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# Testing mechanistic explanations for mammalian predator responses to habitat edges

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**Abstract** Increased predator activity along habitat edges (the edge effect) is often documented in the temperate zone, but earlier studies have rarely been able to explicitly test the suggested mechanisms underlining this phenomenon. In

this study, we measured the distribution of mammalian predators by scent stations and their main prey (rodents) in four types of landscape elements corresponding to an edge gradient between two habitat types; grassland and forest. We found a contrasting pattern in carnivore activities between years. Whereas carnivores did not exhibit a significant occurrence along the forest–grassland edge in the first year with low prey abundance, they were more likely to be detected along habitat edges in the subsequent year with high prey abundance. Our results do not suggest that the increased activity of carnivores at habitat edges arises as a consequence of predator overflow from higher quality habitat through the edge into lower quality habitat, but showed that most predator species focus their activity specifically to the edge structure. On the other hand, our data do not provide straightforward support for the hypothesis that predator edge preferences are caused by a spatial gradient in carnivores' main prey—rodents.

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Mesopredators · Nest predation · Prey distribution

## Introduction

Anthropogenic habitat fragmentation primarily includes reductions in habitat patch sizes and increases in patch isolation and the habitat edge/interior ratio (Andrén 1995). These landscape changes often alter ecological processes, which result in shifts in the distribution and/or abundances of many species. High rates of fragmentation can lead to declines in population densities and even to local extinctions due to overall habitat loss, the adverse effects of metapopulation dynamics and higher risks of inbreeding depression (reviewed by Fahring 2003).

In addition, negative consequences of habitat fragmentation are assumed to result from altered intraspecific interactions. Such negative impacts of fragmentation are often associated with changes to the structure and density of predator communities (Chalfoun et al. 2002). Fragmented landscapes generally maintain a higher number of predators, particularly mammalian mesopredators (e.g., Crooks 2002; Crooks and Soulé 1999; Winter et al. 2006) and corvids (Corvidae), compared to non-fragmented habitats. These predators often exhibit increased activity along habitat edges (hereafter the edge effect; e.g., Andrén 1992), which enhances negative impacts on native biota (Schmidt 2003; Wilcove 1985).

Several mechanisms have been proposed to explain the pattern of predator distributions along habitat edges (Lidicker 1999; Ries et al. 2004; Ries and Sisk 2004). These mechanisms usually assume causal links between habitat-specific resources and predator occurrence (Ries et al. 2004; Ries and Sisk 2004): (1) a neutral (no) predator response to an ecotone gradient is predicted if there is no difference in resources between the habitats. This represents the null model. (2) If predator abundances vary between two habitats due to different resource availability, penetration of predators from the habitat interior with more abundant predator fauna (e.g., farmland) into the second habitat (e.g., forest) may cause a gradual gradient of predation through the transect between adjacent habitats (the spillover model; the matrix effect, sensu Lidicker 1999; see also Andrén 1995; Wilcove 1985). In contrast, the ecotonal effect (sensu Lidicker 1999) occurs when the distribution of predators along habitat edges cannot be explained by simple overflow (see above). This situation is generally predicted in the following cases: (3) resources may be concentrated specifically in an edge structure; or (4) alternatively, if a core habitat contains complementary resources (qualitatively different), predators will profit from the exploitation of the habitat edge due to the spatial proximity of both types of resources (Ries et al. 2004). These complementary resources may include, for example, foraging opportunities in one habitat vs. effective dispersal (i.e., the travel line hypothesis Bider 1968) or vegetation cover for special thermoregulation requirements (e.g., Jędrzejewska and Jędrzejewski 1998; Zub et al. 2008, 2009) in the second habitat. Finally, (5) predator specialists typical for one habitat may mix with predators typical for the second habitat. These three latter predictions (3–5) result in increased abundance of predators along edges.

