GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

The paradox of invasion in birds: competitive superiority or ecological opportunism?

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Abstract Why can alien species succeed in environments to which they have had no opportunity to adapt and even become more abundant than many native species? Ecological theory suggests two main possible answers for this paradox: competitive superiority of exotic species over native species and opportunistic use of ecological opportunities derived from human activities. We tested these hypotheses in birds combining field observations and experiments along gradients of urbanization in New South Wales (Australia). Five exotic species attained densities in the study area comparable to those of the most abundant native species, and hence provided a case for the invasion paradox. The success of these alien birds was not primarily associated with a competitive superiority over native species: the most successful invaders were smaller and less aggressive than their main native competitors, and were generally excluded from artificially created food patches where competition was high. More importantly, exotic birds were primarily restricted to urban environments, where the diversity and abundance of native species were low. This finding agrees with previous studies and indicates that exotic and native species rarely interact in nature. Observations and experiments in the field revealed that the few native species that exploit the most urbanized environments tended to be opportunistic foragers, adaptations that should facilitate survival in places where disturbances by humans are frequent and natural vegetation has been replaced by man-made structures. Successful invaders also shared these features, suggesting that their success is not a paradox but can be explained by their capacity to exploit ecological opportunities that most native species rarely use.

Keywords Colonization · Ecological niche · Behavioral flexibility · Community assemblage · Urbanization

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Introduction

Coming from distant regions, invaders are often confronted with a variety of new environmental challenges to which they are unlikely to be fully adapted. It is not surprising then that most human-mediated past introductions of plants and animals have failed to establish self-sustaining populations (Williamson and Fitter 1996). Nevertheless, despite the inherent difficulty of invading a new region, a selected number of species appears to be extremely successful wherever they are introduced and often can even become more abundant than most native species (Williamson 1996; Blackburn et al. 2009). The reasons for this puzzling observation, referred to as the invasion paradox by Sax and Brown (2000), are not yet fully understood, although some possibilities have been advanced (see below).

The success of a species in a novel environment is likely to depend on a variety of factors, including natural enemies and the physical environment (Shea and Chesson 2002; Duncan et al. 2003; Blackburn et al. 2009; MacLeod et al. 2009), but one that is critical to ensure survival and reproduction is resource availability (Tilman 2004). Invaders can acquire resources by either displacing native species from those available or exploiting resources that are little used by native species (Tilman 2004; Vilà et al. 2005; Bando 2006). This suggests two main pathways to succeeding in new environments. The first is to behave aggressively over the available resources so as to displace locally adapted native species from their niches ("competition hypothesis", hereafter). The second is to exploit niche opportunities generated by human activities that most native species are incapable of using ("opportunism" hypothesis). Although there is some evidence for the case-by-case importance of the competition and opportunism hypotheses (Holway et al. 2002; Vilà et al. 2005), there has been little effort to investigate to what extent either of these hypotheses provides a solution to the invasion paradox.

Here, we contrast the competition and opportunism hypotheses with an analysis of birds from New South Wales (NSW, Australia). In birds, there is little evidence that competition or attributes associated with competition such as body size influence establishment success (reviewed in Duncan et al. 2003; Blackburn et al. 2009). In contrast, the opportunism hypothesis has gained credence from two macroecological observations. First, exotic birds are frequently restricted to human-modified habitats—mainly urbanized habitats and agricultural areas—which offer new ecological opportunities yet contain few native competitors (Diamond and Veitch 1981; Case 1996; Blair 2001). Second, the species' attributes that best identify successful invaders are ecological generalism and foraging flexibility (Mclain et al. 1995; Cassey et al. 2004; Sol et al. 2005, 2008), properties that should facilitate the exploitation of novel foraging opportunities.

However, the above macroecological observations are by themselves insufficient to resolve the invasion paradox, because what counts ultimately is how exotic and native birds interact over the resources available in the recipient region, and this is seldom considered and rarely documented in the literature (but see MacLeod et al. 2009). Thus, there is an urgent need for studies at relatively finer scales in which the interactions between exotic and native species over resources may be assessed. Our study seeks to address this by combining field observations and experiments along gradients of urbanization. The field observations served to assess whether and how exotic and native birds interact within habitats and overlap in resource use. The field experiments were designed to test for differences between exotic and native birds in their ability to compete

for food, to adopt new foraging opportunities and to tolerate feeding close to humans. Combined with previous evidence from broader comparative analyses (reviewed in Duncan et al. 2003; Blackburn et al. 2009), our findings support Sax and Brown's (2000) view that, rather than competitive superiority, the success of invaders is primarily attributable to their ability to exploit ecological opportunities that most native species cannot.

Materials and methods

Study area

NSW Australia provides an excellent opportunity to contrast possible solutions to the invasions paradox. On the one hand, the process of urbanization is relatively recent, leaving intact remnants of natural bush that maintain a high diversity of native birds (Major et al. 2001). On the other hand, some of the most abundant birds are alien species (Duncan et al. 2001; Barrett et al. 2003), making a case for the invasion paradox.

