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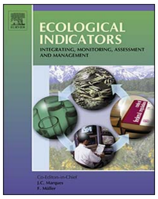

Research paper

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

Irene L. Gorosito[a,*], Mariano Marziali Bermúdez[b], María Busch[a]

[a] *Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina; Instituto de Ecología, Genética y Evolución de Buenos Aires, Universidad de Buenos Aires – Consejo Nacional de Investigaciones Científicas y Técnicas, Intendente Güiraldes 2160 – Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina*

[b] *Departamento de Física, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina; Instituto de Física de Buenos Aires, Universidad de Buenos Aires – Consejo Nacional de Investigaciones Científicas y Técnicas, Intendente Güiraldes 2160 – Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina*

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ABSTRACT

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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* Corresponding author.
E-mail address: iree26@gmail.com (I.L. Gorosito).

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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.

2.4. Habitat characterization

Every season we recorded vegetation characteristics of each linear habitat studied. We recorded habitat variables at all trapping stations that had captures and at a similar number of randomly selected trapping stations without captures. Vegetation variables were selected according to previous habitat selection studies of the rodent species (Ellis et al., 1997; Busch et al., 2001): *per-cent total plant cover*, *per-cent green plant cover*, *per-cent graminoid cover*, and *mean vegetation height* (in centimeters). Variables were estimated within a 1-m-radius circle centered on one trap station. We also determined the width of each linear habitat using the software Google Earth (Google Inc. 2016; Map data ©2016 CNES/Airbus; image date: July 25, 2013), since high vegetation density made direct measurements difficult. For macrohabitat analyses, we pooled all rodent captures and averaged the values of vegetation variables throughout each transect to obtain the corresponding covariates.

3. Statistical analyses

We analyzed capture data at micro- and macrohabitat scales, by means of two types of models: GLMs/GLMMs and OMs. We used each trap as a sampling unit for microhabitat analyses and each transect as a sampling unit for macrohabitat analyses. We treated data from each of the three nights as repeated measurements with respect to habitat characteristics and rodent distribution, but included the fact that detectability may change over time. We accounted for this short-term temporal variability in captures by including the factor *night* (with levels first, second or third trapping night). Although *season* was treated as a factor (with levels *autumn*, *winter*, *spring*, and *summer*), transects sampled during more than one season were considered as different transects for the purpose of analysis (i.e., all traps of any particular transect were assigned a different value of the random term *transect* for each season). Therefore, we made no distinction between CMR transects surveyed many times and removal transects surveyed once. In Table 1 we summarize key definitions and in the following paragraphs we provide details about the procedures for both scales and types of model.

For both scales and types of models, we adopted a multi-model inference approach (Burnham and Anderson, 2002). We devised a set of many candidate models including different combinations of covariates. Each model was evaluated and its weight (i.e., its likelihood of being the best model among the set of candidate models) was calculated based on Akaike or leave-one-out information criteria (AIC or LOOIC, see below for details). In order to identify which covariates best predicted habitat use, we determined the *relative importance* of each covariate as the sum of weights of all models having that covariate (Burnham and Anderson, 2002). In addition, for factors with multiple levels, the difference between two levels was considered statistical significant if their 95%-confidence intervals did not overlap.

3.1. Statistical analyses at microhabitat scale

To determine if microhabitat variables were correlated, we calculated the Pearson's product moment correlation (Zar 2010). Largest correlation coefficients were those between *graminoid* and *green plant cover* (-0.36), and between *graminoid* and *total plant cover* (0.27). No other strong correlations were found (< 0.2). Therefore, we calculated the residuals of the bi-linear fit of *graminoid cover* with *total* and *green plant cover* as independent variables and used these instead of the measured values.

At the microhabitat scale, sampling units corresponding to the same transect are not independent; thus, we addressed lack of independence by introducing the random effect term "transect" in the models to avoid pseudoreplication problems (Millar and Anderson 2004; Zuur et al., 2009). In addition, we excluded data from transects where a species was never found when evaluating microhabitat use by that species. Used data consisted of 2544 observations for *A. azarae*, 548 for *O. flavescens*, and 492 for *O. rufus*. We assessed microhabitat selection without explicitly accounting for detectability by means of GLMMs, using R package lme4 (Bolker 2013). The response variable $y_{t,k}$ was the number of mice captured at trap t during night k, which we treated as a binomial variable (i.e., $y_{t,k} = 0$ or 1). The corresponding probability of capture success $p_{t,k}$ was logit-linked to a linear predictor in terms of the vegetation variables measured at the corresponding unit, *season* and *night* (full model). For each trap in removal sites, we considered only capture histories up to the first capture, thus only the nights when they were active contributed to the total likelihood function. Correlation among traps of the same transect was modeled through the introduction of a random effect term varying among transects. To obtain the final model, we ranked the full model and all reduced models based on the *small-sample-size* corrected version of Akaike information criterion (AICc), as described by Burnham and Anderson (2002). We kept and averaged models with ΔAICc < 6 with respect to the best model (lowest AICc) using the R package MuMIn (Bartoń 2013).

In order to account for non-constant detectability, we also assessed habitat selection at microhabitat scale by OMs (MacKenzie et al., 2006), in which mean abundance (λ) and individual probability of detection (δ) were explicitly modeled in terms of covariates through log and logit link functions, respectively. According to our design, the closure assumption was not met at this scale of analysis because animals likely moved from one trapping station to another during the sampling period. Although this leads to biased estimates of detectability and occupancy, Gorosito et al. (2016) found that covariates affecting habitat selection can still be successfully identified. Therefore, abundance is not to be taken literally as such, but as a relative measure of the intensity of use. For this analysis, we used the same response variable $y_{t,k}$ as in GLMMs, but we did not model $p_{t,k}$ directly in terms of covariates. Instead, following Royle and Nichols (2003), we considered the probability of detecting one out of N individuals near a trap to be

Table 1
Definitions of variables and parameters used in the models.