Although many studies have detected increased predation pressure along the edges of various habitat types (e.g., Bayne and Hobson 1997; Dijak and Thompson 2000; Donovan et al. 1997; Malt and Lank 2007), only a few were able to explicitly test the competing mechanistic explanations of the edge effect as outlined above. This

might be due to drawbacks associated with experimental designs. First, predation risk and/or the presence of predators often were not found throughout the entire edge gradient (i.e., in the habitat edge and both adjacent habitats; Albrecht 2004; Chalfoun et al. 2002; Heske 1995), which means that it was not possible to determine if the edge effect arose as a consequence of predator penetration into the adjacent habitat or due to specifically enhanced activity of edge specialist predator species along the habitat edge. Second, since most studies did not collect data on prey distribution (e.g., Dijak and Thompson 2000; Donovan et al. 1997; Hilty and Merenlender 2004), habitat qualities could not be sufficiently evaluated. Third, most studies failed to reliably determine particular predator species (e.g., Huhta et al. 1998; Pasitschniak-Arts and Messier 1995; Storch et al. 2005). Therefore, they could not determine if the edge effect arose due to the specific preferences of some species for edge structures (see alternatives (3) and (4) above) or solely due to exploitation of the habitat edge by interior specialists from both habitat interiors (see alternative (5) above).

The aim of this study is to test mechanisms resulting in the emergence of the edge effect in Central Europe in a landscape fragmented by agriculture. To do this, we simultaneously studied the distribution of mammalian predators and the distribution of their main prey, rodents (Goszczyński 1986; Lanszki and Heltai 2007; Lanszki et al. 2007; Martinoli et al. 2001), in four types of landscape elements corresponding to an edge gradient between two habitat types, secondary mixed forest and hay-producing meadows. Our experimental design enabled us to confront empirical data with predictions underlining the alternative hypothetical mechanisms leading to the edge effect discussed above.

## Study area and methods

### Study area

The study area was situated in southern Bohemia (the Czech Republic) in the Písecké hory Mts. region (49°11'–49°18' 14° 09'–14°22', 350 a.s.l., 60.3 km<sup>2</sup>). The area was formed by a complex of coniferous, deciduous, and mixed production forests surrounded by farmland consisting mostly of hay-fields, extensively used pastures, and cultivated fields that were partitioned by line habitats such as shrub and tree growth along draining channels and roads (see more on habitat description in “Mesopredator distribution”).

### Mesopredator distribution

The spatial distribution of mammalian predators was studied using scent stations because this is the most

efficient technique for carnivore sampling both in economic and logistic aspect (Barea-Azcón et al. 2006). The scent stations were placed during May 2006 and May 2007 and were constructed as a 1×1-m square filled with a 2-cm thick layer of fine-grained masonry sand. To analyze predator distribution on a relatively small spatial scale, and hence to avoid alluring animals from greater distances, domestic rabbit urine was used as a mild attractant (Linhart and Knowlton 1975). Rabbit urine in a 1.5-ml micro-centrifuge tube was fixed to a wooden stick and placed in the center of each scent station, approximately 15 cm above the ground. Scent stations were monitored every morning for five consecutive days.

In total, 80 scent stations were installed both years at the same localities ( $n=20$ ), with four landscape elements represented: (1) grassland interior, (2) forest interior, (3) grassland edge, and (4) forest edge. Whereas interior scent stations were set up 100 m away from the nearest forest/grassland edge, edge scent stations were installed 5 m from the forest/meadow border (i.e., parallel distance between scent stations was 10 m). Although this distance between the forest and grassland edge scent stations may seem low, in the intensively managed landscape of Central Europe, forest and grassland edges are completely different type of elements with extremely sharp transition gradients (~2 m). They differ markedly in the composition and cover of herbal, shrub, and canopy vegetation (for a detailed description, see below). In order to achieve independence of replicate sites, the minimum distance between adjacent scent stations within a locality was 100 m, and the minimum distance between neighboring localities was 300 m (e.g., Gehring and Swihart 2003). Moreover, to ensure predefined habitat and distance criteria for scent station positions, sites were prior selected using digitized aerial orthophoto maps of the study area using GIS software (ArcView GIS 3.2a).

