

Parental investment and fecundity, but not brain size, are associated with establishment success in introduced fishes

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Summary

1. Classical theory predicts that colonizing ability should increase with fecundity. Additionally, it has recently been shown that successful establishment of birds was correlated with relative brain size, which was suggested as possibly universal among vertebrates.
2. I conducted a comparative study of establishment success in global fish introductions, controlling for regional geographic differences, to test these hypothesized correlates.
3. In 133 introductions of 17 fish species, establishment success was negatively associated with fecundity while there was no evidence for an effect of relative brain size. In analysis of partially overlapping data, there was no evidence of a correlation between relative brain size and establishment rate across 39 species.
4. One explanation for the negative association with fecundity is that parental investment might be more important to establishment than fecundity. In 126 introductions of 14 species, reproductive behaviours associated with parental investment were significantly associated with establishment success. These results suggest that the correlation between brain size and establishment success is not universal.

Key-words: biological invasion, brain size–environmental change (BS–EC) hypothesis, cognitive innovation, establishment, parental investment

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Introduction

Establishment success of introduced species is influenced by many factors, including propagule pressure (Cassey *et al.* 2004; Lockwood *et al.* 2005), features of the recipient environment (Levine & D'Antonio 1999; MacIsaac *et al.* 2000; Blackburn & Duncan 2001), and characteristics of the introduced species (Kolar & Lodge 2001; Cassey 2002; Marchetti *et al.* 2004a). While classical theory suggests that colonizing ability should increase with fecundity (MacArthur & Wilson 1967), it has recently been found that establishment success of introduced birds was correlated with relative brain size (Sol *et al.* 2005), possibly because larger brains are associated with individual response to novel environments and increased propensity for innovative use of habitat or resources (the brain size–environment change or BS–EC hypothesis). If this pattern were universal across taxonomic groups (or even just vertebrates) it would be an important unifying principle in ecology and evolution (Marino 2005).

Recent work on species establishment in aquatic ecosystems has emphasized ecological phenomena such as inter-specific facilitation and taxonomic distinctiveness (Ricciardi 2001; Ricciardi & Atkinson 2004), physical mediation of species interactions (Byers 2002), the occurrence of pathways for overland dispersal and invasion corridors (Buchan & Padilla 1999; MacIsaac *et al.* 2001), and characteristics of invaded watersheds (Gido & Brown 1999; Marchetti *et al.* 2004b) or habitats (Palmer & Ricciardi 2004). Two previous studies have looked at characteristics of colonizing fishes in the Great Lakes (Kolar & Lodge 2002) and in California (Marchetti *et al.* 2004a,c). Parental investment was found to be a significant risk factor for establishment in California (Marchetti *et al.* 2004c), but not the Great Lakes (Kolar & Lodge 2002). Neither study found a significant relationship between fecundity and establishment success. To my knowledge, no study has tested for an effect of relative brain size on establishment success in fishes.

Prior evidence suggests that encephalization might well correlate with a species ability to colonize new habitats (i.e. the BS–EC hypothesis), particularly if cognition plays a role in establishment. Introductions of non-indigenous fishes presumably often fail because features of the new environment, particularly prey variety, are different than those to which the organism's

life-history has adapted (Kolar & Lodge 2002). Thus, species exhibiting relatively superior cognition or more plastic behaviour sets (e.g. food selectivity, mechanisms to evade predation) might more rapidly adjust to their new environments. Kotrschal *et al.* (1998) further argue that spatial learning and problem solving in fish are associated both with visual orientation and habitat structure, and they find that the size of particular brain structures is associated with different habitats or styles of feeding. Perhaps most strikingly, particular brain sizes tend to be associated with particular habitats even across families, with ecological variables such as prey availability, habitat choice and habitat complexity commonly correlating with brain size (Kotrschal *et al.* 1998). However, while there is evidence for relationships both between total relative brain sizes and the relative sizes of various structures with species individual life-histories, the role of cognition remains uncertain

(Bshary *et al.* 2002). Thus, while it does not follow from a correlation between brain size and establishment success that it is cognitive adaptation affecting establishment success, confirmation that brain size is not a factor would strongly suggest the irrelevance of cognition.