Our study area was centred in Newcastle, a city on the eastern coast of Australia, with the limits being Sydney to the south, Nelson Bay to the north, and the Blue Mountains to the interior (see Table S1 in the Electronic Supplementary Material). Field work was carried out from June to August 2007, a period during which many native birds start or are ready to start reproduction. Because most common species in the studied area were resident, and because the temperatures in the region rarely fall below 10°C, the results should be little affected by seasonal changes. We focused our attention on terrestrial species, as introductions of marine birds are very rare (Lever 2006).

Field surveys and observations

To estimate the abundance of exotic and native birds and assess the way they use available resources, we identified 24 gradients of urbanization at least 500 m apart, each extending from the downtown city core to relatively undisturbed wildland areas. In each gradient, we distinguished three habitats: (1) commercial and residential areas dominated by buildings (urban habitat), (2) suburbs dominated by lawns, shrubs and trees (suburbs), and (3) bush fragments where native vegetation predominated (wildland). Thus, these habitats fundamentally differed in the degree of human frequentation and the availability of natural vegetation. We recorded the number of birds observed in transects well within each habitat type during 20 min within a 50-m belt. Most species were recorded by sight although some particularly secretive native species

were identified by sound. A single count was carried out in each of the habitats within each gradient on the same day, either in the morning or the evening, taking care to randomize the order in which each habitat was prospected. The list of species, with scientific names and abundances, are presented in the online appendix (Table S2).

For each solitary bird observed, we also noted its main behavior (feeding, resting, preening, sexual display) during a 15-s focal observation period. When we observed a group, the focal observation was restricted to a single individual selected at random, noting also the number of individuals in the group. If the bird was observed feeding, we noted whether it was feeding on natural food (insects, fruits, flowers, seeds, or plant matter) or on food deliberately or accidentally provided by humans (food remains, waste, food available in feeding stations, or food directly provided by people). During the transects, we also noted all agonistic interactions (i.e. supplanting attacks and aggressions) between native and exotic birds.

Field experiments

The competition hypothesis focuses on contest competition over resources rather than on exploitation competition, as from a theoretical point of view it is unlikely that a species that has not evolved in an environment is more proficient in exploiting the resources than native species that have had more opportunity to adapt. If exotic species were competitively superior to native species, we would expect them to be more capable of monopolizing defendable food patches. To test this prediction, we conducted a food competition experiment (competition experiment, hereafter) in 15 open areas within gardens (experimental site, hereafter) in which native and exotic birds coexisted. At each site, we ran a test in which we deposited a pile of food distributed within a 2-m-diameter circle and waited until both exotic and native species were attracted to feed. We used a mixture of seeds and dog pellets in order to increase the range of species potentially interested. When at least one native and one exotic species had been attracted to the patch, we monitored focal individuals for a maximum of 1 min, noting the seconds the individual was either inside or outside the food patch. The proportion of time spend inside the patch was used to assess whether individuals had access or not to the new food opportunity. In two of the gardens, we only attracted common mynas and consequently these tests were excluded from the analyses. The analyses were based on 274 focal observations on 4 exotic species and 11 native species.

The alternative to the competition hypothesis is that exotic species take advantage of opportunistic food resources derived from human activities. To investigate opportunistic foraging, we ran two types of field experiments in each habitat of the urbanization gradients. In the first experiment (food opportunity experiment, hereafter), we located a foraging bird and dropped small pieces of bread to attract it. We used bread because this is one of the food opportunities more likely to be found in human settlements. We noted whether the individual responded or not to the food opportunity. If it responded, we recorded the time until a piece of bread was handled. The experiment was capped after 3 min. To control for motivation and other confounds, we noted the time of day, gradient and group size for each experiment. We carried out 124 tests in five exotic species and 106 tests in 13 native species.

The capacity of animals to feed close to humans should also be one of the main behavioral demands of urban habitats (Fernández-Juricic et al. 2001; Blumstein 2006; Møller 2009). Birds incapable of reducing the fear to humans are unlikely to succeed in establishing themselves in urban habitats (Møller 2009). Avoidance of human presence was evaluated by measuring flight distances in response to an approaching human (Fernández-Juricic et al. 2001). When an individual was located foraging on the ground, the observer moved at a normal walking speed towards the individual and recorded with a meter the distance at which the individual took flight. We also noted the location, time of day and group size, as well as the type of habitat. We obtained 163 measures of flight distance for 5 exotic bird species, plus 207 measures for 29 native species.

Analyses

We used two main approaches to analyze the data: generalized linear mixed models (Bates and Martin 2009; Bolker et al. 2009; Zuur et al. 2009) and conditional classification trees (Crawley 2002; Hothorn et al. 2006).

Generalized linear mixed models

The generalized linear mixed model (GLMM) framework was used to deal with the possible lack of statistical independence on the data due to the clustering of observations within species, higher taxonomic levels, and geographic location. This approach also allowed us to deal with two additional difficulties of the field experiments. First, differences in behavior across habitats were expected to be found both within and between species, and hence these two levels of variation had to be taken into account in the analyses. Second, observations of behavior across species led to unbalanced samples, reflecting the fact that some species were more abundant and/or more active than others.

