

Are threat status and invasion success two sides of the same coin?

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Global change increases both the number of threatened species and the impacts of invasives. These two problems are sometimes assumed to be opposite sides of the same coin, with invasive species having the opposite characteristics of endangered species. However, the validity of this assumption has never been tested. We analysed 20 life-history and other traits of all European and North American freshwater fish and birds. For these 1813 species, we compared the determinants of invasion success and IUCN-threat status and found that traits favouring invasion are not simply the opposite of those that favour endangerment. The size and life history of species are correlated more strongly with threat status than invasiveness. On the other hand, association with humans is the best predictor of invasiveness but is not correlated with threat status. Thus, the rise of invaders is caused by different aspects of global change than the imperilment of endangered species.

What determines extinction risk? and What determines invasion success? are both important biological questions. It is sometimes assumed that these two questions are tightly linked: “The traits commonly listed as increasing vulnerability to extinction are similar, although opposite in sign, to those listed as increasing the probability of being a ‘good invader’” (p. 561 in Lockwood 1999). But is it really valid to think of condors and other red-listed species as one side of a coin that shows starlings and other invasives on the flip side? We address this question here, testing the hypothesis that the characteristics of endangered species are the opposite of those of invaders.

This hypothesis reflects the belief that globally abundant species, and invaders in particular, share certain characteristics that are absent in threatened species. For example, abundant species are sometimes thought to have a “fast” life history (or are r-selected) and rare species a “slow” life history (or are K-selected), although empirical evidence is equivocal (Lodge 1993, Rejmánek and Richardson 1996, McKinney 1997, Musick 1999, Foufopoulos and Ives 1999, Kolar and Lodge 2001, McMahon 2002, Reznick et al. 2002, Reynolds 2003, Fisher and Owens 2004, Davis 2005, Lockwood et al. 2005, Bishop and Peterson 2006, Ferguson and Higdon 2006, Jeschke and Strayer 2006, Moyle and Marchetti 2006, Cardillo et al. 2006, Olden et al. 2006, Duyck et al. 2007; for general information on r/K-selected species and fast-slow life histories, see Pianka 1970, Sæther 1987, Reznick et al. 2002, Reynolds 2003, Jeschke et al. in press, Jeschke and Kokko unpubl.). Two quotes may better illustrate the implicit assumption made

in many of these studies that invasive and threatened species have opposite characteristics: “Most invasive species with major ecological impacts [...] have r-selected life-history and reproductive traits that allow them to achieve massive population densities soon after invading a new habitat” (p. 1242 in McMahon 2002). On the other hand, “K-selected species provide low maximum sustainable yields and recover slowly from overfishing. [...] K-selected species were the most vulnerable” (p. 1 in Musick 1999).

Published analyses of several specific factors support the opposite-characteristics hypothesis. For example, the larger the geographic range, the less likely is extinction but the more likely is introduction to a new environment by humans, and thus invasion (McKinney 1997, Purvis et al. 2000, Jones et al. 2003, Fisher and Owens 2004, Koh et al. 2004, Cardillo et al. 2005, 2006, Keane et al. 2005, Reynolds et al. 2005, Jeschke and Strayer 2006, Payne and Finnegan 2007). Similarly, habitat and diet generalists tend to be less likely to become extinct than specialists but more likely to become invasive (McKinney 1997, Foufopoulos and Ives 1999, Purvis et al. 2000, Reynolds 2003, Fisher and Owens 2004, Koh et al. 2004, Van Valkenburgh et al. 2004, Keane et al. 2005, Kotiaho et al. 2005, Reynolds et al. 2005, Jeschke and Strayer 2006, Moyle and Marchetti 2006).

However, other specific factors that have been investigated raise doubts as to whether the characteristics of endangered species are simply the opposite of those of invaders. Although the intensity of sexual selection within a species is often thought to increase extinction risk and

diminish invasion success, available empirical data neither support nor contradict this belief (Andersson 1994, Prinzing et al. 2002, Kokko and Brooks 2003, Doherty et al. 2003, Fisher and Owens 2004, Morrow and Fricke 2004, Koh et al. 2004, Jeschke and Strayer 2006). Evidence about the influence of hunting is contradictory: while hunting has imperilled or extinguished species, it is positively correlated with invasion success because hunted species are more likely to be introduced than non-hunted species (Wilson 1992, McKinney 1997, Bodmer et al. 1997, Fisher and Owens 2004, Jeschke and Strayer 2006).

