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Where is the optimum nesting site in anthropogenic landscapes? Adaptation of Barn Swallows along an urban–rural environmental gradient

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Abstract

Urban and rural environments are often treated as contrasting habitat types, but they can also be interpreted as the two ends of a continuous land-use gradient shaped by human activities. Along such gradients, organisms may experience trade-offs among different ecological resources. Here we introduce the Goldilocks hypothesis, which predicts that breeding activity is maximized under intermediate environmental conditions between urban and rural environments. To test this hypothesis, we investigated the distribution of Barn Swallow (Hirundo rustica) nests along urban–rural gradients in three regions of Kyushu, Japan (Nagasaki, Fukuoka, and Kagoshima). Environmental gradients were quantified using principal component analysis (PCA) based on land-cover composition within 500 m grid cells. Nest abundance showed a consistent unimodal pattern across all regions, peaking at intermediate environmental conditions. Potential nesting sites increased toward the urban end of the gradient, whereas potential foraging habitats increased toward the rural end, indicating a spatial trade-off between key breeding resources. These findings support the Goldilocks hypothesis and highlight the ecological importance of intermediate landscapes where elements of contrasting human-modified environments overlap, providing insights for landscape management and biodiversity conservation under ongoing urbanization.

1 Introduction

Over the past century, rapid human expansion and land-use change have dramatically transformed landscapes across the globe, reshaping ecosystems and biodiversity patterns. As a result, many organisms now inhabit environments strongly influenced by human activities.

Urban and rural environments are both secondary natural systems formed through human activities (Ellis and Ramankutty 2008). Urban areas are highly developed environments in which biological resources are limited, and species diversity is often reduced compared with less developed environments (McKinney 2002; Aronson et al. 2014). At the same time, urban environments may experience lower hunting pressure and predation risk for some species (Møller 2012; Gallo et al. 2019; Vincze et al. 2017), and thus may provide suitable habitats for certain urban-adapted species capable of persisting under altered resource conditions (McKinney 2006; Shochat et al. 2006).

In contrast, rural areas have been transformed from primary natural ecosystems through agriculture and forestry, resulting in secondary natural landscapes characterized by farmland, satoyama-like mosaics, and adjacent forests and aquatic systems. These environments often maintain relatively high levels of biodiversity. Although both urban and rural environments are secondary natural systems shaped by human activities, their biotic and abiotic conditions are considered to represent opposite ends of habitat suitability for wildlife (McDonnell and Pickett 1990).

However, when viewed in terms of the intensity of human development, urban and rural environments should not be regarded as dichotomous categories, but rather as the two extremes of a continuous environmental gradient. This gradient-based perspective has been widely recognized as a fundamental

framework in urban landscape ecology (McDonnell and Hahs 2008). For example, green space area, water surface area, residential density, population size, traffic volume, and agricultural land area tend to change gradually along urban–rural gradients (Hou et al. 2015; Grünwald 2024). Such continuous spatial transitions are characteristic features of urban–rural gradients and provide an important basis for gradient-based ecological analyses (Antrop 2004; McDonnell and Hahs 2008). Along such urban–rural environmental gradients, both the quantity and quality of resources available to organisms are expected to vary, leading to corresponding changes in species diversity and population abundance. Such gradients provide a useful framework for understanding how organisms respond to spatial variation in human-modified landscapes.

Despite this, ecological studies explicitly focusing on continuous urban–rural gradients remain limited (Blair and Johnson 2008; Gao et al. 2024; Della Rocca et al. 2026). Most existing studies instead distinguish urban and rural environments as discrete categories and compare population size or species diversity between them (Ortega-Álvarez et al. 2011; Sultana et al. 2023; García-Arroyo et al. 2025; Givelas et al. 2025).

Typical rural environments with high naturalness are generally considered more favorable for the survival and reproduction of many organisms than highly developed urban environments because of their richer food resources. However, within a continuously changing urban–rural gradient, it is not necessarily true that environments closer to rural conditions always provide better habitats. For example, predator abundance may increase with increasing naturalness. Indeed, previous studies have reported higher predator richness and activity in less urbanized environments compared to urban centers (Bateman and Fleming 2012; Fischer et al. 2012).

Therefore, we introduce the Goldilocks Hypothesis, which predicts a unimodal response of breeding performance along a continuous urban–rural gradient, where intermediate environments may provide the most suitable conditions for the survival and reproduction of certain organisms. This hypothesis is conceptually related to several ecological theories that highlight the ecological importance of intermediate conditions or environmental heterogeneity, including the intermediate disturbance hypothesis (Connell 1978; Huston 1979), habitat heterogeneity hypothesis (Tews et al. 2004), and productivity–diversity relationships (Mittelbach et al. 2001).