We used the R package "lme4" to build the GLMMs (Bates and Martin 2009), using Laplace approximations to estimate the parameters (Bolker et al. 2009). Differences in AIC were used to define the optimal structure of the random component in full models (i.e. with all fixed and random effects) fitted with REML (function "lmer") for Gaussian models and with maximum likelihood (function "glmer") for binomial and Poisson models (Bolker et al. 2009). In some cases, the inclusion of random factors did not improve the fit of the model, and hence we used generalized linear models instead. The variables of interest plus a set of nuisance variables were included as fixed factors, along with the interactions between them and with the random effects. The structure of fixed effects was simplified by removing those nuisance variables and interactions that were non-significantly associated with the response variable, according to a Wald t test (Bolker et al. 2009). Below, we detail the type of model and the full structure of fixed and random effects used for each response variable; the minimum adequate models (MAM) are presented in the "Results".

Changes across the urbanization gradient in native species richness were modeled with a Poisson error and log-link (Crawley 2002). The response variable was the number of native species recorded per habitat in each transect. Habitat and hour were coded as fixed effects whereas gradient and date were considered random effects.

The proportion of exotic species relative to native species was modeled in a similar way as native species richness, yet, because the response was binomial in this case, we used a binomial error structure and a logit link (Crawley 2002).

Changes in abundance of exotic and native species along the urbanization gradient were modeled with GLMM with Poisson error structure and log-link (Crawley 2002). The response variable was the total abundance of each species (i.e. sum of all individuals of each species observed) in each habitat. The full model included status (exotic vs. native), habitat (urban, suburban and wildland) and the interaction between these two variables as fixed factors, and taxonomic variables (order, family, and species, in a nested structure) as random factors.

For the competition experiment, the response variable was the proportion of seconds the focal individual spent inside the patch. We modeled this response with a GLMM with binomial errors and logit link. The status of the species (i.e. exotic vs. native) was included in the full model as a fixed effect along with hour of the observation and size of the group as nuisance variables. The clustering of observations within experimental sites, dates and the taxonomic hierarchy (species nested within families, and families nested within orders) was modeled by including these variables as random factors.

In the food opportunity experiment, the response variable was whether the focal birds ate or not the food. The latency to eat the food was not used because many birds did not respond to the stimulus, making the variable right-censored. We modeled the binary response variable with a GLMM with binomial errors and logit link. Each bird tested was classified in one of four categories (urbanized exotic, urbanized native, non-urbanized exotic, non-urbanized native), and this variable was included as a fixed effect in the full model along with nuisance variables (hour and group size). The structure of random effects included gradient, date of the observation, and the taxonomy (species nested within families, and families nested within orders).

Finally, the flight distances were modeled using a similar structure of fixed and random effects to that used for the food opportunity experiment, but in this case we used the function "lmer" to fit a GLMM with a Gaussian error and a log-link.

For all the above models, diagnostic plots were examined to check for outliers and heteroscedasticity. In two of the models (see "Results"), we detected autocorrelation in the observations within gradients. Even when we included gradient in the model as random factor, this did not correct for spatial autocorrelation due to the spatial distribution of the gradients. To assess whether this source of spatial autocorrelation was important, we used the geographic coordinates of each transect to calculate the Moran's I for the residuals of the models, using the package Ape (Paradis 2006). We found no evidence for spatial autocorrelation in any of the models (probability of Moran's I being different from random = 0.52 and 0.89, respectively), indicating no need for further corrections besides adding gradient as random factor (Crawley 2002).

For some scarce species, we failed to obtain enough experimental data. To test whether the resulting model parameters and significances were robust, we repeated the analyses (1) excluding species with five or less observations, and (2) using Markov chain Monte Carlo simulations (MCMC), based on "MCMCglmm" packages (Hadfield 2010). For the MCMC analyses, we used both default priors and informative priors (Hadfield 2010; see details in the ESM). The results were insensitive to the type of prior used, and in the ESM we present those obtained with the informative priors.

Conditional classification tree

The conditional classification tree approach (Crawley 2002; Hothorn et al. 2006) was used as an heuristic tool to identify differences between exotic and native birds in the way they exploited the resources. Conditional trees estimate a regression relationship by binary recursive

partitioning, and repartition is shown as bar plots in the terminal nodes (Hothorn et al. 2006). The advantage of the tree classification approach is that it allows one to identify complex interactions between variables that are difficult to detect with linear modeling approaches. We developed our classification tree with the function "ctree" available in the R package "Party" (Hothorn et al. 2006). Our response variable was status (exotic vs. native) and the predictors were the habitat (wildland, suburbs and urban) and type of food (natural, accidentally derived from human activities and deliberately provided by humans). As species on which we recorded more observations would have an undue weight on the outcome, we weighted each observation by the inverse of the number of observations for that species (Steinberg and Colla 1995).

Results

Five of the most abundant species in the study area were exotic: common myna, feral pigeon, house sparrow, European starling and spotted turtle-dove (Figs. S1, S2). These successful invaders, which have also been extremely successful in other regions within and outside Australia (Lever 2006), are the ones that pose a challenge to ecological theory, and are thus the primary focus of the subsequent analyses.

