Ecological Indicators 85 (2018) 1–10

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Research paper

# Advantages of combining generalized linear models and occupancy models to find indicators of habitat selection: Small mammals in agroecosystems as a case study

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A R T I C L E I N F O

*Keywords:*
Small mammal
Macrohabitat
Microhabitat
Generalized linear models
Occupancy models

A B S T R A C T

Models of habitat variables can be used to find indicators for a quantitative prediction of the likeliness of species occurrence or abundance. Methodological bias due to variable detectability can be critical to properly determine habitat use and, thus, for understanding species ecology, distribution, and requirements for survival. In spite of recent advances in dealing with imperfect detection through detailed modeling, this approach requires large amounts of data and usually leads to larger standard errors in parameter estimates. In this work, we explore the advantages of combining generalized linear models (GLMs) and occupancy models (OMs) for the detection of variables that may be used as indicators of habitat suitability for rodent species. As a case study, we analyzed live trapping data of three rodent species that inhabit agroecosystems at micro- and macrohabitat scales. Both methods provided complementary information: while OMs revealed that some habitat features believed to be selected by studied species actually affected detectability, some effects could only be detected by GLMs. Moreover, for some covariates apparently affecting habitat selection at both scales, comparing results between scales allowed us to determine for which it was actually relevant rather than a reflection of the other. Therefore, we advise applying complementary modeling approaches at multiple scales for habitat selection studies. A variety of outcomes and their implications are thoroughly discussed and may guide other researchers facing similar situations.

## 1. Introduction

Quantitative assessment of resources in a habitat may indicate the quality or suitability of that habitat for a species (Jorgensen 2002). For such quantitative data to serve as good indicator, knowledge about what resources are relevant for the species is required. Moreover, habitat selection by animals occurs at multiple spatial scales. These scales range from the geographic distribution of a species to the choice of suitable macrohabitats for individuals' home ranges and the differential use of microhabitats therein (Johnson 1980). Understanding this complex hierarchy is important for making informed management and conservation decisions.

Ecologists frequently study habitat selection by measuring variations in abundance or presence of species according to habitat characteristics. This requires detecting target species' using some habitat units among (a sample of) available units. Detection techniques vary across taxa and environments, either by directly observing or capturing animals, or by means of animal signs. The fact that animal detectability is rarely either perfect or constant due to methodological limitations (Nichols et al., 2000) may lead to biased estimates of habitat preferences, especially when detectability differs among habitat units (Gu and Swihart 2004; MacKenzie and Royle 2005).

Statistical modeling based on resource selection functions (Manly et al., 2002) is a common approach for the identification of relevant resources and habitat features. In addition, models of habitat variables can be used to find indicators for a quantitative prediction of the likeliness of species occurrence or abundance. In this context, generalized linear models (GLMs) and generalized linear mixed models (GLMMs) are widely used due to their greater availability and ease of application. On the other hand, Occupancy Models (OMs), which address imperfect

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http://dx.doi.org/10.1016/j.ecolind.2017.10.003
Received 18 May 2017; Received in revised form 22 September 2017; Accepted 2 October 2017

detection of species explicitly (MacKenzie 2003), need several observations over time to correctly determine detectability (Banks-Leite et al., 2014) and require more computational efforts. Advantages and disadvantages of using models that either do *or* do not account for imperfect detection have been discussed by various authors (e.g., MacKenzie et al., 2006; Banks-Leite et al., 2014). In this work, we explore whether the application of *both* approaches at different spatial scales may help to obtain more detailed insights into the habitat requirements of species than either model type and scale alone. Our focus is not on accurate abundance or occupancy estimations, but on the correct identification of habitat features *related* to species occurrence and use of habitat.

### *1.1. A case study*

Agroecosystems are landscapes with high intensity of land use and maintain large food resources, which could favor uncommon, endangered or pest species (Tscharntke et al., 2005). Agricultural landscapes are dominated by cropfields surrounded by a variety of habitats inhabited by different rodent species: corridors of remnant grassland, railway terraces invaded by trees, intensive breeding farms, small woodlots, riparian habitats and human settlements. In agroecosystems, rodents are a concern for causing economic losses and spreading animal and human diseases (Ellis et al., 1997). Therefore, proper recognition of ecological indicators of rodent presence in agroecosystems is relevant for pest control and management decisions. Rodent habitat selection studies are mostly based on point count data from live trapping surveys (Jorgensen 2002). In this context, imperfect detection of animals may arise as a consequence of differential animal behavior due to trap shyness, trap baiting, moonlight, as well as by habitat characteristics that may enhance or reduce capture probability (Jorgensen 2002). Several studies on rodent habitat selection in agroecosystems failed to detect habitat partitioning in the past (e.g., Mills et al., 1991), possibly due to the lack of adequate statistical methods to deal with imperfect detection.

