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Behavioural flexibility predicts invasion success in birds introduced to New Zealand

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A fundamental question in ecology is whether there are evolutionary characteristics of species that make some better than others at invading new communities. In birds, nesting habits, sexually selected traits, migration, clutch size and body mass have been suggested as important variables, but behavioural flexibility is another obvious trait that has received little attention. Behavioural flexibility allows animals to respond more rapidly to environmental changes and can therefore be advantageous when invading novel habitats. Behavioural flexibility is linked to relative brain size and, for foraging, has been operationalised as the number of innovations per taxon reported in the short note sections of ornithology journals. Here, we use data on avian species introduced to New Zealand and test the link between forebrain size, feeding innovation frequency and invasion success. Relative brain size was, as expected, a significant predictor of introduction success, after removing the effect of introduction effort. Species with relatively larger brains tended to be better invaders than species with smaller ones. Introduction effort, migratory strategy and mode of juvenile development were also significant in the models. Pair-wise comparisons of closely related species indicate that successful invaders also showed a higher frequency of foraging innovations in their region of origin. This study provides the first evidence in vertebrates of a general set of traits, behavioural flexibility, that can potentially favour invasion success.

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The earth's biota is being rapidly homogenised as human activities increasingly introduce species outside their natural range (Brown 1989, Lodge 1993). Even though most invaders fail to colonise new areas and those that succeed have a generally low environmental and economic impact, the cumulative negative effect of exotic species has been and will continue to be large (Williamson 1996). Ecologists have long wondered why some animals are extremely successful invaders, while close relatives are often not (Ehrlich 1989). Determining the relative importance of factors influencing the success or failure of species' introductions can help us understand how communities are organised, as well as offer an important tool in conservation (Griffith et al. 1989).

Many biogeographic, ecological, genetic and physiological attributes have been proposed to account for a species' chance to establish new populations outside its natural range (Ehrlich 1989, Lodge 1993, Williamson 1996). Empirical evidence does not always support these a priori distinctions, however, and until recently none appeared compelling. One reason for this failure is the lack of detailed data. First, unsuccessful attempts are more difficult to detect than successful ones (Lodge 1993, Simberloff 1995), potentially biasing the data. Second, introduction effort is generally unknown (Veltman et al. 1996). Third, it is increasingly recognised that community characteristics can be as important as invader attributes or introduction effort in influencing

success (Lodge 1993). For all these reasons, we lacked until recently a general framework for explaining why some animals are successful invaders while their close relatives are often not.

New Zealand is a set of islands that have proven exceedingly vulnerable to occupation by exotics (Thomson 1922, Long 1981, Baker 1991, Duncan et al. 1999; but see Sol in press). The history of avian introductions to New Zealand was extensively documented by Thomson (1922), who not only reported the outcome of a large number of species introduced by humans, but also details of the introduction effort. Thomson's data thus provide a unique opportunity to analyse the attributes of successful invaders. Based on Thomson's data, Veltman et al. (1996) analysed the importance of different life history traits in determining the success or failure of introduced avian species and found that, when controlling for the effect of initial population size, species that migrate in their native ranges were less likely to establish themselves in the islands than non-migratory species. Green (1997) also found, using a similar data set, a positive effect of body size on the probability of successful establishment, and a negative effect of clutch size and latitude of origin; however, the significance of these variables was sensitive to taxonomic (within vs between family comparisons) and statistical (presence vs absence of Bonferroni corrections) decisions. Finally, Sorci et al. (1998) found that dichromatic species (i.e. those with strong sexual selection on plumage colour; see Møller and Birkhead 1994) experienced reduced chances of establishing themselves in New Zealand when compared with monochromatic species, a result that is consistent with a previous finding by McLain et al. (1995).

