

Spacing pattern, intersexual competition and niche segregation in American mink

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Many animals, especially mustelids, show a spacing pattern known as intrasexual territoriality in which territorial animals defend areas against individuals of the same sex and there is extensive overlap between sexes. It has been argued that this overlap leads to sharing of food resources between territorial individuals of different sexes which has a net cost for territorial individuals. Several mechanisms have been proposed to reduce competition between sexes, many of them derived from sexual dimorphism, which is closely related to intrasexual territoriality. Among the suggested mechanism is spatial segregation between animals with overlapping areas, although it remains largely untested. We hypothesized that sexual spatial segregation in mustelids could be a consequence of a niche partition in habitat between sexes due to different optimums. We conducted a fine-grained radio tracking survey of seven feral American minks in winter. We compared home ranges, relative spatial positions and characteristics of radio-locations of different sexes. We also considered relative distances between simultaneous locations of overlapping individuals to test for dynamic territorial interactions. There were differences in the home range composition of males and females, and in their relative spatial location, proving spatial segregation between sexes. The comparison of locations showed that females preferred smaller streams as opposed to males that preferred large streams. In addition relative spatial position of female locations was independent of location of males in overlapping pairs, suggesting niche segregation caused by different sexual habitat preferences. Sexual habitat segregation is discussed as a powerful means of avoiding intersexual competition in species exhibiting intrasexual territoriality as a spacing pattern.

Introduction

Most animals limit their activities of food gathering, mating and caring for young into more or less confined areas called home ranges (Powell 2000). When individuals use their home range

exclusively or preferentially defending it against other conspecifics we speak of territoriality (Begon *et al.* 2006). However territorial behaviour only takes place under certain conditions, and under different environmental conditions a species may show different spacing patterns

ranging from group living territories to nomadism (Macdonald 1983, Kruuk 1989, Powell 1994). Traditionally invoked benefits to individuals defending territories are: access to mates and exclusive or preferential use of food or other resources, while among disadvantages there are the net costs of defending a territory (energetics, risk of injuries, etc.) and others (Powell 1994). However, for territoriality to take place, its benefits to individuals must outweigh its costs (Davies 1978, Macdonald 1983, Powell 2000, Begon *et al.* 2006). Intrasexual territoriality is a spacing pattern exhibited by many species and typical of mustelids and other small carnivores (Powell 1979, Macdonald 1992, Palomares & Delibes 1994). In such a spacing pattern males defend territories against males and females defend territories against females, while there is an extensive overlap between sexes. It has been argued that this overlap leads to sharing food resources between territorial individuals of different sexes in overlapping areas, intrasexual territoriality having a net cost for territorial individuals (Powell 1994, Yamaguchi & Macdonald 2003). This cost might be higher in case of carnivores, for the behaviour of some prey species changes after a predator enters a patch, lowering their vulnerability, and thus their availability, and remains altered for as long as a day or more causing resource depletion (Jedrzejewski & Jedrzejewska 1990). Several adaptations have been invoked to overcome this handicap: (1) Sexual dimorphism, often found in species with intrasexual territories (Powell 1979), has been proposed as a mechanism for niche separation and resource partitioning between sexes (Birks & Dunstone 1985, Thom *et al.* 2004). Different sexes being better adapted to consume different prey reduce the effect of home range overlap on competition for resources (Thom *et al.* 2004). (2) In the same way, sexual segregation in the activity patterns has also been proposed as a means of reducing competition between overlapping individuals of different sexes, with sexes using patches at different times (Zalewski 2001, Marcelli *et al.* 2003). (3) Finally, that males and females rarely use the same suitable patches of overlapping areas, creating a spatial segregation between sexes (Gerell 1970, Erlinge 1977, Lodé 1996) has also been proposed. However, little

attention has been paid to this last hypothesis that remains largely untested.

The habitat concept might be misleading, for different people have used it with different meanings (Hall *et al.* 1997, Garshelis 2000). Based on Hutchinson's concept of niche, defined as a hypervolume of n dimensions with a dimension for each environmental condition and resource required for the species (Begon *et al.* 2006), here we consider habitat as the ranges of a set of physical variables within the niche's hypervolume. Therefore, in this paper habitat is considered a species-specific characteristic, as a more or less differentiated part of the ecological niche. Research on trophic apparatus has shown that there is interspecific and intraspecific (intersexual) character displacement, which is thought to be related to niche partitioning as a consequence of competition (Dayan *et al.* 1989, Dayan & Simberloff 1994, Thom *et al.* 2004). In the same way, interspecific or intrasexual competition could provoke niche partition in other facets such as habitat, although little attention has been paid to this.