		Microhabitat	Macrohabitat
Sampling unit		Trap	Transect
Binary response variable		Capture (or not) of an individual of the target species at a given trap during a specific night.	Capture of at least one individual (or none) of the target species in a given transect during a specific night.
Model	Parameter		
GLM/GLMM	p	Probability of capture success: how likely it is to capture one individual of the target species at a particular trap during one night.	Probability of capture success: how likely it is to capture at least one individual of the target species in the whole trap line during one night.
OM	λ	Mean abundance: expectancy of the number of individuals in the vicinity of a trap.	Occupancy probability: probability of species presence in the transect.
	δ	Individual detectability: probability of capturing a particular individual given that it is in the vicinity of a trap.	Species detectability: probability of capturing at least one individual given that the species is present in the transect.

$p_{N,\delta} = 1 - (1 - \delta)^N$.

Since actual abundance is unknown, the number of rodents in the proximity of each trap was modeled as a Poisson-distributed random variable with expectation value λ. The resulting log-likelihood function is

$$\log \mathcal{L} = \sum_{k=1}^{3} \sum_{t=1}^{T} \log \mathcal{L}_{t,k},$$

with

$$\mathcal{L}_{t,k} = \sum_{N=0}^{\infty} p_{N,\delta_{t,k}}^{y_{t,k}} \left(1 - p_{N,\delta_{t,k}}\right)^{1-y_{t,k}} \frac{\lambda_t^{N} \exp(-\lambda_t)}{N!} = \begin{cases} \exp(-\lambda_t \delta_{t,k}), & \text{if} y_{t,k} = 0 \\ 1 - \exp(-\lambda_t \delta_{t,k}), & \text{if} y_{t,k} = 1 \end{cases}$$

where λ_t is the mean abundance at trap t, and $\delta_{t,k}$ is the individual detection probability at trap t during night k. To take into account that traps with captures were not replaced in removal transects, we set their corresponding $\delta_{t,k} = 0$ after the first capture (and, of course, $y_{t,k} = 0$ too), thus only the nights when they were active contributed to the total likelihood function.

We constructed 186 models, including different sets of covariates for λ and δ. All these models were derived from two alternative full models:

a) all vegetation variables, the factor season, and the random effect transect as covariates for λ; the factor night as covariate for δ.
b) the factor season and the random effect transect as covariates for λ; all vegetation variables and the factor night as covariates for δ.

From each of these models, 31 additional models were obtained by selecting different subsets of vegetation variables (considering all possible combinations including/excluding one, two, three or all vegetation variables) and by including/excluding the random effect term. This resulted in a total of 62 unique models. From each of these, three variations were further obtained by either considering

1. uniform detectability throughout nights (i.e., without the factor night as covariate),
2. equal detectability for second and third nights,
3. different detectability for each night.

In order to compare these three types of models, the coefficient corresponding to the third night expressed the difference with respect to the second night. This differs from GLMMs, in which both second and third night coefficients express the difference with respect to the first night.

Parameter estimation for OMs was conducted within a Bayesian framework, using a Markov Chain Monte Carlo (MCMC) method as implemented in the software *WinBUGS* 1.4.3 (Lunn et al., 2000), by means of R package R2WinBUGS (Sturtz et al., 2005). MCMC offers a simple way to estimate both fixed and random-effect parameters and provides probability distributions of parameter values conditional on the observed data (posterior distributions), from which credible intervals can be obtained (Bolker, 2008; Royle and Dorazio, 2008; Kéry and Schaub, 2011). Our non-standard likelihood function was introduced into the model using the zeros trick (*WinBUGS help*). Vague priors were chosen for all parameters. For each model, we ran 7 MCMC chains for 9052 iterations. After 4526 burn-in iterations, a subset of 1022 samples was taken to reduce autocorrelation.

In addition to posterior distributions, *WinBUGS* also calculates models' Deviance Information Criterion (DIC, Spiegelhalter et al., 2002), which favors goodness of fit and penalizes model complexity, providing a way to select and/or average over models. However, it has been argued that DIC is not suited for Bayesian occupancy models (Broms et al., 2016). Therefore, for each species, all 186 models were ranked and corresponding weights were calculated based on models' leave-one-out cross validation information criterion (LOOIC, Gelman et al., 2014; Vehtari et al., 2016a). We performed an efficient approximate calculation of LOOICs by means of R package loo (Vehtari et al., 2016b), using the posterior distributions of parameters provided by *WinBUGS*. We averaged all models with ΔLOOIC < 6 to obtain the final values of the parameters and their credible intervals (Burnham and Anderson, 2002).

3.2. Statistical analyses at macrohabitat scale

After pooling capture data for each transect, per season (nine transects sampled in four seasons, plus 29 transects sampled once) and trapping night (three nights), the resulting dataset for macrohabitat analysis consisted of 195 ($3 \times [4 \times 9 + 29]$) observations for each rodent species.

We applied binomial GLMs to evaluate macrohabitat selection without accounting detectability explicitly (i.e., assuming detectability = 1). The response variable at transect t during night k was $y_{t,k} = 1$ if one or more individuals of the target species were captured or $y_{t,k} = 0$ otherwise. The corresponding success probability $p_{t,k}$ was logit-linked to a linear predictor in terms of *width*, *season*, *night*, and vegetation variables averaged throughout the corresponding transect (full model). To obtain the final model we ranked the full model and all reduced models based on the AICc, as described by Burnham and Anderson (2002). Models with ΔAICc < 6 with respect to the best model (lowest AICc) were selected and averaged using the R package MuMIn (Bartoń 2013).