To test this hypothesis, we selected the Barn Swallow, a species that breeds in Japan, as our focal study organism. This species is well adapted to human-dominated landscapes and utilizes a wide range of environments from urban to rural areas, making it an ideal model species. Previous studies have shown that Barn Swallows exhibit high behavioral flexibility and strong associations with human settlements (Møller 2009), and that their habitat choice and breeding performance are influenced by environmental conditions at multiple spatial scales (Ambrosini and Saino 2010). These characteristics make Barn Swallows a suitable model species for urban–rural ecological studies. In typical urban environments, both food resources (small flying insects) and suitable soil conditions for nest construction are likely to be limited. In contrast, typical rural environments may provide abundant food resources but fewer

artificial structures for nesting, as well as higher predation pressure from natural enemies such as snakes that prey on eggs and chicks. Thus, we assume that the most suitable breeding conditions for this species occur somewhere along the urban–rural environmental gradient between these two extremes.

In this study, we first examined whether the fundamental assumptions required for the Goldilocks Hypothesis are satisfied with respect to Barn Swallow breeding ecology, and then tested three predictions derived from this hypothesis. By explicitly formulating assumptions and predictions, we provide a transparent and testable framework for evaluating the Goldilocks Hypothesis along urban–rural gradients.

Assumptions

- Landscape differences: Urban and rural environments are secondary natural systems formed by human activities and possess distinct ecological functions; however, when examined at a continuous spatial scale, their differences can be interpreted as a gradient.
- Advantages of rural environments: The area of open habitats such as farmland and riverbanks, which support high abundances of aerial insects serving as food resources for Barn Swallows, increases from urban to rural areas.
- Advantages of urban environments: In Japan, Barn Swallows primarily nest on artificial structures such as building eaves. Therefore, the availability of suitable nesting sites decreases from urban to rural areas.

Prediction

• H1: Open habitats such as farmland and riverbanks will increase from urban to rural areas, indicating greater foraging opportunities in rural environments.

• H2: The availability of artificial structures suitable for nesting will decrease from urban to rural areas, indicating greater nesting opportunities in urban environments.

• H3: The number of Barn Swallow nests will be maximized in intermediate environments between urban and rural areas, where the trade-off balance between nesting site availability and foraging opportunities is optimized.

2 Methods

2.1 Study area

This study was conducted in three regions of Kyushu, Japan: Nagasaki Prefecture, Fukuoka Prefecture, and Kagoshima Prefecture (Fig. 1). In each prefecture, the survey area was established along major

roads that connected one of the most highly urbanized areas within the prefecture to a typical rural environment where cultivated land constitutes the dominant landscape element.

In Nagasaki Prefecture, the urban endpoint was Nagasaki City (32.737°N, 129.870°E) and the rural endpoint was Isahaya City (32.794°N, 130.076°E) , with a survey route of approximately 35 km.
In Fukuoka Prefecture, the urban endpoint was Fukuoka City (33.591°N, 130.419°E) and the rural endpoint was Itoshima City (33.606°N, 130.159°E), with a survey distance of approximately 30 km.
In Kagoshima Prefecture, the urban endpoint was Kagoshima City (31.560° N, 130.557° E) and the rural endpoint was Aira City (31.796° N, 130.620° E) , with a survey route of approximately 35 km (Fig. 1).

Thus, in each prefecture, typical urban and rural environments were connected within a spatial range of approximately 30-40 km. The total walking distance across all survey routes, including round trips, amounted to approximately 197 km.

2.2 Quantification of the urban–rural environmental gradient

Along each survey route (approximately 35 km in Nagasaki, 30 km in Fukuoka, and 32 km in Kagoshima), square grid cells with a side length of 500 m were established and used as analytical units (Fig. 1).

Seven environmental components were quantified within each grid cell: residential areas, agricultural land, vegetation cover, open water, abandoned farmland, land under construction, and other land-cover types. The proportional area of each component was calculated based on vegetation maps provided by the Biodiversity Center of Japan, Ministry of the Environment (http://gis.biodic.go.jp/webgis/sc-023.html), using QGIS (version 3.16.11). The underlying vegetation survey data were collected between 2022 and 2024 and published by the Ministry of the Environment (2025). To reduce dimensionality, principal component analysis (PCA) was conducted separately for each prefecture because the magnitude and composition of the urban–rural gradient were expected to differ among regions due to differences in landscape structure and land-use composition. The first principal component axis (PC1) primarily captured variation in secondary natural environments and reflected the transition from urban-dominated to rural-dominated landscapes. Therefore, PC1 was adopted as the environmental gradient index (Fig. 2).

2.3 Survey of nest abundance and potential nesting sites

Nest surveys were conducted between 2021 and 2023. The presence of Barn Swallow nests was recorded through direct visual observation while walking along each survey route (Fig. 1). Each route was surveyed once in both directions to minimize oversight, and observers attempted to access all passable roads within the survey area.

The observation range extended 50 m from the roadside toward adjacent building areas without intervening roads. Detected nests included actively used nests, collapsed nests, and clear nesting traces where nest material was absent but characteristic stains or marks remained on walls. All such records were treated as evidence that nesting had occurred and were included in the analyses.

