ 20 ($\bar{X} = 55.4$, $SD = 26.0$) radiolocations. We tested for differences between species and sexes in total home-range size with univariate general linear models weighted by the number of locations per individual. Numbers of locations varied among individuals but did not differ between species (*t*-test: $t = 1.00$, $d.f. = 15$, $P = 0.33$). Parametric assumptions of general linear models were evaluated with residual analysis (Kleinbaum et al. 1988); variables were transformed where appropriate.

American mink tend to be limited to aquatic habitats in the upper River Thames valley and occupy narrow habitat strips along riparian corridors (Yamaguchi et al. 2003). To investigate the relative use of riparian habitats by polecats we calculated the mean and maximum distances of locations from the nearest river or stream, the proportion of locations recorded on a river or stream, and the number of days on which visits were made to the river for each individual in ArcGIS. For this analysis we define "on the river" as within 17.5 m of the river (i.e., the resolution of the data).

Interactions between species and sexes.—Macdonald et al. (1980) defined 2 types of home-range overlap: static interactions, which measure the amount of spatial overlap between 2 animals; and dynamic interactions, which measure the temporal association of 2 animals within their area of overlap. Static overlaps of 0 between 2 individuals in close proximity suggest territoriality. We considered all individuals within 200 m of one another to be neighboring pairs. We quantified the proportion of intra- and interspecific pairs with spatial overlaps at the total home range and the 50% core-area levels. For all pairs exhibiting overlap > 0, we calculated the area of overlap for each individual in the pair. Because area overlaps measured in terms of the area of the range that is overlapped (hereafter, "area overlaps") can be misleading (Kernohan et al. 2001), we also calculated the overlap in terms of the proportion of locations that fall within another individual's range (hereafter, "point overlaps"—cf. White and Garrott 1990). Area overlaps measure the extent of an individual's home range that it shares with a neighbor; point overlaps measure the use that an individual makes of its neighbor's home range. In either, case the degree of overlap is specific to the individual (i.e., $\text{overlap}_{1,2} \neq \text{overlap}_{2,1}$). All

Table 1.—Monthly autumn home-range size of American mink (*Neovison vison*) and polecats (*Mustela putorius*), upper Thames Valley, Oxfordshire, United Kingdom, 2004–2006. Data are median, range (*n*).[a]

	Mink		Polecats	
Estimation method	Males	Females	Males	Females
Length of river (km)	3.4, 2.5−9.0 (5)	2.2, 1.7−3.1 (6)	—	—
100% minimum convex polygon (ha)	—	—	87.7, 43.1−132.2 (2)	71.0, 50.1−124.3 (5)
Restricted edge polygon[b] (ha)	52.5, 42.0−258.8 (5)	36.0, 15.4−55.0 (6)	45.3, 21.9−68.8 (2)	61.7, 34.1−123.2 (5)

[a] Data on individuals in Harrington (2007).

[b] Restriction was 0.75, buffered by the resolution of the radiolocation data.

measures of overlap were calculated in Ranges 7 (Kenward et al. 2003; www.anatrack.com).

Static interactions were assigned to all possible pairwise groups by species and sex, except that we were unable to evaluate intraspecific overlaps in polecats in the analysis because our sample included only 2 male polecats. We used Fisher's exact test to compare the tendency to overlap between groups and randomization tests (Manly 1997) with 999 replicates to examine intergroup differences in area and point overlaps. For all pairs that exhibited static home-range overlaps, we investigated dynamic interactions by calculating a cohesion index that describes the tendency of pairs of animals to be close together at the same time. The index was calculated in Ranges 7 by comparing observed distances between individuals of a pair during simultaneous locations with all possible distances between that pair based on all known locations of each individual. The observed and possible distances were compared using Jacob's index, which gives a value of between +1 (indicating attraction) and −1 (indicating avoidance—Kenward et al. 2003). Finally, we calculated the number, sex, and species of all additional individuals that were detected in each individual's home range.