All studied landscape elements were highly modified by agriculture and other human activities: (1) Grasslands mostly consisted of production hayfields and extensively used pastures. Hayfields were almost entirely drained and reseeded with competitive nitrogen-demanding species such as *Lolium multiflorum*, *Phleum pratense*, *Festuca pratensis*, and *Dactylis glomerata*. (2) Forests were composed of intensively managed stands; the tree canopy was typically dominated by conifers (*Picea abies* and *Pinus sylvestris*), with occasional broad-leaved tree species such as oak (*Quercus* spp.), birch (*Betula pendula*), and beech (*Fagus sylvatica*). Shrub and herbal undergrowth was very sparsely developed. (3) Forest edges were usually fringed with oak, linden (*Tilia* spp.), and managed-stand trees such as spruce, pine, as well as poplar (*Populus* spp.) and birch. The shrub layer was usually dense, consisting mainly of shrubs (*Corylus avellana*, *Prunus spinosa*) and saplings of canopy

trees. This habitat type was also characterized by dense and diversified herbaceous vegetation mainly originating from the nearby grassland. (4) Grassland edge vegetation was sparsely developed in comparison to grassland interior hayfields, but the species composition was mostly identical.

Mammalian predators were identified according to the size and shape of their footprints (Anděra and Horáček 2005). Since closely related species were difficult to distinguish from each other, the following predators were classified: red fox (*Vulpes vulpes*), marten (*Martes martes* and *Martes foina*), small mustelid (*Mustela nivalis*, *Mustela erminea*), western polecat (*Mustela putorius*), European badger (*Meles meles*), domestic cat, domestic dog, and unidentified carnivore.

### Prey distribution

To estimate prey distribution, we examined the abundance of rodents during the same years (2006 and 2007) as the mesopredator survey described above, using a random subsample of the same localities (eight in total) and including all four landscape elements. Rodents were captured using regular snap traps which were baited with wicks dipped in grease and flour. At each of the eight localities, traps were placed in four lines of 35 traps each, with 5 m between traps (so the total length of each line was about 175 m). Thus, a total of 1,120 traps were set each year (eight localities, four lines per locality, with 35 traps per line). Since trap efficiency can be affected by captures from the previous day, all traps were set for just 24 h. Trap lines were positioned using similar habitat and distance criteria as for the scent stations (see above).

### Data analysis

The effect of landscape element on the distribution of mammalian predators was evaluated using a generalized linear model with mixed effects (GLMM), with a predator visit to a scent station as the dependent variable. Since a scent station could have been repeatedly visited by the same predator during the 5-day period of exposure, the predator activity at each particular scent station was fitted as a binary response (present/absent variable) for the whole exposure time, i.e., without estimating the number of individuals. Besides landscape element, effect of year and locality were included in the model. The landscape element, year, and interaction between these variables were considered as fixed effects. The locality was included as a random effect to avoid spatio-temporal pseudoreplications.

The distribution of rodents was also analyzed using a GLMM. Numbers of captured/noncaptured individuals in the lines of 35 traps were analyzed assuming a binomial distribution of errors. Similarly, as with the model above,

landscape element, year, and interaction between these variables were fitted as fixed effects and locality as a random effect.

In all analyses, the significance of a particular explanatory variable was calculated by the change of deviance between the model containing that variable and the reduced model (deletion tests; Crawley 2002). The best minimal adequate model (the model with the lowest parsimony and all variables being significant) was achieved by backward elimination of non-significant effects. All analyses were performed in R software (R Development Core team 2008).

The mechanisms leading to the emergence of the edge effect were assessed by pooling specific levels of landscape element (a posteriori analyses; Crawley 2002). To evaluate the suggested predator preferences for ecotones, interior elements and edge elements (i.e., grassland edge+forest edges and grassland interior+forest interiors, respectively) were pooled. Then, by pooling grassland interior with grassland edge and forest interior with forest edge, we tested whether predators penetrate from habitat interiors to the edges.

## Results

### Mesopredator distribution

We recorded 72 visitations by seven predator species during 800 station nights ( $9.0\% \pm 0.07$  SE visitation probability per night, Online Resource 1). The species with the highest visitation rates included house cat (*Felis silvestris catus*, 18×), small mustelids (11×), red fox (10×), and domestic dog (*Canis lupus familiaris*, 8×). However, since dogs usually follow the movement of their owners, they were excluded from subsequent analyses. Nevertheless, the exclusion of domestic dog did not affect the conclusions of further statistical analyses.