Materials and methods

DATA

I obtained from the FishBase 2000 data base (<http://fishbase.org/>; Froese & Pauly 2005), data on establishment success and the geographical region into which fish were introduced (FAO area; <http://www.fao.org/>), brain mass (milligrams), wet body mass (grams; maximum individual weight on record for the species), parental investment (levels: live bearers, species that guard their eggs and non-guarding species) and estimates of minimum and maximum brood size for 39 species (Table 1). FishBase is the most comprehensive tabulation of fish introductions available. Introduction records in FishBase were compiled from the UN Food and Agriculture Organization (FAO) data base on the movement of inland fish species between countries, records in the published literature, and FAO questionnaires. Of course, any such data base will be incomplete. In particular, introductions that failed to result in establishment are probably underrepresented due to underreporting of introductions that failed immediately. Nonetheless, a considerable number of failed introductions were observed (65 out of 207).

Whether or not introduction resulted in a population established in the wild was coded in the original data set as 'no', 'probably no', 'probably yes', 'yes' and 'unknown'. For this analysis, 'no' and 'probably no' were pooled and 'yes' and 'probably yes' were pooled, while records for which establishment was unknown were discarded, resulting in records for 207 introductions of 39 species. The effect of this decision was evaluated using a binary variable to distinguish certain records ('yes' or 'no') from uncertain records ('probably yes' or 'probably no'). I log_e-transformed minimum and maximum fecundity data and used the centre of the interval between these two quantities as a measure of fecundity. Following Sol *et al.* (2005), a linear model for the relationship between log_e-transformed brain mass and log_e-transformed body mass was fit and the residuals were retained as an allometrically scaled measure of relative brain size, elsewhere referred to as the encephalization quotient (Jerison 1985).

ANALYSIS

To test the hypothesis that relative brain size was associated with establishment success, I performed logistic regression with establishment success as the dependent variable and relative brain size, geographical region of introduction, certainty of the recorded introduction outcome (as a check on the decision to

Table 1. Introduced fish species used to test effect of brain size on population establishment

