Stop and ask for directions: factors affecting anuran detection and occupancy in Pampa farmland ponds

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Abstract There is a great need to understand the effects of man-made land transformation on freshwater biodiversity, because agricultural landscapes provide habitat for many aquatic and semi-aquatic organisms. However, not all forms of land use are equal in their capacity to support wildlife. Cattle grazing leads to a change in pasture vegetation structure, whereas conversion to commercial crop-based agriculture promotes structural and chemical degradation of the ecosystem. From 2010 to 2012, in the Pampa biome, southern Brazil, we modelled anuran occupancy for 39 farmland ponds. Specifically, we determined detection probabilities associated with survey- and pond-specific variables and examined tadpole occupancy in relation to land use in southern Brazil. We recorded eleven anuran species, but only five were detected at levels suitable for occupancy modelling. Species detectability varied with water temperature, extent of floating macrophyte cover, and sampling date. For three species, detection-adjusted occupancy models indicated a relationship between occupancy and agricultural activities and/or livestock management. Agriculture areas negatively affected occupancy by *Odontophrynus americanus* and *Physalaemus gracilis*. The presence of livestock within a 500 m radius positively affected pond occupancy by *Hypsiboas pulchellus*. Other species were negatively associated with pond area or fish presence. Our results demonstrate that traditional extensive livestock farming can provide a buffer that protects freshwater environments, because it did not greatly modify the grassland matrix. We argue that further species-based approaches will be critical for developing effective conservation strategies for anurans, particularly in the context of the expanding rice production/exotic forests in southern Brazil.

Keywords Grasslands · Land use · Southern Brazil · Tadpoles · Uruguayan savanna

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Introduction

Over the past two decades, numerous studies have indicated that amphibian populations are declining in many places worldwide. Despite the increased awareness of remnant amphibian populations and factors responsible for their declines (Eterovick et al. 2005; Becker and Zamudio 2011), we still do not completely understand how these factors operate at the population level (Beebee and Griffiths 2005; Pimenta et al. 2005; Mann et al. 2009; Blaustein et al. 2010). Although the causes of population declines may vary from region to region and even within different populations of the same species (Blaustein et al. 2010), there is currently a consensus that species declines occurring at low elevations are very frequently associated with habitat loss or modification (Cushman 2006; Gallant et al. 2007; Becker and Zamudio 2011).

Agricultural lands cover about a third of Brazil, a proportion which is likely to increase as demand for food and biofuels increases (Sparovek et al. 2010; Ferreira et al. 2012). Therefore, habitat loss associated with agricultural expansion is probably the principal cause of declining anuran populations (Gallant et al. 2007). As with other organisms, habitat loss affects amphibian species through reduced natural habitats, population isolation, inbreeding and factors associated with edge

effects (e.g. changes in microclimate and interaction with exotic species; Ficetola and De Bernardi 2004; Cushman 2006; Dixo et al. 2009; Watling et al. 2011; Machado et al. 2012). Wetlands in agricultural landscapes often accumulate pollutants (Mann et al. 2009) and have altered hydroperiods (Venne et al. 2012) that negatively affect amphibians. Moreover, studies in modified landscapes have shown that the ability of amphibian populations to persist over time is related to individual species characteristics (dispersal ability, reproductive mode and habitat preference) (Ficetola and De Bernardi 2004; Cushman 2006; Fischer et al. 2015). Thus, amphibian assemblages that use disparate resources may be affected differently by historic land use.

The Pampa biome extends through Uruguay, Argentina and southern Brazil and is characterized by a mosaic of grasslands, scrub savannas and gallery forests (Miñarro and Billenca 2008; MMA 2011). These formations exhibit varying degrees of degradation depending on the nature and extend of past and current land uses practices. Nevertheless, agricultural (rice/soybean) and silvicultural (*Eucalyptus* spp. and *Pinus* spp.) land use practices have greatly expanded since the second half of the twentieth century. This is leading to both local- and landscape-scale changes within the Pampa biome (Miñarro and Billenca 2008). Land use changes in southern Brazil have been poorly documented compared with other regions of the country (Overbeck et al. 2007). About 50 % of the original Brazilian Pampa remains (MMA 2011), though untouched native grasslands and forests have been reduced by almost 90 % (Cordeiro and Hasenack 2009). For Pampas-dwelling amphibians, identification of priority areas for conservation has mainly focused on bioclimatic variables and on species with restricted distributions, whereas including land cover to explain species distribution is still uncommon (Bernardo-Silva et al. 2012; Zank et al. 2014).