Existing information cannot, however, adequately test the hypothesis that threat status and invasion success are two sides of the same coin. This is surprising, given how frequently the assumption is made, either explicitly (Lockwood 1999) or implicitly as a basis of higher-level hypotheses (see, for example, the above paragraph on fast and slow life histories). The only study that systematically considered multiple characteristics of introduced and imperilled species is Blackburn and Cassey (2004) where introduced birds were compared to re-introduced species which are often globally threatened. Yet, not all introduced species become invasive (most of them do not, not all re-introduced species are threatened (35 out of 84 species in Blackburn and Cassey (2004)), and not all threatened species are re-introduced (only a subset selected by humans; 35 out of 1186 species in Blackburn and Cassey (2004)), hence the results by Blackburn and Cassey do not provide direct information on the opposite-characteristics hypothesis. Studies do exist that looked at the correlates of invasion success or of threat status (see above for references), but no previous study looked at both simultaneously, i.e. for a single set of species and data.

Here, we use a large data set on European and North American fish and birds to analyse the correlates of threat status. We compare these findings with the correlates of invasion success reported in a previous study (Jeschke and Strayer 2006) where the same data set and types of analysis were used. We test the opposite-characteristics hypothesis by investigating if species traits correlate to threat status in the opposite way they correlate to invasion success.

Material and methods

We analysed all freshwater fish and birds that are native to either Europe or North America, following the ordinary geographical definition of Europe but defining North America as Canada and the United States except Hawaii. Species that are native to both continents were excluded, leaving 1813 species which were also investigated by Jeschke and Strayer (2005, 2006) and Jeschke and Kokko (unpubl.). These studies additionally included mammals, but these data were not available for the current study.

We considered the same independent variables as in Jeschke and Strayer (2006): as an index of propagule pressure (Lockwood et al. 2005), we used the number of countries (Europe) or states and provinces (North America) where a species was separately introduced; more exact data on propagule pressure were not consistently available. We expect that species often introduced beyond their native range are rarely endangered. Human affiliation is a binary

variable denoting whether a species lives in close association with humans. Specifically, human affiliates include domestic animals; other species deliberately raised for pets, food, or sport in large numbers; and species that reach high population densities in human settlements (e.g. rats or house sparrows). Species strongly affiliated with humans should not normally be endangered. Hunting is a binary variable denoting whether a species has been deliberately sought and harvested from the wild in substantial numbers, whether for sport, individual consumption, or commercial harvest. Hunting is the third variable directly associated with humans. We included three variables on population size and extent: population density, defined as the average number of individuals in areas actually inhabited by a given species (only available for birds), latitudinal range in the native continent, and the native continent itself (Europe or North America). The two variables on diet were carnivory as opposed to herbivory and diet breadth, quantified as the number of the following nine different food types included in the diet: nectar, pollen, gum, flowers; fruits, mushrooms; grain, seeds; grass, herbs; leaves, shoots, branches, bark, roots, tubers; detritus; microorganisms not found on detritus (bacteria, hyphae, algae, protozoans, microorganic metazoans); macroorganic invertebrates; vertebrates. Data on diet were available only for birds. We included three variables on adult body size: body mass, body length, and relative brain mass, the latter was only available for birds and calculated as the residual of linear regressions of \log_{10} -transformed adult brain masses versus \log_{10} -transformed adult body masses. Finally, the nine life-history variables included were clutch size, egg size (diameter or mass for fish or birds, respectively), clutch mass (no data for fish), clutches yr^{-1} , offspring yr^{-1} , the degree of parental care (an ordinal variable in case of fish: 0 = no parental care, 1 = builds nests, 2 = guards eggs, 3 = guards young; age of independence in case of birds), female age of first reproduction, maximum lifespan, and sexual dimorphism, defined as sexual dichromatism or sexual differences in similar secondary sex characteristics such as elongated feathers; following Jeschke and Strayer (2006) and references therein, we used sexual dimorphism as a conservative indicator for the intensity of sexual selection and did not consider sexual differences in body size because these can reflect differences in the ecological niche occupied rather than the intensity of sexual selection. Data on these variables for all investigated species are freely available as a supplement to Jeschke and Strayer (2006).

