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# Behavioural flexibility and invasion success in birds

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Behavioural flexibility has long been thought to provide advantages for animals when they invade novel environments. This hypothesis has recently received empirical support in a study of avian species introduced to New Zealand, but it remains to be determined whether behavioural flexibility is a general mechanism influencing invasion success. In this study, we examined introduction success of 69 bird species in different regions of the world as a function of their degree of behavioural flexibility. Specifically, we predicted that species with relatively large brains and a high frequency of foraging innovations in their area of origin should show a higher probability of establishing themselves where they were introduced than species with small brains and low innovation frequencies. An analysis with general linear modelling (GLM) supported the prediction for relative brain size, even when controlling for phylogenetic biases and potential confounding variables. The only covariates that remained with relative brain size were plumage dimorphism, human commensalism and nest site. A pairwise comparison of closely related species also revealed that successful invaders showed a higher frequency of foraging innovations in their region of origin. This result held even when differences in research effort between species were considered. Overall, the results confirm and generalize the hypothesis that behavioural flexibility is a major determinant of invasion success in birds.

Conventional wisdom in animal ecology states that species that have the capacity to occupy a wide niche are more likely to succeed at invading novel environments than species that are highly specialized (Mayr 1965; Myers 1986; Ehrlich 1989; Williamson 1996). In Mayr's (1965) diagnostic of successful avian invaders, for example, three out of six characteristics are correlates of niche generalism: ecological flexibility, a tendency to discover unoccupied habitats and an ability to shift habitat preferences. Yet the hypothesis that ecological generalism is a general determinant of the invasive capacity of animals is mostly supported by case histories of single species that are already established. In birds, the most intensively studied group (Kolar & Lodge 2001), comparative analyses have generally failed to find a link between opportunistic generalism and invasion success (e.g. Newsome & Noble 1986; Veltman et al. 1996).

A major difficulty in testing hypotheses on opportunistic generalism is quantification of this variable (Lefebvre 2000). Dietary generalism has often been used as a rough surrogate, but at present, evidence supporting a link between this variable and invasion success is rare (e.g. Newsome & Noble 1986; Veltman et al. 1996; but see McLain et al. 1999). Recently, Lefebvre and collaborators (Lefebvre et al. 1997, 1998; Nicolakakis & Lefebvre 2000) have proposed that the frequency of new and unusual feeding behaviours reported in the short note section of ornithology journals may be a good operational definition of flexible, opportunistic generalism in the field. A taxonomic group in which large numbers of new feeding behaviours are observed is likely to change its foraging techniques or diet frequently, to eat a surprisingly large range of foods and to use handling behaviours and novel situations in a way that strikes ornithologists by its complexity and flexibility. Innovation frequency has been found to be a good predictor of experimental measures of flexibility like learning (Gossette 1968; Sasvarï 1985, reanalysed by Timmermans et al. 2000) and problem solving (Webster & Lefebvre 2001). Since behavioural flexibility is likely to be favoured by a larger information-processing capacity, one would also expect this to be associated with a larger neural substrate. Indeed, variation in feeding innovation rate has been found to be correlated with forebrain size, and in particular, the avian equivalent of the mammalian neocortex, the hyperstriatum ventrale and neostriatum (Rehkämper & Zilles 1991) in five areas of the world (Lefebvre et al. 1997, 1998; Timmermans et al. 2000; Nicolakakis & Lefebvre 2000). In primates, Reader & Laland (in press) and Reader (2000) have found an association between feeding innovation rate, relative size of the neocortex, social learning and tool use.

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Sol & Lefebvre (2000) recently used foraging innovations and one of its neural correlates, relative brain size, to test the hypothesis that behavioural flexibility may provide some advantage to species invading novel environments. They found that, in birds introduced to New Zealand, species with relatively larger brains and a higher frequency of foraging innovations in their area of origin tended to be more successful invaders than species with smaller brains and lower innovation frequencies. This study is based on introductions carried out in a single geographical zone, however, and thus allows little generalization. A species that succeeds at establishing itself in a particular place is not necessarily a successful invader in all regions, as some traits may simply preadapt it to live in this particular place. For example, it has been suggested that one of the reasons for the success of the Mandarin duck, *Aix galericulata*, in invading Great Britain might have been the existence of a vacant ecological niche for a hole-nesting duck feeding largely on aquatic vertebrates in spring and summer, and on acorns, chestnuts and beechmast in autumn and winter (Long 1981). The Mandarin duck has in fact had little success in other places where it has been introduced (Long 1981). To support the hypothesis that behavioural flexibility is a general mechanism influencing invasion success, it is necessary to demonstrate that the local trend found in New Zealand is a global one. Here, we examine introduction success of 69 bird species in different regions of the world in relation to variation in behavioural flexibility. We predict that an avian species with a larger neural substrate and a higher frequency of new and opportunistic behaviours should show a higher probability of establishing itself wherever the species is introduced than one that is less flexible.