One set of traits that has received surprisingly little attention in this literature is behavioural flexibility. Behavioural flexibility, in the form of learning, cognition and/or rapid adjustment to new conditions, allows animals to respond more rapidly to changes in the environment and can therefore be an advantage when invading novel habitats. For instance, a species that readily exploits new food sources may be more pre-adapted to live in a novel environment that a more specialised one. Behavioural flexibility is thought to be associated with relative size of the forebrain, and, in particular for birds, with size of the hyperstriatum ventrale and neostriatum, the avian equivalents of the mammalian neocortex (Rehkämper and Zilles 1991). Animals that have larger forebrains are assumed to deal more efficiently with environmental complexity and respond more rapidly to changes in the environment, adopting new food types and handling techniques at a faster rate (e.g. Wyles et al. 1983, Joliceur et al. 1984, Dunbar 1992, Lefebvre et al. 1997, 1998). Lefebvre et al. (1997) used frequency of foraging innovations in the short note sections of ornithology journals as an operational measure of behavioural flexibility and found that it was positively associated with mean relative forebrain size per avian order in both Europe and North America. Recent work shows that the trend also holds for birds of Australia and New Zealand (Lefebvre et al. 1998) and cannot be accounted for by confounding variables like population size, species number, research effort, ornithologist interest, reporting bias, mode of juvenile development or common ancestry (Lefebvre et al. unpubl., Nicolakakis et al. unpubl.). Invasion success, which should logically be influenced by opportunism and flexibility, could very well be related to the variables studied by these authors. In this paper, we use data of avian species introduced to New Zealand to test the hypothesised link between forebrain size, innovation frequency and invasion success.

Methods

Brain size data were obtained from Crile and Quiring (1940), Portmann (1947), Armstrong and Bergeron (1985) and Boire (1989). Brain mass was available for 39 of the species reported by Veltman et al. (1996) and Green (1997) (Table 1), while forebrain mass was available for 27 species. Because total brain mass is strongly correlated with forebrain mass (Pearson correlation coefficient; $n = 27$, $r = 0.99$, $p < 0.001$; see also Bennett and Harvey 1985), we performed all our analyses with this variable as an estimator of forebrain size; similar results are in any case obtained whether forebrain size only is used. Total brain size is also a very close predictor (95.1% of the variance, Timmermans 1999) of relative size of the neostriatum/hyperstriatum ventrale complex, which is unfortunately available for very few species (Boire 1989, Rehkämper et al. 1991). To control for the allometric effect of body size on brain size (Bennett and Harvey 1985), we used the residuals of log-log regressions against body mass. Body mass was obtained from the same sources as was brain mass and the residuals were taken from a log-log regression on all available species ($n = 208$). When more than one source had data for a given species, we averaged the brain and body mass values for the sources.

Species can generally not be considered independent data points because closely related ones tend to share many characters through common descent rather than independent evolution (Harvey and Pagel 1991). To overcome this problem we used two approaches. Firstly, we tested for the most obvious phylogenetic confounds by comparing the introduction success of the large order Passeriformes, which includes almost half of the species in our data set, to all other orders (see Green 1997, Sorci et al. 1998 for a similar procedure); we found no significant difference in success between the two groups (Yates corrected $X^2 = 1.85$, d.f. = 1, $p = 0.174$). see Green (1997) and Sorci et al. (1998) also

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reported no difference at the level of the order and the family using a larger sample of the same data set. In addition, we also found no differences in the mean and variance of brain size residuals between Passeriformes and all other orders (t-test for equality of means, $p > 0.23$ in all cases; Levene's test for equality of variances, $p > 0.17$ in all cases). Secondly, we applied the phylogenetic-subtraction method (Stearns 1983, Harvey and Pagel 1991) to remove any phylogenetic effects from the multivariate models. This method consists in using categorical codes for each taxon to remove phyletic differences between species (see below).

To test for the link between relative brain size and invasion success, we conducted logistic regressions similar to those used in the three previous studies on New Zealand birds (Veltman et al. 1996, Green 1997, Sorci et al. 1998). A binomial error with a Logit link was implemented using GLIM (Crawley 1993). The outcome of the introduction was the dependent variable, which took a value of 0 when the species failed in establishing itself and 1 when it succeeded. All the variables used by Veltman et al. (1996) and Sorci et al. (1998) were included as control variables in the logistic models. In addition, we included three other variables: (1) mode of juvenile development (nidicolous vs nidifugous), which is correlated with relative brain size (Bennett and Harvey 1985), (2) the source of the brain size data (Portmann (1947) vs other sources), and (3) the type of nest (categorised as ground nesters, canopy + shrub nesters and non-excavators hole nesters), which has been suggested by Newsome and Noble (1983) as a possible determinant of invasion success. To test for potential phylogenetic confounds and subtract them if they are significant, the taxon (order) was also introduced in the model. Taxonomic designations follow Sibley and Monroe (1990). Following Green (1997), introduction effort was entered as a categorical variable with three levels: 2–10 individuals introduced; 11–100 individuals; more than 100 individuals; preliminary analyses show that this measure leads

Table 1. Avian species introduced in New Zealand before 1907 and for which information on brain size was available.