As response variable, we used threat status which is binomially distributed and classifies a species as either red-listed (classified as near threatened, conservation dependent, vulnerable, endangered, critically endangered, extinct in the wild, or extinct in the 2004 IUCN Red List of Threatened Species) or not listed (not included in the list or classified as least concern); the variable threat status has no value for species categorised as data deficient by the IUCN (2004). Note that all bird species have been evaluated by the IUCN but not all fish species, so we cannot exclude the possibility that some non-listed fish species are actually threatened.

We decided to use the binary variable threat status instead of an ordinal variable that discriminates among the different IUCN categories because it allowed us to perform the same analyses as in Jeschke and Strayer (2006) and

make direct comparisons to this study where invasion success was a binary response variable. A successful invader was defined as a species that was (deliberately or accidentally) introduced from Europe to North America or vice versa, has established one or more self-sustaining populations in the wild in the exotic continent, and has spread substantially from its point of introduction. The data on this variable are provided in the supplement to Jeschke and Strayer (2006). We used the 2004 Red List rather than the most recent one to have a similar point of time where data for the two response variables were collected. The value of the variable threat status for each species is given in the Supplementary material.

We repeated the analyses of Jeschke and Strayer (2006) except that we used threat status instead of invasion success as the response variable. In both fish and birds, we compared red-listed with non-listed species by means of A) univariate and B) multivariate analyses of the raw data plus C) multivariate analyses of phylogenetically independent contrasts. Since geographic range is considered as an indicator for threat status by the IUCN (2004) and our variables latitudinal range and threat status are hence potentially correlated, we repeated the univariate analyses with range as the independent variable and all multivariate analyses after excluding those species that were classified by the IUCN as threatened only on the basis of their distribution (species that met IUCN criterion B or D2 but no other criterion: 91 fish and 3 bird species, Supplementary material). Statistics were calculated with SPSS 12.0.1. Details of the three types of analysis are as follows (cf. Jeschke and Strayer 2006).

A) For univariate analyses, we performed two-tailed binomial tests, U-tests, and t-tests for dichotomous, ordinal, and metric variables, respectively. We did the t-tests with \log_{10} -transformed data, if this was necessary to normalise their distribution. We also calculated Hedges' d effect sizes (Gurevitch and Hedges 2001), e.g. for body mass, d is: (mean body mass of red-listed species – mean body mass of non-listed species) \times J/pooled standard deviation of body mass of red-listed and non-listed species, where J is $1-3/(4 \times (n_{\text{all species}}-2) - 1)$, a correction factor for smaller sample sizes. A value of |d| between 0.5 and 0.8 is usually interpreted as a medium effect, and a value >0.8 is a large/strong effect (Gurevitch and Hedges 2001).

B) For multivariate analyses of the raw data, we ran stepwise forward (likelihood ratio) logistic regressions with an entry probability of 0.05 and a removal probability of 0.10. Because only species with no missing data can be included in these analyses, we used a limited data set here: we excluded variables with missing data for $>30\%$ of the species and those that did not have a medium or strong effect on threat status (i.e. $|d| < 0.5$ in Table 1). As a result, we excluded clutch size, egg size, offspring yr^{-1} , parental care, age of first reproduction, maximum lifespan, and sexual dimorphism for fish; and population density, brain mass, clutches yr^{-1} , offspring yr^{-1} , and maximum lifespan for birds.

