Frogs taste nice when there are few mice: Do dietary shifts in barn owls result from rapid farming intensification?

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ABSTRACT

Biodiversity ecosystem services in agroecosystems are negatively affected by farmland homogenisation due to intensive agriculture. The Pampas, an important worldwide region producing commodity crops, have been greatly homogenised with the expansion no-tillage and herbicide-tolerant transgenic soybeans since the 1990s. Here, we tested the hypothesis of that dietary changes in barn owls will be associated with the loss of semi-natural habitats derived from farming intensification. We characterised the dietary habits of western barn owls by analysing their pellets between two sampling periods (2004–2005 and 2010–2012). We also assessed the habitat loss due to cropping intensification through fencerow removal and pasture conversion to annual crops during the same period. We observed that barn owls shifted from eating mostly rodents in the first sampling period to eating a higher proportion of anurans in the second sampling period. Between sampling, rodent proportion in pellets decreased from 80% to 61.6%, while anuran proportion increased from 20% to 37.7%. A rapid farming intensification occurred on the farm between both sampling periods. Pastures were ploughed to grow annual crops. Thus, the annually cropped area increased by 60% from 2004 to 2012, while the area with pastures was reduced in about 80%. During the same period, nearly two-thirds of fences on the farm were removed to enlarge the cropped area. Our findings suggest that dietary habits of barn owls may shift to consume more anurans when rodent availability declines in association with the loss of semi-natural habitats, which resulted from rapid farming intensification on the studied farm. We suggest monitoring the population size and diet of barn owls for evaluating environmental changes produced in agroecosystems by farming intensification, as well as the adaptive responses of different rodent and anuran species to such changes.

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1. Introduction

Agricultural intensification has promoted farmland homogenisation, resulting from enlarging cropland area. This was due to fencerow removal to enlarge fields and the conversion of pastures and semi-natural habitats to grow annual crops (Tscharntke et al., 2005). Hence, habitat loss and landscape transformation promoted biodiversity decline, which has impacted on the associated ecological processes (Fahrig et al., 2011). Semi-natural habitats surrounding cropped areas contribute to fulfil many ecological requirements of animal populations (e.g. shelter, feeding areas, movement corridors, and breeding sites), as well as providing habitat for non-crop plants (Marshall and Moonen, 2002; Poggio et al., 2010). However, biodiversity in agroecosystems has been threatened by farming intensification, promoting habitat loss and fragmentation and reducing habitat quality for wildlife (Tscharntke et al., 2005; Fahrig et al., 2011).

The Pampas of Argentina are among the most productive regions worldwide for growing commodity crops, such as soybean, maize, and wheat. Grasslands have dominated the Pampas until around a century ago, being later transformed to mosaics of cultivated fields and pastures. They were interconnected by a network of semi-natural habitats along wire fences, roadsides and streams. Farmlands in this region have been intensely homogenised due to agricultural intensification, particularly since the 1990s, when no-tillage and glyphosate-tolerant, transgenic soybean varieties were rapidly adopted (Baudry et al., 2010).

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In such intensively farmed lands, semi-natural areas along linear landscape features have been identified as key habitats for providing shelter and food for many animal taxa, such as arthropods, birds and small rodents (Hodara and Busch, 2010; Medan et al., 2011; Torretta and Poggio, 2013; Molina et al., 2014). Moreover, small mammals play a key role in food webs in agroecosystems (Medan et al., 2011). Small rodents are omnivorous feeding on seeds, plants and arthropods (Ellis et al., 1998), and they are also prey for foxes (*Pseudolopex gymnocercus*), opossums (*Didelphis albiventris* and *Lutreolina crassicaudata*), ferrets (*Galactis cuja*), feral cats (*Leopardus geoffroyi* and *L. colocolo*), and avian raptors as owls (Medan et al., 2011).

The western barn owl (*Tyto alba* Scopoli 1769, Birds, Tytonidae), the most commonly studied avian raptor worldwide (Marks et al., 1999), is an opportunistic predator, even though it feeds mostly on small mammals in southern South America (Teta et al., 2012). Barn owls can be expected to choose the prey species that are most profitable (i.e. nutrients obtained versus energy expended for hunting) to be an optimal forager (Love et al., 2000). Barn owls feeding strategy is based on food availability (Bellocq, 2000; Taylor, 2004), and can easily switch among prey species when availability changes (Taylor, 2004; Marti, 2010). Rodent proportion in the barn owl diet varies seasonally and regionally according to human activities prevailing in the region (Massa et al., 2014). Barn owl diet comprises more than 90% of rodents during winter, when rodent population density increases, whereas the rodent proportion measured in pellets decreases to 80% in warmer seasons, when amphibians, birds, arthropods and other mammal taxa (small lagomorphs and marsupials) are more abundant (Bellocq and Kravetz, 1993; González Fischer et al., 2011). Native small rodents have been abundant in the composition of barn owl pellets collected in agricultural and undisturbed areas of central Argentina (Bellocq, 2000; Leveau et al., 2006; González Fischer et al., 2011). However, little is known about the extent of shifts in barn owl dietary habits due to rapid agricultural intensification.