Genus	Species	Introduced populations	Established populations	Establishment rate (%)
<i>Abudefduf</i>	<i>saxatilis</i>	1	1	100.0
<i>Acipenser</i>	<i>transmontanus</i>	2	1	50.0
<i>Arapaima</i>	<i>gigas</i>	1	0	0.0
<i>Astronotus</i>	<i>ocellatus</i>	7	4	57.1
<i>Chelon</i>	<i>labrosus</i>	1	0	0.0
<i>Cichlasoma</i>	<i>severum</i>	1	0	0.0
<i>Dicentrarchus</i>	<i>labrax</i>	3	0	0.0
<i>Dussumieria</i>	<i>elopsoidea</i>	2	2	100.0
<i>Epinephelus</i>	<i>tauvina</i>	1	1	100.0
<i>Epinephelus</i>	<i>merra</i>	1	0	0.0
<i>Esox</i>	<i>lucius</i>	6	4	66.7
<i>Etroplus</i>	<i>suratensis</i>	3	1	33.3
<i>Fistularia</i>	<i>commersonii</i>	2	2	100.0
<i>Gasterosteus</i>	<i>aculeatus</i>	4	4	100.0
<i>Hemichromis</i>	<i>bimaculatus</i>	3	3	100.0
<i>Heterotis</i>	<i>niloticus</i>	6	6	100.0
<i>Lebistes</i>	<i>reticulatus</i>	24	19	79.2
<i>Lepomis</i>	<i>gibbosus</i>	12	12	100.0
<i>Lutjanus</i>	<i>argentimaculatus</i>	2	0	0.0
<i>Lutjanus</i>	<i>kasmira</i>	1	1	100.0
<i>Lutjanus</i>	<i>fulvus</i>	1	1	100.0
<i>Lutjanus</i>	<i>gibbus</i>	1	0	0.0
<i>Mugil</i>	<i>cephalus</i>	2	1	50.0
<i>Mullus</i>	<i>barbatus</i>	1	0	0.0
<i>Oryzias</i>	<i>latipes</i>	5	4	80.0
<i>Oryzias</i>	<i>melastigma</i>	1	1	100.0
<i>Platycephalus</i>	<i>indicus</i>	1	1	100.0
<i>Pungitius</i>	<i>pungitius</i>	1	0	0.0
<i>Rastrelliger</i>	<i>kanagurta</i>	1	1	100.0
<i>Salmo</i>	<i>salmo</i>	16	4	25.0
<i>Saurida</i>	<i>undosquamis</i>	1	1	100.0
<i>saxatilis</i>	<i>plumierii</i>	1	1	100.0
<i>Scomberomorus</i>	<i>commersonni</i>	1	1	100.0
<i>Siganus</i>	<i>rivulatus</i>	1	1	100.0
<i>Siganus</i>	<i>lurida</i>	1	1	100.0
<i>Tilapia</i>	<i>nilotica</i>	39	27	69.2
<i>Tilapia</i>	<i>mozambica</i>	30	21	70.0
<i>Tilapia</i>	<i>rendalli</i>	18	14	77.8
<i>Umbr</i>	<i>krameri</i>	2	1	50.0
Average establishment rate				64.3

pool observations), and fecundity as independent variables. Because several species were introduced on more than one occasion, and because species vary in relatedness, the data are expected to be clustered (Sol *et al.* 2005). Some studies have used hierarchical mixed effects models to include phylogenetic contrasts at different levels (e.g. Blackburn & Duncan 2001; Cassey *et al.* 2004; Sol *et al.* 2005). As this approach was precluded by lack of data, to confirm that results were not an artefact of non-random sampling I also performed a linear regression with the fraction of introductions that were successful for each species (after arcsin-square root transformation) modelled as a function of relative brain size. This analysis has reduced power (because it depends on a smaller number of observations), but ensures independence at the species level.

I considered the effect of parental investment in a separate analysis because not all variables were available for all species. Reproductive behaviour was considered because species highly invested in their offspring might produce fewer eggs, confounding effects of fecundity. Maximum egg diameter was considered as a covariate because it has previously been shown that egg size was a predictor of nuisance status of introduced fish species in the Great Lakes, though not of establishment success (Kolar & Lodge 2002). The maximum was selected because it was more frequently reported than other summary measures (e.g. average).

Results

Because of missing data not all records could be used for all analyses. Therefore, for each test statistic, I also report the number of observations (n) and number of species (S) represented by the analysis. Details of statistical results are available online.

As expected, brain size was strongly dependent on body mass ($P < 0.0001$, $n = 133$, $S = 17$; Fig. 1). Estimates of relative brain size (the residuals from the regression of brain size and body mass), were not correlated with body mass (Pearson's $\rho \approx 0$, $P \approx 1$) resulting in a correctly rescaled measure of encephalization. There was no evidence of a correlation between relative brain size and fecundity (Pearson's $\rho = -0.045$, $P = 0.61$). In logistic regression, only fecundity was a significant predictor of establishment success (fecundity: $P = 0.008$; relative brain size: $P = 0.111$; certainty of introduction record: $P = 0.127$; geographical region $P > 0.99$; $n = 133$, $S = 17$; See Supplementary Table S1). Simple linear regression confirmed that there was no detectable effect of relative brain size on the fraction of populations that established ($P = 0.692$, $n = 39$, $S = 39$; Supplementary Table S2), suggesting that relative brain size was not associated with establishment success. The significant, but relatively weak, negative effect of fecundity on establishment success was retained in univariate analysis ($P = 0.0077$; Fig. 2).