Measuring site occupancy on a landscape scale is recognized as an effective technique for monitoring populations of secretive, low-density and/or territorial species, such as amphibians (MacKenzie et al. 2006; Durso et al. 2011; Sewell et al. 2012). Studies of amphibian occupancy and detectability have mainly focused on call-based survey data, or concentrated on the methodologically most tractable segments of the community (e.g. terrestrial species caught in pitfall traps). Few studies have focused on ecological aspects of larval stages or the seasonal variation in detection probabilities (Curtis and Paton 2010). However, several characteristics of tadpoles make them good subjects for field inventories and aquatic monitoring studies, including their generally high abundance and more extended presence in aquatic habitats than adults (Andrade et al. 2007).

In this study, we modelled tadpole occupancy as a function of land use in 39 farmland ponds located in the Pampa biome. First, we determined detectability associated with pond- and survey-specific covariates. Then, we determined whether pond occupancy was associated with land use and cover type. We predicted that occupancy estimates would be higher with land use types that did not greatly modify the grassland matrix (e.g. livestock). Various negative effects of silviculture on both larval and adult anuran assemblages have been identified in southern Brazil (Machado et al. 2012). In addition, many of the chemical formulations regularly used in soybean and rice plantations in the Pampa (such as glyphosate-based herbicide and related dispersal agents) are specifically hazardous to the aquatic environment (Peltzer et al. 2008; Attademo et al. 2011). Thus, traditional extensive livestock is probably more compatible with maintaining anuran diversity than are many other potential uses of these private lands in the Pampa landscape.

Methods

The study area is located in the southern half of Rio Grande do Sul ($28°36.6'$–$31°44.64'$S, $52°31.08'$–$57°30.18'$W), within the Pampa biome (Fig. 1). Livestock farming (40 %), native grasslands (30 %), and crop-based agriculture (20 %) dominate the land use patterns. Native grasslands are mainly used as traditional livestock ranches. The subtropical climate includes a wide range of temperatures, and although it may freeze or snow in some regions, temperatures can reach 40 °C in summer. Annual rainfall varies from 1200 to 1700 mm year^{-1} and is concentrated in spring and autumn (Rossato 2011). Currently, the anuran fauna known from the region includes 48 species, of which 43 breed in lentic water bodies (Maneyro and Carreira 2012). However, information on the distribution and natural history of many species is scarce and fragmented. In the Uruguayan savanna, three species types comprise the pond-dwelling anuran assemblages: (i) those with prolonged calling activity and slow larval development (e.g. *Hypsiboas pulchellu*s and *Pseudis minuta*), (ii) those with prolonged calling and rapid larval development (*Dendropsophus minutus*, *Physalaemus gracilis*, *Scinax squalirostris*) and (iii) explosive breeders with rapid larval development (*Melanophryniscus* spp., *Odontophrynus* spp., *Rhinella* spp.) (Canavero et al. 2010; Zank et al. 2014).

We selected 39 ponds located 11–500 km apart to represent variability in the regional landscape (Fig. 1). The ponds were selected using the following criteria: distance between ponds, presence of dams, pond size and distance from nearest road. We selected ponds that were at least 10 km apart, did not have dams, were within 200 m of the nearest road, and were less than 1 ha. Many of the ponds in the region are modified for pisciculture or by cattle ranching. Because our focus was on natural ponds, we avoided those that had been dammed or dug. Selecting ponds close to roads allowed us to sample more locations and standardize distance to the road, a factor that may affect anuran distribution (Carr and Fahrig
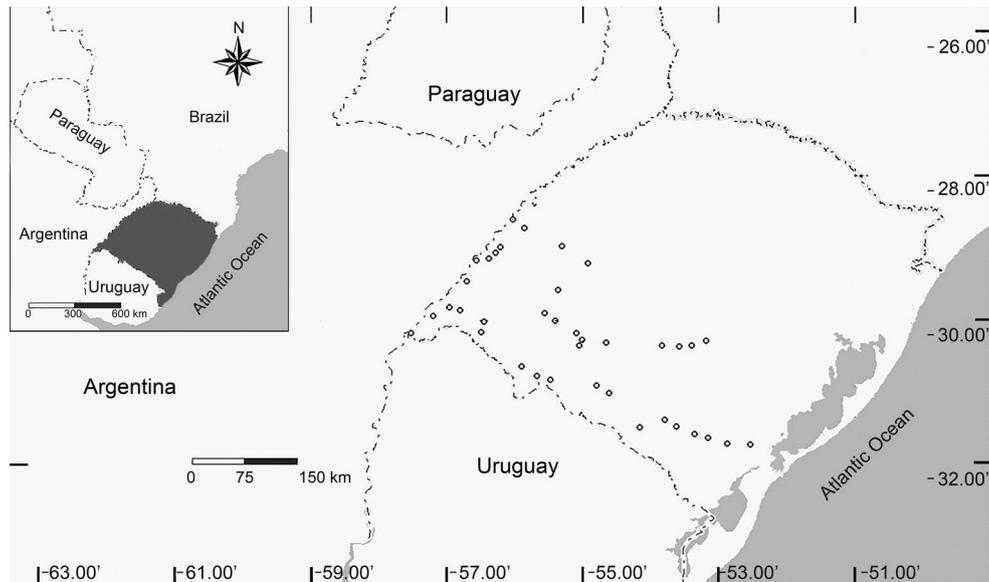
Fig. 1 Location of study region and study sites in the Pampa biome. *Inset* vicinity map; *dark shading* indicates Rio Grande do Sul, in southern Brazil. *Open circles* represent ponds sampled in Rio Grande do Sul