The American mink is a mustelid native to North America that has been introduced in many areas where it now is widely distributed (Macdonald & Harrington 2003). It is sexually dimorphic and exhibits intrasexual territoriality (Dunstone 1993, Yamaguchi & Macdonald 2003). Its population is structured along water courses, it is susceptible to more intraspecific competition pressure since it has linear home ranges. Animals can respond to changes in quality of the home range (for instance to resource depletion or depression caused by conspecifics) by expanding it. However, this expansion would be more costly in mink due to the linear shape of their home ranges.

We hypothesized that carnivores with intrasexual territories and sexual dimorphism show spatial segregation and habitat segregation as a means of avoiding intersexual competition, mainly as a consequence of a niche partition in habitat between sexes. Therefore, we expected that habitat composition and use of home range varies with sex and that males and females use different areas as a means of avoiding competition. In the same way, we expected to find differences in the areas used by males and females as indication of niche segregation.

We conducted a spatially explicit radio-tracking study of habitat use of American mink at a very fine-grained scale during winter and early spring, and we performed (1) dynamic interactions analysis (Kenward 2001) to test whether overlapping individuals of different sexes showed spatial segregation, and (2) niche comparison analysis to test whether spatial segregation was a consequence of niche partition between sexes as predicted by our hypothesis.

Materials and methods

Study area

The study was conducted in the Butron river system, Biscay, northern Spain. This is a small catchment 40-km long along its main axis and whose area is 174 km². Climate is oceanic, with annual rainfall around 1200 mm. Winters are mild and there is no summer drought. The study was focused on 20 km of the medium part of the river system and its tributaries, where the biggest stretch of the main river is 10 m wide and 1.5 m deep under normal weather conditions, although most stretches are between 3- and 6-m wide and between 30- and 50-cm deep. Riverbank vegetation is composed of alder trees (*Alnus glutinosa*) and willows (*Salix alba*), and heliophytic vegetation forming dense undergrowth especially where tree species are absent. Locally riverbank vegetation has been completely extirpated due to grazing. Main land uses are forest cultures in upper and step areas and grasslands and cattle rearing in the middle flatter ones. The medium and lower parts of the study area were mainly composed of rich lowland area, where cattle rearing has created meadows and kilometres of ditches for drainage. Small villages and farms are scattered all across the area. The oldest report of feral American mink in the area goes back to 1993, but the population is suspected to have originated from a local fur farm closed more than 20 years ago (Zuberogoitia & Zabala 2003). Rabbits are absent from the study area. The American mink are the largest semi-aquatic carnivores in the study area; otters are absent, polecats (*Mustela putorius*) are very rare, and European mink (*Mustela lutreola*) are scarce, occur-

ring mainly in the upper reaches and medium tributaries (Zabala *et al.* 2005, Zabala 2006). Mink scats collected during the study contained crayfish, fish, small mammals, poultry and berries (own unpubl. data).

Trapping and radio-tracking

Animals were live-trapped in single-entry cage traps (25 × 25 × 45 cm). Trapping sessions were carried out in streams from November 2004 to January 2005. After immobilisation with 0.8 mg of Zooletil (Virbac, Carros, France) per 100 g of animal weight, individuals were fitted with radiotransmitters (Biotrack, Dorset, UK). Radio-collars weighed ca. 15 g, i.e. less than the 3% of the animal weight. After radio-collaring, mink were closed in the trap again and set in concealed areas (bramble patches), where we observed them until they completely woke up and then let them free. During all the handling, mink were kept warm using rags to prevent hypothermia. Animals were aged according to tooth wearing into three categories: subadults, adults and old. We caught 5 adult males and 6 adult females, and 10 of them (5 males and 5 females) were fitted with radiocollars. A hand-held 3-element Yagi antenna, and TRX-1000S (Wildlife Materials Inc. Carbondale, USA) and Sika (Biotrack, Dorset, U.K.) receivers were deployed on foot. In addition, a RX8910 receiver (Televilt International AB, Sweden) with an H-shaped antenna was used at close distances. Fixes were achieved by homing-in (White & Garrot 1990) or triangulation at close distances (normally less than 5 m) with an accuracy of 1-2 m² and variables describing an area of 25 m² around the point were measured in the field. Each data set of variables describing 25 m² around a location or randomly created point will be hereafter named a point descriptor. Then fixes were located in high resolution aerial photographs (0.5 m pixel) implemented in a Geographic Information System (GIS) with an accuracy of 3 m². Animals were classified as either active or inactive according to the level of variations in the radio signal strength (Kenward, 2001). Mink were radio tracked twice a week starting the next day after capture until early April. Tracking periods are detailed in Table 1. At the beginning we took