We also evaluated macrohabitat selection by OMs to assess the effect of imperfect detectability. We modeled each transect occupancy (whether the target species was present on the transect) and per-night detection (capturing at least one individual, given that the species was present) as binomial-distributed random variables. The value of occupancy at a given transect is 1 if the species is present during the survey, with probability λ, and 0 otherwise; whereas detection takes value 1 if the species is detected during one night, with probability δ conditional on positive transect occupancy, and 0 otherwise. However, since actual non-occupancy cannot be ascertained where a species was not detected at all, the marginal likelihood of non-detection has contributions of both non-occupancy and non-detection conditional on positive occupancy. The resulting log-likelihood function was

$$\log \mathcal{L} = \sum_{t=1}^{T} \log \mathcal{L}_t,$$

with

$$\mathcal{L}_t = \lambda_t \prod_{k=1}^{3} \delta_{t,k}^{y_{t,k}} (1 - \delta_{t,k})^{1-y_{t,k}} + (1 - \lambda_t) \prod_{k=1}^{3} (1 - y_{t,k}).$$

In this model, the species detectability is evaluated, instead of the individual detectability. Since a high abundance enhances the probability of detecting at least one individual of a species at a given site, this detectability reflects not only individual capturability, but also the effect of local abundance.

Occupancy and detection probabilities were logit-linked to linear predictors in terms of transect-averaged vegetation variables and border *width*; trapping *night* and *season* were also included in the predictor of detectability. Models with all possible combinations of covariates (without repetition) were evaluated, totaling 972 models. To prevent potential boundary estimates (i.e., biased occupancies either towards 1 o 0) due to low sample size, we implemented a penalized likelihood method to improve parameter estimation, after Hutchinson et al. (2015). This approach avoids large values of the parameters by adding an *ad hoc* term to the deviance:

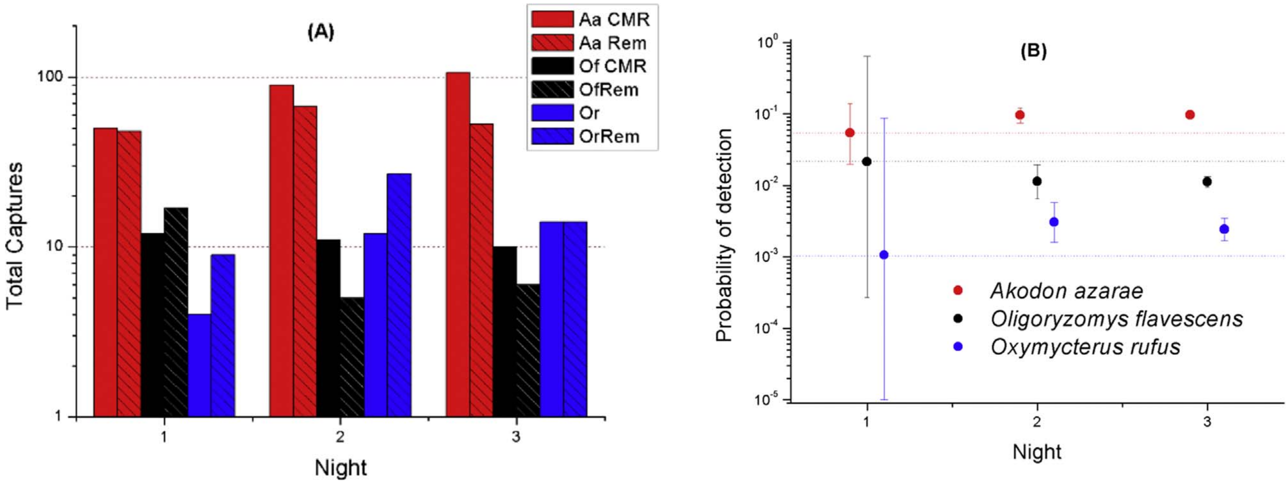

Fig. 1. (A) Total number of captures of each species (*O.f.* = *O. flavescens, A.a.* = *A. azarae, O.r.* = *O. rufus*) per night throughout the whole survey, split between capture-mark-recapture surveys (CMR) and removal samplings (Rem). (B) Individual detection probabilities fitted at microhabitat scale for the three trapping nights. Error bars for the first night indicate uncertainty in the absolute value of detectability; error bars of the second and third night represent the uncertainty in detectability *variation* with respect to the previous night, showing statistically significant changes with respect to the first night (dotted line).

Table 2
Relative importance (RI), mean value (Mean), and standard error (SE) of model-averaged estimates from GLMMs at microhabitat scale. The number of averaged models (ΔAICc < 6) for each species is indicated next to their name.