2001). Ponds that matched all these criteria were sampled on four occasions between 2010 and 2012: twice at the end of winter (September 2010 and 2011) and twice at the end of summer (March 2011 and 2012).

Two trained field observers sampled tadpoles in five 50×50 cm plots randomly distributed in each pond (Shaffer et al. 1994). All tadpoles within each plot were removed with a dipnet (10 cm diameter, 250 mm mesh). Each plot sampling ended when no additional tadpoles were captured with 10 sweeps of the dipnet. Collected tadpoles were anaesthetized in a 5 % solution of benzocaine, then immediately fixed in 10 % formaldehyde. Voucher specimens were deposited in the Coleção de Herpetologia of the Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Brazil. Data for pond- and survey-specific factors thought to influence detection probability were collected, based on previous survey programs (Weir et al. 2005; Kroll et al. 2008). These included data related to water temperature, water depth, time of day, date, and type of vegetation cover. Water temperature was measured in three places for each survey, and measurements were taken 15 cm below the water surface. Water depth was measured using a ruler in five places per pond. For water depth and temperature, mean values were used in the analysis. Time of day was registered in minutes from 07:00 h to the end of each survey. Date corresponded to the month and year of the sampling event (e.g. September 2010). Vegetation cover was visually estimated using five classes of aquatic macrophytes (emergent and floating: 0 = no vegetation, 1 = <5 %, 2 = 5–25 %, 3 = 25–75 %, 4 = >75 %).

We also considered local and landscape covariates that could potentially contribute to variation in the site occupancy of amphibian communities (Werner et al. 2009; Silva and Rossa-Feres 2011; Moreira and Maltchik 2012). Pond area was measured in situ in September 2010 using a 100 m tape to measure length and width and extrapolated to full pond size based on the formula of an ellipse (area $= a \times b \times \pi$, where a = maximum pond width and b = maximum pond length). Presence of predatory fishes was recorded during tadpole sampling.

Four landscape covariates were measured within two circular buffer areas (500 and 3000 m radius) centred on each pond, using ArcGIS 10 (Esri 2010). The variables were the proportions of agricultural areas, livestock ranches, and silviculture. We used the soil use classification system developed by the Universidade Federal do Rio Grande do Sul at a scale of 1:250,000 (Hasenack 2006). We transformed the classification scheme into raster (matrix) data with a 5 m resolution (pixel size 5×5 m) and applied the distances for landscape analysis. The classified images were cut into windows and Fragstats 4.1 (McGarigal et al. 2012) was used to extract the area of each class from the processed images. We selected radii of 500 and 3000 m based on estimates of amphibian migration and dispersal (Semlitsch 2008).

For our analysis of occupancy estimates, we used a multi-season occupancy model that explicitly accounts for imperfect detection (MacKenzie et al. 2006). A detection history was constructed for each species, assigning "1" to those sampling plots in which the species was detected, and "0" if not. If a pond dried out, we considered tadpole occupancy as a missing value for that sampling event. We incorporated pond-specific, survey-specific, and landscape covariates for occupancy (ψ) and detection probability (d) into the models through a logit link function. Because our main focus was how occu-

pancy changes, we assumed that the probability of colonization (γ) and probability of extirpation (ε) were constant over the study period. Estimates of the probability of occupancy in sampling seasons were obtained by a smoothing-based method (Weir et al. 2009). We used 100 bootstrap iterations to compute standard errors of derived parameter estimates, as recommended by MacKenzie et al. (2006).