C) To correct for phylogenetic dependence in the raw data, we ran stepwise forward (entry probability = 0.05, removal probability = 0.10) multivariate linear regressions of independent contrasts which were calculated with Mesquite 1.05 and its PDAP module 1.06 (Felsenstein

Table 1. Results of univariate analyses with threat status as response variable. The numbers are Hedges' d effect sizes, where positive values indicate higher values for red-listed species, e.g. body mass was higher for red-listed than for non-listed fish. Significant medium or strong effects are highlighted by a grey background ($|d| \geq 0.5$). For comparison, significant strong effects ($|d| \geq 0.8$) with invasion success as the response variable are framed (cf. Jeschke and Strayer 2006). We used a lower threshold of effect size d in case of threat status because here, effect sizes were generally lower than with invasion success as the response variable. Even using this more moderate threshold clearly shows that different variables are correlated with threat status than with invasion success. Independently of effect sizes, we also performed significance tests: two-tailed binomial tests in case of dichotomous variables (sexual dimorphism, carnivory, human affiliation, hunting), U-tests in case of the ordinal variable parental care in fish, and t-tests in case of metric variables (for unequal variances and/or with \log_{10} -transformed data, if necessary); * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

Variable	Fish (n ≤ 933)	Birds (n ≤ 880)
A) Association with humans		
Propagule pressure	-0.16***	-0.09
Human affiliation	-0.10	-0.24***
Hunting	0.00	0.31***
B) Population size and extent		
Population density	no data	-0.30**
Native latitudinal range	-0.74***	-0.78***
	-0.54*** ^a	-0.74*** ^a
Native continent Europe ^b	0.23***	-0.06
C) Diet		
Carnivory	no data	-0.35***
Diet breadth	no data	0.17
D) Body size		
Body mass ^l	0.20	0.64***
Body length ^l	0.12	0.45***
Relative brain mass	no data	0.02
E) Life history		
Clutch size ^l	0.05	-0.10
Egg size ^l	0.19	0.76***
Clutch mass	no data	0.41 ^l **
Clutches per year	-0.54*	-0.37**
Offspring per year ^l	0.01	0.31
Parental care	0.00	0.85***
Age of first reproduction	0.38	1.08**
Maximum lifespan ^l	0.36	0.40
Sexual dimorphism	0.06	0.02

^aSpecies excluded that were classified by the IUCN as threatened based on their range only.

^bThe variable "native continent Europe" is dichotomous where 1 denotes Europe and 0 denotes North America. Thus, a positive effect size means in this case that European species are more frequently red-listed than North American species.

^lIf a superscript ^l is given in the leftmost column of a row, all data were \log_{10} -transformed for that row; if the ^l is given in a single cell, only the data for that cell were \log_{10} -transformed.

1985, Garland et al. 1993, 1999, 2005, Garland and Ives 2000, Maddison and Maddison 2004, Midford et al. 2005). The phylogeny used for this calculation is given by Jeschke and Strayer (2006). Because hypothetical ancestors attain intermediate values of categorical variables, our response variable was not binomially distributed in this case, and we performed linear instead of logistic regressions. We used the same reduced data set as for the raw-data regressions but \log_{10} -transformed some of the variables before calculating the contrasts in order to normalise and homogenise the data. We transformed the same variables as for the univariate analyses (Table 1).

These three analyses are complementary, each one allowing different insights. From A to C, their complexity increases: as multivariate analyses, B and C consider intercorrelations between variables, and C additionally considers phylogenetic relationships among species. On the other hand, statistical power decreases from A to C: the multivariate analyses cover a smaller data set than the univariate analyses, and the consideration of phylogenetic relationships results in a further reduction of power. In fact, the statistical tests performed on the large samples in A were so powerful that they often showed significant differences where effect sizes were small. We discount such small differences as biologically not very meaningful and consequently do not dwell on them in the Results and the Discussion. Instead, we focus on variables that were significant and had medium to large effect sizes ($|d| \geq 0.5$).

Results

Of the 1813 species in the data set, 276 (15.2%) were red-listed (205 fish and 71 bird species) and 27 (1.5%) were invasive (17 fish and 10 bird species). Of the 276 red-listed species, seven were introduced from Europe to North America or vice versa: *Polyodon spathula* (paddlefish), *Hucho hucho* (huchen), *Anser canagica* (emperor goose), *Colinus virginianus* (northern bobwhite), *Tympanuchus cupido* (greater prairie chicken), *Tympanuchus pallidicinctus* (lesser prairie chicken), and *Crex crex* (corncrake). One of these introduced species established itself (*C. virginianus*), but none became invasive.