## METHODS

We gathered data on avian introductions for as many species as possible from sources yielding information on both success and failure. We used the work of Long (1981) as a starting point, and then included information from Newsome & Noble (1986), Simberloff (1992), Brooke et al. (1995), McLain et al. (1995), Moulton & Sanderson (1996), Veltman et al. (1996), Green (1997), Hagemeijer & Blair (1997) and Purroy (1997). We excluded introduction events that were carried out after 1975 (to ensure an accurate assessment of the outcome), those whose outcome was considered uncertain (Case 1996) and those that were natural colonizations or reintroductions. In some cases, a species was introduced two or more times in the same place; to avoid pseudoreplication, we considered these cases as single introductions (Case 1996). Following Sol & Lefebvre (2000), we made separate tests for the brain and foraging innovation data (see below).

### Invasion Success and Relative Brain Size

The best neural predictor of innovation rate, size of the neostriatum/hyperstriatum ventrale complex (Timmermans et al. 2000), was only available for 32 species. However, total brain size is a good predictor of the size of this complex (95.1% of the variance, Timmermans 1999), and it may thus be used as a surrogate when it is the only measure available for a broader sample of species. Data on brain mass were taken from Crile & Quiring (1940), Portmann (1947), Armstrong & Bergeron (1985) and Boire (1989). Brain mass was available for a total of 69 species in the introduction data, comprising 501 introduction events (mean attempts per species=6.96, range 1–39), of which 231 were successful (Appendix, Table A1). All the species were land or freshwater species, and for 88%, the main mode of introduction was deliberate release.

As in previous studies, to control for the allometric effect of body size on brain size, we used the residuals of log–log regressions of brain mass against body mass (see Bennett & Harvey 1985; Lefebvre et al. 1997; Sol & Lefebvre 2000). These residuals are referred in the text as 'relative brain size' (Bennett & Harvey 1985).

In birds, the traits that have been shown to influence invasion success include nesting habits (Newsome & Noble 1986; McLain et al. 1999), sexually selected traits (McLain et al. 1995, 1999; Sorci et al. 1998), migratory behaviour (O'Connor 1986; Veltman et al. 1996), fecundity (Green 1997), body size (Green 1997), diet (McLain et al. 1999) and parental care (McLain et al. 1999). We also considered these traits in the analyses to ensure that the effect of relative brain size on invasion success did not result from its covariation with a third variable. We scored the variables as follows: nest location (ground, bush/tree or hole), sexually selected trait (sexual monochromatic or dichromatic in plumage; McLain et al. 1995, 1999), migratory behaviour (migratory, partially migratory or sedentary; Veltman et al. 1996), fecundity (mean number of eggs per clutch; Veltman et al. 1996), body size (body mass in grams; Veltman et al. 1996), diet (herbivorous, omnivorous, insectivorous, granivorous or carnivorous) and parental care (monoparental or biparental; Sorci et al. 1998). We also considered three additional variables that could bias the results: (1) mode of juvenile development, a confounding variable of avian brain size (Bennett & Harvey 1985), scored as nidicolous and nidifugous; (2) human commensalism, measured as the use of urbanized habitats and scored as infrequent and frequent; and (3) the number of introduction attempts per species. We gathered the data from Bull & Farrand (1977), Pizzey (1980), Bennett & Harvey (1985), Scott (1987), Forshaw (1990), Veltman et al. (1996), Ehrlich et al. (1994), McLain et al. (1995) and Sorci et al. (1998).