Family	Species	Introduction outcome	Relative brain size	Source of brain data
Anatidae	*Alopochen aegyptiacus*	0	−0.480	A
Anatidae	*Anas acuta*	0	−0.090	A
Anatidae	*Anas penelope*	0	−0.610	B
Anatidae	*Anas platyrhynchos*	1	−0.440	B
Anatidae	*Anser anser*	0	−0.250	B
Anatidae	*Cygnus olor*	1	−1.050	B
Charadridae	*Vanellus vanellus*	0	−0.380	B
Alaudidae	*Alauda arvensis*	1	0.309	B
Corvidae	*Corvus frugilegus*	1	2.276	B
Corvidae	*Corvus monedula*	0	1.394	B
Fringillidae	*Acanthis cannabina*	0	0.057	B,C
Fringillidae	*Agelaius phoeniceus*	0	0.557	C
Fringillidae	*Carduelis carduelis*	1	0.116	B
Fringillidae	*Carduelis spinus*	0	0.142	B,C
Fringillidae	*Emberiza citrinella*	1	−1.200	C
Fringillidae	*Fringilla coelebs*	1	−0.030	B
Muscicapidae	*Eritachus rubecula*	0	−0.070	B
Muscicapidae	*Turdus merula*	1	0.134	B
Muscicapidae	*Turdus philomelos*	1	0.094	B
Passeridae	*Passer domesticus*	1	0.423	A,B,D
Passeridae	*Poephila guttata*	0	−1.320	D
Passeridae	*Prunella modularis*	1	0.146	B
Sturnidae	*Sturnus vulgaris*	1	0.564	A,B
Sylvidae	*Sylvia atricapilla*	0	0.709	C
Phasianidae	*Colinus virginianus*	1	−1.780	C,D
Phasianidae	*Coturnix coturnix*	0	−2.060	B,D
Phasianidae	*Gallus gallus*	0	−2.510	B,D
Phasianidae	*Lagopus lagopus*	0	−1.410	A,C
Phasianidae	*Lophortyx californicus*	1	−1.390	C
Phasianidae	*Lophura nycthemera*	0	−1.040	B
Phasianidae	*Numida meleagris*	0	−1.660	A,D
Phasianidae	*Perdix perdix*	0	−1.670	B,D
Phasianidae	*Phasianus colchicus*	1	−1.460	A,B,D
Phasianidae	*Alectoris chuckar*	0	−1.290	D
Phasianidae	*Tetrao tetrix*	1	−1.470	B
Psittacidae	*Melopsittacus undulatus*	0	0.294	B,D
Strigidae	*Athene noctua*	1	1.196	B
Strigidae	*Strix aluco*	0	1.765	B
Tytonidae	*Tyto alba*	0	1.471	B

Introduction outcome: 0 = failure; 1 = success. Source of brain data: A = Crile and Quiring (1940); B = Portmann (1947); C = Armstrong and Bergeron (1985); D = Boire (1989).

Table 2. Closely related species used in the comparison of foraging innovations between successful and unsuccessful invaders. Numbers are frequency of foraging innovations recorded in their region of origin.