Competition hypothesis

If exotic species were competitively superior to native species, they should be more capable of exploiting experimental food patches where contest competition is high. Our competition experiments revealed that, in contrast, the proportion of time spent inside the food patch was not higher for exotic species than it was for native species (binomial GLMM, with experimental site and species as random factors: Wald test, $z = 1.54$, $P = 0.12$; Table S3; Fig. 1a). Using as a null model the average proportion of time spent by focal birds in the centre of the patch (mean = 0.37, bootstrapped 95% confidence interval: 0.319–0.429), the probability of finding an exotic species in the centre was lower than expected for all the exotic species but the feral pigeon (common myna: $P = 0.029$; starling: $P < 0.001$; the turtle-dove: $P < 0.001$; and feral pigeon: $P = 0.5$; Fig. 1a). This lack of success in monopolizing the food patch was unsurprising given that most exotic species were small relative to the most successful native competitors (Fig. 1b). The house sparrow was the only species that was never observed trying to use the experimental food patch, despite being present in nearby trees in three of the experimental sites and readily responding to novel food opportunities when alone (see below).

Field observations also revealed that, while some native species (notably Australian magpie, noisy miner and Australian raven) were very aggressive towards other species over food resources, exotic species rarely initiated disputes, and, furthermore, were frequently displaced from foraging sites by more aggressive species (Fig. 2; Table S4). For example, the common myna, which was the most abundant exotic species in the region (Fig. S2), was attacked more frequently by Australian magpies than the reverse (21 attacks received out of 22 interactions between both species), and did not win any encounter. Again, the house sparrow was the only exotic never observed interacting with native species, but this was to be expected given that the most aggressive invaders were much larger. The only exotic species that could perhaps be regarded as an aggressive competitor was the feral pigeon, the largest exotic species in the region, which was capable of monopolizing resources in urban habitats and was often observed displacing native species such as Australian magpies and silver gulls (Fig. 2).

Fig. 1 Proportion of time spent at the centre of the artificial food patch over all field experiments (**a**) and mean body mass (g) taken from the literature (**b**) for native and exotic species. *Asterisks* indicate alien species
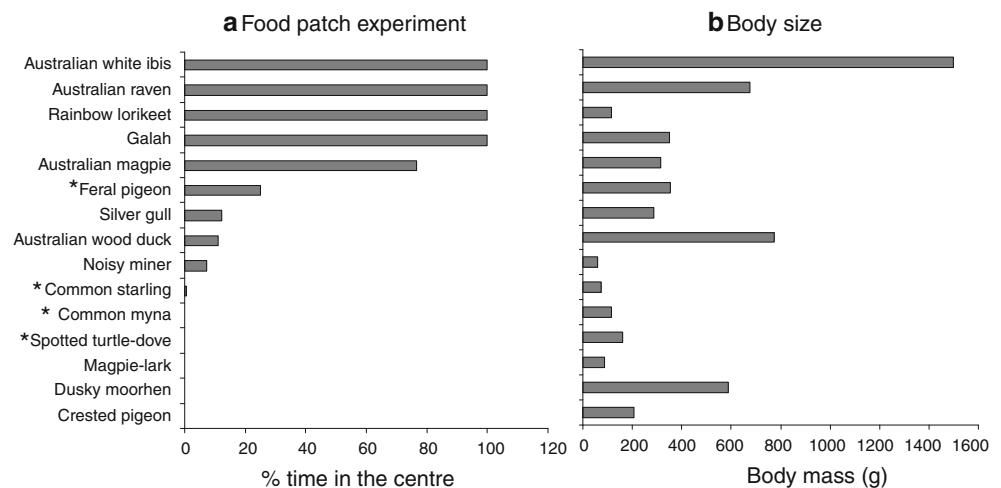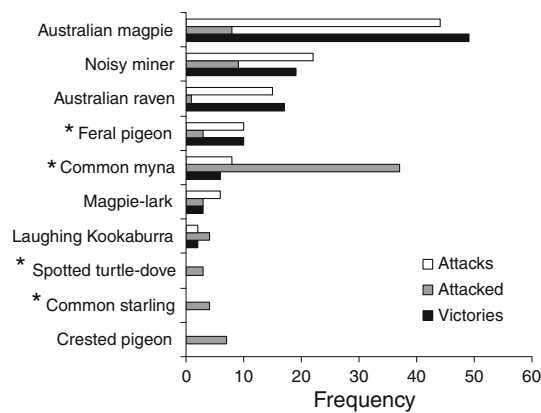
Fig. 2 Number of interactions (attacks initiated or received) and outcome of the interactions for native and exotic species recorded during the transects. *Asterisks* indicate alien species

Opportunism hypothesis

The diversity of native species decreased with the degree of urbanization (Table 1; Fig. 3a), a pattern well known in birds. In contrast to native species, exotic species reached the highest diversity (Table 1; Fig. 3b) and abundance (Table 2; Fig. 3c) in the most urbanized environments, yet they were almost absent in the wildland.