two fixes per day at different times, but locations tended to be the same or very close, so, in order to avoid bias due to data pseudo-correlation, only one fix per day, obtained at different time, was considered for analysis (Aebischer *et al.* 1993). Similarly, we initially radio-tracked mink at randomly selected times during day and early night hours, but we found almost no activity at the nighttime locations, which were usually very close to the daytime ones. Therefore, we decided to continue radio-tracking during daytime only (for further information on mink activity patterns at the study area see Zuberogoitia *et al.* [2006a]). Linear home ranges were calculated as the length (meters) of waterway used by mink considering the 100% of the locations (White & Garrot 1990, Dunstone 1993, Yamaguchi *et al.* 2003). We performed incremental analyses in order to determine the number of locations needed for home-range calculations. To delimitate areas used by individuals we built density estimators with the locations using an *ad hoc* cell size of 25 metres. For setting the window size we performed the Least Square Cross Validation (LSCV) (Powell 2000, Kenward 2001), but it did not consider streams as paths and yielded different window sizes for different individuals depending on the scattering of their locations, so we used an *ad hoc* window size of 150 metres. Using digital cartography overlaid on aerial photographs we defined two type of streams based on cartographic generalization (Corsi *et al.* 2000): main streams were

those represented in 1:50 000 scale, and tributary or secondary ones were represented only in larger scales (1:25 000, 1:5000 but not 1:50 000). To gain insight into the spatial arrangement of the population, using the GIS we measured the position of locations with regard to main axis (i.e. main river). To find out if there was dynamic territoriality, i.e. temporal avoidance between animals in the shared patches, we measured the distance between simultaneous locations of overlapping individuals of different sex and compared it with one set of potential distances between obtained locations.

Variable selection

We selected a set of 7 variables describing habitat features (Table 2). Mink habitat use is known to be correlated with the vegetation present along the edge of water, mainly trees and scrub, with some differences in preferences between sexes (Yamaguchi *et al.* 2003, Zabala *et al.* 2003, 2007). Therefore we considered two vegetation variables describing the degree of forest cover and scrub cover (i.e. how dense, tangled and impenetrable the scrub was). In both cases estimations were made on a categorical scale from 0 (lowest cover) to 5 (highest cover) regardless of the plant species; tall rank grass was included in scrub. We also measured the size of scrub patches (length \times width \times height) or estimated it

Table 1. Detailed tracking periods, MMV stands for male American mink and FMV for female American mink. Locations shows the number of independent locations used to build home ranges (capture point included), and Active and Inactive the number of independent locations obtained from each individual during activity and resting periods, respectively. Animals marked with asterisks (*) are not considered in the analyses due to scarce radio-tracking data.

Individual	Tracking period	Number of locations	Active	Inactive	Home range length (m)	Tributary length (m)	Percentage of home range in tributaries
MMV1*	16 Nov.–13 Dec. 2004	6	2	3	2237	0	0
MMV2	16 Nov. 2004–23 Feb. 2005	32	11	19	4085	391	9.3
MMV3*	23 Nov.–1 Dec. 2004	4	0	2	1017	36	3.5
MMV4	26 Nov. 2004–24 Jan. 2005	19	4	14	1193	123	9.6
MMV5	13 Jan.–7 Apr. 2005	26	14	11	15874	10167	64.1
FMV1	18 Nov. 2004–28 Feb. 2005	28	6	21	10486	5161	49.2
FMV2*	24 Nov.–7 Dec. 2004	3	1	1	332	55	83.4
FMV3	13 Jan.–7 Apr. 2005	30	14	15	2099	1539	73.3
FMV4	14 Jan.–7 Apr. 2005	26	14	11	4063	2300	56.6
FMV5	15 Jan.–7 Apr. 2005	27	13	13	3051	1111	36.4

when measuring was not possible. Scrub patches of different sizes could either be dense patches (scrub cover 5) or sparse ones (scrub cover 1–2). In addition we measured the width of the stream at each location and estimated its mean depth. Finally, we included the distance from the location point to the water and the slope of the bank, although these last two variables only were considered in the case of resting animals.