Introduction effort (i.e. the minimum number of individuals released in each place, Veltman et al. 1996) was not available in most cases. This was none the less known for 39 species introduced to New Zealand (Veltman et al. 1996) and/or Australia (Newsome & Noble 1986), which allowed us to test the key assumption that more flexible species are not introduced in larger numbers than the less flexible ones. Following Green (1997) and Sol & Lefebvre (2000), we measured introduction effort as a categorical variable with three levels: 2–10 individuals introduced;

11–100 individuals; more than 100 individuals (data from Long 1981; Veltman et al. 1996; Newsome & Noble 1986; respectively). To avoid pseudoreplication, when a species was introduced two or more times in the same place we considered the sum of individuals released across all the attempts (see Veltman et al. 1996; Green 1997; Sol & Lefebvre 2000 for similar procedures). This is justified given that (1) multiple introductions were generally close together in time and (2) the number of individuals released in one place is strongly correlated with the number of introduction attempts (Veltman et al. 1996). We found no relationship between relative brain size and introduction effort, either in Australia (Kruskal–Wallis analysis of variance, ANOVA, by ranks: $\chi^2_2=1.69$, $P=0.42$) or in New Zealand ($\chi^2_2=4.34$, $P=0.11$). In the case of New Zealand, where the $P$ value approached significance, the differences went against the hypothesis (i.e. species with relatively larger brains being introduced in lower numbers). We are therefore confident that the results obtained here are not biased by introduction effort.

We used general linear models (GLM) to test whether relative brain size predicts differences in invasion success between species. For analysing the proportion of successful introductions per species, a GLM model with binomial error and logit link function is the most appropriate tool (Crawley 1993; Tella et al. 1999). Instead of using the percentage of successful introductions, which loses information on the sample size from which the proportion is estimated, this procedure uses the number of successful introductions as the response variable and the number total of introductions as the binomial denominator. Use of this method allowed us to include species with few introduction events; note that the situations where a single introduction event was available are similar to those found in previous studies at a regional scale. We first used a univariate approach to determine whether relative brain size, when considered alone, was significantly associated with introduction success. Then, we tested the effect of potential confounding variables using multivariate models. The best models were determined by removing from the full model those variables that did not improve it. We tested the influence of each variable on invasion success with a likelihood ratio test that compared each model to its lower-order version that excluded the particular variable being tested. At each step, the less significant variable was removed until the model retained only significant predictors. We investigated the significance of alternative models by adding the previous variable removed from the model. We carried out a test of the robustness of the best models following Crawley (1993). All analyses were carried out with GLIM 4 (1992, Royal Statistical Society, London).

Species cannot generally be considered independent data points because closely related species tend to share many characters through common descent rather than independent evolution (Harvey & Pagel 1991). Due to this effect, interspecific variation in invasion success could be heavily skewed towards a particular phyletic group. We dealt with this problem as follows. We first used a nested ANOVA on the proportion of successful introductions per species to identify the taxonomic level that accounted for the largest amount of variation in introduction success. Most of the variance (72.4%) was accounted for by species within genera, justifying the use of species as independent data points. Because part of the variance (20.6%) was also found at the order level, however, we decided to apply the phylogenetic subtraction method (Stearns 1983; Harvey & Pagel 1991) to remove any phylogenetic effects from the multivariate models. This method consists in using categorical codes for the taxon (the taxon order, in our case) to remove phyletic differences between species (see also Veltman et al. 1996; Tella et al. 1999). Taxonomic designations follow Sibley & Monroe (1990).

## Invasion Success and Foraging Innovations

Innovation frequency could not be compared directly for all species using the GLM approach, since the birds originated from different parts of the world and the total number of foraging innovations varied greatly between regions (e.g. 54 for New Zealand, over 700 for Europe). We therefore analysed the difference in foraging innovations between successful and unsuccessful invaders by means of pairwise comparisons of closely related species (same genus or family) originating from the same continent or subcontinent. This method effectively controls for confounding variables, as well as common ancestry, since closely related species are more generally similar with respect to ecology, morphology, physiology and anatomy (Ehrlich 1989; Møller & Birkhead 1992; Veltman et al. 1996). Our previous analysis of avian introductions to New Zealand (Sol & Lefebvre 2000) indicated that the link between innovation frequency and invasion success was not biased by differences in introduction effort. Innovation frequencies were taken from an augmented version of the corpus studied by Lefebvre et al. (1997, 1998). Cases are included in this database if the authors of a report and/or the editors of the journal judged the food or feeding technique used by a bird to be new, previously unknown, unusual, opportunistic or worthy of attention (see Lefebvre et al. 1997, 1998 for examples). The database presently includes a total of 1787 innovations from six areas of the world (Nicolakakis & Lefebvre 2000; Timmermans et al. 2000). In a few cases where a family contained more than one possible pair, we randomly chose the two species for the comparison. We used a total of 29 pairs (58 species) in this analysis (Appendix, Table A2). Innovation frequency may be biased because some species are more investigated than others. To deal with this problem, we estimated research effort by counting the number of papers on each of the species in the Zoological Record during 1993–2000. We found a significant correlation between log (innovation frequency+1) and log (research effort), all 58 species pooled together ($R^2=0.11$, $F_{1,57}=6.87$, $P=0.01$). We therefore used the residuals of this regression to compare successful and unsuccessful invaders on innovation rates that were not biased by research effort.