Activity patterns.—To compare activity patterns of mink and polecats, we calculated the proportion of radiolocations during which each individual was moving. We used general linear models on arcsine-transformed variables, weighted relative to the number of locations per individual ($\sqrt{n}$, $n =$ number of fixes), to evaluate relationships of activity with time of day, species, and individual (individual was nested within species to account for repeated use of the same individuals over different times). We only used 1 record per hour for each individual to ensure independence of records, but when multiple fixes for an individual were available within an hour, we scored that hour as active if at least 1 fix showed evidence of movement by that animal. For this analysis, the important test was the statistical significance of the interaction term time × species, which tests whether the effect of time is dependent on species.

All statistical analyses were carried out in Minitab 13 (www.minitab.com; Minitab 15 for Fisher's exact tests); macros for randomization tests were from Butler et al. (2003; http://www.ceh.ac.uk/products/software/minitab/download.asp). Statistical significance was accepted at $P < 0.05$; all tests were 2-tailed unless otherwise stated.

RESULTS

We radiotracked and described home ranges for 11 mink (5 males and 6 females) and 7 polecats (2 males and 5 females). We also obtained a limited number of radiolocations ($n = 9$–30 per individual) for 5 additional polecats (3 males and 2 females), 3 of which (all males) appeared either to be transients or to have home ranges on the edge of our study site and 2 of which (females) were tracked in the 1st year of the study (2004–2005) but prematurely lost their radiocollars. None of these 5 individuals were detected within or close to the home ranges of the 7 polecats for which we were able to describe home ranges, or in areas where mink occurred. We did not include these 5 individuals in analyses of home-range size or overlap but we did include them in analyses of activity patterns.

Mean weights of study animals were: male mink, 1,260 g ($n = 5$, $SD = 173.3$ g); female mink, 750 g ($n = 6$, $SD = 60.2$ g); male polecats, 1,560 g ($n = 2$, $SD = 187.0$ g); and female polecats, 980 g ($n = 5$, $SD = 127.3$ g). Three mink (2 males and 1 female) and 2 polecats (1 male and 1 female) were subadults (individuals between 6 months and 1 year of age, having reached adult body size but not yet bred—cf. Yamaguchi and Macdonald 2003); all other individuals were adults. Because our study was carried out in the autumn–winter, after the period in which juveniles disperse, both adults and subadults should be settled in stable home ranges (Dunstone 1993).

Home-range characteristics.—Autumn home-range size (restricted edge polygons) did not differ statistically between sexes or species (total home-range size, reciprocal-transformed restricted edge polygon, sex: $F = 1.43$, $d.f. = 1, 15$, $P = 0.250$; species: $F = 0.44$, $d.f. = 1, 15$, $P = 0.519$; Table 1). Similarly, no intersexual difference was detected in home-range sizes of mink or polecats measured by length of river used or minimum convex polygon, respectively (mink: $F = 4.19$, $d.f. = 1, 9$, $P = 0.075$, after excluding 1 male outlier whose home range was large [9.04 km] because it included several parallel-running watercourses; polecats: $F = 0.01$, $d.f. = 1, 5$, $P = 0.946$, reciprocal-transformed variables in both cases; Table 1).

Mink occupied linear home ranges along waterways. Polecats occupied 2-dimensional ranges using hedgerows and copses bordering the river. Mink also used small ditches adjoining the river, although the farthest that a mink was recorded from a river or stream was approximately 400 m and, on average, mink remained within approximately 200 m of the river. In contrast, polecats tended to move within an area between the river and approximately 700 m from the river (Table 2). Neither mink nor polecats used open fields. There was no intersexual difference in either median or maximum distance from the river for either mink or polecats (mink: median distance: $t = -0.19$, *d.f* = 4, $P = 0.857$; maximum distance: $t = -0.78$, *d.f.* = 5, $P = 0.473$; polecats: median distance: $t = 0.58$, *d.f.* = 2, $P = 0.619$; maximum distance: $t = 0.20$, *d.f.* = 2, $P = 0.863$). Four of 7 polecats were recorded on a river at least once, the other 3 came within 50 m of the river. The relative proportion of locations on the river was significantly greater for mink than for polecats ($t = 8.46$, *d.f.* = 15, $P < 0.001$; Table 2). Three polecats had >5% of their locations on the river; these individuals all made multiple visits to the river on separate days (2–3 days, 14–22% of total days tracked).