Statistical analyses

To test for dynamic interactions (attraction/avoidance of overlapping conspecifics of different sex) we compared observed distances with expected ones. Based on Kenward's (2001) procedure, we calculated a minimum distance between simultaneous locations of overlapping conspecifics. Expected locations were obtained by randomising all possible pairs of locations at which the animals were detected, i.e. distances from locations of an individual to non-simultaneous locations of overlapping individuals. However, rather than using minimum distances between locations, we used minimum watercourse distance between locations, which we calculated using the GIS. Then we compared observed distances and expected distances using Man-Whitney's *U*-test. For analyses we used simultaneous locations, obtained in less than 30 minutes intervals.

To determine differences in niches between sexes we plotted active locations of males against those of females and inactive locations of males against those of females, and compared them using a Logistic Regression Analysis (LRA). For the LRA we used the stepwise method and the Wald statistic (Morrison *et al.* 1998). The LRA

is a type of multivariate analysis that allows the inclusion of categorical variables (Ferrán 1996). The Stepwise method is an exploratory tool allowing identification of the best predictors from the pool of potentially useful parameters (Ferrán 1996). In this approach, variables are entered into the LRA individually provided that they fulfill some requirements. The selection of variables ends when no further increase in the accuracy of the model can be achieved. For the LRA analyses, we randomly selected 20 point descriptors plus 8 more for each variable in the analysis, following the recommendations of Morrison *et al.* (1998). In total, we used 60 locations for the activity LRA and other 80 for the inactivity locations LRA. The dependent variable was in both cases the sex of mink (male against female), and the independent variables were those listed in Table 2. The number of locations of male mink was similar to that of female in both analyses.

Subsequently, selection of classes within determinant categorical variables after the LRA was tested using the χ^2 -test corrected with Bonferroni's inequality (Manly *et al.* 1993). For the comparison of distances data sets we used Mann-Whitney's *U*-test and Wilcoxon's paired test (Zar 1999). $\alpha = 0.05$ in all cases.

Results

Trapping and radio-tracking

We captured and tagged 10 American minks, five males and five females, and successfully radio-tracked seven of them (Table 1). MMV3 and FMV2 took off the collar few days after tagging. MMV1 disappeared shortly after radio-tagging

Table 2. Variables describing locations as measured *in situ*. "Activity" or "rest" show whether they were considered to characterize each period.

Variable	Description	Activity	Rest
Scrub cover	Density of shrubs within 5 m from each location	Yes	Yes
Forest cover	Density of trees within 5 m from each location	Yes	Yes
Scrub size	Size of the shrubs concealing mink	Yes	Yes
River width	Width of the water stretch in the river's adjacent point to each mink location	Yes	Yes
Depth	Depth of the water stretch in the river's adjacent point to each mink location	Yes	Yes
Distance to bank	Distance from each location to the adjacent water	No	Yes
Bank	Angle of the bank closest to each location	No	Yes

and was not found despite searching along the entire catchment and adjacent areas; radio-tag failure and poaching were suspected (Table 1). Indeed during the study period, poaching was confirmed in the case of MMV2, FMV1 and other three untagged animals.

Home range size, composition, use and overlap

The mean size of a male home-range, considering only those tracked sufficiently, was 7092 (SD = 6763) metres, while that of females was 4925 (SD = 3793) m. The male MMV5 had a total home range much larger than the others, however its large home range (15874 m, Table 1) is the result of acquiring the whole of MMV2's adjacent home range (4085 m) a week after the latter was poached. This individual was a very old male and, although its home range was much larger than the others, it could not be considered as nomadic because it regularly moved along 10 km of river stretches since its tracking started, regularly returning to the same points. Incremental analyses showed that males rapidly revealed their territory, indeed MMV2 and MMV4 revealed 100% of their territories at 14 and 8 locations, respectively. MMV5 revealed 90% of its territory at 16 locations, just a week after MMV2 was poached and it had overtook its territory. In order to reveal territory sizes for females, about 20 locations were necessary. After taking 15 locations FMV1, FMV2 and FMV3 respectively revealed 30%, 40% and 60% of their territories, while FMV5 revealed 90% at only 10 locations.