We used a classification tree to describe differences between exotic and native species in the use of food resources across the urbanization gradient. The best tree revealed that birds changed the way they used the resources along the urbanization gradient: as expected, the higher the degree of urbanization, the higher the tendency of birds to rely on food deliberately or accidentally provided by people (Fig. 4). Interestingly, exotic species primarily relied on food deliberately or accidentally provided by humans rather than on natural foods, suggesting that opportunism is a major feature of exotic species.

We used field experiments to test more formally whether opportunistic feeding is an important feature of exotic

birds. As predicted by the opportunism hypothesis, exotic birds were more likely to eat the meal offered during the food opportunity experiments and showed shorter flight distances to an approaching human than non-urbanized birds, yet they did not differ in any of these aspects from the most urbanized native birds (Table 3; Table S5). Within exotic species, individuals inhabiting urban environments were also more opportunistic than those found in the suburbs, both in terms of foraging opportunism (binomial GLMM, with species as random factor and urbanized birds set to zero: 3.438 ± 0.726, $t = 4.74$, $P < 0.0001$, $n = 125$) and flight distance (Gaussian GLM, with urbanized birds set to zero: -0.835 ± 0.087, $t = -9.58$, $P < 0.0001$, $n = 163$).

There were nonetheless differences among exotic species in the response to new food opportunities and in their flight distances (Table 4; Fig. 5). In particular, the spotted turtle-dove and the common starling showed longer latencies to eat the meal offered during the food opportunity experiments and exhibited longer flight distances than the other species. Interestingly, these less opportunistic species showed lower densities in urban environments than the most opportunistic exotics (Fig. 6, S4).

Discussion

Because the environments faced by introduced species differ in many aspects from their ancestral environments, invaders often have to deal with a variety of ecological challenges that can severely limit their survival and reproduction. It should therefore come as no surprise that most species introduced to Australia failed to become established there (Duncan et al. 2001), and that even those exotics that eventually became abundant and widespread often did so only after having failed to become established following multiple earlier introductions (Newsome and Noble 1986; Lever 2006; see Fig. S3). Despite the obvious

Table 1 Differences in the richness of native species and the proportion of exotic species (relative to native species) along the gradient of urbanization

Fixed effects	Richness of native species				Proportion of exotic species			
	Parameter	SE	t	P	Parameter	SE	z	P
Intercept	2.708	0.062	43.24	<0.0001	−5.541	1.002	−5.53	<0.0001
Habitat								
Wildland	0.000[a]	–	–	–	0.000	–	–	–
Suburb	−0.466	0.101	−4.62	<0.0001	3.644	1.026	3.55	<0.0001
Urban	−0.841	0.114	−7.37	<0.0001	4.733	1.017	4.65	<0.0001

Species richness has been modeled with a generalized linear model with Poisson error and log-link whereas the proportion of exotic species has been modeled with a binomial error and logit link

[a] The significance of the parameters is relative to wildland, which is set to be zero
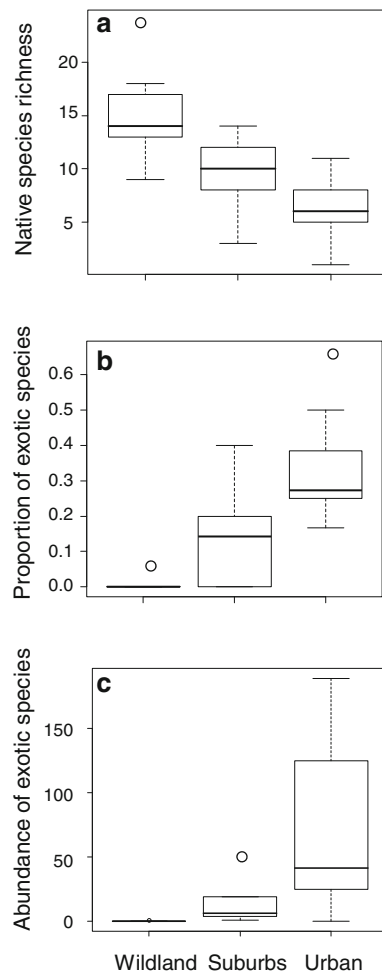
Fig. 3 Changes (median and percentiles) in the richness of native species (**a**), the proportion of species that were exotic (**b**) and the abundance of those exotic species (**c**) along gradients of urbanization

difficulties of invading the continent, a few species succeeded there and are nowadays more abundant than many native species (Duncan et al. 2001; Barrett et al. 2003). These species have also been extremely successful when introduced to other regions within and outside Australia (Lever 2006). The question is why.

According to the competition hypothesis, invaders may succeed in new regions if they are aggressive enough to displace native species from the available resources. The success of alien species in NSW does not seem to be primarily associated with a competitive superiority over native species, however. On the one hand, the most successful avian invaders were smaller and less aggressive than many natives, and were excluded from food patches where competition was high. It should be noted that in the study region there are some native species, such as Australian magpie, Australian raven and noisy miner, that are well known for their aggressiveness towards other species (Garden et al. 2006). The only exotic species that could

perhaps be regarded as an aggressive competitor was the feral pigeon, the largest exotic species in the region, which was capable of monopolizing resources in urban habitats and was often observed displacing native species. Yet, this species also behaved very opportunistically when foraging (see below), suggesting that aggressiveness is not the sole explanation for its success.