Potential nesting sites were defined as roofed, semi-open structures exceeding approximately 2.0 m in height and 1.5 m in width, including piloti spaces, garages, house eaves, and cattle sheds. The number of such potential nesting sites was counted within each grid cell.

2.4 Statistical analyses

To examine how Barn Swallow nest abundance varied along the urban–rural environmental gradient, generalized linear models (GLMs) were constructed using the number of nests per grid cell as the response variable and the environmental gradient index (PC1) as the explanatory variable. Because the count data exhibited overdispersion, a quasi-Poisson error distribution with a log link function was applied. To test for a unimodal (hump-shaped) response along the gradient, a quadratic term of the environmental gradient index was included in the model.

To evaluate changes in the availability of potential nesting sites along the environmental gradient, generalized linear models with a Poisson error distribution and log link function were constructed, using the number of potential nesting sites per grid cell as the response variable and the environmental gradient index as the explanatory variable.

To quantify available foraging habitat, circular buffers with a radius of 500 m were generated around each confirmed nest location (Ambrosini et al. 2002; Bryant and Turner 1982). The combined area of agricultural land, vegetation cover, and abandoned farmland within each buffer was calculated and defined as foraging habitat area. Linear regression models were then constructed using foraging habitat area as the response variable and the environmental gradient index as the explanatory variable. All statistical analyses were conducted in R.

3 Results

3.1 Environmental gradient index

The first principal component (PC1) derived from the PCA represented an urban–rural environmental gradient in all three regions. Residential areas loaded negatively on PC1 (urban direction), whereas farmland, vegetation, and abandoned farmland loaded positively (rural direction) (Fig. 2).

The characteristics of PC1 were consistent across the three independent regions: Nagasaki (31.3% variance explained) , Fukuoka (28.3%) , and Kagoshima (36.2%) (Fig. 3).

3.2 Environmental gradient index and number of Barn Swallow nests

Along the urban–rural environmental gradient, the number of nests showed a unimodal pattern. Nest numbers were low in highly urban environments, increased toward intermediate environments, and decreased again toward rural environments (Fig. 3).

Thus, the highest number of nests was observed under intermediate environmental conditions. The quadratic term of the model was statistically significant in Nagasaki ($t = -2.39$, $p = 0.019$) and Fukuoka ($t = 2.32$, $p = 0.023$), but not in Kagoshima ($t = -0.96$, $p = 0.34$), although the overall pattern was similar across the three regions.

3.3 Environmental gradient index and potential nesting sites

The number of potential nesting sites increased toward the urban end of the gradient, where building density was high. This negative relationship between PC1 (rural direction positive) and potential nesting sites was consistent across regions: Nagasaki ($z = -13.69$, $p < 0.001$, pseudo-$R^2 = 0.36$), Fukuoka ($z = -12.50$, $p < 0.001$, pseudo-$R^2 = 0.38$), and Kagoshima ($z = -14.74$, $p < 0.001$, pseudo-$R^2 = 0.33$). The relationship was monotonic across all three regions.

3.4 Relationship between environmental gradient and foraging habitat area

The area of potential foraging habitat (farmland, vegetation, open water, and abandoned farmland) increased significantly toward the rural end of the environmental gradient. This positive relationship was consistent across Nagasaki ($R^2 = 0.84$, $p < 0.001$), Fukuoka ($R^2 = 0.64$, $p < 0.001$), and Kagoshima ($R^2 = 0.57$, $p < 0.001$) (Fig. 5).

In all regions, more rural environments were associated with larger areas of potential foraging habitat. Together, these results demonstrate opposing trends of nesting-site availability and foraging habitat area along the urban–rural gradient.

4 Discussion

The findings of this study are consistent with a gradient-based perspective in which urban and rural environments are positioned not as dichotomous categories, but as the two ends of a continuous environmental gradient. Our results provide empirical support for the Goldilocks Hypothesis. Across all three regions examined, we consistently observed that (1) the number of Barn Swallow nests peaked in

intermediate environments along the urban–rural gradient, (2) the availability of potential nesting sites increased toward the urban end of the gradient, and (3) the area of potential foraging habitat increased toward the rural end.

Together, these findings suggest that Barn Swallow nesting distribution is maximized in landscapes where structural elements of both environments overlap.

As the environmental gradient index became more urban-oriented, artificial structures such as roofs and building walls increased, resulting in greater availability of potential nesting sites. In urban areas, many nesting opportunities were associated with garages, piloti spaces, and other semi-open parking structures—features characteristic of densely built environments but rarely found in rural landscapes.