We located 36 den sites for 10 mink and 19 den sites for 7 polecats. Mink used hollow and fallen tree trunks and tree stumps on the riverbank (50% of den sites) and rabbit burrows (31%); polecats used predominantly rabbit burrows (79%). Mink dens were generally found on or near the riverbank (61.1% of dens ≤17.5 m from the river; Table 2). Polecat dens were generally found further from the river (Table 2) but 31.6% were found on or near the riverbank (≤17.5 m from the river).

Sex and species interactions.—Of 23 possible neighboring pairs, there were 8 intraspecific pairs of mink, 13 interspecific pairs, and 2 intraspecific pairs of polecats; the polecat–polecat pairs were excluded from statistical analysis because of small sample size. Six (75%) of the 8 pairs of mink and 9 (69%) of the 13 interspecific pairs had home ranges that overlapped in area to at least some extent. Of these, however, only 1 pair of mink and 2 interspecific pairs also had overlapping 50% core areas. Trends in the tendency to overlap were similar for point overlaps, with 6 (75%) of 9 intraspecific and 6 (46%) of 13 interspecific pairs showing overlap to some extent at the total home-range level. At the 50% core-area level, however, 3 pairs of mink (50% of the pairs showing overlap) and 5 interspecific pairs (83%) showed some overlap. The proportion of pairs that showed overlap did not differ significantly between groups in any case (Fisher's exact tests, all $P > 0.37$). Both intraspecific pairs of polecats overlapped at the home-range level, and 1 pair overlapped at the 50% core-area level. The spatial arrangement of home ranges in the study site is depicted in Fig. 1.

The area of an individual's home range that was overlapped by another individual ranged between <1% and 82% for all groups combined, and differed statistically between groups ($P = 0.039$; Fig. 2a). Area overlaps were highest for pairs of mink of opposite sexes and lowest for pairs of mink of the same sex. On average, area overlaps for interspecific pairs were low (18% mean overlap for mink–polecat pairs of the same sex and 22% mean overlap for mink–polecat pairs of different sexes), but overlap in mink–polecat pairs was extensive for a few individuals (44% for a same-sex pair and 82% for a different-sex pair; Fig. 2a). Intersexual overlaps for the 2 pairs of polecats were 0.11–0.18% and 15–21%. Although pairwise overlaps could be highly asymmetrical within a pair, particularly in intersexual pairs, area overlaps in interspecific pairs tended to be symmetrical ($P = 1.0$; Fig. 3a). There was no difference among groups in point overlaps ($P = 0.196$; Fig. 2b), and a high (>40%) proportion of points were recorded within the home range of a neighbor in at least a few cases for all groups. As for area overlaps, asymmetrical point overlaps occurred in a few pairs. Generally, asymmetrical overlap occurred in intersexual pairs, but there was no tendency for greater overlap by one sex or another. The proportion of locations of mink falling within the home range of a neighboring polecat and the proportion of locations of polecats falling within the home range of a neighboring mink did not differ ($P = 1.0$; Fig. 3b). Overlap areas tended to occur on rivers or riverbanks.

Table 2.—Proximity of American mink (*Neovison vison*; $n = 11$) and polecats (*Mustela putorius*; $n = 7$) to riparian habitats in the upper Thames Valley,[a] Oxfordshire, United Kingdom, 2004–2006. Data on animal locations are summarized as mean, range of data for individuals. Data on den sites are median, maximum.

	Mink	Polecat
Median distance from nearest waterway per individual (m)	18,[b] 11–50	480, 82–1,240
Maximum distance from nearest waterway per individual (m)	180, 27–380	710, 320–1,310
% locations on the river per individual	49.5, 22–66	5.7, 0–23
Den distance from river (m)	15, 64	140, 1,310

[a] Within our study site, that is, within 1 km of the river.

[b] Note that this is approximately equal to the resolution of the tracking data, meaning that, in effect, mink locations tend to be on the river. Note also that because of the imprecise nature of radiolocations, the figures presented here serve as relative measures between the 2 species, not as absolute measures for either species.