Our study was motivated by the observation of unexpected dietary changes in western barn owls. We noticed a lower proportion of rodent bones in barn owl pellets than in previous records for the Pampas (ca. 80%, Bellocq and Kravetz, 1993), in particular for the Inland Pampa (ca. 98% in winter and 80% in summer, González Fischer et al., 2011), where our study site was located. Therefore, we hypothesised that dietary changes in barn owls will be associated with the loss of semi-natural habitats derived from the rapid farming intensification in the study site. Habitat loss due to cropping intensification was assessed through both fencerow removal and pasture conversion to annual crops during the studied period. Our findings provide valuable information to better understand the impact of agricultural intensification on complex food webs in agroecosystems.

2. Methods

2.1. Study area

The study was conducted at a farm belonging to the University of Buenos Aires (Estancia San Claudio, 5442.92 ha), located in the Inland Pampa (35 53′S, 61 12′W, Province of Buenos Aires, Argentina). Climate is temperate sub-humid. Mean temperature ranges between 8.2 °C in winter (July) and 23.4 °C in summer (January). Mean annual rainfall is 1090 mm. Rains are homogeneously distributed throughout the year, without either marked wet seasons or severe droughts. Annual precipitation records measured at the farm varied between 699 and 828 mm during the first sampling session (2004–2005), while they ranged between 738 and 931 mm for the second (2010–2012). Soils are Typic Hapludolls with deep, well drained top horizons, rich in organic matter (2.5%).

Pristine grasslands have been fragmented by farming and transformed into farmlands. Farmland mosaics mainly consist of mixtures of crop fields and grazing paddocks, delimited and interconnected by narrow vegetation corridor networks associated with fencerows, roadsides and streams. Remnant native grasslands are restricted to linear semi-natural vegetation along railways, roadsides, fencerows and field margins (Poggio et al., 2010, 2013), as well as old fields or successional pastures (Tognetti et al., 2010). Mixed plant communities are currently dominated by naturalised weedy grasses (*Festuca arundinacea, Cynodon dactylon, Sorghum halepense* and *Lolium multiflorum*), exotic tall forbs (*Carduus acanthoides* and *Conium maculatum*), and native tussock grasses, such as *Paspalum quadrifarium*, *Bromus catharticus* and *Deyeuxia viridiflavescens*.

Field crops on the farm are sown using no-till practices, being maize and soybean the prevailing summer crops. While soybean represented less than 16% of the farm area in the early 2000s, it increased nearly to 40% by 2012. Both maize and soybean markedly differ in their agronomic management, particularly regarding herbicide and fertiliser applications (Poggio et al., 2013).

2.2. Data collection

Dietary habits of western barn owls were characterised by collecting and analysing their pellets with the procedure summarised by Marti (1987). Assuming that owls hunt according to prey species availability, prey items found in pellets are a reliable indicator of the seasonal variation in prey availability within the hunting range of owls in agricultural agroecosystems (Marti, 2010; González Fischer et al., 2011). Previous studies in the Pampas collected pellets in precarious and abandoned buildings, mills, water reservoirs, silos and palm trees surrounding rural dwellings (Teta et al., 2012). Pellets were not found in any other locations in the study site, despite several intensive searches during both sampling periods. Pellets were collected in the same sites during both sampling periods and their total numbers were recorded for each sampling site. Each pellet was manually dissected and then immersed in a Sodium hydroxide solution to dissolve soft materials, such as fur and feathers. Finally, the recovered skeletal materials were washed in water and dried. Mammalian skeletal remains were identified to species by examining skulls and teeth (Pardiñas et al., 2010). Abundance of each mammalian species was determined by counting the number of skulls or pairs of lower mandibles. Birds and anurans were determined by counting pairs of humeri and femurs, respectively.

2.3. Data analysis

Number of prey individuals per species or taxa was divided by the number of owl pellets collected at each site to obtain statistically comparable data. Goodness-of-Fit test was used to compare prey proportions consumed during the 2010–2012 with values previously documented for barn owls in the Inland Pampa (80% rodents in summer, see González Fischer et al., 2011). Frequency distributions of rodent species in barn owl pellets in autumn were compared between sampling periods by using a Chi Square Test for Homogeneity (χ^2).