**Table 1.** General linear models with binomial error and logit link testing the relationship between invasion success and relative brain size

| | Univariate model | | Multivariate model | |
|---|---|---|---|---|
| | Estimate | SE | Estimate | SE |
| Variable of interest | | | | |
| Relative brain size | 0.601 | 0.095 | 0.875 | 0.300 |
| Confounding variables | | | | |
| Order | — | — | −5.824–1.570 | 0.631–13.55 |
| Sexual dimorphism | — | — | −0.091 and −0.599 | 0.292 and 0.505 |
| Use of urban habitats | — | — | 1.567 | 0.342 |
| Nest site | — | — | −1.315– −0.091 | 0.505–0.745 |
| Introduction attempts | — | — | 0.033 | 0.014 |
| Explained variance | 22.2% | | 62% | |

Only parameter estimates that were significant at $P<0.05$ are shown. See text for details.

## RESULTS

### Invasion Success and Relative Brain Size

A univariate GLM model for the 69 species showed that invasion success was positively associated with relative brain size ($\chi^2_1=44.1$, $P<0.0001$; Table 1). This link did not appear to be an artefact due to a third variable, as this remained significant ($\chi^2_2=9.504$, $P=0.002$; Table 1) when variables that could confound the results were included in the model. The best model also showed that invasion success varied between different orders ($\chi^2_9=21.71$, $P=0.009$), and was higher in monomorphic species than in dimorphic ones ($\chi^2_1=4.24$, $P=0.039$), and in those that use urban habitats ($\chi^2_1=22.18$, $P<0.0001$). The location of the nest was also significant ($\chi^2_2=9.46$, $P=0.009$), success being higher for ground nesters than for species from the two other nesting categories. Finally, some bias due to differences in the total number of introductions per species was also detected ($\chi^2_1=5.17$, $P=0.023$). This could be the result of human influence, with species that generally succeed at invading being introduced more frequently than those that frequently fail.

### Invasion Success and Foraging Innovations

A pairwise comparison of closely related species classified as successful and unsuccessful invaders (Appendix, Table A2) showed that the former had a higher frequency of foraging innovations than the later (Wilcoxon matched-pairs signed-ranks test: $Z=2.74$, $N=29$, one-tailed $P=0.003$): in 15 of 29 pairs, innovation frequency was higher for the successful species than it was for the unsuccessful one. Of the remaining pairs, 11 showed identical innovation frequencies, and only three yielded a higher innovation frequency for the less successful species. The conclusion held when the comparison was done on the residuals of a log–log regression of innovation frequencies against research effort ($Z=2.61$, $N=29$, one-tailed $P=0.003$).

## DISCUSSION

We found that species with relatively larger brains and a higher frequency of foraging innovations tended to have a higher probability of introduction success than species with smaller brains and a lower frequency of innovations. The results of our study, therefore, confirm and generalize the hypothesis that behavioural flexibility may be advantageous for surviving and reproducing in novel environments.

Although our focus is behavioural flexibility, we identified three other traits that could also influence invasion success in birds. The analyses revealed that dichromatic species tended to be less successful than monochromatic ones, a result that is consistent with previous findings by McLain et al. (1995, 1999) and Sorci et al. (1998). Plumage dimorphism is generally thought to have evolved by sexual selection and this could impose costs for viability of small populations due to production and maintenance of sexual characters, demographic stochasticity, predation and a trade-off between disease resistance and sexual selection (McLain et al. 1995; Sorci et al. 1998; A. P. Møller, personal communication). The second trait identified in our analyses was human commensalism: species that frequently live in close association with humans tended to be better invaders than those that rarely occur in this type of habitat. This result is specially relevant because numerous observations report that invading birds are particularly successful in anthropogenically modified habitats (see Green 1984; Diamond & Veitch 1981; Simberloff 1992; Case 1996). Avian invaders seem thus to establish themselves in habitats they are preadapted to, but to which many native species are often not preadapted (Sax & Brown 2000). Finally, the results suggest that the location of the nest is also an important factor, ground nesters tending to be better invaders than species nesting in other sites. This result is contrary to the one found by McLain et al. (1999), who reported that ground nesters were the least successful category. The discrepancy is probably the result of our multivariate approach. When nest site was considered alone, ground nesters were worse invaders than the others; it was only when we removed the variance accounted for by other factors in the multivariate models that ground nesters did better. Because of the complexity of these relationships, it is impossible at this point to decide which of the two results are spurious; more work is needed here.

