lection clearly can favor sperm quality (e.g., length) at the expense of sperm quantity, even when males have limited resources for gamete production (*26*).

Although we now understand what drives sperm length evolution, we do not know what is driving the evolution of SR length. Nonetheless, this trait offers an exceptionally tractable system for studying the evolution of a female preference and of male-female interactions. The functional relationship between the female preference and the corresponding male ornament is unambiguous, the preference and ornament are both easy to quantify, the macroevolutionary pattern of coevolution between the preference and ornament has been established (*17*), costs of relative expression of each have been quantified (*19, 23, 26*), and each is amenable to genetic analysis and artificial selection (*27*).

Our results are consistent with several models developed to explain the evolution of female mate preferences. Linkage disequilibrium between the female preference and male ornament is consistent with the Fisherian runaway process and "good genes" models (*28*). Also consistent with good genes models, recent studies have suggested a link between male condition and sperm quality (*29*), including sperm length (*30*). Next, interactions between the sexes are rife with conflict in *D. melanogaster* (*31*) and the coevolution of sperm and SR length may be sexually antagonistic, as has been suggested for sperm length and sperm-storage tubule length in birds (*15*). Finally, data reported here refute predictions of two sexual selection models as applied to this system. First, the "direct benefits" model (*28*) cannot apply, as the long sperm tails are not absorbed by females and have not evolved to serve a post-fertilization function (*32*). Second, the "sensory exploitation" model (*28*) is not applicable, as phylogenetic analysis reveals a pattern of correlated evolution between the female preference and male trait (*17*) rather than a pattern of the male trait evolving in response to a preexisting female bias.

The sperm-female coevolution demonstrated here has important implications for diversification and speciation. Rapid morphological divergence of sperm has been reported for numerous taxa, including primates (*33*). Such divergence has been shown to drive correlated divergence of important life history traits (*19, 26*). Further, as sperm morphology and sperm usage by females are central to successful reproduction, their divergence will likely contribute to reproductive isolation between populations and the formation of new species (*1, 7, 34*).

References and Notes

1. W. J. Swanson, V. D. Vacquier, *Nature Rev. Genet*. **3**, 137 (2002).
2. G. J. Wyckoff, W. Wang, C.-I. Wu, *Nature* **403**, 304 (2000).
3. K. A. Sutton, M. F. Wilkinson, *J. Mol. Evol*. **45**, 579 (1997).
4. V. D. Vacquier, *Science* **281**, 1995 (1998).
5. W. J. Swanson, A. G. Clark, H. M. Waldrip-Dail, M. F. Wolfner, C. F. Aquadro, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 7375 (2001).
6. W. R. Rice, *Nature* **381**, 232 (1996).
7. G. A. Parker, L. Partridge, *Philos. Trans. R. Soc. London Ser. B* **353**, 261 (1998).
8. A. G. Clark, D. J. Begun, T. Prout, *Science* **283**, 217 (1999).
9. S. Gavrilets, *Nature* **403**, 886 (2000).
10. W. J. Swanson, Z. Yang, M. F. Wolfner, C. F. Aquadro, *Proc. Natl. Acad. Sci. U.S.A.* **98**, 2509 (2001).
11. G. Arnqvist, L. Rowe, *Evolution* **56**, 936 (2002).
12. B. G. M. Jamieson, *The Ultrastructure and Phylogeny of Insect Spermatozoa* (Cambridge Univ. Press, Cambridge, 1987).
13. L. W. Simmons, *Sperm Competition and Its Evolutionary Consequences in the Insects* (Princeton Univ. Press, Princeton, NJ, 2001).
14. C. W. LaMunyon, S. Ward, *Proc. R. Soc. London Ser. B* **269**, 1125 (2002).
15. J. V. Briskie, R. Montgomerie, T. R. Birkhead, *Evolution* **51**, 937 (1997).
16. M. J. G. Gage, *Proc. R. Soc. London Ser. B* **258**, 247 (1994).
17. S. Pitnick, T. A. Markow, G. S. Spicer, *Evolution* **53**, 1804 (1999).
18. T. R. Birkhead, *Evolution* **54**, 1057 (2000).
19. S. Pitnick, T. A. Markow, G. S. Spicer, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 10614 (1995).
20. G. T. Miller, S. Pitnick, data not shown.
21. Female and male body sizes were measured. Initial analyses of P2 by analysis of covariance (ANCOVA), with female and male lines as main factors and male and female sizes as covariates, revealed that size and its interaction with other variables were never significant and inclusion of body sizes never improved model fit. Entering the variable "remating interval" as a covariate was only justified in the analysis for the third replicate experiment.
22. E. H. Morrow, M. J. G. Gage, *Proc. R. Soc. London Ser. B* **268**, 2281 (2001).
23. G. T. Miller, S. Pitnick, *J. Evol. Biol.*, in press.
24. S. Pitnick, unpublished data.
25. T. C. M. Bakker, A. Pomiankowski, *J. Evol. Biol*. **8**, 129 (1995).
26. S. Pitnick, *Am. Nat.* **148**, 57 (1996).
27. G. T. Miller, W. T. Starmer, S. Pitnick, *Heredity* **87**, 25 (2001).
28. M. Andersson, *Sexual Selection* (Princeton Univ. Press, Princeton, NJ, 1994).
29. A. Rakitin, M. M. Ferguson, E. A. Trippel, *Can. J. Fish. Aquat. Sci.* **56**, 2315 (1999).
30. L. W. Simmons, J. S. Kotiaho, *Evolution* **56**, 1622 (2002).
31. S. Pitnick, F. García-González, *Proc. R. Soc. London Ser. B,* **269**, 1821 (2002).
32. T. L. Karr, S. Pitnick, *Nature* **379**, 405 (1996).
33. M. J. G. Gage, *Proc. R. Soc. London Ser. B* **265**, 97 (1998).
34. P. E. Eady, *J. Zool. (London)* **253**, 47 (2001).
35. S. Pitnick, G. T. Miller, J. Reagan, B. Holland, *Proc. R. Soc. London Ser. B* **268**, 1071 (2001).
36. We thank J. Reagan and D. Trinkaus for technical assistance and J. Alcock, T. R. Birkhead, A. Bjork, W. D. Brown, T. L. Karr, L. A. McGraw, M. Polak, R. R. Snook, W. T. Starmer, and L. L. Wolf for comments on an earlier draft of the manuscript. Supported by NSF grants DEB-9806649 and DEB-0075307 (S.P.).