Overlaps of core areas (both area and point) tended to be <10% for all groups. There were only 3 cases where either area or point overlaps of 50% core areas exceeded 20%: reciprocal overlaps between 2 female mink (area overlaps: 67–68%; point overlaps: about 40% for both individuals) and the overlap of a male polecat by a male mink (area: 33%; points: 45%). Neither area nor point overlaps differed between pairs of mink or interspecific pairs at the 50% core-area level (area overlaps: $P = 0.332$; point overlaps: $P = 1.0$; sample sizes were insufficient to test statistically for differences among groups subdivided by sex).

Jacob's index varied between −0.01 and 0.55 ($n = 10$ pairs tracked simultaneously) and was higher for mink–polecat pairs (0.25, $n = 4$ pairs) than for pairs of mink (0.06, $n = 5$ pairs). The mean distance observed between individuals in a pair was >100 m in all cases (>200 m in 8 of 10 cases). Seven of 10 pairs of overlapping neighbors were never recorded in the overlap area at the same time, and individuals that were occasionally recorded ≤200 m apart were rarely recorded active at the same time. Detailed observations were limited, but 1 male–female pair of mink that exhibited almost complete home-range overlap were rarely recorded active at the same time and 2 mink–polecat pairs also appeared to maintain spatial segregation on different waterways although both individuals of the pair used the same waterways on different days. The closest simultaneous locations recorded for pairs were 2 female

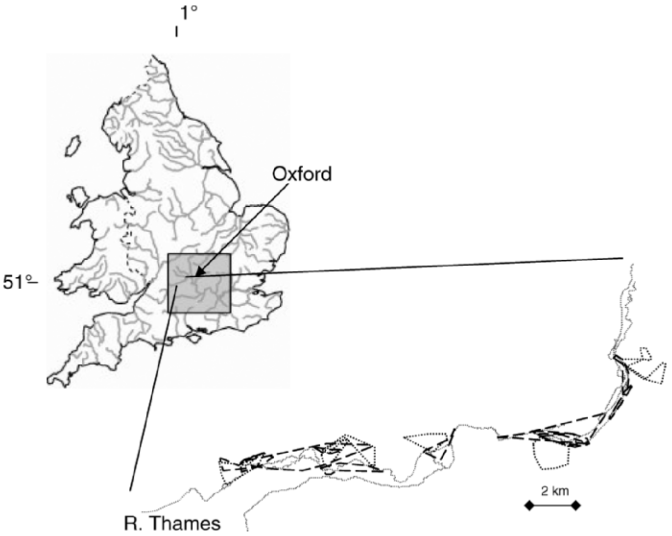

Fig. 1.—Autumn home ranges of mink (*Neovison vison*; dashed lines, $n = 11$) and polecats (*Mustela putorius*; dotted lines, $n = 7$) on a 20-km stretch of the River Thames, 2004–2005. Home ranges are restricted edge (concave) polygons with a restriction distance at 75% of range span. Insert shows location of the study site in the United Kingdom, relative to the city of Oxford.

minks that occupied dens within 50 m of each another and a mink–polecat pair that occupied dens in a riverside copse approximately 25 m from each another on a single occasion.

On average, male mink ($n = 6$) shared their home range with 1.17 ($SD = 0.41$) female mink, 0.67 ($SD = 0.52$) male mink, and 1.33 ($SD = 1.0$) polecats. Female mink ($n = 6$) shared their home range with 0.33 ($SD = 0.52$) female mink, 1.17 ($SD = 0.98$) male mink, and 0.83 ($SD = 0.75$) polecats. Female polecats ($n = 5$) shared their home range with 0.6 ($SD = 0.55$) male polecats and 2.0 ($SD = 1.4$) mink. Male polecats ($n = 3$) shared their home range with 1.0 ($SD = 0$) female polecat and 1.67 ($SD = 0.58$) mink. We did not detect any intrasexual overlap among polecats within our study area.

Activity patterns.—Activity of mink appeared to be confined to the daylight hours (0800–1600 h), whereas activity of polecats, although quite variable, was predominantly nocturnal, with little or no activity recorded during the middle of the day (Fig. 4). The difference between the 2 species was statistically significant (general linear model, time × species interaction: $F = 2.74$, $d.f. = 5, 74$, $P = 0.025$).