The hypothesis that threat status and invasion success are two sides of the same coin was not supported. Only one of the 20 variables tested, latitudinal range, agreed with it: it was the only important correlate of both threat status and invasion success where the two correlations had the opposite direction (species with a large range had a relatively high invasion success but a low threat status). While association with humans was the most important group of variables affecting invasion success, body size and life-history variables (such as age of first reproduction and sexual dimorphism) were particularly important to threat status. This conclusion is supported by the univariate analyses reported in Table 1, the multivariate regressions of raw data reported in Table 2, and the multivariate regressions of

phylogenetically independent contrasts reported in Table 3. Although correlations between effect sizes of threat status and invasion success as response variables were negative, they were weak and not significant ($r = -0.304$, $p = 0.271$, $n = 15$ for fish; $r = -0.208$, $p = 0.379$, $n = 20$ for birds; Fig. 1). Thus, none of these approaches back the opposite-characteristics hypothesis.

When we take a closer look at the five groups of variables, the first group – association with humans, consisting of propagule pressure, human affiliation, and hunting – was most important to invasion success but had almost no effect on threat status.

Of the three variables quantifying population size and extent – population density, latitudinal range, and native continent – latitudinal range was the most important correlate of threat status. For birds, this was true for all analyses, whereas for fish, the native continent appeared to be slightly more important than the range in the multivariate analyses that excluded species that were red-listed only based on their range. As expected, the correlation between range and threat status was negative. Range also correlated with invasion success but positively so; hence this variable matched the opposite-characteristics hypothesis, whether all species were analysed or excluding those that were red-listed based only on their range. Population density was important to neither threat status nor invasion success. Finally, European species were more often red-listed than North American ones, but there was no important difference relative to invasion success.

Data for the third group, diet, were only available for birds where it was not important to threat status. However, both variables – carnivory and diet breadth – were significantly correlated to invasion success and had high effect sizes in the univariate analysis (herbivores had a higher invasion success than carnivores, and species with a broad diet were better invaders than species with a narrow diet).

Body size was important to threat status but not to invasion success. Body mass and length were significantly positively correlated with threat status in birds in the univariate analyses. In the multivariate analyses, which consider intercorrelations, body mass or length was included in the final regression models in both groups. They were never included together because of their high correlation with each other. Relative brain mass was not important

Table 2. Results of multivariate logistic regressions with threat status vs invasion success as response variable. The regressions were run stepwise forward. Each cell gives the entry order of significant variables together with regression coefficients B.

	Threat status		Invasion success (from Jeschke and Strayer 2006)
	All species	Without species that were red-listed based on range	
Fish ($n = 305$, 283 for all species, reduced dataset, respectively; Cox-Snell $r^2 = 0.21$, 0.16)	–0.20 latitudinal range 0.01 body length –2.46 clutches yr^{-1} 0.84 native continent Europe	1.96 native continent Europe <0.01 body mass –0.10 latitudinal range –3.04 clutches yr^{-1}	0.34 propagule pressure 0.90 egg size
Birds ($n = 159$, Cox-Snell $r^2 = 0.15$)	<0.01 body mass –0.12 latitudinal range 2.77 sexual dimorphism	Identical to all species	19.6 propagule pressure 0.60 clutch mass 139 clutches yr^{-1} –0.25 body mass 1.95 egg size

Table 3. Results of multivariate linear regressions of phylogenetically independent contrasts with threat status vs invasion success as response variable. The regressions were run stepwise forward. Each cell gives the entry order of significant variables together with standardised regression coefficients β .

	Threat status		Invasion success (from Jeschke and Strayer 2006)
	All species	Without species that were red-listed based on range	
Fish (n=304, 282, respectively; adjusted $r^2=0.14, 0.11$)	-0.33 latitudinal range -0.16 clutches yr^{-1} 0.13 native continent Europe	0.29 native continent Europe -0.14 latitudinal range -0.12 clutches yr^{-1}	0.41 propagule pressure
Birds (n=158, adjusted $r^2=0.12$)	-0.36 latitudinal range	Identical to all species	0.47 propagule pressure 0.17 human affiliation

to threat status or invasion success in the species we analysed.