	A. azarae (5)			*O. flavescens* (32)			*O. rufus* (25)		
Variable	RI	Mean	SE	RI	Mean	SE	RI	Mean	SE
Intercept		−2.55	0.20		−2.80	0.33		−3.69	0.37
H	1.00	0.50	0.14	0.73	0.57	0.29	0.57	0.45	0.27
TP	0.97	1.45	0.55	0.24	−0.28	1.10	0.50	1.52	1.17
GP	0.26	−0.06	0.25	0.44	0.72	0.60	0.34	0.47	0.54
G	0.26	−0.06	0.24	0.72	−1.13	0.59	0.26	0.10	0.51
2nd night	1.00	0.55	0.15	0.89	−0.69	0.33	1.00	1.11	0.33
3rd night	1.00	0.46	0.15	0.89	−0.76	0.33	1.00	0.69	0.35
Winter	1.00	0.88	0.21	0.80	−0.32	0.45	0.12	0.64	0.59
Spring	1.00	−0.05	0.23	0.80	0.15	0.39	0.12	0.57	0.54
Summer	1.00	0.54	0.20	0.80	−0.87	0.42	0.12	0.21	0.52

$$Deviance = -2\log\mathcal{L} + \alpha\sum parameter^2,$$

where α is a penalization weight. We searched for an optimal value of α (for each species) by means of a 5-fold cross validation procedure. Trapping data was randomly assigned to 5 subsets of similar size and the model averaging procedure described below was conducted using only data from 4 subsets. The model obtained was then evaluated on the excluded data and its unpenalized likelihood was calculated. The process was repeated sequentially excluding a different subset, and deviances of these five iterations were tallied. We considered that the optimum α was that which minimized the total deviance of excluded data (Fig. 1). Afterwards, this value of α was used for fitting all candidate models to the full dataset.

For each species, all candidate models were fitted using the Broyden–Fletcher–Goldfarb–Shanno algorithm as implemented in the optim function in R (R Core Team, 2014) and ranked according to their AICc values. Models with ΔAICc < 6 were selected and averaged according to their Akaike weights and the relative importance of the parameters were also calculated (Burnham and Anderson, 2002). The relative importance of each variable for predicting capture success, occupancy/abundance or detectability was estimated as the sum of the weights of all models in which that variable was included (Burnham and Anderson, 2002).

4. Results

A total of 517 rodents were captured. The three species were detected every season, but the number of captures per night was not constant during each survey, and varied differently for each species (Fig. 1A). *Akodon azarae* was the most frequently captured species, with a total of 378 individuals (found in 90.7% of the transects and 20.9% of the traps), followed by *O. rufus* with 79 (44.62% of the transects and 4.4% of the traps), and 60 *O. flavescens* (46.15% of the transects and 3.5% of the traps). In most removal sites (24 out of 28), at least half of the traps remained unused during the sampling period, with only 14 removal sites having more than 6 captures. In all sites, at least 9 traps were active throughout the whole sampling period.

The range of measured vegetation variables were 0.1–1.0 for *per-cent total plant cover* (mean = 0.91), 0.0–1.0 for *per-cent green plant cover* (mean = 0.57), 0.04–3.33 m for *average vegetation height* (mean = 0.83 m), and 0.0–1.0 for *per-cent graminoid cover* (mean = 0.43). Transect means ranged between 0.58–1.00 for *per-cent total plant cover*, 0.03–0.94 for *per-cent green plant cover*, 0.11–1.56 m for *average vegetation height*, and 0.00–0.91 for *per-cent graminoid cover*. Border *widths* ranged between 2 and 35 m with mean 12.6 m.

4.1. Habitat selection at microhabitat scale

Final averaged models are presented in Table 2 (GLMMs) and Table 3 (OMs), including the total number of averaged models (those with ΔAICc or ΔLOOIC < 6), mean values and confidence/credible intervals of the coefficients, and relative importance (RI) of the covariates. For the three species, none of the OMs that assumed constant detectability through all nights entered in the average due to their large values of LOOIC, highlighting the non-constant detectability through nights. Results obtained by both statistical methods for each species are presented below.

Results from GLMMs indicate that capture success of *A. azarae* varied seasonally (high RI of *season*) and was higher in winter and summer than in autumn and spring. OMs were consistent with the seasonal pattern, but all credible intervals overlapped so seasonal abundance variations were not statistically significant. *Total plant cover* and *vegetation height* had high RI and affected capture success positively in GLMMs. Among vegetation variables, *vegetation height* was also the most important predictor of *A. azarae*'s detectability in OMs, having a slight positive effect. However, vegetation variables were not strong predictors of *A. azarae*'s occupancy or detectability, as suggested by their low RI values which did not exceed 0.57 in any case. All averaged OMs included the random-effect term (*transect*), suggesting that there were differences in the abundance of *A. azarae* among transects not

Table 3
Relative importance (RI), mean value (Mean), and lower (LCL) and upper confidence limits (UCL) of model averaged estimates from OMs at microhabitat scale. Coefficients of covariates included in occupancy and detectability are identified by sub-indices o and d. The number of averaged models (ΔLOOIC < 6) for each species is indicated next to their name. RI of terms included in all candidate models were omitted.

	A. azarae (26)				*O. flavescens* (82)				*O. rufus* (52)			
Variable	RI	Mean	LCL	UCL	RI	Mean	LCL	UCL	RI	Mean	LCL	UCL
Intercept$_{o}$		0.35	−0.67	1.37		1.07	−3.25	5.40		2.76	−1.79	7.32
H$_{o}$	0.51	0.24	−0.03	0.51	0.38	0.21	−0.13	0.55	0.17	0.07	−0.08	0.21
TP$_{o}$	0.5	0.76	−0.15	1.67	0.15	0.04	−0.30	0.38	0.24	0.35	−0.39	1.08
GP$_{o}$	0.13	0.00	−0.06	0.06	0.25	0.19	−0.21	0.59	0.14	0.04	−0.13	0.21
G$_{o}$	0.2	−0.03	−0.13	0.07	0.42	−0.47	−1.19	0.25	0.15	0.00	−0.15	0.16
winter$_{o}$		0.85	0.45	1.25		−0.25	−1.12	0.63		0.59	−0.57	1.75
spring$_{o}$		−0.02	−0.46	0.41		0.17	−0.60	0.93		0.60	−0.52	1.71
summer$_{o}$		0.53	0.16	0.90		−0.82	−1.65	0.00		0.22	−0.86	1.31
Intercept$_{d}$		−2.86	−3.90	−1.82		−3.82	−8.23	0.59		−6.85	−11.35	−2.35
H$_{d}$	0.49	0.29	−0.05	0.62	0.31	0.20	−0.14	0.54	0.18	0.07	−0.08	0.22
TP$_{d}$	0.42	0.67	−0.25	1.58	0.08	−0.02	−0.22	0.19	0.24	0.35	−0.40	1.10
GP$_{d}$	0.20	−0.02	−0.14	0.09	0.17	0.14	−0.18	0.47	0.14	0.04	−0.13	0.22
G$_{d}$	0.13	−0.02	−0.09	0.06	0.30	−0.35	−0.97	0.26	0.15	0.00	−0.16	0.16
2nd night		0.62	0.34	0.89		−0.65	−1.21	−0.10		1.06	0.41	1.71
3rd night	0.34	0.01	−0.08	0.10	0.22	−0.01	−0.18	0.16	0.55	−0.23	−0.59	0.13