Composition of the home range was different between sexes, with males encompassing mainly

main river stretches and females a bigger proportion of tributaries (Table 1). This tendency is clearer if we pay attention to the location of the areas used inside animals' home ranges (Table 3), with males having most of their areas on main streams and females preferentially on tributaries. Spatial position of the radio-locations was different, males tended to be closer to the main stream than females (Mann-Whitney: $U = 1865.0$, $p < 0.001$, $n = 163$). This pattern held for both activity (Mann-Whitney: $U = 265.0$, $p < 0.006$, $n = 60$) and resting locations (Mann-Whitney: $U = 548.5$, $p < 0.001$, $n = 99$), and also held when mink locations on a main stream (i.e. when mink were not on a tributary, therefore with a 0 value) were not considered in the analysis (Mann-Whitney: $U = 437.0$, $p < 0.001$, $n = 98$).

Dynamic interactions and niche segregation

There were no differences between the distances between simultaneous locations and the set of possible distances among randomly selected locations of overlapping individuals (2 pairs, 33 simultaneous locations; 1st pair, 10 simultaneous locations Mann-Whitney: $U = 2002.0$, $Z = -0.543$, $p = 0.587$, $n = 172$; 2nd pair, 23 simultaneous locations $U = 4798.5$, $Z = -0.306$, $p = 0.760$, $n = 304$) suggesting that males and females neither attracted nor avoided each other during the study period.

When comparing the characteristics of resting sites used by males and females, the LRA produced a two step model, which extracted the variables River Width and Scrub Cover, both reaching statistical significance (Table 4). Therefore, there

Table 3. Composition of the activity areas.

Individual	Length of main stream (m) within activity areas	Length of tributary (m) within activity areas	Percentage of activity areas in tributaries	Percentage of home range included in activity areas
MMV2	1878	159	7.8	46
MMV4	607	0	0	50
MMV5	3011	1295	30.1	17
FMV1	250	1489	86.6	32
FMV3	0	1390	100	34
FMV4	531	1177	68.9	27
FMV5	500	789	61.2	81

were clear differences between sexes in their resting sites, with females using resting sites in narrower streams (i.e. small tributaries) and areas with less bramble and scrub cover while males rested preferentially in dense bramble patches in main stream stretches. In the same way, the LRA with activity locations produced a single step model that extracted the variable River Width, reaching statistical significance (Table 4), indicating that there were statistically significant differences in the areas used by sexes, with females preferring smaller streams than males.

We tested for differential use of categories of the variable Scrub Cover during rest and found statistical differences in the categories 2 and 0 (Table 5). Females used areas with medium-low scrub cover more often than did the males (Scrub category 2), and also used more often areas with no scrub cover at all (Scrub category 0, mainly dens in buildings) (*see Zabala et al. [2007]* for a description of resting sites).

Discussion

Studies on the American mink ecology from other areas reported disruption of the spatial

organization during late winter as a consequence of males being highly mobile with a great degree of immigration and emigration (Yamaguchi & Macdonald 2003, Yamaguchi *et al.* 2003). This could pose a serious problem to our study design, however the fact that incremental analyses showed that male mink revealed over 95% of their territories in about 14 locations suggests high territorial stability. In addition, sign surveys were conducted parallel to the radio tracking to assess different census techniques (Zubero-goitia *et al.* 2006b). During the sign survey we detected 8 signs of untagged mink in the gaps between territories (note that a single individual could leave more than one), and a single one in a tributary at the edge of a male's territory, likely a female as deduced from the track size. Therefore, in opposition to studies from northern areas neither territorial disruption nor male emigration or immigration was detected.

American mink in the study area showed sexual spatial segregation in the location and use of their home ranges. The home range of males were mainly situated along main river stretches while those of females were primarily along tributaries and included only small proportions of the main river, usually at the tributary's junc-

Table 4. Results of the Logistic Regression Analyses comparing male and female locations.

Step	Included variables	β	Wald	df	p	r	Correctly classified (%)
Resting							
1	River width	0.266	11.59	1	0.001	0.215	75.3
2	Scrub cover		11.50	5	0.042		
	River width	0.334	6.64	1	0.010	0.369	79.4
Activity							
1	River width	0.180	4.167	1	0.041	0.081	56.7

Table 5. Differential use of categories of the variable Scrub cover during rest. We plotted proportion of use by males against proportion of use by females. Upper and lower values of confidence intervals and observed value for each category are quoted.