Life-history variables were relatively more important to threat status than to invasion success. Moreover, those

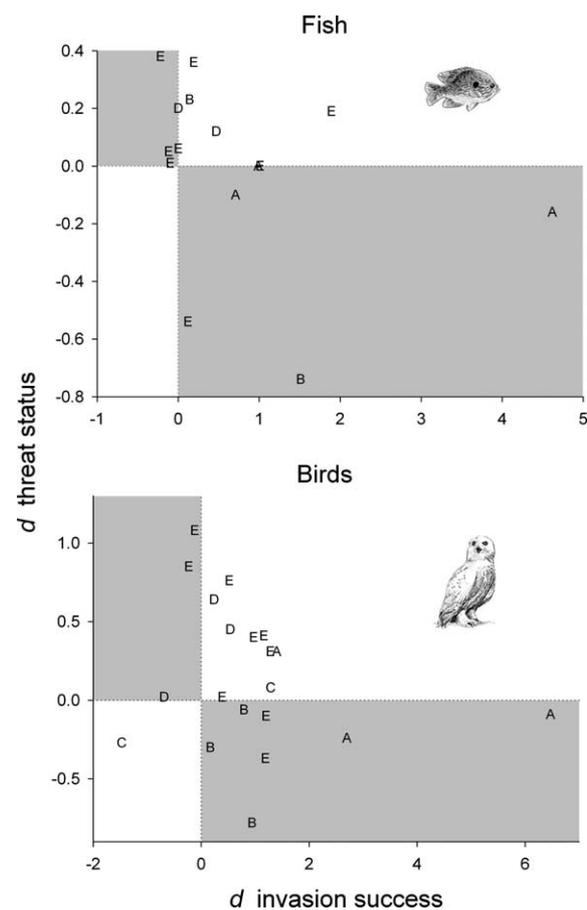


Fig. 1. Effect sizes d with invasion success and threat status as response variables. Each data point is given as a letter, indicating the group of variables it belongs to (cf. Table 1; A = association with humans, B = population size and extent, C = diet, D = body size, E = life history). If threat status and invasion success are two sides of the same coin, traits that are negatively correlated with invasion success should be positively correlated with threat status and vice versa, so data points should lie in the grey areas. This was only partly true, however, and although the observed correlations were negative, they were not significant ($r = -0.304$, $p = 0.271$, $n = 15$ for fish; $r = -0.208$, $p = 0.379$, $n = 20$ for birds). Note that axes have different scales. Credit for drawings: U.S. Fish and Wildlife Service/Bob Savannah.

variables that were important to invasion success (e.g. egg size and parental care in fish) were not important to threat status. Red-listed fish had fewer clutches per year than non-listed fish. In birds, egg size, the degree of parental care, age of first reproduction, and sexual dimorphism were all important to and positively correlated with threat status. The influence of sexual dimorphism was not apparent from the univariate analyses, probably because it was negatively correlated with body size which, in turn, was positively correlated with threat status. This indirect negative effect on threat status balanced the direct positive effect, leading to the absence of an effect in the univariate analyses.

Discussion

Threat status and invasion success are not opposite sides of the same coin for European and North American fish and birds. Although the native latitudinal range was conversely correlated with threat status and invasiveness, this was not true for the other 19 variables tested. Our finding is in line with Blackburn and Cassey (2004) who wrote: “[T]here seems little reason a priori to expect species on the lists of introductions and re-introductions to share common characteristics or ancestry. Surprisingly, however, our analyses reveal as many similarities as differences” (p. 431).

With respect to specific factors, we found in agreement with previous studies that geographic range correlated negatively with threat status but positively with invasion success (McKinney 1997, Purvis et al. 2000, Jones et al. 2003, Fisher and Owens 2004, Koh et al. 2004, Cardillo et al. 2005, 2006, Keane et al. 2005, Reynolds et al. 2005). Diet generalists have sometimes been found to be less likely to become extinct than specialists and more likely to become invasive, but diet breadth of birds was not an important factor for imperilment in our analyses (McKinney 1997, Purvis et al. 2000, Fisher and Owens 2004, Van Valkenburgh et al. 2004, Keane et al. 2005, Kotiaho et al. 2005).