accounted for by variations in vegetation variables. Both GLMMs and OMs displayed higher capture success and detectability, respectively, during nights 2 and 3 than in the first night (Fig. 1B). There was no difference in capture success nor in detectability between nights 2 and 3.

According to GLMMs, capture success of *O. flavescens* was lower in summer than in other seasons, OMs showed similar results but, as for *A. azarae*, credible intervals overlapped. GLMMs indicated a positive effect of *vegetation height* and negative effect of *green plant cover* on capture success, both had high RI (0.73 and 0.72, respectively). On the contrary, in OMs the RI of all vegetation variables did not exceed 0.39, neither for occupancy nor detectability, meaning that none was a strong predictor. Models with the random-effect term yielded similar LOOIC values than models without it, suggesting that *O. flavescens*'s occurrence was less variable between transects than *A. azarae*'s. Capture success in GLMMs and detectability in OMs were not uniform through nights, decreasing from the first night to the second and then remaining similar for the third night.

Unlike the other species, no differences in capture success of *O. rufus* were observed among seasons in GLMMs. GLMMs indicated that *vegetation height* had a slight positive effect on capture success of *O. rufus*. However, according to OMs none of the vegetation variables scored a RI greater than 0.28, neither for occupancy nor detectability, so none was a strong predictor. All averaged OMs included the random-effect term (*transect*), which suggests that there were differences in *O. rufus*'s abundance among transects not accounted by the vegetation variables considered. Capture success and detectability during nights 2 and 3 were higher than in the first night in GLMMs and OMs, respectively.

4.2. Habitat selection at macrohabitat scale

Through cross validation we found different optimum values of the penalization weight α for each species. The deviance of excluded data as function of the penalization weight is shown in Fig. 2. *O. flavescens* and *O. rufus* required smaller values of α, suggesting that OMs fitted to part of the data could adequately predict remaining data. In contrast, *A. azarae* required a larger α to improve model fitting, indicating that models were prone to over fit data. Final averaged models are presented in Table 4 (GLMs) and Table 5 (OMs), including the total number of models averaged (those with ΔAICc < 6), mean values of confidence/credible intervals of the coefficients, and RI of the covariates.

High RI of the factor *season* in GLMs support seasonal variations in capture success of *A. azarae*, which was higher in winter and summer than in autumn and spring. Seasonal variations in detectability were not statistically significant in OMs due to overlapping confidence intervals, but the trend in mean values of the coefficients was consistent with GLMs. In addition, while only *total plant* had high RI in GLMs, with a

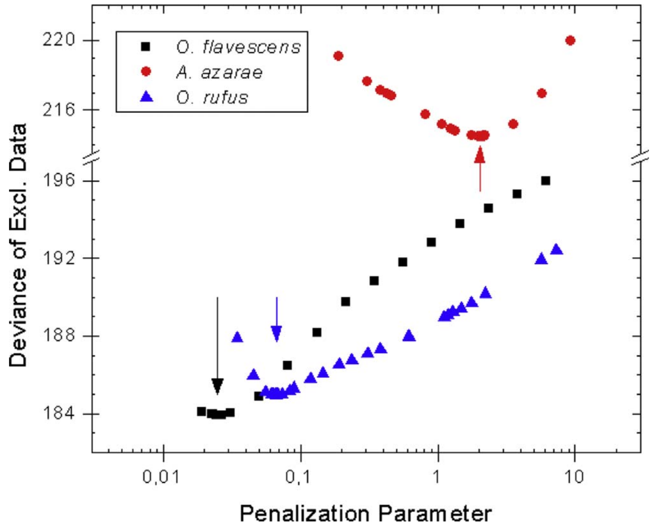

Fig. 2. Deviance of excluded data as function of the penalization parameter (α) in five-fold cross-validation for the three species. Arrows indicate values of the penalization parameter used for final model fitting, corresponding to minimum deviance.

Table 4
Relative importance (RI), mean value (Mean), and standard error (SE) of model averaged estimates from GLMs at macrohabitat scale. The number of averaged models (ΔAICc < 6) for each species is indicated next to their name.