Conversely, in rural environments, rivers, agricultural land, abandoned farmland, and vegetation cover were more abundant, increasing the availability of potential foraging habitats. These opposing spatial trends indicate a structural trade-off along the gradient: nesting-site availability increases toward urban environments, whereas foraging habitat area increases toward rural environments. The unimodal response of nest abundance suggests that breeding performance is maximized under intermediate conditions where these contrasting resources overlap at sufficient levels. Although nest abundance does not directly measure reproductive success, it provides a useful proxy for breeding habitat suitability at the landscape scale. Importantly, this pattern was consistent across Nagasaki, Fukuoka, and Kagoshima, despite substantial differences in topography, urban structure, population density, and industrial composition among the regions. Although the magnitude and steepness of the environmental gradients may vary among prefectures, the functional relationship between nesting-site availability, foraging habitat area, and nest abundance showed a consistent structure.

The spatial variation in potential nesting sites documented here reflects biological responses to differences in landscape structure shaped by human activities in urban and rural environments. Similar responses to urban–rural gradients have been reported for avian species richness and population abundance (Blair and Johnson 2008). By focusing on a single synanthropic species, this study adds mechanistic insight into how gradient-dependent trade-offs influence breeding distribution. Further investigation of dietary composition and niche breadth along urbanization gradients would contribute to urban planning and biodiversity conservation (Blair and Johnson 2008).

Several environmental factors not explicitly quantified in this study may also influence breeding success. Although urban areas provide abundant artificial nesting substrates, ground surfaces are often paved, potentially limiting access to soil used as nesting material (Kim et al. 2023). In addition, newer building materials may reduce nest adhesion success (Chen et al. 2025), indicating that the quality—not only the quantity—of nesting sites may vary along the gradient.

In rural environments, food resources are likely more abundant; however, predation risk from snakes and corvids may be higher (Ambrosini et al. 2002). Such factors may partly explain regional variation in the shape or position of the response curves observed among the three study areas.

Under intermediate environmental conditions, negative effects typically associated with either highly urbanized or highly rural environments may be partially mitigated. Where nesting sites remain available while foraging habitats are sufficiently present, urban and agricultural landscape elements may overlap, creating structurally heterogeneous landscapes that can support bird communities and associated ecosystem functions (Smith et al. 2022). These environments may represent the ecological realization of the “Goldilocks” condition—where anthropogenic influence is neither too strong nor too weak. The present study therefore provides a concrete example of a gradient-dependent breeding strategy in which Barn Swallows utilize intermediate landscapes that balance opposing ecological constraints. These findings highlight the importance of considering intermediate landscapes in conservation and urban planning, where multiple ecological resources may coexist and support species adapted to human-modified environments.

Declarations

Competing interests

The authors declare no competing interests.

Ethics approval

No birds were captured, handled, or experimentally manipulated in this study.

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Author Contribution

T.C.A. conceived and designed the study, collected and analysed the data, and wrote the first draft of the manuscript. N.M.Y. supervised the study, contributed to the interpretation of the results, and critically revised the manuscript. Both authors read and approved the final manuscript.