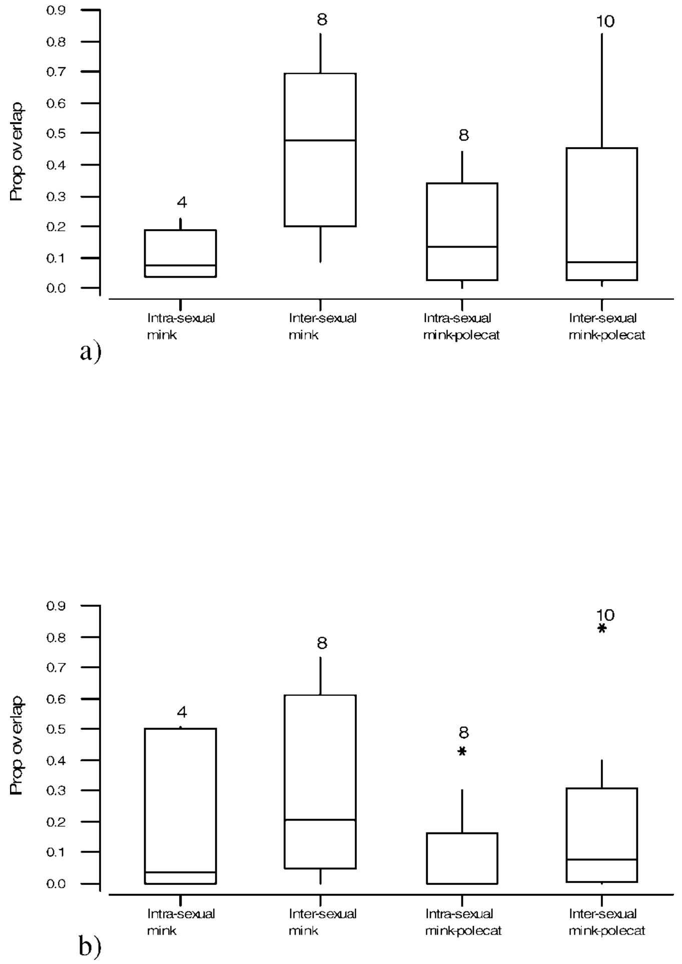

Fig. 2.—Home-range overlaps among species–sex groups of mink (*Neovison vison*) and polecats (*Mustela putorius*), upper Thames Valley, Oxfordshire, United Kingdom, in autumn–winter 2004–2005 and 2005–2006. Graphs depict median, interquartile range, range, and outliers for a) area overlaps, and b) point overlaps. Proportion overlaps for a) are the proportion of an individual's home range that was overlapped by the home range of its neighbor, and for b) are the proportion of an individual's radiolocations that were recorded within the home range of its neighbor. n (shown above bars) = the number of neighboring pairs.

DISCUSSION

We found that mink and polecats are not exclusively territorial, either intra- or interspecifically. As reported by Yamaguchi and Macdonald (2003), we found that there is some spatial overlap between neighboring mink, even within the sexes. We never trapped a polecat of the same sex within another polecat's home range. However, the fact that we also failed to trap additional polecats of the same sex within several kilometers of a radiotracked polecat's home range in areas of apparently suitable terrestrial habitat unoccupied by mink suggests that the lack of intraspecific overlap among polecats recorded in our study was due to the low population density of polecats. Cores areas were generally not shared either within or between species. Nevertheless, the relatively high tendency for individuals to be located on at least a few occasions within the core area of a neighbor demonstrated that even core areas are not completely exclusive. This, and the small proportion of home ranges that overlapped on average, suggests that overlaps reflect incursions by neighbors that cannot be prevented rather than lack of territoriality (cf. Wolff 1993).

The area of an individual's home range that it shared with its neighbor, and the extent to which an individual utilized its neighbor's home range, varied greatly between members of pairs. As expected, area overlaps (but not point overlaps) were greatest for intersexual pairs of mink. Otherwise, we did not detect any significant differences in the extent of spatial overlaps at the home-range level between species–sex groups.