We followed a two step process for building occupancy models (Kroll et al. 2008; Roloff et al. 2011). First, we held occupancy constant while modelling those covariates considered most likely to influence detection probabilities (Table S1). Only species with a detection probability ≥0.15 were used for occupancy modelling. Species with a constant detection probability < 0.15 were deemed unsuitable for unbiased occupancy modelling (O'Connell et al. 2006). Second, we examined nine occupancy models (Table S2) where ψ was allowed to vary with local and landscape covariates using the best model for the probability of detection. We used corrected Akaike's information criteria (AICc; Burnham and Anderson 2002) to rank the candidate models for each species. Because our models were chosen to evaluate factors that we considered would influence parameter estimates, we calculated factor weights to gauge the overall importance of each covariate for each species. The factor weight for a particular covariate was calculated by summing up the AICc weight (w_i) of each model in which the covariate had appeared. Potential correlation of local and landscape covariates were explored to avoid entering combinations of correlated covariates in models. Moran's I analyses (Legendre and Legendre 1998) were used to assess the degree of spatial autocorrelation for each species. Analyses were carried out in the R statistical computing environment (R Development Core Team 2013), and its extension

packages *spdep* (Bivand and Piras 2015), *vegan* (Oksanen et al. 2013), and *unmarked* (Fiske and Chandeler 2011).

Results

Of the 39 ponds with water in the winter of 2010 sampling, only 13 still contained water during the following summer sampling event (Table S3). During the winter 2011 sampling, 22 ponds contained water, and 17 were fully dried-out in the summer 2012. Water temperature was correlated with mean daily temperature (Fig. S1). Nine ponds contained predatory fish (Characidae, Cichlidae, and Erythrynidae). Tables S3 and S4 summarize local and landscape variables. At the fine scale of 500 m, three ponds were surrounded exclusively by steppic savannas.

We recorded 11 anuran species belonging to families Hylidae (06), Leptodactylidae (04), and Odontophrynidae (01) (Table 1). The most frequently encountered species was *H. pulchellus*, encountered in 36 ponds. *D. sanborni* and *P. riograndensis* were the two least frequently encountered species, with one encounter each. In the five ponds with water in 2012, *P. minuta* was the only species recorded. We are able to model occupancy for five species: *D. minutus*, *H. pulchellus*, *O. americanus*, *P. gracilis*, and *S. squalirostris*. Spatial correlation was not included in the occupancy models because Moran's test did not detect significant spatial structure in species occurrence.

Tables S1 and S2 present the full set of ranked candidate models. The best models for detection probability included both pond-specific (floating macrophytes, water depth) and survey-specific (date, temperature) covariates, although the relationship varied from species to species (Table 2). Water temperature explained the

Table 1 Anuran species recorded in 39 farmland ponds, Rio Grande do Sul, Brazil, and corresponding detection probabilities (*d*) for the constant model, from September 2010 to March 2012

Species	*d* (SE)	Number of occurrences				Total[a]
		Sep. 2010	Mar. 2011	Sep. 2011	Mar. 2012	
Hylidae						
Dendropsophus minutus	0.34(0.10)	4	1	1	0	5
Dendropsophus sanborni	0.01(0.01)	1	0	0	0	1
Hypsiboas pulchellus	0.51(0.03)	35	1	10	0	36
Scinax berthae	0.02(0.01)	1	1	0	0	2
Scinax squalirostris	0.27(0.04)	17	3	6	0	18
Pseudis minuta	0.06(0.04)	3	1	2	1	5
Leptodactylidae						
Physalaemus gracilis	0.36(0.09)	7	0	0	0	7
Physalaemus henselii	0.14(0.08)	4	0	2	0	5
Physalaemus riograndensis	0.01(0.01)	0	1	0	0	1
Pseudopaludicola falcipes	0.02(0.01)	2	0	0	0	2
Odontophrynidae						
Odontophrynus americanus	0.29(0.07)	6	0	7	0	13

SE standard error

[a] The total column sums the number of sites where each species was detected at least once

Table 2 Parameter estimates contained in the most well-supported models, selected using AICc (corrected Akaike's information criterion), for factors influencing detection probability