On the other hand, the transects across gradients of urbanization revealed that most alien species were concentrated in the most human-modified habitats, where native species were scarcer, a pattern consistent with previous studies within and outside Australia (Diamond and Veitch 1981; Case 1996; Blair 2001; White et al. 2005; van Heezik et al. 2008). Together with behavioral observations, this finding suggests that exotic and native species rarely interact in nature. These lines of evidence, although do not deny the case-by-case importance of competition, suggests that the competition hypothesis is not a general solution to the invasion paradox in birds (Diamond and Veitch 1981; Simberloff 1992; Smallwood 1994; Case 1996). Of course, it is possible that competition for food may play a greater role in other organisms, such as some fishes and mammals, which are well known for having displaced ecologically similar native species (Hill et al. 1993; Wauters et al. 2002; Seiler and Keeley 2009). We also note that our study focused on the use of food sources, rather than on other types of resources, on the grounds that food is a major factor limiting the abundance of birds (Marzluff 2001; Shochat et al. 2006) and that previous evidence points to foraging plasticity as a major factor in the success of exotic birds (Sol 2007). However, competition over other resources, notably nest sites, may also be important and should be examined in future studies.

The alternative to the competition hypothesis is the opportunism hypothesis, which posits that the success of exotic species relates to their ability to exploit ecological opportunities that most native species cannot use. The urban environment is characterized by a substitution of natural vegetation for man-made structures and an increase in human density, which is expected to affect the way birds exploit available food resources (McKinney 2002; Shochat et al. 2006). Previous comparative work has found that bird species that are adapted to urban habitats are characterized, among other things, by short flight distances and enhanced foraging opportunism (Bonier et al. 2007; Liker and Bókony 2009; Møller 2009; but see Kark et al. 2007). Our results further emphasize the importance of feeding close to humans and exploiting food resources derived from their activities in the success of native birds in urbanized environments. More importantly for the present study is nonetheless the finding that these same capacities were also key in the success of exotic birds in urbanized environments. Our fine-scale observations and experiments

Table 2 Abundance of each species in all transects as a function of their status, habitat and the interaction between status and habitat

Fixed effects	Parameter	SE	z	P
Intercept	0.834	0.192	4.33	<0.0001
Status				
Native	0.000[a]	–	–	–
Exotic	−3.112	1.167	−2.66	0.008
Habitat				
Wildland	0.000	–	–	–
Suburb	−0.218	0.069	−3.15	<0.0001
Urban	−0.855	0.084	−10.09	<0.0001
Interactions				
Exotic wildland[a]	0.000	–	–	–
Exotic suburb[a]	4.718	1.007	4.68	<0.0001
Exotic urban[a]	6.900	1.004	6.86	<0.0001
Random effects	Variance	SD		
Species	1.920	1.385	–	–

Abundance has been modeled with a Poisson GLMM, including species as a random factor

[a] Comparisons are relative to a reference level, which is set to be zero

Fig. 4 Conditional classification tree based on foraging observations to identify differences in the use of resources between exotic and native birds. The *histograms* show the fraction of exotic species for terminal nodes
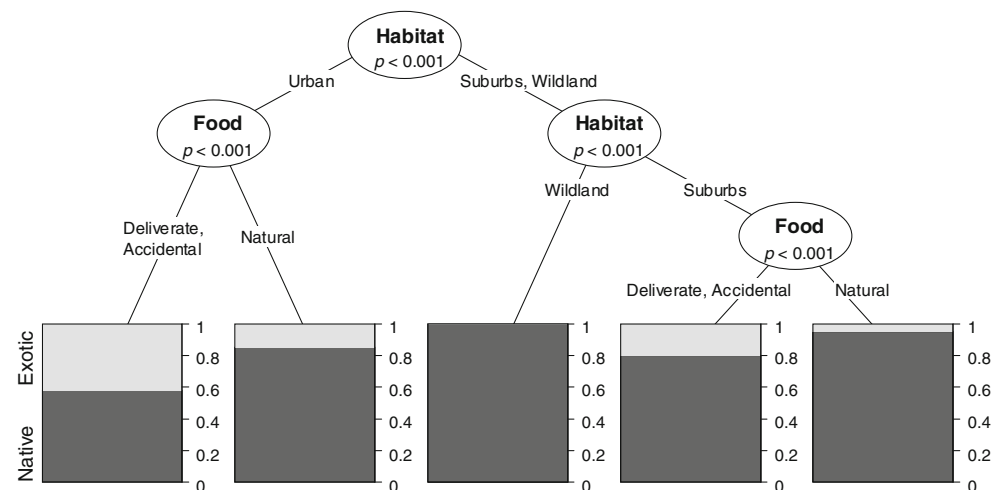
revealed that exotic birds established in the region readily adopted new feeding opportunities and were little afraid to forage close to humans compared to native species that occur in less urbanized habitats, but did not differ in any of these aspects from the most urbanized native birds. Likewise, laboratory experiments on the common myna, the most abundant exotic species in the study area, show that the species has a remarkable ability to explore and adopt new food types, and that these abilities are more pronounced in individuals inhabiting the most urbanized habitats (Sol et al. 2011).