Most of traits that have been consistently found to influence invasion success in birds primarily explain why certain species repeatedly fail to establish themselves in a novel environment, but they say much less about why others are so successful (e.g. migratory behaviour: O'Connor 1986; Veltman et al. 1996; presence of sexually selected traits: McLain et al. 1995; Sorci et al. 1998). This is to be expected, however, since adaptations that are optimal in one environment are often less useful in others. Instead, behavioural flexibility provides a more general explanation for why species differ in their invasive capacity. It is easy to imagine, for example, that a species that readily tastes new foods or adopts novel foraging strategies is more preadapted to survive and reproduce in a novel environment than a more specialized species that persists with the behaviours of its area of origin. The blackbird *Turdus merula* is a case in point: it is highly flexible in its native Europe (23 reported foraging innovations) and has progressively invaded urban areas all over the continent (Hagemeijer & Blair 1997). In Sasvarï's (1985) comparative study, it was the fastest learner of the seven passerines tested. In an experimental field test, Marples et al. (1998) also showed very low neophobia in most individuals tested. As an introduced bird, the blackbird has successfully established itself in half of the countries where it has been introduced and is one of the few species that has invaded pristine habitats (Diamond & Veitch 1981). Innovations have also been recorded in introduced populations, suggesting that they play an important role in the lifestyle of the species. In Australia, for example, the blackbird has been recorded preying on copper skink and lizards, as well as hawking insects in the evening in cities.

Behavioural flexibility is a rubric for several different aspects of decision making. In this study, we have used innovation frequency and one of its neural correlates, relative brain size, as operational measures of behavioural flexibility. Our choice was based on the availability of quantitative data for these measures on a large number of species. Obviously, several other flexibility correlates could contribute to invasion success. For instance, neophobia (Greenberg 1983, 1989; Greenberg & Mettke-Hoffmann 2001) affects the likelihood that a species will approach new environmental features, an obvious first step to innovative feeding and adaptation to new environments. Comparative experiments in birds have shown that neophobia is lower in generalist birds than it is in specialists (Greenberg 1983, 1989; Webster & Lefebvre 2001). Exploration is also likely to affect the adaptation of animals to novel environments (Greenberg & Mettke-Hofmann 2001). Components of behavioural flexibility are often positively correlated. For example, innovations are associated with social learning in primates (Reader & Laland, in press), and with problem solving (Webster & Lefebvre 2001) and individual learning in birds (reanalysis of Gossette 1968 and Sasvarï 1985 in Timmermans et al. 2000). In some cases, however, the different components of behavioural flexibility are uncorrelated (e.g. exploration and neophobia in parrots: Greenberg & Mettke-Hoffmann 2001; Mettke-Hofmann et al., in press) or context specific (e.g. Coleman & Wilson 1998). The relationship between invasion success and other flexibility correlates like neophobia and exploration is worth studying, but more work is needed on quantitative estimates of these variables in a large variety of avian orders.

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## Appendix

**Table A1.** List of the species for which brain data were available, with the number of successful introductions and the number total of introductions