Species and model[a]	ΔAICc	w_i[b]	Evidence ratio[c]
Dendropsophus minutus			
Ψ (.), d (Temperature)	0.00	0.35	
Ψ (.), d (Temperature^2)	0.67	0.25	1.4
Ψ (.), d (− Emergent macrophyte, Temperature)	0.88	0.23	1.5
Hypsiboas pulchellus			
Ψ (.), d (Floating macrophyte, − Temperature)	0.00	0.65	
Ψ (.), d (− Temperature^2)	1.78	0.27	2.4
Odontophrynus americanus			
Ψ (.), d (Date)	0.00	0.65	
Ψ (.), d (Temperature^2)	2.41	0.19	3.4
Physalaemus gracilis			
Ψ (.), d (− Depth)	0.00	0.58	
Ψ (.), d (Emergent macrophyte, Temperature)	3.46	0.10	5.8
Scinax squalirostris			
Ψ (.), d (− Floating macrophyte, Temperature)	0.00	0.94	
Ψ (.), d (− Floating macrophyte)	7.07	0.03	31.3

[a] Ψ indicates the occupancy portion of the model; d denotes the detection portion of the model. (.) The parameter was constant. − indicates a negative relationship

[b] w_i: Akaike model weight. Models with ΔAICc ≥ 2.0 were included in some species only for comparison

[c] Evidence of the best model (ΔAICc = 0) in relation to an alternative model

variation in detection probability for three species with positive effects on detectability found for *D. minutus* and *S. squalirostris*, and a negative association for *H. pulchellus*. The percentage of floating macrophytes contributed to the variation in detection probability for *H. pulchellus* and *S. squalirostris*. The detection probability for *P. gracilis* was negatively associated with water depth. The best models presented considerably high evidence in their favour only for *P. gracilis* and *S. squalirostris* (Table 2). Substantial evidence showed that detection probabilities for *O. americanus* should be modelled as date specific, with the probability of detecting tadpoles during a visit to an occupied pond being about ten times higher in September 2011 than other sampling events (Table 2; Fig. 2). For the other four species, detection probability was not found to be consistently related to sampling date (Fig. 2).

In September 2010, naive occupancy ranged from 0.102 for *D. minutus* to 0.923 for *H. pulchellus* (Table 3). In four species, the best models for occupancy had landscape covariates. With the exception of *O. americanus*, the best models did not receive strong support from our data. The presence of agricultural lands within a 500 m radius had a negative effect on *O. americanus* occupancy. *H. pulchellus* occupancy was positively correlated with livestock within a 500 m radius, although the model weight was modest (0.30). Two other competing models (i.e. ΔAICc ≤ 2) that included only the intercept and presence of predatory fish were identified (Table 3). Agricultural area had a negative effect on *P. gracilis* occupancy for both buffer zones. Models including the 3000 m radius buffer had reasonable support (0.58). For *S. squalirostris*, occupancy was negatively associated with both local and landscape covariates, such as pond area and livestock within 500 m. The presence of predatory fish had a negative effect on occupancy of *D. minutus*. Estimated occupancy by tadpoles varied

widely through time with a marked decline in ponds used for anuran reproduction (Fig. 2).

Discussion

Our analysis demonstrates that tadpole occupancy was correlated with land use for three species (*H. pulchellus, O. americanus*, and *P. gracilis*), while the other species were affected by pond area and the presence of predatory fish. In addition, our results showed detection estimates were more closely associated with habitat characteristics than with species phenology. An increasing number of studies have reported that amphibian communities can be affected by local and landscape features (Ficetola et al. 2009; Silva et al. 2011; Denoël et al. 2013). Local variables, such as aquatic vegetation and predatory fish, were directly associated with tadpole survival or with spawning site selection by adults (Kopp et al. 2006; Prado and Rossa-Feres 2014). Furthermore, landscape effects are frequently interpreted in terms of juvenile and adult habitat use, and connection with tadpole occurrence is indirect (Van Buskirk 2003). For amphibian species in modified landscapes, life traits, such as tadpole survival and dispersal ability of post-metamorphic individuals, are crucial in determining colonization dynamics and extinction thresholds (Fonseca et al. 2013). In this sense, the divergences in anuran detectability and occupancy found in our results were not unexpected, because of differences in individual traits for each species, such as dispersal ability and tadpole adaptability.