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Data availability

The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

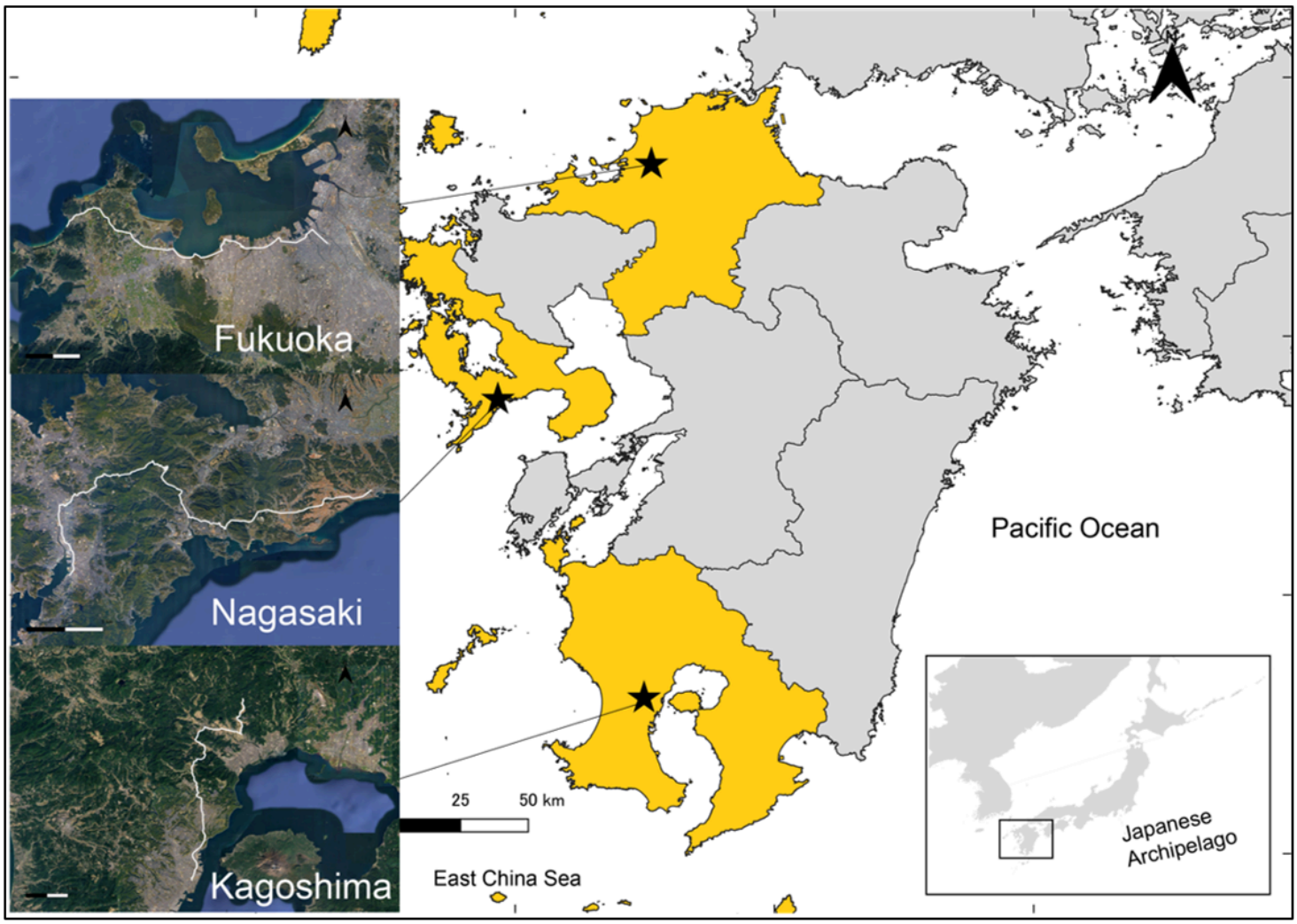


Figure 1

Location of the three study prefectures in Kyushu, Japan (Nagasaki, Fukuoka, and Kagoshima). The aerial images show the urban–rural survey routes (white lines) used in this study. Map data: Natural Earth (https://www.naturalearthdata.com/). Aerial imagery: Google.