	A. azarae (26)			*O. flavescens* (50)			*O. rufus* (14)		
Variable	RI	Mean	SE	RI	Mean	SE	RI	Mean	SE
Intercept		−3.91	1.19		−4.56	2.11		−12.22	3.072
H	0.61	1.18	0.72	0.61	1.25	0.73	1.00	3.31	0.735
TP	1.00	4.36	1.27	0.68	3.49	2.18	1.00	7.17	2.924
GP	0.51	−1.86	1.27	0.35	1.07	1.24	0.27	0.70	1.285
G	0.26	0.48	1.06	0.25	0.02	1.13	0.25	−0.39	1.083
W	0.32	−0.02	0.02	0.80	0.05	0.02	0.25	0.01	0.023
2nd night	0.81	1.17	0.46	0.05	−0.20	0.45	0.59	1.05	0.497
3rd night	0.81	0.62	0.43	0.05	−0.31	0.46	0.59	0.84	0.499
Winter	1.00	1.82	0.66	0.55	−0.40	0.62	1.00	2.21	0.747
Spring	1.00	0.04	0.54	0.55	0.10	0.57	1.00	1.16	0.672
Summer	1.00	1.37	0.56	0.55	−1.16	0.57	1.00	1.80	0.621

Table 5

Relative importance (RI), mean value (Mean), and lower (LCL) and upper confidence limits (UCL) of model averaged estimates from OMs at macrohabitat scale. Coefficients of covariates included in occupancy and detectability are identified by sub-indices o and d. The number of averaged models (ΔAICc < 6) for each species is indicated next to their name.

	A. azarae (433)				*O. flavescens* (194)				*O. rufus* (391)			
Variable	RI	Mean	LCL	UCL	RI	Mean	LCL	UCL	RI	Mean	LCL	UCL
intercept_o		0.04	−0.62	0.70		−2.70	−6.15	0.75		−2.31	−4.38	−0.24
H_o	0.16	0.00	−0.11	0.11	0.25	−0.43	−1.39	0.54	0.75	1.79	0.32	3.27
TP_o	0.25	0.10	−0.13	0.33	0.19	0.13	−0.92	1.18	0.20	0.12	−0.40	0.64
GP_o	0.16	0.01	−0.10	0.12	0.17	0.01	−0.62	0.65	0.37	0.69	−0.49	1.86
G_o	0.17	0.03	−0.10	0.16	0.22	0.40	−0.59	1.39	0.27	−0.30	−1.01	0.41
W_o	1.00	0.49	0.19	0.80	1.00	0.71	−0.10	1.52	0.75	0.07	−0.00	0.14
intercept_d		0.62	0.05	1.19		−3.02	−6.00	−0.05		−2.36	−5.35	0.64
H_d	0.39	0.17	−0.11	0.46	0.91	1.35	0.44	2.27	0.66	0.97	−0.03	1.98
TP_d	0.35	0.16	−0.12	0.44	0.52	1.58	−0.51	3.67	0.46	1.14	−0.47	2.74
GP_d	0.17	0.01	−0.09	0.10	0.19	0.08	−0.33	0.50	0.21	0.02	−0.46	0.50
G_d	0.22	0.06	−0.09	0.21	0.18	−0.09	−0.42	0.25	0.35	0.43	−0.35	1.21
W_d	0.24	−0.00	−0.01	0.01	0.20	0.00	−0.01	0.01	0.26	−0.00	−0.02	0.01
2nd night	0.62	0.44	0.01	0.87	0.03	−0.01	−0.03	0.02	0.62	0.68	0.00	1.35
3rd night	0.62	0.21	−0.10	0.52	0.03	−0.01	−0.04	0.02	0.62	0.51	−0.07	1.09
Winter_d	0.46	0.23	−0.09	0.56	0.60	−0.31	−0.91	0.29	0.02	0.02	−0.03	0.07
Spring_d	0.46	−0.10	−0.34	0.15	0.60	−0.12	−0.65	0.41	0.02	0.02	−0.02	0.06
Summer_d	0.46	0.29	−0.09	0.67	0.60	−0.85	−1.70	−0.01	0.02	0.02	−0.02	0.05

positive effect on capture success, no vegetation variable was important for occupancy or detectability in OMs. *Width* had a positive effect on occupancy, but it had low RI for detectability and capture success. GLMs and OMs showed an increase in capture success or detectability, respectively, from the first to the second night.

GLMs for *O. flavescens* indicated that capture success was lower during summer than during the other seasons; the same effect was observed for detectability through OMs. However, moderate RI of season in both methods indicated little support for seasonal variations. *Vegetation height*, *total plant cover* and *width* had a positive effect on capture success and were the three most important predictors in GLMs. According to OMs, *width* was a strong predictor of occupancy, while *vegetation height* was positively related to species detectability. No variations in detectability nor in capture success among nights were observed.

Capture success of *O. rufus* was higher during winter and summer, and lowest during autumn (RI of *season* 1.0 in GLMs). Conversely, *season* was not an important predictor in OMs. Among vegetation variables, *total plant cover* and *vegetation height* were the only important predictors in GLMs; both had positive effects on capture success. These two vegetation variables affected detectability positively in OMs, but their moderate RI provides little support for this effect. *Vegetation height* also affected occupancy positively, with better support from its RI than for detectability. Both detectability in OMs and capture success in GLMs were higher for the second and third nights, but with moderate RI. *Width* had high RI and a positive effect on occupancy in OMs, but not on capture success in GLMs.

5. Discussion

We evaluated habitat use of three small-rodent species in agroecosystems at two spatial scales. These scales were defined according to the typical range of movements of individuals rather than habitat features, which were described *a posteriori*. Raw proportions of occupied transects and traps showed that *A. azarae* was ubiquitous in the study area, whereas the other species were found at only a small fraction of sampling units. For the three species, three-night trapping periods may have not been long enough to accurately estimate detectability. OMs yielded smaller individual detectability for *O. flavescens* than for *A. azarae*, and even smaller for *O. rufus*. The extremely low individual detectability estimated for *O. rufus* is most likely due to statistical method bias associated with the violation of the closure assumption (Gorosito et al., 2016). At macrohabitat scale, some bias could also be expected due to different sampling schemes applied to CMR and removal sites. However, it is unlikely that the probability of detecting a species' presence at a site was significantly affected by the small number of traps that became inactive and removed individuals.