| Species | Successes | Total | Relative brain size |
|---|---|---|---|
| *Agapornis fischeri* | 2 | 2 | 1.433 |
| *Alauda arvensis* | 6 | 9 | 0.309 |
| *Alectoris chukar* | 7 | 16 | −1.287 |
| *Alopochen aegyptiacus* | 2 | 6 | −0.475 |
| *Anas acuta* | 1 | 2 | −0.088 |
| *Anas penelope* | 0 | 1 | −0.612 |
| *Anas platyrhynchos* | 4 | 5 | −0.437 |
| *Anser anser* | 0 | 2 | −0.245 |
| *Athene noctua* | 2 | 2 | 1.196 |
| *Cacatua sulphurea* | 2 | 2 | 1.738 |
| *Cardinalis cardinalis* | 3 | 4 | 0.641 |
| *Carduelis cannabina* | 0 | 4 | 0.057 |
| *Carduelis carduelis* | 7 | 11 | 0.116 |
| *Carduelis spinus* | 0 | 3 | 0.142 |
| *Cathartes aura* | 3 | 3 | 1.765 |
| *Chrysolophus pictus* | 1 | 8 | −0.833 |
| *Cinclus cinclus* | 0 | 1 | 0.222 |
| *Colinus virginianus* | 5 | 28 | −1.778 |
| *Columba livia* | 21 | 21 | −0.729 |
| *Columba palumbus* | 0 | 1 | −1.253 |
| *Corvus brachyrrynchos* | 1 | 1 | 2.276 |
| *Corvus frugilegus* | 1 | 1 | 1.534 |
| *Corvus monedula* | 2 | 2 | 1.394 |
| *Coturnix chinensis* | 3 | 8 | −1.622 |
| *Coturnix coturnix* | 3 | 11 | −2.059 |
| *Crex crex* | 0 | 2 | −0.801 |
| *Cygnus olor* | 4 | 5 | −1.046 |
| *Dromaius novaehollandiae* | 1 | 3 | −1.601 |
| *Emberiza citrinella* | 1 | 3 | −1.198 |
| *Erithacus rubecula* | 0 | 4 | −0.067 |
| *Fringilla coelebs* | 2 | 4 | −0.028 |
| *Gallinula chloropus* | 1 | 2 | −0.718 |
| *Gallus gallus* | 5 | 20 | −2.505 |
| *Geopelia cuneata* | 0 | 4 | −1.428 |
| *Grus virgo* | 0 | 1 | 0.107 |
| *Lagopus lagopus* | 5 | 16 | −1.411 |
| *Lophortyx californicus* | 7 | 16 | −1.387 |
| *Lophura nycthemera* | 1 | 12 | −1.036 |
| *Meleagris gallopavo* | 9 | 19 | −1.969 |
| *Melopsittacus undulatus* | 1 | 6 | 0.294 |
| *Numida meleagris* | 10 | 25 | −1.661 |
| *Ocyphaps lophotes* | 2 | 6 | −0.560 |
| *Parus caeruleus* | 0 | 1 | 0.691 |
| *Parus major* | 1 | 2 | 0.661 |
| *Passer domesticus* | 33 | 39 | 0.423 |
| *Pavo cristatus* | 5 | 11 | −1.399 |
| *Perdix perdix* | 2 | 8 | −1.672 |
| *Phalacrocorax carbo* | 0 | 1 | −0.052 |
| *Phasianus colchicus* | 12 | 33 | −1.457 |
| *Phoenicopterus ruber* | 1 | 1 | −0.194 |
| *Pica pica* | 1 | 1 | 1.710 |
| *Prunella modularis* | 1 | 2 | 0.146 |
| *Psittacula eupatria* | 1 | 1 | 2.013 |
| *Rhynchotus rufescens* | 0 | 2 | −1.204 |
| *Serinus canaria* | 2 | 9 | 0.198 |
| *Streptopelia risoria* | 3 | 3 | −1.296 |
| *Struthio camelus* | 1 | 2 | −0.558 |
| *Sturnus roseus* | 0 | 1 | 0.377 |
| *Sturnus vulgaris* | 23 | 30 | 0.564 |
| *Sylvia atricapilla* | 0 | 1 | 0.709 |
| *Taeniopygia guttata* | 1 | 4 | −1.320 |
| *Tetrao tetrix* | 2 | 12 | −1.467 |
| *Tetrao urogallus* | 1 | 8 | −1.62 |
| *Trichoglossus novaehollandiae* | 0 | 1 | 0.629 |
| *Turdus merula* | 3 | 6 | 0.134 |
| *Turdus migratorius* | 0 | 2 | 0.876 |
| *Turdus philomelos* | 2 | 5 | 0.094 |
| *Tyto alba* | 3 | 6 | 1.471 |
| *Vanellus vanellus* | 0 | 2 | −0.375 |