Scrub cover	Upper limit	Lower limit	Observed value	Statistical significance
5	0.820	0.327	0.394	No
4	0.122	-0.056	0.014	No
3	0.349	-0.021	0.056	No
2	0.080	-0.047	0.085	Yes
1	0.122	-0.056	0.014	No
0	0.080	-0.047	0.127	Yes

tion. In addition, the location of the activity centres (Table 3) indicates that females used main streams as corridors between tributaries, because we rarely detected them on main streams. Contrary to males, females ventured far into tributaries and smaller streams, and tended to stay far from the main rivers for most of the time while males tended to remain on them. The fact that males did travel less than females into tributaries suggests that they used them only marginally and mainly near the junction with the main streams. MMV5 included 10 km of tributaries within its home range, and used them more often than other males, but still far less than females. This was partially a consequence of the inclusion of the largest tributary of the area into its territory. We also radio-tracked a female on that tributary (FMV4), whose territory followed the main stem but the female used third order streams while the main stem of the tributary was used by the male. The spatial organization pattern is similar to that observed by others for similar species. Kruuk (1995) found that in freshwater areas most Eurasian male otters (*Lutra lutra*) were caught in main streams while females and subadults were in streams and lakes. Similar spacing patterns have been reported for the North American river otter (*Lontra canadensis*) (Reid et al. 1994), and other otter species (review in Kruuk 2006).

The comparison of male locations against female locations yielded river width as a key variable for niche differentiation. This, reinforced by the different composition of home ranges and the differences in distances from radio-locations to main stream, strongly suggests differential habitat use by sexes. Although we cannot state whether there are differences in habitat quality between male and female areas, our results suggest that there is no exclusion of either sex by the other from preferred areas. The fact that there were no differences between the distances between simultaneous locations and the set of possible distances among randomly selected locations of overlapping individuals indicates that there is neither attraction nor avoidance between individuals of different sexes, although we can not be conclusive here due to the low number of overlapping individuals tracked simultaneously. Therefore, our data do not support the hypothesis of males driving females out to suboptimal

habitats. In addition, if this were true, we could expect females to enter the main streams when males are absent, but we did not find such tendency. Notwithstanding, male's scats and other marks could inform females and keep them out, but the fact that females did cross large sections of main streams when moving from one tributary to another, and also used dens and resting sites in them does not support this hypothesis. Our results, strongly suggest that the observed segregation arises from different sexes having different habitat preferences and different optimum habitats, as predicted by our hypothesis, and in consequence using different clues for making decisions on where to settle and which areas to use. Similarly, Kruuk (1995) also suggested different habitat use between sexes, with males using poorer quality habitats in his studies.

Interspecific competition is supposed to lead to compression from fundamental niche to realized niche, thus allowing species with moderate niche overlap to coexist by segregating the niche (Begon et al. 2006). Intraspecific competition can also drive sexual dimorphism as a result of different selective pressures acting over sexes and lead to niche partition (Dayan & Simberloff 1994, Bolnick & Doebeli 2003). Dimorphic sexes must therefore match different challenges and mustelid females being smaller have different energetic requirements and different thermal tolerance (Peters 1983, Harlow 1994, Zalewski 2001) and probably different predators. This would explain the second variable extracted by the LRA for resting sites. Females used significantly more areas with low scrub cover as resting sites, but all of them were dens inside buildings and their use was associated with snow or cold days (Zabala et al. 2007). Assuming that during winter nights dens inside buildings are warmer than those outside, females using buildings seems to be related to lower thermal tolerance.

Although niche and habitat are commonly treated as species' specific, they actually are characteristics of individuals and much of their variation is due to individual specialization (Bolnick et al. 2003). We suggest that in dimorphic mustelids individuals of the same sex will have more similar niche than individuals of different sexes, due to similar sizes and same selective pressures acting over individuals of the

same sex. In addition, this would not only be valid for time budgets or trophic niche (Sidorovich *et al.* 2001, Thom *et al.* 2004) but also for habitat issues as suggested by our results. Different habitat preferences, or different clues for assessing habitat quality, lead to spatial segregation according to the distribution of preferred patches, and to reduced intersexual competition. Indeed, some studies have reported spatial segregation between overlapping couples in mustelids (Gerell 1970, Erlinge 1977, Lodé 1993, Yamaguchi *et al.* 2003) although they did not test for habitat segregation between sexes. Our results strongly suggest that the intersexual pressure caused by intrasexual territoriality amongst American mink is, at least partially, lessened by differential use of habitat by sexes. More studies are needed to test whether our results can be extrapolated to other seasons and areas, and especially to other species showing intrasexual territoriality.