Although the Uruguayan savanna has a high anuran richness of about 50 species (Canavero et al. 2010; Maneyro and Carreira 2012), tadpole richness recorded in our study represented around 60 % of species richness observed in farmland ponds of the Pampa (Peltzer et al.
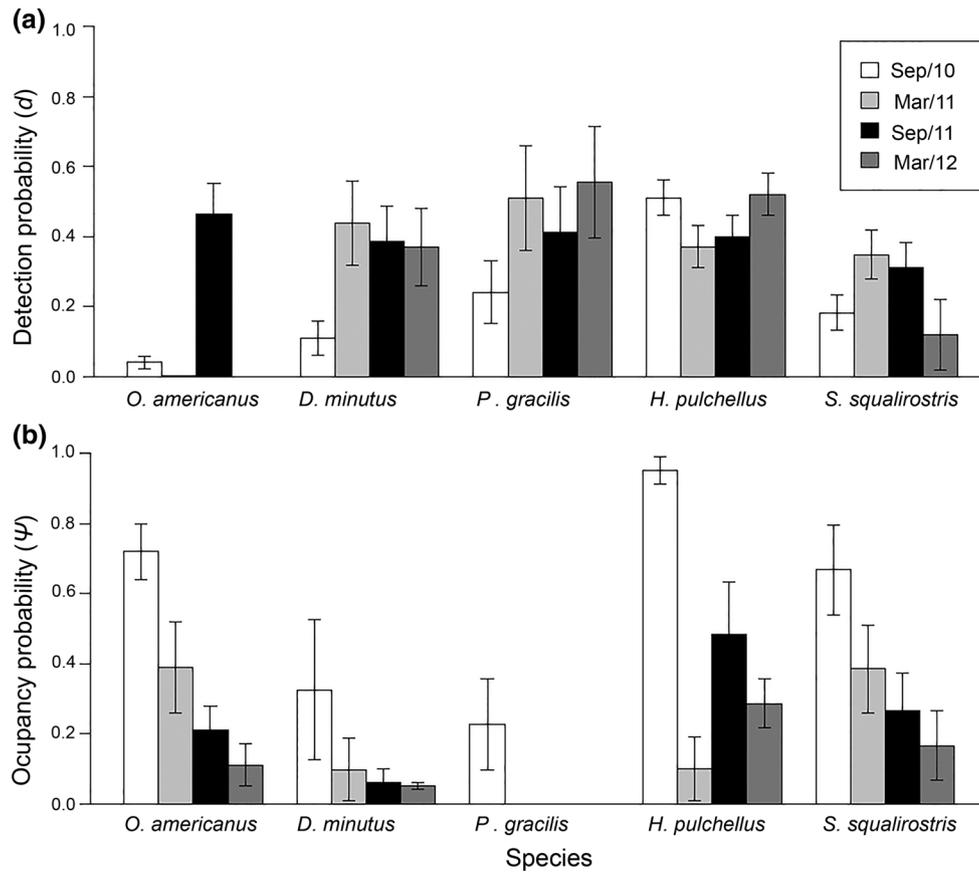
Fig. 2 Detection probability (*d*) and pond occupancy (ψ) estimates for five anuran species across 39 ponds in southern Brazil. *Bars* represent standard errors of 100 bootstrap iterations. See results for a list of full species names

Table 3 Naive occupancy and parameters estimates contained in the most supported models selected using AICc (corrected Akaike's information criterion) for pond occupancy

Species and model[a]	Naive occupancy[b]				ΔAICc	w_i^c
	Sep/2010	Mar/2011	Sep/2011	Mar/2012		
Dendropsophus minutus	0.102	0.077	0.028	0.00		
ψ (− Predatory fish), *d* (Temperature)					0.00	0.32
ψ (.), *d* (Temperature)					0.85	0.21
Hypsiboas pulchellus	0.923	0.077	0.286	0.00		
ψ (Livestock 500 m), *d* (Floating macrophyte, − temperature)					0.00	0.30
ψ (.), *d* (Floating macrophyte, − temperature)					0.15	0.28
ψ (Predatory fish), *d* (Floating macrophyte, − temperature)					1.58	0.14
Odontophrynus americanus	0.154	0.00	0.200	0.00		
ψ (− Agriculture 500 m), *d* (date)					0.00	0.80
ψ (− Silviculture 3000 m), *d* (date)					5.30	0.06
Physalaemus gracilis	0.179	0.00	0.00	0.00		
ψ (− Agriculture 3000 m), *d* (− depth)					0.00	0.58
ψ (− Agriculture 500 m), *d* (− depth)					1.57	0.27
Scinax squalirostris	0.436	0.231	0.171	0.00		
ψ (− Pond area), *d* (− floating macrophyte, temperature)					0.00	0.29
ψ (− livestock 500 m), *d* (− floating macrophyte, temperature)					0.01	0.29
ψ (.), *d* (− floating macrophyte, temperature)					1.11	0.16