While invaders tended to be highly opportunistic in foraging behavior, the species differed in the way they used new feeding opportunities and in the distance at which they tolerated humans when feeding. In particular, the spotted turtle-dove and the common starling showed less response to food provisioning and longer flight distances than other exotic species. Most comparative studies assume that there

is a unique way to living in the city, yet these results highlight that less opportunistic exotic species can also be successful in urban environments provided that they find easy-to-access food. Interestingly, the most opportunistic exotic species in the study area, common myna, feral pigeon and house sparrow, were also the most abundant species. Although there are a variety of factors that may facilitate population growth in urbanized environments (Marzluff 2001; Yeh and Price 2004; Anderies et al. 2007), our results fit well with the view that the exotic species that opportunistically exploit the abundant food accidentally or deliberately produced by human activities may reach high population densities (Marzluff 2001; Piper and Catterall 2006; Shochat et al. 2006).

Taken together, the evidence provided in our study yields support for the widely accepted but rarely tested view that the success of exotic species relates to the

Table 3 Variation in response to experimental food provisioning (binomial error, 0 = ignore food, 1 = feed food) and in flight distance (Gaussian error) in exotic and native individuals found in either urban or non-urban (suburbs and wildland) habitats; gradient and species were random effects

Fixed effects	Opportunistic foraging							
	All species (n = 230 observations)				Species >5 observations (n = 214 observations)			
	Parameter	SE	z	P	Parameter	SE	z	P
Intercept	3.073	1.037	2.961	0.003	2.579	1.131	2.28	0.022
Category								
Urbanized exotics	0.000[a]	–	–	–	0.000[a]	–	–	–
Urbanized natives	−1.888	1.153	−1.64	0.101	−1.840	1.258	−1.46	0.144
Non-urbanized birds[b]	−3.556	0.899	−3.96	<0.001	−3.715	0.953	−3.89	<0.001
Random effects	Variance	SD			Variance	SD		
Species	3.249	1.802	–	–	4.249	2.061	–	–
Gradient	2.824	1.680	–	–	2.511	1.584	–	–
Fixed effects	Flight distance							
	All species (n = 370 observations)				Species >5 observations (n = 334 observations)			
	Parameter	SE	z	P	Parameter	SE	z	P
Intercept	0.121	0.046	2.61	0.009	0.120	0.045	2.69	0.007
Category								
Urbanized exotics	0.000[a]	–	–	–	0.000[a]	–	–	–
Urbanized natives	0.021	0.074	0.29	0.773	0.075	0.077	0.96	0.337
Non-urbanized birds	0.678	0.058	11.52	<0.001	0.673	0.058	11.54	<0.001

[a] The significance of the parameters is relative to urbanized exotics, which is set to be zero

[b] During model simplification (Crawley 2002), non-urbanized exotic and native species were grouped together as they did not differ in the response variables

invasion of vacant niches. Under this view, the invasion paradox is not such a paradox but can be understood if we consider that successful invaders are occupying empty ecological niches associated with human activities, which many native species are unable to use (Sax and Brown 2000). Future studies will have to examine to what extent the opportunism hypothesis provides a general explanation for the invasion paradox in other regions and organisms. Given the great success achieved by many exotic animals in cultivated areas and urbanized environments, we suspect that the explanation may be quite general. In birds, the subset of the species selected for introductions is known to be non-random with respect to their life history and ecological traits (Blackburn and Duncan 2001), and hence it is quite conceivable that the species more common around human settlements were significantly more likely to have been chosen for introduction. There have been few tests of character selectivity for introduced birds, although, for those introduced to Australia, a high proportion of species were ground foragers that use grassland, cultivated, or urbanized habitats (Newsome and Noble 1986).

However, the question remains as to why invasive species are able to survive and reproduce in human-altered habitats, while many native species are not able to do so. The varying success of animals in human-modified environments is usually held to be produced by the differing adaptations of species to survive and reproduce in such environments, causing some species to be common and others rare (McKinney 2002; Bonier et al. 2007). A species may succeed in a human-altered environment because it has specific adaptations to this particular environment or because it has general adaptations to invade empty niches, regardless of whether they have been altered or not (reviewed in Sol 2007). In birds, the idea that successful invaders have specific adaptations to human-altered environments lacks empirical support. Indeed, there has been little success in assembling evidence that highly urbanized birds tend to be more successful when introduced into new regions than species that do not use human-altered environments (Veltman et al. 1996; Sol et al. 2002, 2008), although it is worth noting that previous studies did not distinguish between urban exploiters and adapters (Kark et al. 2007). On the contrary, there is firm evidence for two general adaptations—ecological generalism and behavioral plasticity—that seem to facilitate the establishment in novel environments (Mclain et al. 1999; Cassey et al. 2004; Sol et al. 2005). These two adaptations are found

Table 4 Variation in response to experimental food provisioning (GLMM with binomial error, response 0 = ignore food, 1 = feed food) and in flight distance (GLM with Gaussian error) between exotic species