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References

- Aebischer, N. J., Robertson, P. A. & Kenward, R. E. 1993: Compositional analysis of habitat use from animal radio-tracking data. — *Ecology* 74: 1313–1325.
- Begon, M., Townsend, C. R. & Harper, J. L. 2006: *Ecology. From individuals to ecosystems*. — Blackwell Publishing, Oxford.
- Birks, J. D. S. & Linn, I. J. 1982: Studies of home range of the feral mink, *Mustela vison*. — *Symp. Zool. Soc. Lond.* 49: 231–257.
- Birks, J. D. S. & Dunstone, N. 1985: Sex-related differences in the diet of the mink *Mustela vison*. — *Holarctic Ecology* 8: 245–252.
- Bolnick D. I. 2004: Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. — *Evolution* 58: 608–618.
- Bolnick D. I. & Doebeli, M. 2003: Sexual dimorphism and adaptive speciation: two sides of the same ecological coin. — *Evolution* 57: 2433–2449.
- Corsi, F., de Leeuw, J. & Skidmore, A. 2000: Modeling species distribution with GIS. — In: Boitani, L. & Fuller, T. K. (eds.), *Research techniques in animal ecology. Controversies and consequences*: 389–434. Columbia University Press, New York.
- Davies, N. 1978: Ecological questions about territorial behaviour. — In: Krebs, J. R. & Davies, N. (eds.), *Behavioural ecology, an evolutionary approach*: 317–350. Blackwell Scientific Publications, Oxford.
- Dayan, T. & Simberloff, D. 1994: Character displacement, sexual dimorphism, and morphological variations among British and Irish mustelids. — *Ecology* 75: 1063–1073.
- Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. 1989: Inter- and intraspecific character displacement in mustelids. — *Ecology* 70: 1526–1539.
- Dunstone, N. 1993: *The mink*. — T&AD Poyser Ltd., London.
- Erlinge, S. 1977: Spacing strategy in stoat *Mustela erminea*. — *Oikos* 28: 32–42.
- Ferrán, M. 1996: *SPSS para Windows*. — McGraw-Hill, Madrid.
- Garshelis, D. L. 2000: Delusions in habitat evaluation: measuring use, selection and importance. — In: Boitani, L. & Fuller, T. K. (eds.), *Research techniques in animal ecology. Controversies and consequences*: 111–164. Columbia University Press, New York.
- Gerell, R. 1970: Home ranges and movements of the mink *Mustela vison* Schreber in southern Sweden. — *Oikos* 21: 160–173.
- Harlow, H. J. 1994: Trade-offs associated with the size and shape of American martens. — In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. & Powell, R. A. (eds.), *Martens, sables and fishers. Biology and conservation*: 391–403. Cornell University press, Ithaca.
- Powell, R. A. 1994: Structure and spacing of *Martes* populations. — In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. & Powell, R. A. (eds.), *Martens, sables and fishers. Biology and conservation*: 101–121. Cornell University press, Ithaca.
- Hall, L. S., Krausman, P. R. & Morrison, M. L. 1997: The habitat concept and a plea for standard terminology. — *Wildl. Soc. Bull.* 25: 173–182.
- Jedrzejewski, W. & Jedrzejewska, B. 1990: Effect of a predator's visit on the spatial distribution of bank voles: experiments with weasels. — *Can. J. Zool.* 68: 660–666.
- Kenward, R. E. 2001: *A manual for wildlife radio tagging*. — Academic Press, London.
- Kruuk, H. 1989: *The social badger*. — Oxford University Press, Oxford.
- Kruuk, H. 1995: *Wild otters. Predation and populations*. — Oxford University Press, Oxford.
- Kruuk, H. 2006: *Otters. Ecology, behaviour and conservation*. — Oxford University Press, Oxford.
- Lodé, T. 1993: Diet composition and habitat use of sympatric polecat and American mink in western France. — *Acta Theriol.* 38: 161–163.
- Lodé, T. 1996: Conspecific tolerance and sexual segregation in the use of space and habitats in the European polecat. — *Acta Theriol.* 41: 171–178.
- Macdonald, D. W. 1983: The ecology of carnivore social behaviour. — *Nature* 301: 379–385.