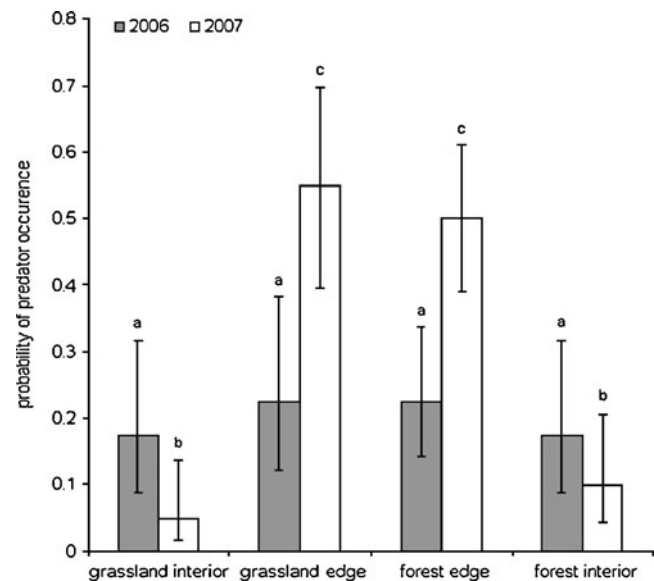
We found a significant interaction between year and landscape element (Table 1, Fig. 1), suggesting inconsistency in carnivore occurrence in elements over time.

**Table 1** GLMM results for probability of the occurrence of a mammalian predator at scent stations in southern Bohemia, 2006 and 2007

Factors	$\Delta df$	AIC	$\chi^2$	<i>P</i>
Habitat	3	182.394	13.795	0.003
Year	1	191.043	1.171	0.279
Habitat × year	3	180.605	8.619	0.035

Domestic dog was excluded from the analysis

AIC Akaike's information criterion



**Fig. 1** Mean probability ( $\pm$ SE of difference) of predator occurrence in particular habitat types of southern Bohemia in 2006 and 2007, based on predictions of the GLMM. Domestic dog was excluded from the analysis. In 2007, habitat types where the scent stations were visited with the same intensity in a given year are marked by the same symbols (see “Results”)

Although predator visits to scent stations were slightly higher in 2007 (30.0%) than in 2006 (22.5%), the year main effect was not significant after eliminating the year vs. landscape element interaction from the model (Table 1). On the other hand, deletion of the landscape element main effect from the model resulted in a significant increase of the residual deviance (Table 1). Due to the significance of this year vs. landscape element interaction in the initial model, we further analyzed differences in the probability of visits to particular localities for each year separately. Whereas in 2006, no difference was found between particular landscape elements ( $\chi^2=0.31$ ,  $\Delta df=3$ ,  $P=0.957$ ), in 2007 the effect of landscape element was significant ( $\chi^2=21.56$ ,  $\Delta df=3$ ,  $P<0.001$ ). In addition, pooling interior elements (i.e., forest and grassland interiors) and edge elements (i.e., forest edge and grassland edge) did not lead to a significant change of the residual deviance ( $\chi^2=0.37$ ,  $\Delta df=1$ ,  $P=0.544$ ). The posterior comparisons revealed that predators used forest and grassland interiors ( $\chi^2=0.37$ ,  $\Delta df=1$ ,  $P=0.544$ ) and forest and grassland edges ( $\chi^2=0.10$ ,  $\Delta df=1$ ,  $P=0.749$ ), respectively, with comparable intensity. However, the significant contrast between forest edge and forest interior ( $\chi^2=8.16$ ,  $\Delta df=1$ ,  $P=0.004$ ), and grassland edge and grassland interior ( $\chi^2=13.42$ ,  $\Delta df=1$ ,  $P<0.001$ ), indicated that carnivores visited edges more frequently than habitat interiors in 2007 (Fig. 1).

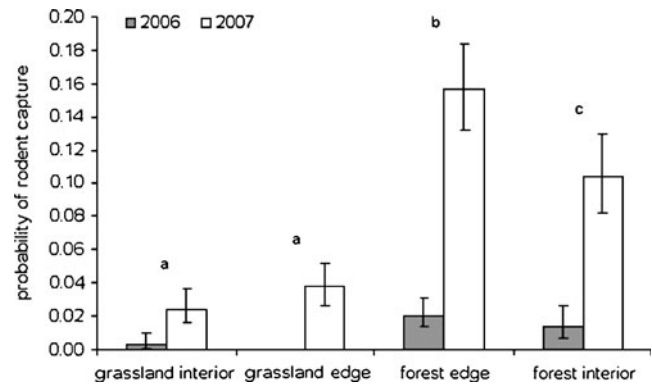
Prey distribution

In total, 104 rodents were captured during 2006 and 2007 (Online Resource 2). However, in 2006, rodent numbers were almost nine times lower ( $1.4 \pm 0.19$  SE numbers per line) than in the following year ( $11.8 \pm 0.35$  SE numbers per line).