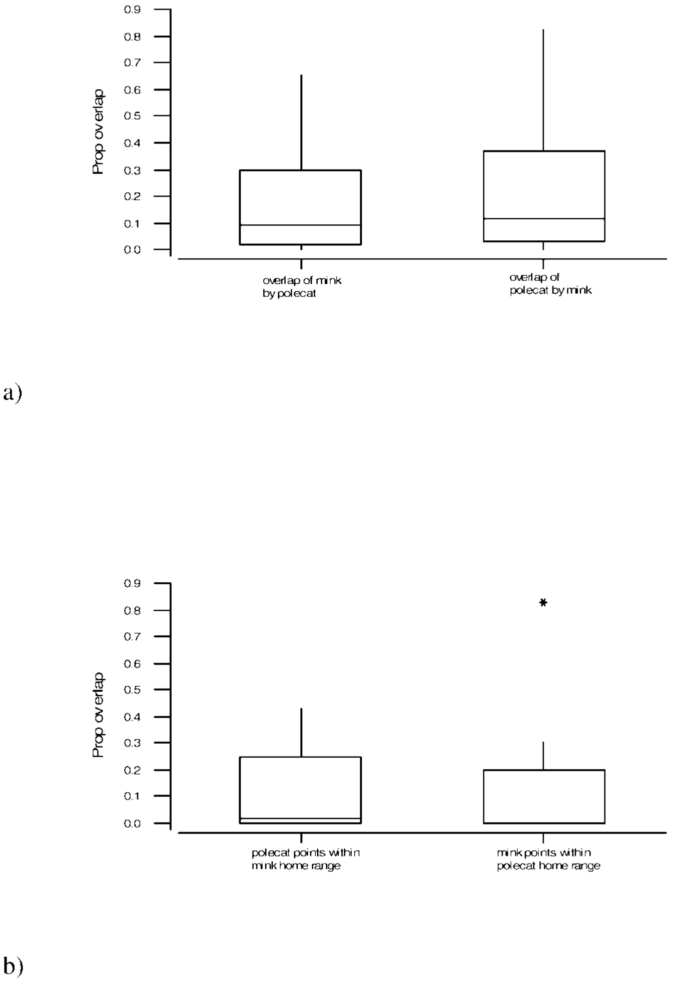

FIG. 3.—Interspecific home-range overlaps between mink (*Neovison vison*) and polecats (*Mustela putorius*), upper Thames Valley, Oxfordshire, United Kingdom, in autumn–winter 2004–2005 and 2005–2006. Graphs depict median, interquartile range, range, and outliers for a) area overlaps, and b) point overlaps. Proportion overlaps for a) are the proportion of an individual's home range that was overlapped by the home range of its neighbor, and for b) are the proportion of an individual's radiolocations that were recorded within the home range if its neighbor. $n = 9$ neighboring interspecific pairs.