As hypothesized, reproductive behaviour and fecundity were significantly correlated ($F_{2,11} = 19.574$,

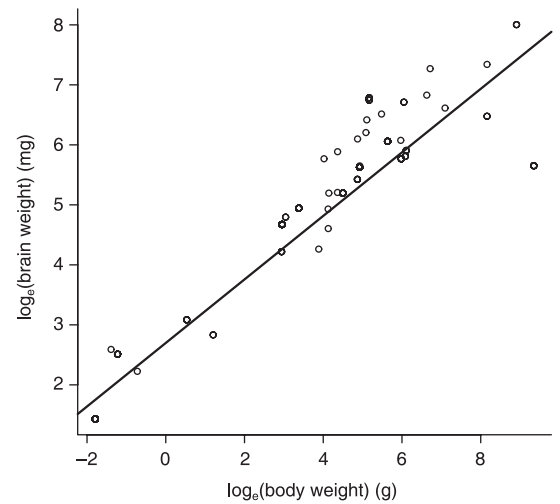


Fig. 1. Relationship between brain mass and body mass of introduced fish species. Following Sol *et al.* (2005), the residuals from this regression line are used as an allometrically rescaled measure of relative brain size.

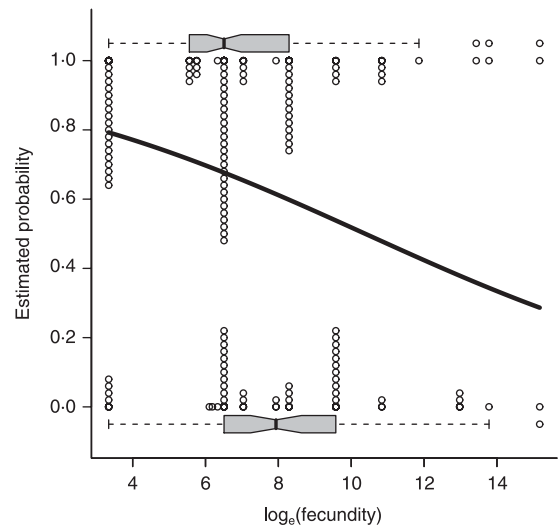


Fig. 2. Probability of successful establishment is negatively associated with fecundity. Following de la Cruz Rot (2005), stacks of open circles (dit plots) corresponds to individual introductions that fail ($y = 0$) or succeed ($y = 1$). Box- and whisker plots summarize these raw data. The solid line shows the estimated logistic model of establishment probability as a function of \log_{10} -transformed fecundity at the maximum likelihood estimates of model coefficients. Null deviance: 173.95 on 132 degrees of freedom. Residual deviance: 166.27 on 131 degrees of freedom. AIC: 170.27.

$P = 0.0002$, $n = 14$, $S = 14$; Supplementary Table S3). Not surprisingly, when establishment success was fit to fecundity and reproductive behaviour simultaneously, neither variable had a significant effect ($\alpha = 0.05$; Supplementary Table S4). However, in univariate analysis (logistic regression, $n = 126$, $S = 14$; Supplementary Table S5), non-guarding species were less likely to establish than live bearing species ($P = 0.0010$), though there was no evidence of a difference between live-bearers and guarding species ($P = 0.82$). Notably,

relative brain size was associated with reproductive behaviour ($F_{2,123} = 4.66$, $P = 0.011$, $n = 126$, $S = 14$; Supplementary Table S6), but explained a relatively small fraction of the total variance ($R^2 = 0.055$). When fit simultaneously ($n = 126$, $S = 14$; Supplementary Table S7), the effect of reproductive behaviour was retained ($P = 0.0004$), while relative brain size was marginally insignificant ($P = 0.055$).