Seasonal and sampling period effects on proportions of anurans in barn owl pellets were analysed with a generalised linear mixed model (GLMM with a binomial distribution). The model included two main fixed factors: season (spring-summer and autumn) and period (2004–2005 and 2010–2012). Pellets collection sites were included as a random factor. The GLMM analysis was conducted by using the *glmer* function (*lme4* package, R Development Core Team, 2014). The Akaike Information Criterion (AIC) was used for choosing the best-fitting model as a minimal adequate one. Thus,

the model with the lowest AIC value was selected. The analysis was performed with R 3.0.3 (R Development Core Team, 2014). Significance was set at $P < 0.05$ level in the analysis.

3. Results

All rodent species identified in owl pellets were native Sigmodontinae (*Akodon azarae*, *Calomys laucha*, *C. musculinus*, and *Oligoryzomys flavescens*). A total of 782 prey-items (630 rodents, comprising 72.5% *Calomys* spp., 13.5% *O. flavescens*, and 15.0% *A. azarae*, and 152 anurans), which were identified from 156 owl pellets collected in 10 sites visited during 2004–2005 (Table 1). Total prey-items were 2882 in 2010–2012 (1776 rodents, comprising 79.7% *Calomys spp.*, 5.1% *O. flavescens*, and 15.2% *A. azarae*, 1087 anurans and 19 birds), which were identified in 478 owl pellets collected at 11 sites (Table 1).

3.1. Shift in barn owl diet between samplings

Number of prey-items per pellet (mean ± SE) was lower in the first than in the second sampling period (5 ± 1.0 and 6 ± 1.0). Average item number per pellet was 4.4 ± 2.1 and 2.3 in autumn of each sampling periods, whereas the number per pellet increased during spring from 5.7 ± 2.1 in 2004 to 7.4 ± 2.1 in 2010–2012.

Rodent proportions in owl pellets changed between sampling periods. Prey-items in pellets collected in 2004–2005 comprised 80% rodents and 20% anurans (Table 1). However, prey-item proportions changed in the second sampling (61.6% rodents, 37.7% anurans, and 0.7% birds), which significantly differed from the values historically documented for the Inland Pampa ($\chi^2 = 577.6$, d.f. = 1, P < 0.0001, Table 1). Frequency distributions of rodent species consumed by barn owls differed between sampling periods during autumn ($\chi^2 = 17.41$, d.f. = 2, P < 0.001). *A. azarae* was consumed less frequently than expected, while *Calomys* spp. was consumed than expected.

Anuran proportion in barn owl pellets significantly differed between seasons depending on the period (GLMM Season–Period $\chi^2_{(1)} = 50.41$, P < 0.0001, see Table 1). Greater anuran proportion was consumed during spring-summer 2010–2012 in comparison to both spring-summer 2004–2005 and autumn during both periods.

3.2. Loss of semi-natural habitats due to rapid farming intensification

A rapid farming intensification occurred on the farm between both sampling periods. Pastures were ploughed to grow annual crops. Thus, the annually cropped area increased by 60% from 2004 to 2012, while the area with pastures was reduced in about 80% (Table 2). During the same period, nearly two-thirds of fences on the farm were removed to enlarge the cropped area (Table 2). Annual cropping and fence removal rapidly homogenised the landscape, which was sown mainly with soybean, thus reducing semi-natural habitats for wild flora and fauna. Hence, habitat loss due to cropping intensification between both samplings was from 0.24% to 0.08% in fencerows, and from 43% to 14% in uncropped

areas, which mostly resulted from pasture ploughing. Consequently, the crop field proportion increased from 50% to 80% between both samplings (Table 2).

4. Discussion

We observed from our results that barn owls shifted from eating mostly rodents in the first sampling period to eating a higher proportion of anurans in the second sampling period, when barn owls consumed 53.5% anurans in spring and summer (Table 1). This percentage was three times higher than the values documented for the Inland Pampa (17%, González Fischer et al., 2011) and twice those obtained in the first sampling session (27.2%, Table 1). Our findings do not support those by Roulin and Dubey (2013), who concluded that barn owls rarely capture amphibians because they apparently have not developed such ability.

High anuran consumption in our study can be attributed to two possible reasons. Western barn owls usually hunt rodents along patches covered in tall and dense vegetation, where owls are more likely to find and capture rodents (Bellocq and Kravetz, 1990). Because of landscape homogenisation, vegetation cover in field margins has been reduced or even removed, which associated with reductions in rodent abundance in these habitats, particularly during spring and summer (Hodara and Busch, 2010). As rodent availability changes, barn owls respond to the lower rodent abundances by changing their diet, consuming more anurans. Anurans usually feed on arthropods within fields, but cropped areas are unfavourable habitats for anurans due to pesticides, desiccation and predation, which increase mortality rates (Attademo et al., 2005). Conversely, ponds with shore vegetation and semi-natural field margins intermingled in homogeneous soybean croplands provide favourable habitats for anurans. These habitats ensure survival and reproductive success in anurans, because they provide water, shelters, calling sites, refuge from pesticide contamination, and oviposition sites.