The GLMM model revealed that numbers of rodents changed significantly between years and landscape elements, but the interaction between these variables was insignificant (Table 2). The highest numbers of rodents were recorded at forest edges and the lowest in grassland interiors (Fig. 2). Posterior comparisons indicated similar rodent abundance between the interiors and edges of particular elements. However, while grassland edge with grassland interior were pooled without significant change to the residual deviance ( $\chi^2=0.49$ ,  $\Delta df=1$ ,  $P=0.484$ ), the contrast between forest edge and forest interior was significant ( $\chi^2=3.93$ ,  $\Delta df=1$ ,  $P=0.048$ ). On the other hand, pooling both edges ( $\chi^2=30.69$ ,  $\Delta df=1$ ,  $P<0.001$ ) and both interiors ( $\chi^2=18.44$ ,  $\Delta df=1$ ,  $P<0.001$ ), respectively, led to significant changes to the residual deviance.

Discussion

Interestingly, our data show a large temporal variation in the carnivore distribution along the interior/edge continuum. In the first year of our study, carnivores did not increase their activity in any particular landscape elements, suggesting that under some circumstances, carnivores do not respond to forest/grassland edges in agricultural landscapes. This result is partly in support of the null hypothesis (i.e., no response of predators to transitions between two habitats). However, a contrasting pattern of predator distribution was found in the subsequent year when our data indicated, as have many previous studies (e.g., Dijak and Thompson 2000; Donovan et al. 1997), the increased activity of predators specifically along habitat edges. Moreover, in 2007, predator activity within grassland and forest interiors was significantly lower than in edge structures and did not differ between these habitat types. Hence, the possibility that the occurrence of



**Fig. 2** Mean probability ( $\pm$ SE of difference) of rodent capture per one trap and one night in particular habitat types, southern Bohemia, 2006 and 2007, based on predictions of the GLMM. Habitat types with statistically different abundances of rodents are marked by different symbols

mammalian predators in edge elements was the result of overflow from one habitat through the habitat edge into the second habitat (i.e., the spillover model; the matrix edge effect, sensu Lidicker 1999) was not supported during the second year. Although the spillover model has been supported by empirical data in several cases (Andrén and Angelstam 1988; Heske 1995), many studies have not been able to test this hypothesis because predation patterns have rarely been measured across the whole ecotone continuum (but see Gates and Gysel 1978; Ratti and Reese 1988).

The higher activity of carnivores along grassland/forest edges in 2007 clearly supports the ecotonal edge effect model, which implies the emergent property of predator distribution across the edge continuum (Lidicker 1999). In this study, two alternative explanations for the ecotonal edge effect model were evaluated. Firstly, increased predator abundance along an edge may appear due to the mixture of predator faunas that differ between adjacent habitats (Ries et al. 2004). Alternatively, some species of predators may focus their activity specifically around edge structures (i.e., edge habitat specialist; Larivière and Messier 2000). Our data lends support to the second possibility, consistently with other studies performed in Central-European landscapes (Červinka 2010; Šálek 2009) because all species detected in our study tended to more likely occur at the edge of habitats compared to the interiors. In addition, we found no species that tended to prefer the grassland interior over the other landscape structures.

Increased predator activity along habitat edges may arise as a consequence of the habitat-specific distribution of resources, as recently suggested for example by Ries and Sisk (2004). Rodents, that may form up to 80% of the diet of mammalian mesopredators (Goszczyński 1986; Lanszki and Heltai 2007; Lanszki et al. 2007; Martinoli et al. 2001)

**Table 2** GLMM results for rodent abundance in southern Bohemia, 2006 and 2007

Factors	$\Delta df$	AIC	$\chi^2$	$P$
Habitat	3	208.604	53.322	<0.001
Year	1	168.161	78.971	<0.001
Habitat $\times$ year	3	124.406	2.432	0.488