Unexpectedly, there was no evidence for a correlation between fecundity and egg diameter (Pearson's $\rho = -0.29$, $P = 0.48$, $n = 59$, $S = 8$), though the small number of species for which both variables were available resulted in relatively low power. Logistic regressions of establishment success were fit to egg diameter and brain size both with and without fecundity as a covariate ($n = 59$, $S = 8$). In neither case was maximum egg diameter statistically significant (without fecundity as a covariate: $P = 0.17$; with fecundity as a covariate: $P = 0.90$), and, as above, relative brain size was not significant (without fecundity as a covariate: $P = 0.71$; with fecundity as a covariate: $P = 0.22$).

Discussion

BS–EC HYPOTHESIS

Marino (2005) remarked that the BS–EC hypothesis has only been tested with data on birds and primates, and recommended considering other groups. As relative encephalization is greatest in birds and mammals (Jerison 1985), it is plausible that the effects of cognition and behavioural plasticity on establishment success might obtain only for those groups. This study of establishment success in fish found no evidence for a correlation with brain size ranging over either 17 species (for a model in which covariates were fit) or 39 species (for a model without covariates). Consequently, the BS–EC hypothesis was not supported. I also did not find a significant effect of introduction region on establishment success. Further, I found a negative effect of fecundity on establishment success, contrary to conventional theory (MacArthur & Wilson 1963; Richter-Dyn & Goel 1972) but consistent with a recent hypothetical counterexample (Drake 2006).

Detailed consideration of the logistic regression is instructive and aids interpreting these results while avoiding incorrectly asserting the null hypothesis of no effect of brain size. The hypothesis test on the parameter for the effect of relative brain size was only marginally not significant ($P = 0.093$), suggesting that perhaps the test was hindered by low power. However, the estimate of the effect (the estimated value of the coefficient) was negative ($\beta = -0.67$; 95% confidence interval $[-1.504, 0.088]$) suggesting that, if anything, the increased relative brain size reduced the probability of establishment. Indeed, exponentiating the upper 95% confidence interval indicates that at most, relative brain size increases the odds of establishment by $e^{0.088} - 1 \approx 9\%$ and more likely decreases it by half. Thus, although it

is possible that additional data would reverse the conclusion that relative brain size does not increase the chance of establishment, it more likely would confirm a negative effect.

In the future, three potentially confounding factors that could not be controlled for in this study should be considered. First, true effects of cognition on colonization success could be habitat-specific, for instance if species with relatively larger brains are more successful at colonizing suboptimal habitats than other species. Such a subtle effect probably is undetectable in highly heterogeneous data such as used here. Second, brain size might be affected by relatedness among introduced individuals (the extreme case of this is in introductions of the same species) so that data are not independent. Kotrschal *et al.* (1998) report that there is a 'coarse' trend towards increased brain size with phylogenetic development, exemplified by the difference between agnathans, exhibiting relatively small brains, and perciforms, featuring larger brains. With more data, a hierarchical model with random effects might be used to perform nested phylogenetic contrasts (cf. Sol *et al.* 2005), though the regression analysis reported here for the fraction of introduced populations vs. relative brain size suggests that a more complicated model is unlikely to reveal patterns not identified here. Finally, it is known that propagule pressure is a common correlate of establishment success across taxonomic groups (Lockwood *et al.* 2005) and that correlations between propagule pressure and other factors thought to contribute to establishment success has confounded previous analyses (Cassey *et al.* 2004). Propagule pressure has two aspects. The effect of multiple introductions, that is, as long as there is some non-zero chance of colonization success repeated introductions will eventually result in establishment, is accommodated here by the fact that introduction records correspond to introduction events. Unfortunately, for these introductions there are no estimates of the number of individuals that were introduced on each occasion (introduction size), which is a second aspect of propagule pressure known to correlate with establishment success (Marchetti *et al.* 2004a; Lockwood *et al.* 2005). The finding by Cassey *et al.* (2004) suggested that introduction size is commonly correlated with other factors postulated to affect establishment success does not confound interpretation of the finding reported here. Even if the questionable extrapolation of results by Cassey *et al.* (for birds) to this study (on fish) is justified, the direction of the effect is opposite that which would result in spurious inference.