[a] ψ indicates the occupancy portion of the model; *d* denotes the detection portion of the model. (.) The parameter was constant. − indicates a negative relationship. 500 and 3000 m correspond to different radii used in landscape cover
[b] Naïve occupancy: proportion of sites where the species was detected at least once
[c] wi: Akaike model weight. Models with ΔAICc ≥ 2.0 were included in some species only for comparison

2006; Bolzan et al. 2014; Moreira and Maltchik 2014). Low richness has been attributed to the ability of only generalist species to persist in agricultural landscapes (Babbitt et al. 2009; Piatti et al. 2010). Indeed, many of the recorded species are widely distributed in southern Brazil and might be considered generalists associated with open areas (Maneyro and Carreira 2012). Adults of the five modelled species give mating calls when they are on waterlogged ground close to grass tufts, and, among macrophytes, up to 0.5 m above water (Moreira et al. 2007). Thus, calling site preferences could explain the occurrence of the studied species in farmland ponds. Furthermore, tadpoles are known to exhibit various different forms of adaptability, including developmental time, swimming ability, and microhabitat preferences (Wells, 2007). For example, tadpoles of *O. americanus* and *P. gracilis* are known to actively select specific portions of the microhabitat based on substrate colour (Scarabotti et al. 2007; Ximenez et al. 2012).

Consistent with our predictions, agriculture negatively affected *O. americanus* and *P. gracilis*. However, the importance of agriculture varied according to the species. Studies on diet from other agricultural areas within the Pampas have shown that tadpoles in agricultural areas consume fewer food items and have poorer body condition than tadpoles from non-cultivated areas (Bionda et al. 2012, 2013). In the neotropics, agrochemical application on many crops tends to be seasonal and concentrated in the early rainy season for various crops (e.g. Schiesari and Grillitsch 2011). Thus, one may reasonably assume that agricultural runoff affects water quality and therefore affects tadpole survival (Peltzer et al. 2008, 2013). We know that the presence of tadpoles depends, at least in part, on the location selected for egg-laying by adults (Eterovick and Ferreira 2008; Kato et al. 2010). In addition, the effects of agricultural practices on anurans differ between different species groups (e.g. fossorial frogs vs. semi-aquatic frogs; Kato et al. 2010; Moreira and Maltchik 2014). Many crop fields are open and bare during spring in southern Brazil. Thus, adults of semi-aquatic species may face a high risk of desiccation during their breeding migrations. Fossorial frogs, such as *O. americanus*, can burrow into the ground, thereby moderating desiccation risks. A failure of adults to reach ponds surrounded by large agricultural areas can indirectly affect tadpole occupancy. This is a plausible explanation for the results for *P. gracilis* in the present study, because adults rely only on soil cracks and crevices to serve as daytime retreats (Moreira and Maltchik 2014).

Many ranches in the Pampa retain a relatively large portion of native vegetation and associated animal species (Pillar et al. 2009). Open areas of low grasslands are likely to represent a hostile matrix for those amphibian species prone to desiccation and with low dispersal ability. However, grazed grasslands constitute a mosaic of intensely grazed plants and tussock grasses that are unattractive to cattle such as shrubby and/or thorny species (Overbeck et al. 2007). The patchy distribution of

shrubs might improve anuran movement ranges by changing microclimate conditions (e.g. lower temperatures, higher humidity). Such patches may provide adequate shelter for some species, such as *H. pulchellus*, that known to use shrubland habitats. In the Pampa, many hylid species (e.g. *D. sanborni*, *H. pulchellus*, *S. squalirostris*) are frequently found in association with *Eryngium* spp. (Apiaceae) and such tall tussock grasses as *Andropogon*, *Cortaderia*, *Eryanthus* species (Peltzer et al. 2006; Maneyro and Carreira 2012). Terrestrial frogs may also benefit from vegetation patches that reduce desiccation risk in open areas (Dorado-Rodrigues et al. 2015). However, trampling by cattle may reduce tadpole survival, and decrease water quality (Jofré et al. 2007; Schmutzer et al. 2008). Since benefits and drawbacks are likely to be specific for different cattle management regimes, we can expect that only species with higher adaptability will be able to occupy ponds surround by areas used for cattle. However, more directed research will be required to identify the most important features involved in this trade-off.