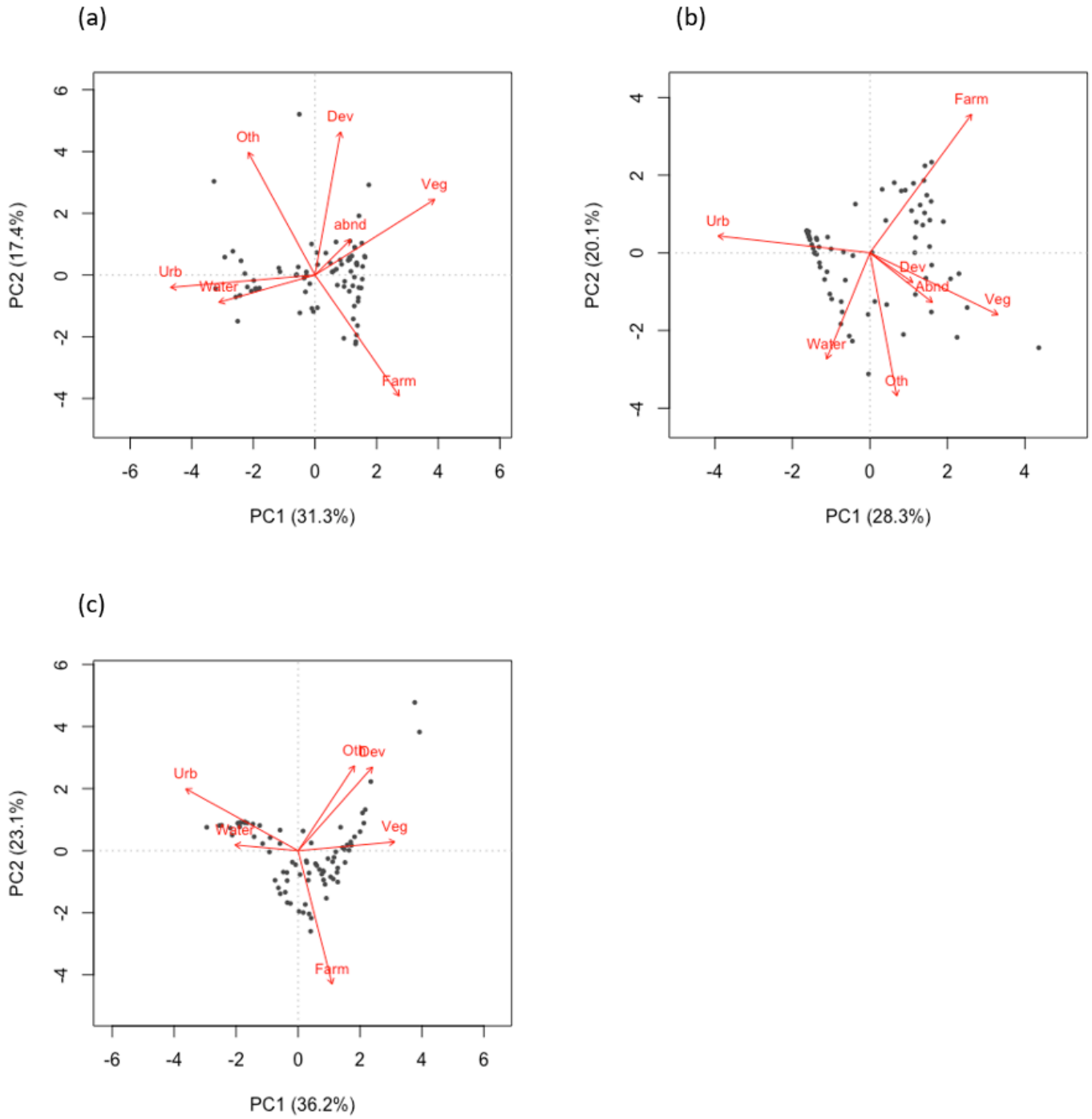


Figure 2

Principal component analysis (PCA) of seven environmental variables measured within 500 m grid cells. Panels show results for Nagasaki, (b) Fukuoka, and (c) Kagoshima. Arrows indicate the direction and strength of loadings for each environmental variable (Urb: Urban area; Dev: Developed land; Veg: Vegetation; Wat: Wetland; Farm: Farmland; Abnd: Abandoned land; Oth: Other). Percentages shown on the axes represent the proportion of variance explained by each principal component. PC1 primarily represents the degree of urban development along the urban–rural gradient, whereas PC2 captures variation in natural landscape components.