AIC Akaike’s information criterion

were previously found to affect the habitat preferences of mesopredators in fine spatial scales (Šálek et al. 2010). Particularly, opportunistic predators such as fox and mustelids may increase their activity in localities with high prey abundance (numerical response; Korpimäki et al. 1991, 2005). However, our study does not provide straightforward evidence for an association between the habitat-specific quantity of food resources and predator distribution. Although the abundance of rodents was approximately 3–4 times higher in forest compared to grassland habitats in both study years (irrespective if measured in edges or interiors), we did not observe the predicted spatial shift in the distribution of mammalian carnivores (i.e., both forest and meadow habitats were visited with similar intensity). It is possible that forest rodent species (particularly *Apodemus* sp.) are more difficult for carnivores to capture than grassland species (particularly *Microtus* sp.) because they are better climbers and may use various escape tactics due to the more complex structure of forest habitats (Jędrzejewski and Jędrzejewska 1993; Jędrzejewska and Jędrzejewski 1998). However, we did not find any evidence of higher carnivore occurrence in grassland elements. Our study did not quantify the habitat-specific distribution of alternative food resources that may supplement part of the carnivore diet, such as passerine birds, bird clutches, amphibians, insect, or fruit. Although these resources are usually a less important part of the diet of mammalian carnivores (Goszczyński 1986; Genovesi et al. 1996; Lanszki et al. 2007; Martinoli et al. 2001), most are also likely to be more abundant at forest edges compared to heavily exploited grasslands and forests (Buse and Good 1993; Flashpohler et al. 2001; Lázaro et al. 2005; Šálek et al. 2009). Nevertheless, habitat quality for predators also includes other (complementary) sources than food. Carnivore species with small and slim bodies such as small mustelids have special thermoregulation requirements which significantly alter their habitat choice (Jędrzejewski and Jędrzejewska 1993; Jędrzejewska and Jędrzejewski 1998; Zub et al. 2008, 2009). In addition, these species are subjected to predation by larger predators (Crooks and Soulé 1999; Korpimäki and Norrdahl 1989; St-Pierre et al. 2006). For this reason, they might prefer edges where they can forage near open habitat but have access to forest cover.

On the other hand, since prey abundance at forest edges was higher (1–2 times) compared to forest interiors, the higher abundance of carnivores at forest edges might be at least partly explained by the spatial pattern of food resource distribution. Interestingly, carnivores did not exhibit a significant preference for the forest–grassland edge in the year with low rodent abundance, whereas they were more likely to be detected at habitat edges in the year with high prey abundance (with an eight- to ninefold increase in

rodent abundance). This suggests that carnivores switch their searching efforts from habitat edges, which are most profitable in years with high rodent densities, to a more diverse spectrum of habitats that may provide supplementary resources. As carnivores seek prey in a wider band (Larivière 2003), increased activity might also be observed at grassland edges. Alternatively, carnivores may seek prey only within forest edges and use grassland edges just for moving between preferred landscape segments (i.e., the travel line hypothesis, Bider 1968). However, our experimental design did not allow us to distinguish between these two alternatives because scent stations were placed only 5 m away from both forest and grassland edges. Thus, scent stations could have attracted predators from both edge habitats.

In conclusion, our results suggest that the emergence of the edge effect is not caused by carnivore penetration from habitats with higher predator density into habitats with lower predator density, but rather, it is caused by predator concentration along the edge itself. Although we are not able to provide a proximate explanation for the higher activity of mammalian mesopredators at edges compared to interiors, possibilities include higher prey availability and/or effective displacement along habitat edges. Moreover, our study shows that carnivores preferred edges only in years with high prey abundance. In years of low prey abundance, they used all landscape elements with the same frequency. This suggests a large temporal variation in the spatial distribution of carnivores depending on food availability along time, and that the edge effect hypothesis (sensu Lidicker 1999) cannot be viewed as a general pattern from year to year. Even though the number of predator visits to scent stations was low and the spatial scale tested was relatively limited (60.3 km<sup>2</sup>), we believe that this study is an important step towards understanding the mechanism of the edge effect in European landscapes. Nevertheless, as carnivore distribution and the composition of predator fauna is affected by several other factors acting at the landscape scale (Pita et al. 2009; Virgós et al. 2002), we hypothesize that the magnitude and overall pattern of edge preferences may vary according to landscape features (e.g., landscape composition and connectivity). Nevertheless, further research is needed to resolve this issue.

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