Unsuccessful invaders	Innovations	Successful invaders	Innovations
Europe			
Anas penelope	2	Anas platyrhynchos	5
Anas acuta	0	Cygnus olor	1
Perdix perdix	0	Phasianus colchicus	1
Lullula arborea	0	Alauda arvensis	1
Luscinia megarhynchos	0	Turdus philomelos	5
Erithacus rubecula	5	Turdus merula	14
Corvus monedula	2	Corvus frugilegus	5
Passer montanus	2	Passer domesticus	10
Fringilla montifringilla	1	Fringilla coelebs	3
Carduelis spinus	0	Carduelis chloris	2
Acanthis cannabina	0	Carduelis carduelis	4
Acanthis flavirostris	0	Acanthis flammea	0
Emberiza hortulana	1	Emberiza citrinella	0
Emberiza schoeniclus	0	Emberiza cirlus	0
Australia			
Ocyphaps lophotes	0	Columba livia	1
Coturnix pectoralis	1	Coturnix australis	0
North America			
Aix sponsa	0	Branta canadensis	1
Oreortyx pictus	0	Lophortyx californicus	0
Tympanuchus cupido	0	Colinus virginianus	0

to similar conclusions to the one used by Veltman et al. (1996), minimum number of introduced individuals required for a successful invasion.

The best logistic models were determined by removing from the full model those variables that did not improve it. The influence of each variable on invasion success was tested with a likelihood ratio test that compared each model to its lower order version that excluded the particular variable being tested. The selection procedure was run manually, using the $p = 0.05$ threshold for removal of terms. At each step, the less significant variable was removed until the model retained only significant predictors. The significance of alternative models was investigated by adding the previous variable removed from the model. To evaluate the effect of the use of species with low introduction effort (Sorci et al. 1998), we repeated the analyses using only species with an introduction effort equal or larger than the minimum effort recorded for a successful invader species.

Frequencies of foraging innovations per species were taken from Lefebvre et al. (unpubl.) for birds originating from North America and Australia and Nicolakakis et al. (unpubl.) for species originating from Europe; these data are an augmented version of the data base used by Lefebvre et al. (1997, 1998) and include a total of 930 innovations instead of the previous 430. Foraging innovations were available for 76 of the species reported by Veltman et al. (1996). Because these species originate from different parts of the world, and because the total number of foraging innovations varies between regions (e.g. the Australian total is approximately one third of the European one), absolute

innovation frequencies cannot be compared directly. To control for this effect, as well as possible phyletic ones, we analysed the difference in foraging innovations between successful and unsuccessful invaders by means of pair-wise comparisons of closely related species (same genus or family) originating from the same continent or sub-continent. This method effectively controls for confounding variables, since closely related species are more generally similar with respect to ecology, morphology, physiology and anatomy (Ehrlich 1989, Møller and Birkhead 1992).

However, in order to further control for possible biases and not favour type 1 error, we avoided whenever possible the pairing of species where the unsuccessful one was dimorphic in colour plumage and the other monomorphic (Sorci et al. 1998), and/or where the unsuccessful species was migratory and the other one sedentary (Veltman et al. 1996). In a few cases, a family contained more than one possible pair; the two species were randomly chosen for the paired comparison. In four cases the only possible pair did not meet our other criteria, but these pairs were tentatively included in the analyses to cover the broadest possible range of bird taxa; this decision does not affect our conclusions, as analyses with and without the four pairs yield identical results. A total of 19 pairs of closely related species differing in invasion success were thus available from the feeding innovation data (Table 2). This data set also includes three pairs where the resulting association is against the hypothesis, which further suggests that our methodological decisions are conservative and unbiased. To evaluate the effect of using species with low introduction effort, we repeated the

analyses using only species with an introduction effort equal or larger than the minimum effort recorded for a successful invader species.

Results

Invasion success and relative forebrain size

The data set included 20 species that failed to invade New Zealand and 19 species that succeeded. In his study, Green (1997) excluded three of these species, the mallard, *Anas platyrhynchos*, California quail, *Lophortyx californicus*, and ring-necked pheasant, *Phasianus colchicus*, arguing that their feral populations were the product of captive breeding; we also excluded them from our final analysis, even though preliminary work shows that their inclusion would not have changed the results.

We obtained a unique GLM model (Table 3) in which five variables remained: relative brain size, introduction effort, migration, mode of development and source of the brain data. However, two levels of the variable 'introduction effort' (≤ 100 individuals and > 100) were not significantly different one from another in their parameter estimates. We derived a simplified model by grouping levels that were not statistically different (change in deviance = 6.89 − 6.76 = 0.13). This final model shows that invasion success increases with relative brain size ($X^2 = 18.78$, df = 1, $p = 0.00002$) and introduction effort ($X^2 = 35.30$, df = 1, $p < 0.00001$) and is lower for nidicolous species than it is for nidifugous ones ($X^2 = 13.39$, df = 1, $p = 0.0001$). Migration was also significant ($X^2 = 24.51$, df = 2, $p < 0.00001$), success being highest for partially migratory species and lowest for migratory ones. Finally, a bias in the brain data source was also detected ($X^2 = 13.05$, df = 1, $p = 0.0001$), although the conclusions does not vary if this variable is excluded from the final model. The taxonomic variable 'Order' was not significant in the model.