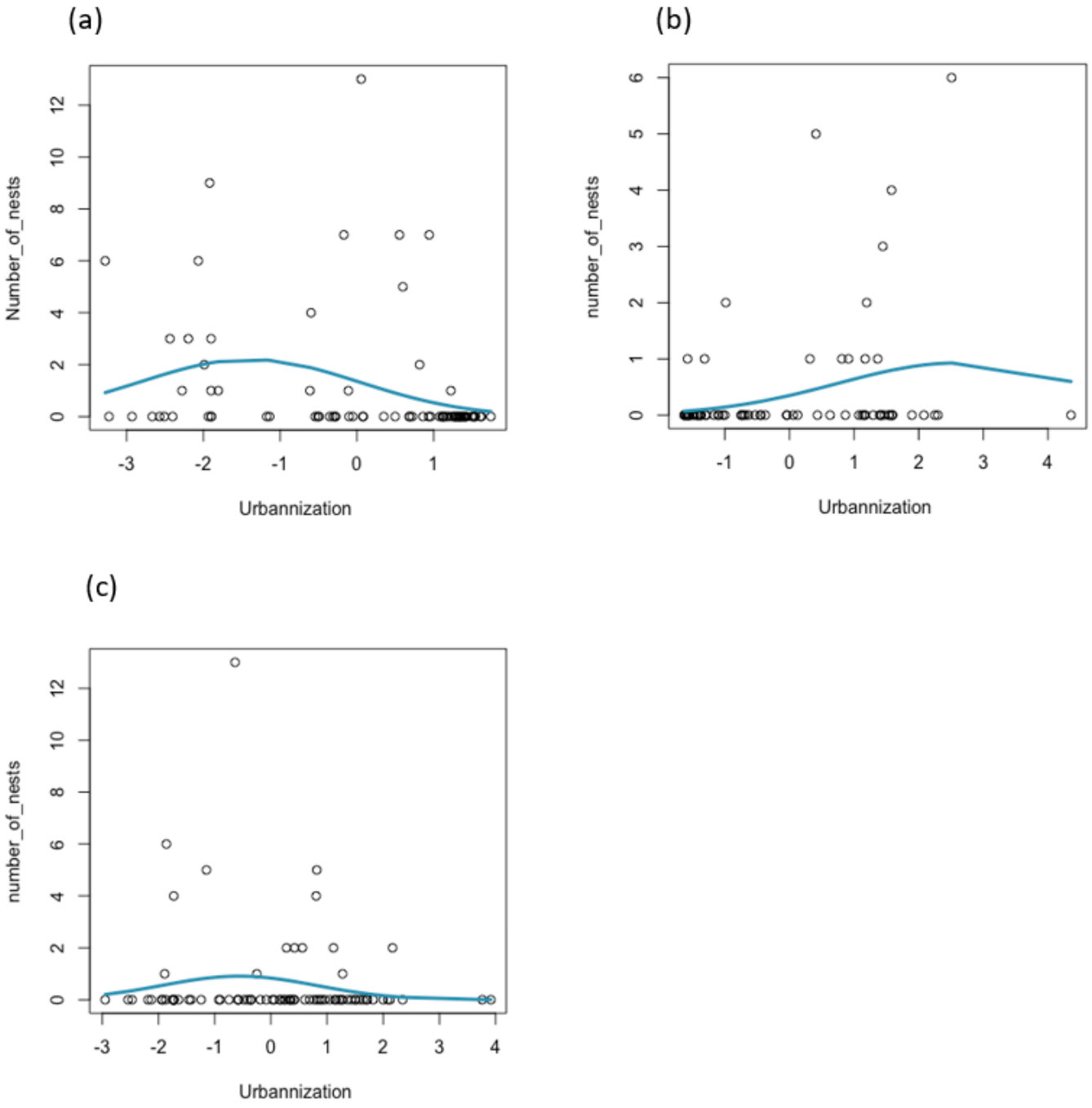


Figure 3

Response of Barn Swallow nest abundance to the urbanization index. Panels show results for (a) Nagasaki, (b) Fukuoka, and (c) Kagoshima. Each point represents the number of nests within a 500 m grid cell, and the solid line indicates the fitted curve in nest abundance along the gradient. In all regions, nest abundance was low at both the urban and rural extremes and peaked under intermediate environmental conditions, showing a unimodal response pattern.

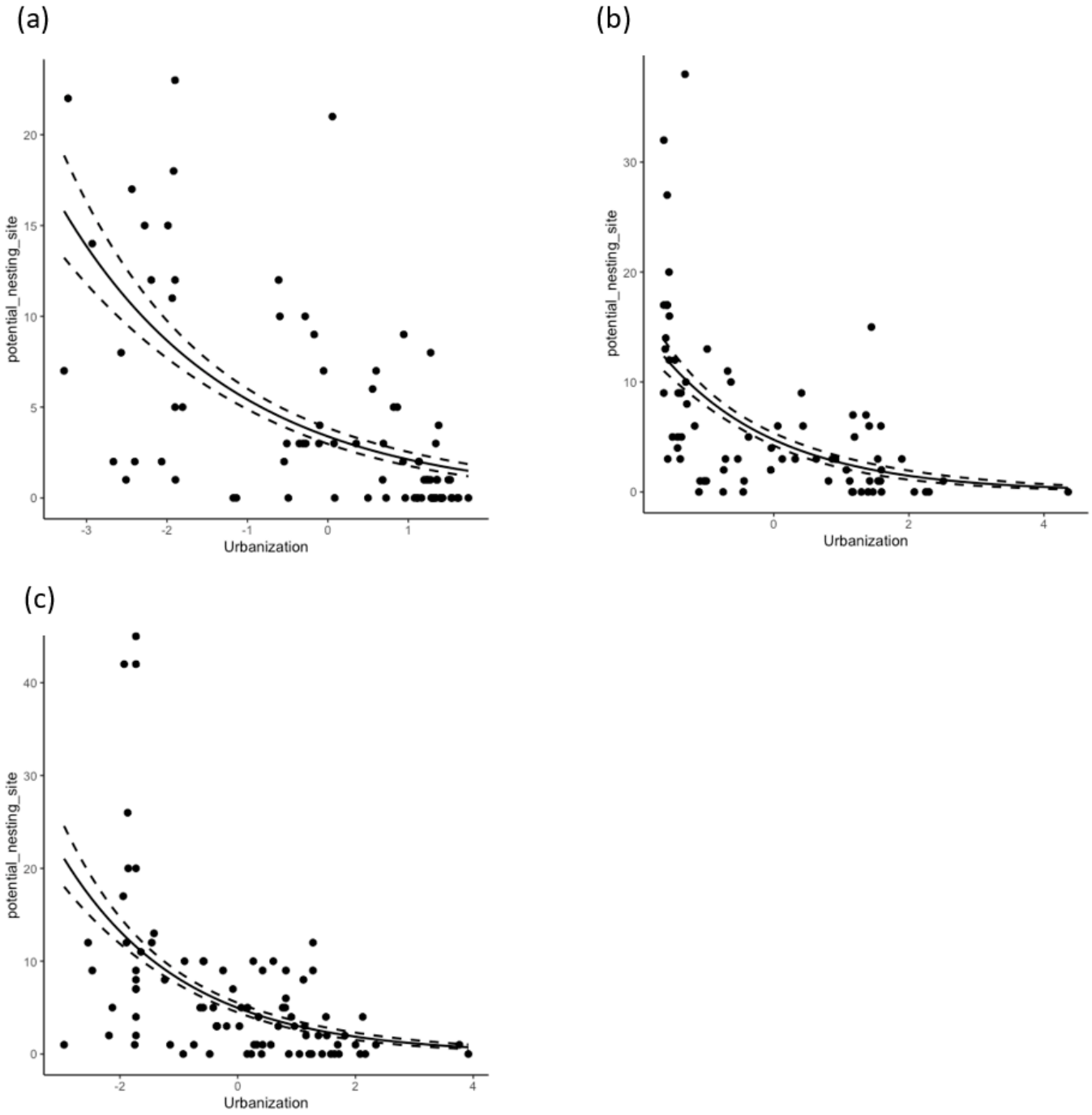


Figure 4

Response of potential nesting-site availability to the urbanization index. Panels show results for (a) Nagasaki, (b) Fukuoka, and (c) Kagoshima. Each point represents the number of potential nesting sites calculated within a 500 m grid cell, and the solid line indicates the fitted curve along the gradient. In all regions, potential nesting-site availability was highest in urban environments and decreased progressively toward rural areas.