Barn owls consumed more anurans due to lower rodent availability, even though hunting anurans demands greater foraging effort in relation to nutrition and energy gained when compared to rodents. More prey items per pellet may indicate more time spent hunting, as well as consuming a larger number of less nutritive preys. Body size of rodent species consumed varied between 12 and 35 g, while anuran species in Pampean agroecosystems are much lighter than rodents. Adult individuals of most anuran species weigh less than 10 g, with the exception of *Odontophrynus americanus* with an average weight of 20 g and *Rhinella arenarum* with more than 40 g (Attademo et al., 2005). Furthermore, as anurans live in exposed places surrounding cropped areas and undisturbed patches, they may be easier to catch than rodents sheltered in dense vegetation.

Western barn owls preferentially consumed *Calomys* spp. during autumn, which is consistent with previous results (Teta et al., 2012). Preference of barn owls for native sigmodontine rodents is well documented for agricultural areas of central Argentina (Bellocq, 2000; González Fischer et al., 2011; Teta et al., 2012). In addition, field margins have been identified as preferred

Table 1
Percentages of seasonal composition of western barn owl diet of agroecosystems in the Inland Pampa during 2004–2005 and 2010–2012 periods. n = individuals consumed. Mean percentages and standard errors are in parenthesis.

Period	2004–2005		2010–2012	
	Spring (n = 412)	Autumn (n = 370)	Spring/Summer (n = 1933)	Autumn (n = 949)
Rodents	72.8 (71.1 ± 7.69)	89.2 (86.5 ± 3.15)	45.8 (45.3 ± 8.97)	93.9 (91.1 ± 2.79)
Anurans	27.2 (28.9 ± 7.69)	10.8 (13.5 ± 3.15)	53.5 (54.0 ± 8.95)	5.5 (6.8 ± 2.43)
Birds	–	–	0.7 (0.7 ± 0.21)	0.6 (2.1 ± 1.11)

Table 2
Representativeness and changes of the main landscape elements in the agricultural mosaic during the two sampling periods (Farm area: 5442.92 ha) conducted on a farm in Buenos Aires Province, Argentina.

Land use type	2004–2005		2010–2012	
	Area (ha)	(%)	Area (ha)	(%)
Annual crops	2725.8	50.08	4359.2	80.08
Pastures	1957.2	35.96	417.2	7.66
Grazed semi-natural grasslands	359.2	6.60	359.2	6.60
Dwellings and woodlots	134.0	2.46	134.0	2.46
Ponds and water bodies	246.8	4.53	162.6	3.0
Fencerows (internal)	13.3 (66641 m)	0.24	4.2 (21191 m)	0.08
Fencerows (perimeter)	6.6 (32942 m)	0.12	6.6 (32942 m)	0.12

habitats by rodents (Hodara and Busch, 2006). However, the impressive expansion of soybean in the last two decades has been associated with the progressive removal of field margins to extend croplands. Thus, *Calomys* individuals would not only have become more abundant preys for barn owls, but also highly vulnerable to these avian predators. While the increase in cropped land may have favoured the growth and spread of *Calomys* spp. populations (Teta et al., 2010), land use intensification has increased predation risk for *Calomys* spp., while reducing food availability, foraging efficiency and movements, all of which result from lack of shelter due to low vegetation cover (Jacob, 2008; Fraschina et al., 2009). Barn owls consumed lower proportion of *A. azarae* than those observed for *Calomys* spp. These differences can be explained by the removal of pastures (80%) and fencerows by about two thirds between 2004 and 2012 (Table 2). Because fencerows and their semi-natural vegetation associated are reported as the selected habitats for hunting by barn owls (Bellocq and Kravetz, 1990).

Landscape changes may have negatively affected the interaction between rodent prey availability and dietary habits of barn owls. Heterogeneous, complex farmlands usually support higher small mammal abundance than homogeneous and intensively cropped farmlands (Fischer et al., 2011). Similar response patterns were observed in small mammal communities due to changes in agricultural landscapes in western France (Millán de la Peña et al., 2003; Michel et al., 2006).

5. Conclusions

Our findings suggest that dietary habits of barn owls may shift to consume more anurans when rodent availability declines in association with the loss of semi-natural habitats, which resulted from rapid farming intensification on the studied farm. Barn owls switched their feeding strategies by increasing anuran consumption to compensate for the scarcity of the preferred rodent preys. Fencerows remaining in the region are key elements for biodiversity conservation in the intensively managed agroecosystems prevailing in the Pampas (Poggio et al., 2010). Nonetheless, fencerows have become scarce and disconnected, thus decreasing rodent survival and, probably, preventing rodent movement in intensively farmed landscapes. We suggest monitoring the population size and diet of barn owls for evaluating environmental changes produced in agroecosystems by farming intensification, as well as the adaptive responses of different rodent and anuran species to such changes.

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