The intensity of sexual selection within a species is often thought to increase extinction risk and diminish invasion success, although previously available data are inconclusive (Andersson 1994, Prinzing et al. 2002, Kokko and Brooks 2003, Doherty et al. 2003, Fisher and Owens 2004, Morrow and Fricke 2004, Koh et al. 2004). Our results suggest that the intensity of sexual selection, measured as the presence of sexual dimorphism, is of minor importance to invasion success but significant to extinction risk: if

Table 4. Usefulness of the fast-slow concept for predicting threat status and invasiveness.

	Red-listed species		Invasive species	
	Predicted	Observed	Predicted	Observed ^b
Fish ^a				
Body size	Large	? ^c	Small	n.i.
Clutch size	Large	n.i. ^d	Small	n.i.
Offspring size	Large	n.i.	Small	Large
Clutches yr ⁻¹	Few	Few	Many	n.i.
Reproduction	Late	n.i.	Early	n.i.
Lifespan	Long	n.i.	Short	n.i.
Birds ^a				
Body size	Large	Large	Small	n.i.
Offspring size	Large	n.i.	Small	n.i.
Reproduction	Late	Late	Early	n.i.
Lifespan	Long	n.i.	Short	Long

^aAccording to Jeschke and Kokko (unpubl.), fish with a “fast” life history have a small body size, small clutch size, small offspring size, many clutches per year, reproduce early and die young, whereas “fast” bird species have a small body size, small offspring size, reproduce early, and die young (clutch size and clutches per year are not part of the fast-slow continuum here). Species with a “slow” life history have the opposite characteristics.

^bSee Jeschke and Strayer (2006).

^cConflicting results.

^dn.i. (“not important”) indicates insignificant correlations or significant ones with small effect sizes; these are biologically not very meaningful.

intercorrelations between variables are accounted for, sexually dimorphic birds are more often red-listed than monomorphic species. Two points of caution need to be added here, however: sexual dimorphism is only a rough indicator for the intensity of sexual selection (see also Discussion in Jeschke and Strayer 2006), and we cannot exclude the possibility that humans tend to classify species more often as threatened if they are pretty.

Hunting has driven many species into or close to extinction (Wilson 1992, McKinney 1997, Bodmer et al. 1997, Fisher and Owens 2004), but we did not find a strong effect of hunting on threat status of European and North American fish and birds. This is perhaps because the direct negative effect of hunting is balanced by an indirect positive effect: especially in Europe and North America, game species are often stocked or otherwise managed by humans.

The concept of fast and slow life histories does not seem to be helpful with respect to invasion success but may apply to threat status, at least for the species analysed here (Table 4). This concept is historically based on the, now outdated, r-K dichotomy (Pianka 1970, Reznick et al. 2002, Jeschke et al. in press) and states that life-history traits of species show co-occurrence patterns that allow classification on a continuum from “fast” to “slow” (Sæther 1987, Reynolds 2003, Jeschke and Kokko unpubl.). The exact definition of the fast-slow continuum differs among taxa: Jeschke and Kokko (unpubl.) analysed the species included in this study and found that different traits define the continuum in fish and birds. These traits are provided in Table 4 which addresses the hypothesis that species with a “fast” life history have a lower threat status and higher invasion success than species with a “slow” life history (see Introduction for references). With respect to threat status, some of the observations match predictions, e.g. large birds with a late start of reproduction tend to be frequently red-listed (McKinney 1997, Purvis et al. 2000, Fisher and Owens 2004, Keane et al. 2005). Many variables defining

“fast” and “slow”, however, are apparently not important to threat status. For invasion success, the classification of species on a fast-slow continuum apparently is not useful at all.

The overall predictability of threat status with the 20 traits included in this analysis was relatively low, lower than the predictability of invasion success (cf. Jeschke and Strayer 2006). Apparently, factors not considered here, e.g. habitat destruction and the degree of human disturbance, are more important determinants of threat status than of invasion success.

In conclusion, as so often in biology, things are not as simple as one might wish them to be. The peril of endangered species has different causes than the success of invasives. Hence, they must be studied separately. Classifying species on the basis of their life history on a continuum from fast to slow may be somewhat useful when the goal is to gain knowledge on threat status but not when their invasiveness is the focus. In general, the size of species and their life history are correlated more strongly with threat status than with invasion success, whereas their association with humans is a better predictor of invasion success than threat status.

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