In the following subsections, we discuss the results obtained by both approaches and at both scales. We remark that generalized linear models and occupancy models are not immediately comparable because only the latter discriminates between use and detectability. However, it is possible to make conclusions from both types of models as long as what is being modeled by each method is clear.

5.1. Habitat feature effects

Our finding that capture success of *A. azarae* was positively related to *total plant cover* at micro- and macrohabitat scale, according to GLMMs/GLMs, agrees with previous studies reported in the literature which did not account for detectability (Ellis et al., 1997; Bilenca and Kravetz, 1998; Busch et al., 2001). From OMs, we could not distinguish whether *total plant cover* mainly affected use or individual detectability at microhabitat scale, but higher RI of this covariate for detectability than occupancy at macrohabitat scale indicates that mean plant cover would not determine the species presence. Higher capture success of *A. azarae* associated with *vegetation height* at microhabitat scale through GLMMs is in agreement with previous observations in crop field borders (Busch et al., 2001). Such outcome could be interpreted as a selection for microsites with taller vegetation. However, OMs indicated that this habitat feature was actually favoring individual detectability, meaning that *A. azarae* individuals were more detectable in traps placed in sites with taller vegetation. This differential behavior towards traps according to vegetation height may be related to an increase in activity in sites with less aerial predation, since rodent activity is strongly affected by predation risk (Ellis et al., 1997).

Consistently with previous authors who studied *O. flavescens* in riparian habitats without explicitly accounting for detectability (Bonaventura et al., 2003; Boiani et al., 2008), we could conclude from GLMs results that the species was more frequent in longitudinal habitats with high mean values of vegetation height. Does it mean that the species inhabited mostly places with taller vegetation or that it was more abundant or just more detectable in taller vegetation? OMs revealed that in such places the species was more detectable, but not more often present. Although species detectability at macrohabitat scale can still be related to either differential species abundance or behavior towards traps, this result rules out *vegetation height* as a factor determining if the species will inhabit a place or not, which may be of central interest, e.g. for predicting *O. flavescens* distribution. Moreover, our finding that *vegetation height* is associated with capture success of *O. flavescens* at microhabitat scale indicated that most captures of this species correspond to microsites with tall vegetation and, therefore, suggest that the effect of the variable observed at macrohabitat scale may be reflecting a microhabitat phenomenon. Unfortunately, we could not distinguish from OMs whether this effect was on individual detection probability or on local abundance. The connection between *O. flavescens* and tall vegetation both in riparian and agrarian ecosystems remains to be further investigated, especially due to *O. flavescens*'s role as a reservoir of hantavirus.

Our results for *O. rufus* indicated that overall tall vegetation favors this species' presence. Therefore, the positive effect of *vegetation height* on species' detectability at macrohabitat scale may be due to greater abundances in habitats with tall vegetation. Consequently, the small effect of *vegetation height* observed at microhabitat scale may be the result of the macrohabitat choice, characterized by overall tall vegetation, rather than a preference for tall vegetation microsites. No association of this species with vegetation height has been reported in previous works, which were conducted in riparian habitats (Bonaventura et al., 2003). Since our study was conducted in agroecosystems, habitat requirements of *O. rufus* could be specific to particular landscapes. Besides, Bonaventura et al. (2003) found *O. rufus* associated to macrohabitats with dense plant cover. Our results from GLMs showed the same association and OMs favored *total plant cover* as a covariate for detectability rather than occupancy. While *total plant cover* does not seem to determine whether the species will inhabit a particular macrohabitat, the observed association may be a consequence of larger abundances in more densely vegetated macrohabitats as well as of differential behavior therein.

In agroecosystems, most longitudinal habitats are borders surrounding cultivated fields, which in general are narrower than railway embankments. Most studies at macrohabitat scale in agroecosystems compared the preferences of rodents between cultivated fields and field borders, concluding that the studied species inhabit mainly field borders (Bilenca et al., 2007; Gómez et al., 2011). Preferences for different types of longitudinal habitats had only been assessed by comparing borders dividing cropfields with those next to roads (Busch et al., 2001), but not borders of different width. In our study, we sampled cropfield edges, which were 2- to 8-m wide, and railway embankments, which ranged from 15 to 35 m in width. For the three species, OMs indicated that *width* affected occupancy, with the predicted probability of occupancy increasing for wider habitats (Fig. 3). Moreover, for very narrow borders (under about 10-m wide), occupancy probability of *O. flavescens* drops abruptly, suggesting that this species may require a minimum width of the linear habitat to accommodate their home ranges. Interestingly, we did not observe the effect of *width* in GLMs for *A. azarae* nor *O. rufus*. Although most transects where these species were never captured were narrow, multiple captures occurred in some narrow transects. Therefore, as GLMs cannot differentiate between multiple captures from a small fraction of narrow sites from low frequency captures in almost all wide sites (as OMs do), transect width appeared to have no effect at all.

5.2. Short-term temporal variability (nights)

In the case study, data was collected during three consecutive nights each survey, which is a common practice in field studies of small mammals (Gorosito et al., 2016). Both at macro- and microhabitat scale we observed night-to-night variation in GLMs/GLMMs and OMs for the three rodent species. Therefore, under the assumption that habitat use remained constant throughout the sampling period, the conclusion with the two methods is the same since the effect of the night in GLMs/GLMMs can only be attributed to a change in detectability. In addition, the evolution of detectability through nights (Fig. 1B) was consistent with the trend observed in the raw data (Fig. 1A).