**Table A2.** Closely related species used in the comparison of foraging innovations between successful and unsuccessful invaders

| Successful species | Successful/total introductions | Innovations | Research effort | Unsuccessful species | Successful/total introductions | Innovations | Research effort | Origin |
|---|---|---|---|---|---|---|---|---|
| *Cygnus atratus* | 4/5 | 0 | 17 | *Dendocygna autumnalis* | 0/3 | 0 | 32 | Australia |
| *Coturnix australis* | 2/2 | 0 | 2 | *Coturnix pectoralis* | 0/2 | 1 | 2 | Australia |
| *Platycercus elegans* | 2/3 | 2 | 17 | *Melopsittacus undulatus* | 1/6 | 0 | 168 | Australia |
| *Lonchura castaneothorax* | 2/3 | 0 | 5 | *Emblema guttata* | 0/4 | 0 | 3 | Australia |
| *Anas platyrhynchos* | 4/5 | 5 | 540 | *Anas penelope* | 0/2 | 2 | 110 | Europe |
| *Cygnus olor* | 4/5 | 1 | 209 | *Anser anser* | 0/2 | 1 | 198 | Europe |
| *Alectoris rufa* | 6/10 | 2 | 67 | *Perdix perdix* | 2/8 | 0 | 212 | Europe |
| *Phasianus colchicus* | 12/33 | 1 | 249 | *Tetrao urogallus* | 1/8 | 0 | 211 | Europe |
| *Columba livia* | 21/21 | 0 | 382 | *Columba palombus* | 0/1 | 1 | 80 | Europe |
| *Streptopelia decaocto* | 5/9 | 1 | 143 | *Streptopelia turtur* | 0/2 | 1 | 143 | Europe |
| *Alauda arvensis* | 6/9 | 1 | 119 | *Lullula arborea* | 0/3 | 0 | 41 | Europe |
| *Carduelis carduelis* | 7/11 | 4 | 53 | *Carduelis cannabina* | 0/4 | 1 | 26 | Europe |
| *Carduelis chloris* | 5/7 | 2 | 73 | *Carduelis spinus* | 0/3 | 1 | 88 | Europe |
| *Fringilla coelebs* | 2/4 | 3 | 184 | *Fringilla montifringilla* | 0/2 | 1 | 78 | Europe |
| *Turdus merula* | 3/6 | 14 | 230 | *Erithacus rubecula* | 0/4 | 5 | 162 | Europe |
| *Passer domesticus* | 33/39 | 10 | 426 | *Passer montanus* | 8/11 | 2 | 159 | Europe |
| *Gallinula chloropus* | 1/2 | 5 | 109 | *Crex crex* | 0/2 | 0 | 165 | Europe |
| *Anas platyrhinchos* | 4/5 | 0 | 540 | *Anser anser* | 0/2 | 0 | 198 | India |
| *Coturnix chinensis* | 3/8 | 0 | 13 | *Coturnix coturnix* | 3/11 | 0 | 130 | India |
| *Francolinus pondicerianus* | 7/9 | 0 | 13 | *Francolinus francolinus* | 5/9 | 0 | 9 | India |
| *Pavo cristatus* | 5/11 | 1 | 49 | *Gallus gallus* | 5/20 | 1 | 324 | India |
| *Streptopelia senegalensis* | 4/4 | 0 | 63 | *Streptopelia decaocto* | 5/9 | 0 | 143 | India |
| *Pycnonotus jocosus* | 9/9 | 1 | 13 | *Pycnonotus cafer* | 2/6 | 4 | 29 | India |
| *Passer domesticus* | 45/51 | 3 | 426 | *Amandava amandava* | 7/15 | 0 | 4 | India |
| *Acridotheres tristis* | 30/36 | 1 | 108 | *Gracula religiosa* | 2/6 | 0 | 23 | India |
| *Branta canadensis* | 7/9 | 1 | 266 | *Aix sponsa* | 1/3 | 0 | 155 | North America |
| *Anas platyrhynchos* | 4/5 | 1 | 540 | *Anas discors* | 0/3 | 0 | 64 | North America |
| *Meleagris gallopavo* | 9/19 | 0 | 198 | *Tympanuchus cupido* | 0/4 | 0 | 56 | North America |
| *Lophortyx californicus* | 9/15 | 0 | 13 | *Colinus virginianus* | 6/29 | 0 | 184 | North America |

Innovations are the frequency of foraging innovations recorded in their region of origin. Research effort is the number of published papers of the species for the period 1993–2000.