- Macdonald, D. W. 1992: *The velvet claw. A natural history of the carnivores.* — BBC Books, London.
- Macdonald, D. W. & Harrington, L. A. 2003: The American mink: the triumph and tragedy of adaptation out of context. — *New Zealand J. Zool.* 30: 421–441.
- Manly, F. J., McDonald, L. & Thomas, D. L. 1993: *Resource selection by animals.* — Chapman and Hall, London.
- Marcelli, M., Fusillo, R. & Boitani, L. 2003: Sexual segregation in the activity patterns of European polecats *Mustela putorius*. — *J. Zool. Lond.* 261: 249–255.
- Morrison, M. L., Marcot, B. G. & Mannan, R. W. 1998: *Wildlife-habitat relationships. Concepts and applications.* — The University of Wisconsin Press, Wisconsin.
- Peters, R. H. 1983: *The ecological implications of body size.* — Cambridge University Press, Cambridge.
- Powell, R. A. 1979: Mustelid spacing patterns: variations on a theme by *Mustela*. — *Zeitschrift für Tierpsychologie* 50: 153–165.
- Powell, R. A. 1994: Structure and spacing of *Martes* populations. — In: Buskirk, S. W., Harestad, A. S., Raphael, M. G. & Powell, R. A. (eds.), *Martens, sables and fishers. Biology and conservation:* 101–121. Cornell University press, Ithaca.
- Powell, R. A. 2000: Animal home ranges and territories and home range estimators. — In: Boitani, L. & Fuller, T. K. (eds.), *Research techniques in animal ecology. Controversies and consequences:* 65–110. Columbia University Press, New York.
- Reid, D. G., Code, T. E., Reid, A. C. H. & Herrero, S. M. 1994: Spacing, movements and habitat selection of the river otter in boreal Alberta. — *Can. J. Zool.* 72: 1314–1324.
- Sidorovich, V. E., Macdonald, D. W., Pikulik, M. M. & Kruuk, H. 2001: Individual feeding specialization in the European mink, *Mustela lutreola* and the American mink, *M. vison* in north-eastern Belarus. — *Folia Zool.* 50: 27–42.
- Thom, M. D., Harrington, L. A. & Macdonald, D. W. 2004: Why are American mink sexually dimorphic? A role for niche separation. — *Oikos* 105: 525–535.
- White, G. C. & Garrot, R. A. 1990: *Analysis of wildlife radio-tracking data.* — Academic Press, London.
- Yamaguchi, N. & Macdonald, D. W. 2003: The burden of co-occupancy: intraspecific resource competition and spacing patterns in American mink. — *J. Mammal.* 84: 1341–1355.
- Yamaguchi, N., Rushton, S. & Macdonald, D. W. 2003: Habitat preferences of feral American mink in the Upper Thames. — *J. Mammal.* 84: 1356–1373.
- Zabala, J. 2006: *Distribution and spatial ecology of semi-aquatic mustelids (Carnivora: Mustelidae) in Biscay.* — Ph.D. thesis, University of the Basque Country.
- Zabala, J., Zuberogoitia, I., Garin, I. & Aihartza, J. R. 2003: Landscape features in the habitat selection of European mink *Mustela lutreola* in south-western Europe. — *J. Zool. Lond.* 260: 415–421.
- Zabala, J., Zuberogoitia, I. & Martínez-Climent, J. A. 2007: Habitat and landscape features ruling the habitat selection and occupancy of the polecat (*Mustela putorius*) in a low density area: a multiscale approach. — *Eur. J. Wildl. Manage.* 51: 157–162.
- Zabala, J., Zuberogoitia, I. & Martínez-Climent, J. A. 2007: Winter habitat preferences of feral American mink *Mustela vison* in Biscay, Northern Iberian Peninsula. — *Acta Theriol.* 52: 27–36.
- Zalewski, A. 2001: Seasonal and sexual variation in the diel activity rhythms of pine marten *Martes martes* in the Białowieża National Park. — *Acta Theriol.* 46: 295–304.
- Zar, J. H. 1999: *Biostatistical analysis.* — Prentice Hall, Upper Saddle River.
- Zuberogoitia, I. & Zabala, J. 2003: Data on the distribution of the American mink in Biscay. — *Galemys* 15: 29–35. [In Spanish with English summary].
- Zuberogoitia, I., Zabala, J. & Martínez-Climent, J. A. 2006a: Diurnal activity and observations of the hunting and ranging behaviour of the American mink. — *Mammalia* 70: 310–312.
- Zuberogoitia, I., Zabala, J. & Martínez-Climent, J. A. 2006b: Evaluation of sign surveys and trappability of American mink: management consequences. — *Folia Zool.* 55: 257–263.