Table 3. Best GLM model for invasion success in birds introduced to New Zealand using a logistic link with binomial error (total deviance = 49.46).

	Parameter estimate	Standard error
Constant	−28.61	34.09
Relative brain size	22.97	11.81
Effort of intro-duction	−28.61 to 64.68	34.09 to 43.76
Migration	−74.63 to 5.49	7.05 to 62.46
Mode of develop-ment	−41.60	22.59
Source of brain data	31.73	17.78
scaled deviance = 6.77		
residual df = 29		

Considerable care must be exercised when interpreting binomial GLM models in cases where they explain only a small fraction of the total variance or are based on marginally significant parameters. Regarding the first point, the model accounted for 86.3% of the variance in invasion success and did not show excessive overdispersion (residual deviance/residual df = 0.24). The second point is also not problematic because all variables entered in the model are significant at the 0.0001 level, and remain so under Bonferroni standards (significance = α/number of variables = 0.05/19).

For seven species, introduction effort was lower than the minimum recorded for a successful invader (i.e. three release events and eight released individuals; see Veltman et al. 1996); the probability that these species could establish itself in the islands was thus very low. This is the case, for example, for the Eurasian jackdaw, *Corvus monedula*, which did not establish itself in New Zealand despite our models predicting it would; introduction effort in this case is very low, with only two release events and three released individuals (Veltman et al. 1996). To test if a possible bias toward such unsuccessful species could have influenced our results, we repeated the analyses with only those cases in which introduction effort was equal or larger than the minimum recorded for a successful invader (see Sorci et al. 1998). The results were similar to those obtained with the whole data set: relative brain size ($X^2 = 20.30$, df = 1, $p < 0.00001$), introduction effort ($X^2 = 26.40$, df = 1, $p < 0.00001$), mode of development ($X^2 = 15.97$, df = 1, $p = 0.0001$), migration ($X^2 = 27.33$, df = 2, $p = 0.0001$) and source of brain data ($X^2 = 13.64$, df = 1, $p = 0.0001$) remain significant.

Because relative brain size and mode of development have opposite effects on the outcome of the introduction, it might very well be that in practice one variable can cancel the effect of the other. This possibility can be tested by removing one of the variables and looking at significance in the other. When mode of development is excluded from the final model, relative brain size still remains significant ($X^2 = 5.43$, df = 1, $p = 0.019$). In contrast, when relative brain size is removed, mode of development becomes non-significant ($X^2 = 0.04$, df = 1, $p = 0.84$). These results show that relative brain size is a more influential variable than mode of development.

Invasion success and foraging innovations

Successful invaders showed a higher frequency of foraging innovations ($n = 28$, mean = 1.96, SD = 3.21) than unsuccessful species ($n = 48$, mean = 0.58, SD = 1.01; Mann-Whitney U-test; $U = 496.5$, $p_{one-tailed} = 0.029$). To control for phylogenetic effects and biases in the origin of data, a pair-wise comparison of closely related species was performed (Table 2). Once again, successful

invaders showed a higher frequency of foraging innovations than did unsuccessful species (Wilcoxon matched-pairs signed-ranks test; $n = 19$ pairs, $z = 2.95$, $p_{one-tailed} = 0.0015$): in 13 out of 19 pairs of closely related species, the frequency of foraging innovations was higher for the successful species than it was for the unsuccessful one. In four of the remaining pairs, the number of foraging innovations was the same for the two members, and in only two did the successful species show a smaller frequency than the unsuccessful one. This result is unlikely to be influenced by the way pairs were formed, because successful invaders had a higher frequency of foraging innovations than unsuccessful species in 21 out of the 38 possible pairs (i.e. also including those pairs that not meet the criteria of selection; see Methods), while the relationship was the opposite in only three pairs. Neither exclusion of the four unsuccessful species for which introduction effort is lower than the minimum required (see above) nor exclusion of the three species eliminated by Green (1997) affect our conclusions; excluding these species yields results that are very similar to those given above ($n = 14$, $z = 2.80$, $p_{one-tailed} = 0.0003$; $n = 16$, $z = 2.69$, $p_{one-tailed} = 0.0004$, respectively). This conclusion seems little affected by differences in the effort of introduction, since in only four of the pairs the introduction effort for the successful species was classified in a higher category than that of the unsuccessful one.