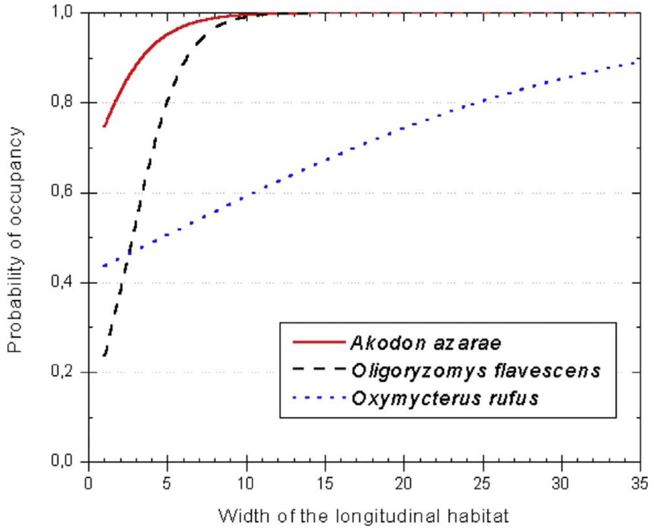

Fig. 3. Fitted occupancy probability as function of width (in meters) with other covariates at their mean values, for each species.

In the present study, environmental factors that could have affected animals' behavior towards traps (e.g., changing weather or moonlight) did not vary substantially during successive trapping nights. The fact that *A. azarae* and *O. rufus* were more detectable after the first night, both at macro and microhabitat scale, suggests that these species need to be acclimated to traps before entering them (neophobia). This effect may be critical when data from surveys of different durations, or with and without pre-baiting, are analyzed together, because initial lower detectability may introduce higher bias. On the other hand, *O. flavescens* was more likely to be detected in the first night than in the following nights at microhabitat scale (neophilia), but the trapping night seemed not to be relevant at macrohabitat scale (RI < 0.05). This apparent contradiction between detectability at micro- and macrohabitat scale for *O. flavescens* may arise if once an individual is trapped, it becomes trap-shy, reducing the average individual detection probability. As non-captured individuals would be equally likely to enter traps on the following night, overall probability of detecting the species in the transect remained unchanged. This explanation also applies to removal samplings, where the probability of detecting a removed individual is null.

5.3. Seasonal variations

Because of well-known abundance cycles of rodent species among seasons, we attributed seasonal variations to species detectability at macrohabitat scale and local abundance at microhabitat scale. Under the assumption that *season* only affects abundance, seasonal covariates in GLMs/GLMMs and OMs have the same meaning and both types of models are expected to yield similar results. This was indeed observed: for all three species OMs showed the same seasonal trend than corresponding GLMs/GLMMs. Moreover, for *A. azarae* and *O. flavescens*, results obtained at both scales were identical, further supporting our assumption of seasonal abundance variation. In contrast, seasonal variations in capture success found at macrohabitat scale for *O. rufus* were not important in OMs nor at microhabitat scale. Most captures of *O. rufus* occurred in removal sampling transects, which were surveyed once. Therefore, different proportions of occupied transects each season may have affected GLMs results, but are to be considered of methodological rather than ecological origin. By excluding transects without any captures of the species for microhabitat analysis and not considering seasonal changes in occupancy, we avoided spurious associations in these models. The absence of notorious seasonal changes in abundance is consistent with reported longevity of *O. rufus*.

6. Conclusions and recommendations

Our findings show how neglecting differential detection probabilities is likely to lead to false conclusions about habitat selection. Thus, actual selection cannot be ascertained solely on the basis of GLMs' results. However, had we relied exclusively on OMs for the evaluation of habitat selection, some covariates affecting species would have gone unnoticed (for instance, *total plant cover* for *A. azarae*). GLMs/GLMMs may identify effects which could be ecologically important (or mere artifacts; see Gu and Swihart, (2004)) and require more effort to be fully understood. Therefore, we encourage researchers to contrast results of multiple models whenever possible in order to obtain a complete picture of a species' ecology and to find the variables that may be useful as indicators of a high probability of use by a given species. When doing so, covariates known to affect detectability should be incorporated into GLMs/GLMMs too (such as we incorporated *night* in GLMs/GLMMs), so that the variability in the outcome of samplings due to these factors does not mask other ecological features. In particular, if data from surveys of different lengths are to be combined, special care must be taken with time-varying detectability as the probabilities of detection may not scale uniformly with survey duration.

It has been argued that habitat selection at small scales "disappears" when larger scales are considered (Morris 1987). Similarly, we observed that selection occurring at a given scale may appear reflected at another scale. To avoid possible confusion, we recommend simultaneously analyzing data at more than one scale.

OMs usually incorporate additional covariates, which reduces estimates' precision and leads to overfitting data. Researchers should pay attention to this issue and look for strategies such as penalized likelihood, cross validation, etc. to avoid overfitting in more complex statistical models.

The large volume of ecological research conducted before modern computational capabilities were developed was restricted to simpler statistical analyses. While all the previous work may provide valuable information, it may be subject to methodological bias and some important ecological aspects might have not been properly identified. We believe that, even for long-studied species, it is important to revisit our knowledge from a fresh perspective and taking advantage of multiple modeling approaches. This is especially true for endangered and disease-bearing species, for which precise knowledge of their habitat requirements may be critical in order to make informed conservation and public health decisions.

Author contributions

ILG and MB planned and conducted the surveys. ILG and MMB analyzed the data. ILG and MB wrote the manuscript.

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