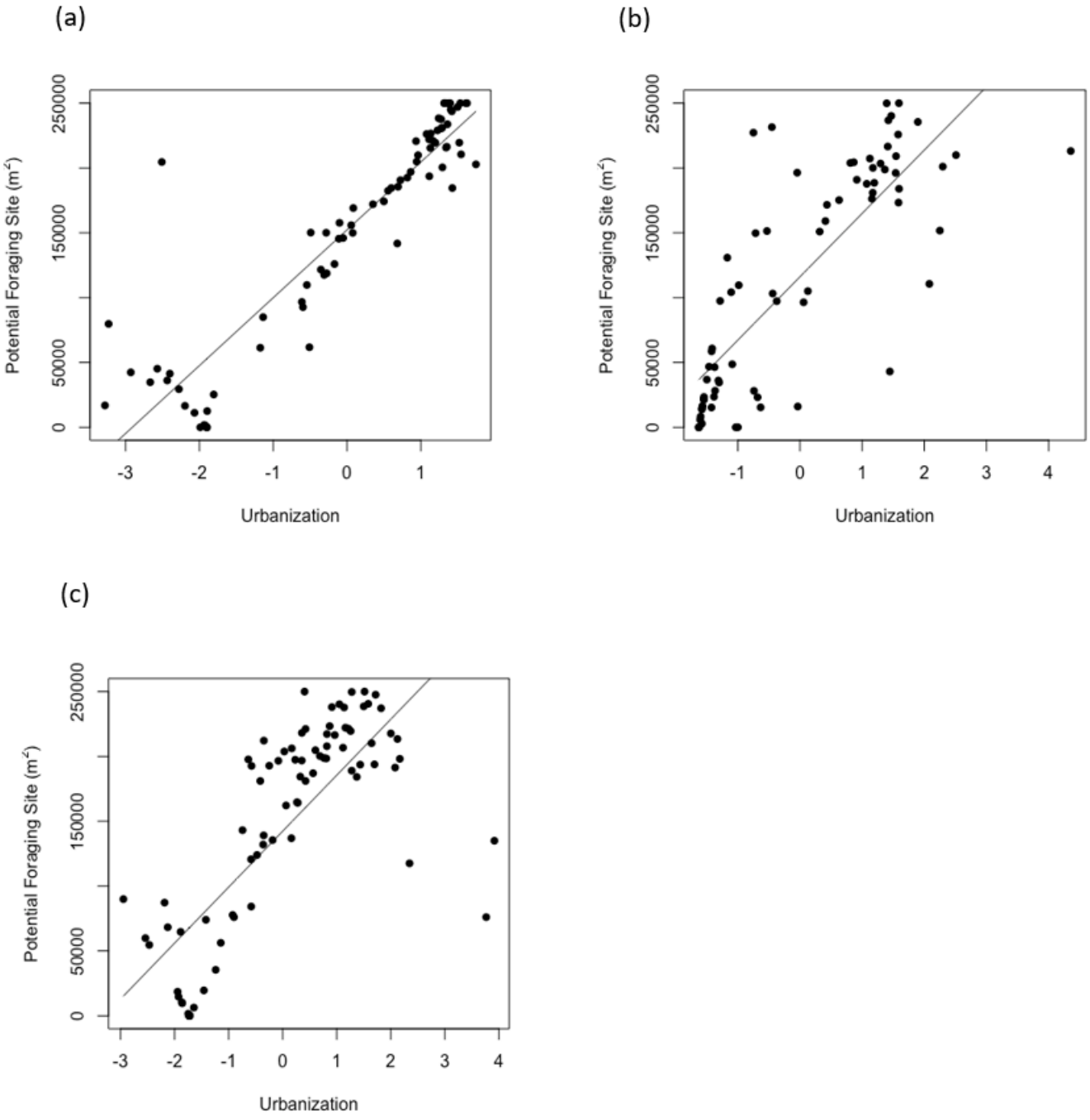


Figure 5

Response of potential foraging habitat area to the urbanization index. Panels show results for (a) Nagasaki, (b) Fukuoka, and (c) Kagoshima. Each point represents the foraging habitat area calculated within a 500 m grid cell, and the solid line indicates the fitted regression line along the gradient. In all regions, foraging habitat area was lowest in urban environments and increased progressively toward rural areas. Together with Figure 4, these results illustrate opposing resource gradients along the urban–rural continuum.