Discussion

Evidence that some intrinsic traits of vertebrates can predispose them to be successful invaders comes from the fact that some species establish themselves in new areas while others fail to do so (Ehrlich 1989). In birds, nesting habits (Newsome and Noble 1983), sexually selected traits (McLain et al. 1995, Sorci et al. 1998), migratory behaviour (Veltman et al. 1996), clutch size (Green 1997) and body mass (Green 1997) have been linked to this difference. Here, we show that behavioural flexibility can also affect the fate of introduction attempts in the most thoroughly documented zone of the world, New Zealand: all else being equal, bird species with relatively large brains and a high frequency of foraging innovations in their area of origin tend to be more successful invaders than species with smaller forebrains and lower innovation frequencies. The trend appears to be robust, given that similar results were reached with different analytical assumptions and approaches.

Our results differ in some aspects from previous analyses on birds introduced to New Zealand (Veltman et al. 1996, Green 1997, Sorci et al. 1998). First, only two of the six variables previously reported as major determinants of invasion success remain significant in our models: introduction effort and migratory strategy. Secondly, a new variable emerges, mode of juvenile development: all else being equal, nidifugous species tend to be better invaders than nidicolous ones. This result should be interpreted with caution, however, since the development was only significant when relative brain size was also included in the model. Lockwood (1999), however, has very recently shown that nidifugous game birds like Anatidae, Phasianidae, Rheidae and Odontophoridae are over-represented in worldwide patterns of invasions, a finding that is consistent with ours despite differences in approach; Lockwood (1999) looks only at successful invasions and focuses on broad taxonomic trends.

When asking why some animals are successful invaders while close relatives are often not, it is equally important to consider why a given species succeeds as it is to ask why its relative does not (di Castri 1990). Although migration and dichromatism might be significant predictors of introduction success, they primarily explain why certain species repeatedly fail to invade a new environment, but say much less about why other species are such good invaders. In contrast, brain size and feeding innovations have a much broader explanatory power. Behavioural flexibility implies a rapid respond to novel environmental conditions and presumably allow animals to exploit a wider variety of ecological contexts (Wyles et al. 1983). A species that, for example, readily exploits new food sources is more likely to be pre-adapted to live in a novel environment than a more specialised species that persists with the foraging behaviours and diet of its area of origin. Indeed, there are several cases where behavioural flexibility has been linked with the differential invasive abilities of closely related species. For example, the contrasting successes in North America of the common starling, *Sturnus vulgaris*, and the closely related Southeast Asian crested myna, *Acridotheres cristatellus*, have been attributed to the fact that, beyond the effects of climate, mynas retained breeding habits appropriate to their homelands, which are less appropriate in British Columbia (Johnson and Cowan 1974, Ehrlich 1989).

In New Zealand, exotic birds are generally excluded from intact, climax forest avian communities and most can only invade urban habitats and browsed forests where the native avian community has been decimated and the forest structure altered (Diamond and Veitch 1981, Duncan et al. 1999, Sol in press). The reduced number of species in such anthropogenically modified habitats presumably leads to the absence of some major exploitation strategies (Simberloff 1995, Williamson 1996). Furthermore, the introduction of exotic species can lead to extinction of native species through predation, competition or disease transmission, as well as alteration of natural habitats by browsing and grazing; such an impact on the structure of natural ecosystems can have a negative effect on the native community and

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create new opportunities for invaders (see Diamond and Veitch 1981). This scenario is compatible with our idea that behavioural flexibility is a key determinant of invading success; it suggests that, in New Zealand, successful invaders are those species that are able to exploit a wider variety of ecological contexts, more than those that interact successfully with native biota.

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