Fixed effects	Parameter	SE	z	P
Opportunistic foraging, $n = 120$ observations				
Intercept	−2.196	1.297	−1.69	0.091
Species				
Spotted turtle-dove	0.000[a]	–	–	–
Common starling	−1.888	1.153	−1.64	0.101
House sparrow	3.528	1.591	2.21	0.026
Common myna	−0.061	1.526	−0.04	0.967
Feral pigeon	3.984	1.623	2.45	0.014

Random effect	Variance	SD		
Gradient	1.654	1.286	–	–

| Fixed effects	Parameter	SE	z	P
Flight distance, $n = 162$ observations				
Intercept	1.058	0.094	11.2	<0.001
Species				
Spotted turtle-dove	0.000[a]	–	–	–
Common starling	−0.164	0.135	−1.21	0.227
House sparrow	−0.569	0.153	−3.71	<0.001
Common myna	−0.579	0.104	−5.54	<0.001
Feral pigeon	−1.527	0.115	−13.25	<0.001

[a] The significance of the parameters is relative to the spotted turtle-dove, which is set to be zero

Fig. 5 Opportunistic foraging in exotic birds: **a** percentage of field observations in which the species was observed feeding on either natural food or artificial food, **b** response of the individuals (i.e. ate or not the food) to experimental food provisioning, **c** time (s) to handle food in food provisioning experiments, and **d** flight distance (m) in foraging birds. *Numbers* in (**b**) and (**d**) are sample size
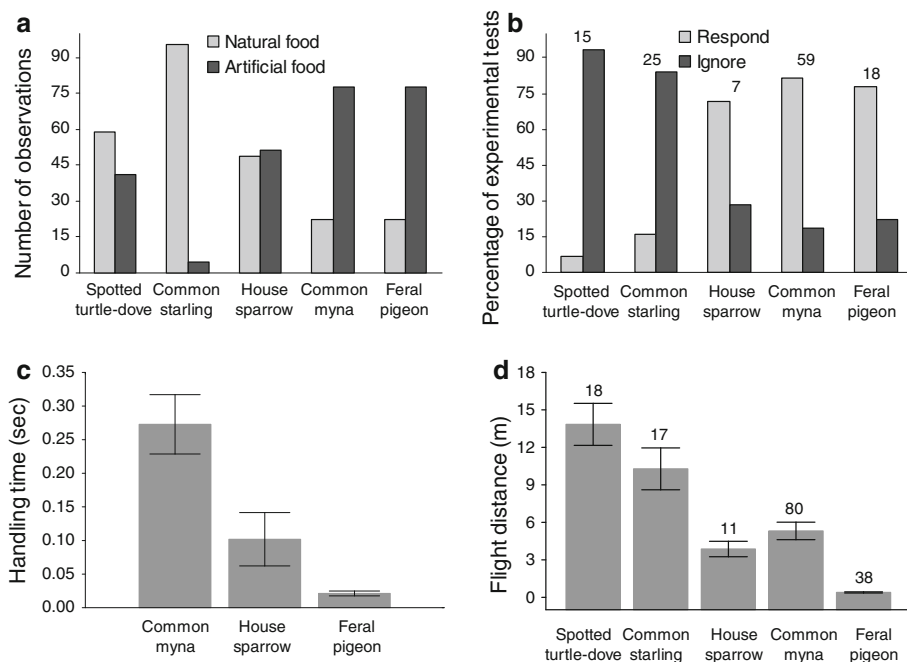
in many introduced species besides those that use urbanized environments in their native ranges, which perhaps explains the lack of success in assembling evidence that highly urbanized birds are more successful invaders.

The observation that most exotic birds occur primarily in human-modified habitats also raises the question of why these species do not colonize more pristine habitats. Although the exact reasons are unclear, two obvious
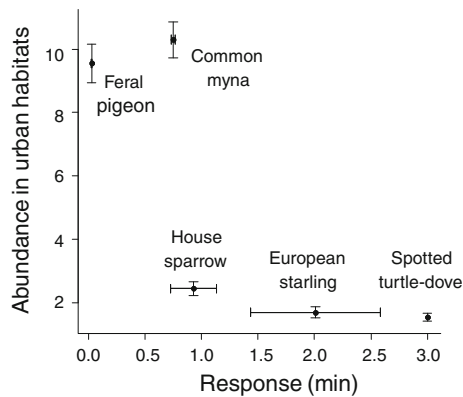
Fig. 6 Relationship (mean and standard errors) between the abundance of exotic species and their response to experimental food provisioning (time to feed, capped after 3 min) in exotics birds

possibilities are the lack of adaptations to efficiently exploit more natural resources and the biotic resistance that offer communities that harbor a greater diversity of native species. Yet, there are exotic species that have been successful in more pristine habitats (MacLeod et al. 2009), and these species present ecologists and evolutionary biologists with a challenging paradox. We suggest that a fruitful avenue for future research would be the study of selected species, such as the blackbird (*Turdus merula*) and red-billed leiothrix (*Leiothrix luthea*), that have succeeded in coexisting with native species in less disturbed environments.

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