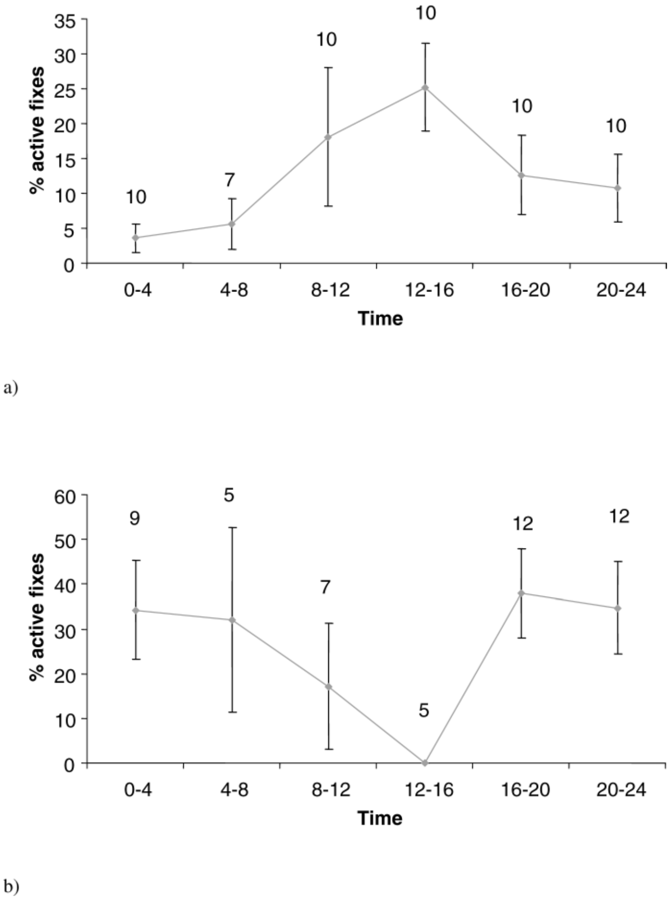

FIG. 4.—Activity patterns of radiotracked a) mink (*Neovison vison*) and b) polecats (*Mustela putorius*), upper Thames Valley, Oxfordshire, United Kingdom, in autumn–winter 2004–2005 and 2005–2006. Data are mean proportion ± *SE* of fixes classified as active for 11 mink and 12 polecats. Individuals are repeated between time periods but not all individuals are included in all time periods. *n* (shown above bars) = number of individuals included within each time period.

Overlaps at the core-area level were small in extent for all but 2 neighboring pairs. The female–female pair of mink involved a subadult originally captured as a juvenile in July within the home range of the other adult female, suggesting that the 2 were mother and daughter. The other pair, a mink–polecat pair composed of 2 males, also involved a subadult mink, although it is unclear in this case why a high overlap of core areas would be tolerated by either individual.

The fact that home ranges of mink were overlapped to a similar extent by both neighboring mink and polecats suggests that a similar degree of territoriality is expressed against polecats as against other mink. Interestingly, mink appear to react with similar interest to the scent of polecats as to the scent of unknown mink (Harrington 2007). Although it is not known what mechanisms are involved in territorial defense in mustelids, it is likely that scent plays a role (e.g., Hutchings and White 2000). Given that the 2 species are very similar in size and hunt many of the same prey species (Birks and Kitchener 1999; Dunstone 1993), it is not unreasonable to suppose that a mink might perceive a polecat to be a similar threat or nuisance as another intruding mink.

Analyses of dynamic interactions suggested that locations of mink and polecats were not affected by the location of their neighbors. Nevertheless, the distances between locations of neighbors were >200 m in most cases. Although home-range overlaps frequently occurred between both mink–mink and mink–polecat neighboring pairs, individuals appeared to avoid simultaneous use of overlap areas. Avoidance was achieved by temporal avoidance, spatial avoidance, or both. Interspecific temporal avoidance was accentuated by almost opposite diel activity cycles.

The similarities in the extent of home-range overlap and the apparent avoidance behavior within overlap areas between both intra- and interspecific neighboring pairs are consistent with the hypothesis that the 2 species exhibit interspecific territoriality

(Murray 1971). However, we cannot exclude the alternative hypotheses that the absence of greater spatial overlap is due to ecological differences rather than interspecific territoriality (Martin and Thibault 1996); or that the limited use of the riverbank by polecats is due to the avoidance of otters. The first alternative is unlikely given the use of riparian habitats by polecats in mainland Europe (Lodé 1994; Rondinini et al. 2006; Sidorovich and Macdonald 2001), and specifically in Poland where polecats occupy linear home ranges along streams in the Białowieża Forest (Brzeziński et al. 1992). Similarly, the fact that dietary overlap between polecats and otters is much less than it is between mink and otters (e.g., Sidorovich et al. 1998) suggests that polecats are more likely to be able to coexist in the same space as otters than are mink, and, thus, the second alternative lacks credibility.

Yamaguchi and Macdonald (2003) suggested that mink maintain home ranges larger than is necessary based on energetic requirements because their home ranges overlap to some extent with those of conspecific neighbors, and they have to compensate for the resulting resource depression (Charnov et al. 1976; Powell 1994). The number of other mink that spatially overlapped a mink's home range in our study was similar to that found by Yamaguchi and Macdonald (2003), but we also found that home ranges of mink were overlapped by an additional 1 or 2 potentially competing, similar-sized mustelids. Similarly, home ranges of polecats were overlapped by those of 1–3 mink. The obvious prediction is that both species would have to maintain even larger home ranges to compensate for the presence of a greater number of spatially overlapping competitors. We do not have comparative data on the size of home ranges of polecats in similar habitats in the absence of mink. However, mink do not appear to have increased the size of their home ranges since the recolonization of our study site by polecats (Harrington 2007). We suggest that resource depression is partly ameliorated by resource partitioning, principally temporal partitioning. The effectiveness of temporal partitioning in reducing resource depression would depend on prey recovery time, which is not known. Partitioning of prey types as a secondary result of the differences in their activity times also could occur.