Pond area and the presence of predatory fish are factors that are known to influence amphibian abundance and richness (Werner et al. 2007a; Both et al. 2009). However, these effects interact within a spatial context (pond connectivity). It is also possible that the likelihood of occupation was affected by random factors such as pond hydroperiod because our study was conducted over a broad geographical area. Hydroperiod is an important aspect that helps to determine the composition of amphibian assemblages, especially in temporary ponds (Both et al. 2009; Venne et al. 2012). Aside from the developmental constraints imposed on tadpoles, hydroperiod length influences pond vegetation structure and predation-prey interactions (Wellborn et al. 1996). Predation by fish can be an important factor at small spatial scales (ponds). However, evidence exists that other environmental features, such as habitat structure and number of ponds, are major factors influencing anuran communities at broad spatial scales (Almeida et al. 2014).

Our results related to the effects of temperature and floating macrophytes on *H. pulchellus* and *S. squalirostris* occupation are in agreement with their known natural history. The former usually breeds early in the fall and overwinters as larvae (Maneyro and Carreira 2012). In contrast, *S. squalirostris* usually breeds in spring and overwinters as adults (Martins 2009). In addition, microhabitat selection by tadpoles can be expected to differ if they occupy different positions of the water column (Eterovick and Barata 2006; Both et al. 2011). Benthic tadpoles with dorso-ventrally depressed bodies and low fins, such as *H. pulchellus*, are found mostly at or near the pond bottom. In contrast, nektonic species with high tail fins and laterally compressed bodies, such as *S. squalirostris*, inhabit open water and move through vegetation (McDiarmid and Altig 1999). The presence of vegetation provides concealment from predators and therefore may constitute a positive factor influencing

tadpole survivorship (Kopp et al. 2006). However, habitat complexity may challenge the locomotion of nektonic tadpoles and favour invertebrate ambush predators, such as water bugs and larval dragonflies (Nomura et al. 2011).

Sampling date consistently affected detection only for *O. americanus*. Because this species has explosive breeding periods associated with heavy rainfall (> 50 mm day^{-1}), a boom of tadpoles is expected following a breeding event (Maneyro and Carreira 2012). Thus, our result was not unexpected because detectability often increases with abundance (MacKenzie et al. 2006; Mazerolle et al. 2007). Within the Pampa, the restricted geographical distributions and explosive nature of the breeding behaviour of some species makes them difficult to find for most of the year (Maneyro and Carreira 2012; Zank et al. 2014). For example, occupancy by species with larval periods of 1–2 months, such as *M. atroluteus* and *R. fernandezae*, may be easily overlooked by our sampling design. We acknowledge that some tadpoles may not be available for detection at any given time because breeding has not started or has already finished. Although we identified downward trends for tadpole occupancy, interpretations should be made with caution. In unpredictable temporary ponds, species are expected to experience repeated breeding failures during their lifetime, and short-term studies (such as ours) are insufficient to make consistent predictions. Marked declines in pond occupancy rates and subsequent increases are expected in long-term surveys of amphibians (Werner et al. 2007b; Cayuela et al. 2012).

Our study provided the first estimates of detectability and site occupancy for Pampa anurans. Despite the high uncertainty for some species, incorporating detection probability into our analyses showed that local and landscape factors associated with land use directly affected pond occupancy by tadpoles. We demonstrated that even widely-distributed and generalist species differ markedly in their responses to land use. The differences we observed may relate to variation in natural history between species. Thus, the incorporation of individual traits of each species (tadpole adaptability, habitat preference, and reproductive mode of adults) is fundamental to the creation of more effective conservation strategies in farmlands. From the perspective of environmental degradation, livestock management leads to a change in local vegetation structure, whereas conversion to agriculture promotes structural and chemical degradation of the environment. Grasslands of southern Brazil have exceptional conditions for agricultural expansion, and man-made land transformation is a critical factor that regulates amphibian distribution (Brum et al. 2013). In addition, global warming is likely to alter natural and agricultural ecosystems, causing relocation of some of the major crop producing regions (Lobell et al. 2011). In this sense, the Pampa is likely to receive more extensive agricultural transformation. We hope our results contribute to a deeper analysis of the effects of land use not only on species, but also on the biotic interaction of local and regional anuran assemblages of the Pampa.

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