ARE INVASIVE FISH DIFFERENT FROM INVASIVE BIRDS?

The long-standing search for general characteristics of colonizing species continues unabated (Kolar & Lodge 2001, 2002; Marchetti *et al.* 2004a,c). Almost certainly there is a taxonomic level above which generalizations

about colonizing ability fail to hold. Sol *et al.* (2005) provided evidence supporting the idea that cognitive innovation may be an important determinant of establishment success in birds. By contrast, perhaps fishes do not exhibit the same degree of cognitive variation so that differential cognitive ability does not discriminate species with respect to colonizing ability, or perhaps behavioural innovations in fishes are too uncommon to influence colonization success. Indeed, crude relative brain size might simply be a poor indicator of the capacity for cognitive innovation (Safi *et al.* 2005). However, these speculations are inconsistent with the emerging picture of relative cognitive complexity for fish (Kotrschal *et al.* 1998; Bshary *et al.* 2002). Alternatively, then, it might be that the relevant behaviours in fishes are instead those that relate to reproduction rather than feeding, such as the guarding behaviours shown here to correlate with establishment success. Reproduction will also be related to individual growth, which has consistently been identified as a reliable predictor of establishment success in fishes (Kolar & Lodge 2002; Marchetti *et al.* 2004a). In conclusion, as establishment success probably depends on ecological characteristics that differ among groups with highly different habits and life-histories, correlates of establishment success are unlikely to be universal among vertebrates (cf. Marino 2005).

RISK FACTORS FOR SPECIES INVASION

Previous studies have identified many risk factors for invasion by fishes (Kolar & Lodge 2002; Marchetti *et al.* 2004a,c), including many such as propagule pressure that point to association with human activities as the critical factor determining success. To my knowledge no previous study has shown a relationship between establishment success and fecundity in fishes, though Kolar & Lodge (2002) found that nuisance fish species had smaller eggs than established species that were not a nuisance. The finding reported here, that establishment success is negatively related to fecundity, is surprising in the light of theory that predicts highly productive species will be more successful colonizers (MacArthur & Wilson 1963; Richter-Dyn & Goel 1972). Although the lack of evidence for this generalization has been pointed out previously (Lodge 1993), most models suggest that establishment success should increase with fecundity. One might speculate that evolution is constrained by a trade-off between fecundity and parental investment. Here, I found that parental care was significantly associated with establishment success, consistent with the results of Marchetti *et al.* (2004a,c), but not with Kolar & Lodge (2002). In conclusion, these results suggest that in these species behaviour (parental care) may be a more important determinant of colonization success than demographic characteristics (fecundity), though the latter continues to be a basis for fruitful theory (Haccou & Iwasa 1996; Haccou & Vatutin 2003). In addition to increasing

understanding of the colonization process, these results support the further identification and analysis of species traits as a basis for risk assessment (Ricciardi & Rasmussen 1998; Kolar & Lodge 2002; Marchetti *et al.* 2004c).

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Supplementary materials

The following supplementary material is available for this article:

Table S1. Summary of logistic regression model for effects of relative brain size, fecundity, FAO area and certainty of the recorded introduction outcome on establishment success

Table S2. Summary of linear regression for effect of relative brain size on the fraction of populations established, by species

Table S3. Summary of ANOVA model for effects of reproductive behaviour on fecundity

Table S4. Summary of logistic regression model for effects of reproductive behaviour and fecundity of establishment success

Table S5. Summary of logistic regression model for effect of reproductive behaviour on establishment success

Table S6. Summary of ANOVA model for effects of reproductive behaviour on relative brain size

Table S7. Summary of logistic regression model for effects of reproductive behaviour and relative brain size on establishment success

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