As a case study, we evaluate habitat use of three rodent species that inhabit agroecosystems using data from a live trapping survey. We apply GLMMs/GLMs and OMs and show how results obtained through both methods at both scales can be integrated. Throughout the discussion, we provide a variety of examples of situations where both types of model agree and disagree, and how to interpret them jointly. Additionally, we discuss possible implications of having relied on a single method instead.

## 2. Materials and methods

### *2.1. Study area*

The study area was located in an agricultural landscape in the Exaltación de la Cruz Department (34°18′ S, 59°14′ W), Northwestern Buenos Aires Province, Argentina, within the Pampean phytogeographic province (Hall et al., 1992). The region has temperate and humid climate (Hall et al., 1992) with mean temperatures of 9.8 °C during winter and 22.5 °C in summer. Main human activities in the area are extensive agriculture and cattle production (Mills et al., 1991). The landscape is dominated by a matrix of crop fields bounded by relatively undisturbed linear habitats, including narrow fence lines and road edges, and wider abandoned railway embankments. Patches of small urbanizations, woodlots, and farms are also present in the area. The plant community in linear habitats consists of a mixture of exotic and native species, which provide suitable habitats for rodents because they are less disturbed than fields. The rodent community is composed of sigmodontines *Akodon azarae*, *Oligoryzomys flavescens*, *Oxymycterus rufus*), *Calomys laucha*, and *Calomys musculinus*, the cavies *Cavia aperea*), and introduced murines *Rattus norvegicus*, *Rattus rattus*, and *Mus musculus*, (Ellis et al., 1997).

### *2.2. Previous knowledge about the species studied*

Of the nine species in the rodent community, we trapped only *A. azarae*, *O. flavescens*, and *O. rufus*, besides small numbers of *C. laucha* and *C. musculinus*. Therefore, we focused on the three most captured species. *A. azarae* and *O. flavescens* adults weigh about 20–30 g (Redford and John, 1992). Both species show seasonal population changes, with minimum abundances in spring and a peak in autumn-winter (Busch et al., 2005). *O. rufus* adults may exceed 60 g (Redford and John, 1992). This species shows no seasonal abundance variations, probably because of its longer lifespan (Cueto et al.,1995).

In agroecosystems, the three studied species are mainly found in field edges and railway embankments rather than inside crop fields. In these habitats, *A. azarae* was associated with high total vegetation cover, green plant cover, and graminoid cover at macro- and microhabitat scales (Ellis et al., 1997; Bilenca and Kravetz 1998; Busch et al., 2001; Bilenca et al., 2007). In riparian habitats, the abundance of *A. azarae* was also associated with high vegetation cover (Bonaventura et al., 2003). In agroecosystems, *O. flavescens* was associated with high plant species richness and cover of forbs at microhabitat scale, while at macrohabitat scale it was associated with high vegetation cover and graminoid richness (Ellis et al., 1997). In riparian habitats, *O. flavescens* was mainly found near stands of tall grass in marshes and along rivers and streams (Boiani et al., 2008). Habitat use of *O. rufus* was described in wetlands and riparian habitats. At macrohabitat scale, the species inhabits mainly tall grass areas adjacent to streams, rivers, and marshes (Cueto et al.,1995), but shows low specificity for habitat types (Suárez 1994). At microhabitat scale, *O. rufus* was associated with high-plant-cover moist grassy areas (Kravetz 1972; Bonaventura et al., 2003). There are no detailed studies regarding habitat use of this species in agroecosystems.

### *2.3. Sampling design*

Four seasonal surveys were conducted in linear habitats (field edges and railway embankments) during May, July, November 2012 and March 2013 (in autumn, winter, spring, and summer, respectively). In each survey, we studied between 15 and 18 sites with a single trap line per site. Each trap line consisted of 25 Sherman live traps (30 × 10 × 10 cm) placed at 10-m intervals. Such proximity is required to obtain enough spatial resolution to evaluate differential microhabitat use within the span of individual home ranges; lack of independence among sampling units is thus unavoidable.

Trap lines were placed along both types of linear habitats (field edges and railroad embankments) randomly chosen among accessible places in the area. In 10 fixed sites, we conducted capture-mark-recapture (CMR) trappings every season (except one site which became unavailable after the first survey). Remaining sites (five, six, eight and nine for autumn, winter, spring and summer, respectively) changed every season because we conducted removal samplings in order to collect samples for an ongoing study of Hantavirus prevalence.

Traps were baited with a mixture of rolled oats and peanut butter, were active for three consecutive nights, and were checked every morning. The number of captured individuals per night and trap was either zero or one. Traps were reset after a capture at CMR sites but remained inactive at removal sites. The total trapping effort was of 4789 trap nights (10 CMR transects in autumn and 9 in winter, spring and summer, each with 25 traps active all three nights, plus 28 removal transects, each with 25 traps active during 1–3 nights). For each individual captured, we recorded capture date and location, species, sex, reproductive condition, corporal weight and length, and tail length. In CMR sites, rodents were ear tagged using individually numbered metal tags and released at the capture site whereas, at removal sites, animals were euthanized. Animals were handled according to the Argentine National Law 14,346 for the protection of animals.