Being active at different times also reduces the probability of aggressive encounters, an important form of competition between carnivores (Macdonald and Sillero-Zubiri 2004). Temporal partitioning is seen in other similar sympatric carnivores, for example, crab-eating foxes (*Cerdocyon thous*) and Pampas foxes (*Lycalopex gymnocercus*) in Brazil (Vieira and Port 2006).

Diurnal activity in mink in autumn is unusual (Dunstone 1993), and although it may facilitate the coexistence of mink and polecats, it is not necessarily caused by competition with polecats. An alternative explanation for diurnal activity in mink at this site is the arrival of otters there and the subsequent avoidance by mink of a dominant competitor (Harrington 2007). Unlike polecats, mink dive for fish and are, therefore, likely to come into direct contact with otters in the river. We do not know whether diurnal activity by mink is unique to this site or whether it occurs more generally in the presence of polecats, otters, or both.

From a conservation perspective, 2 possible outcomes of the interactions between mink and polecats in the United Kingdom are of interest: if the presence of mink prevents recolonization by polecats, and if recolonization by polecats leads to declines in populations of mink (as suggested for otters—Bonesi et al. 2006; McDonald et al. 2007). Neither appears to be supported by our results and the apparent coexistence between mink and polecats in the United Kingdom contrasts with the findings of Sidorovich and Macdonald (2001), who found that polecats in Belarus have declined in riparian habitats since the colonization of these areas by American mink. However, there are 3 important differences between our study site in the United Kingdom and Belarus: in northeastern Belarus, the environment is pristine, with little agricultural land and extensive marshes and swamps bordering the rivers (Sidorovich 2000a); the rivers in Belarus freeze in winter (Sidorovich 2000b); and polecats in Belarus are smaller than they are in our study area, and are smaller there than American mink (Sidorovich et al. 1999). As a result of the type of environment, home ranges of mink in Belarus are oval rather than linear (Macdonald et al. 2002), and are not restricted to a narrow band of habitat along the river as they are in the United Kingdom. When the rivers freeze, American mink switch to a diet of predominantly small mammals (Sidorovich 2000b). Both shape of home ranges and dietary switching in winter result in substantial overlap in space and diet with polecats in Belarus (Sidorovich 2000b), and the larger size of American mink there gives the mink a competitive advantage (Sidorovich et al. 1999). In the lowland agricultural areas in the United Kingdom, the restriction of American mink to linear habitats along the river, as well as year-round access to the river, might allow for sufficient niche partitioning for the coexistence of the 2 species, at least in the short-term. It is perhaps noteworthy that in Belarus, before colonization by American mink, polecats coexisted with European mink (*Mustela lutreola*). The European mink differs from the American mink principally in its greater dependence on the aquatic environment (Sidorovich and Macdonald 2001).

Finally, although our results suggest coexistence, our study was short-term and confined to a single season, thus it is unknown whether this system is stable year-round or over the long-term. Indeed, Powell and Zielinski (1983) suggest that coexistence between similar mustelids is never stable, but rather is temporary and fluctuates in response to fluctuations in prey. Some other species of predators, for example the arctic fox (*Vulpes lagopus*) and the red fox (*V. vulpes*), only show spatial segregation during the breeding season (Dalen et al. 2004). Also, because our study system is currently changing with the concurrent recovery of 2 native mustelids, it is possible that the full effects, particularly on the carrying capacity of the landscape, have not yet been seen. Indeed, Harrington (2007) detected an apparent decline in the body mass of mink since the recovery of otters and polecats, perhaps indicating a decline in body condition. Similarly, although mink have not prevented the recolonization of the area by polecats, it is unclear whether the presence of mink reduces habitat availability for polecats. Future research should focus on these and related questions, such as whether the carrying capacity of the landscape for polecats is increased by the removal of mink and whether an increase in habitat availability is necessary to ensure the long-term viability of the population of polecats in the United Kingdom.

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