5 August 2002; accepted 9 September 2002

Ecological Predictions and Risk Assessment for Alien Fishes in North America

Cynthia S. Kolar*† and David M. Lodge

Methods of risk assessment for alien species, especially for nonagricultural systems, are largely qualitative. Using a generalizable risk assessment approach and statistical models of fish introductions into the Great Lakes, North America, we developed a quantitative approach to target prevention efforts on species most likely to cause damage. Models correctly categorized established, quickly spreading, and nuisance fishes with 87 to 94% accuracy. We then identified fishes that pose a high risk to the Great Lakes if introduced from unintentional (ballast water) or intentional pathways (sport, pet, bait, and aquaculture industries).

Increased trade and tourism associated with globalization have facilitated one of the least reversible human-induced global changes now under way: the homogenization of Earth's biota through the establishment and spread of alien species (*1*, *2*). Given the myriad detrimental impacts attributed to alien species in invaded ecosystems (*3*, *4*) and the limited possibilities for eradication, predicting potential alien species and preventing their establishment are important policy goals (*5*). Invasion biology has, however, been plagued by a paradox that has hindered prevention. On the one hand, there is a widespread perception that diagnostic characteristics of weedy species have long since been identified (*6*). Current risk-screening protocols, such as the Weed Risk Assessment of Australia (*7*) and the Ecological Risk Assessment Framework of the U.S. Government (*8*), are based on largely qualitative categorizations of such putative diagnostic characteristics. On the other hand, there is a widespread perception that predictions about which species will invade are impossible (*9*). This perception has emerged from searching for

---

Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, USA.

*Present address: U.S. Geological Survey Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Road, LaCrosse, WI 54603, USA.

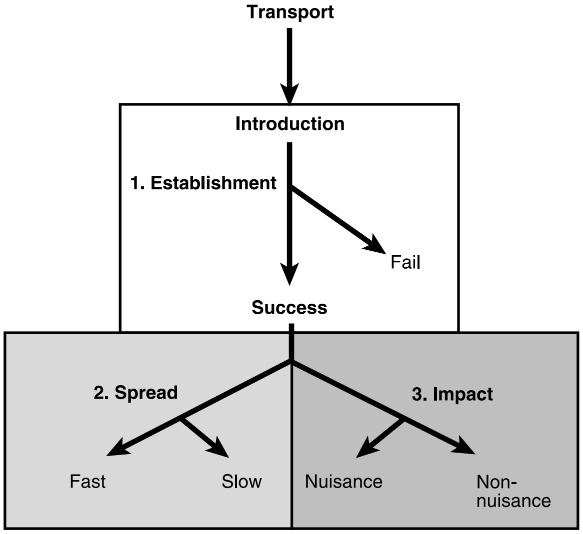
†To whom correspondence should be addressed. E-mail: ckolar@usgs.gov

characteristics that apply generally to all taxonomic groups and in all ecosystems (*6*). It should not be surprising, however, that such overarching characteristics do not exist. Further, growing evidence suggests that characteristics important at the spread stage differ from those important to other stages of the invasion sequence (*10*). Recognition of the incommensurability of these two perceptions, therefore, is the key to the paradox and is the basis on which we build an approach to quantitative, predictive risk assessments of alien species consistent with recommendations of the U.S. National Research Council (*11*).

Here, we develop quantitative models using species characteristics to predict potential alien species and their impact. A similar approach has been used to predict invasiveness of terrestrial plants (*12*, *13*) and provides the foundation of our approach. We control for factors not usually considered explicitly in previous investigations: We examine one ecosystem (the Great Lakes of North America) and one taxon (fishes) and consider invasion stages independently (establishment, spread, and impact) (Fig. 1). We develop and use multivariate models to assess the risk to the Great Lakes from fishes introduced unintentionally from ballast water or intentionally from the aquaculture, bait, sport, or pet industries. Such models and predictions could provide the basis for quantitative risk assessment and management tools essential in reducing the threat of alien species (*5*). This approach could also be extended to other taxonomic groups and ecosystems.

We first identified the 24 established and 21 introduced but not established alien fishes in the Great Lakes (*14*) (table S1), and then further identified the established fishes that spread quickly through the ecosystem (tables S2 and S3) and those that are perceived as a nuisance. We then collected data from the literature on 13 life-history characteristics, 5 habitat needs, 6 aspects of invasion history, and human use (table S4). Unfortunately, we could not perform phylogenetically independent contrasts, because the systematics of fishes is not sufficiently understood. To reduce the likelihood that significant association was due to phylogenetic similarity, we included a variable ranking fish families by degree of derived characters (*15*).

Fig. 1. Invasion by alien species is a process consisting of several transitions, each with an independent probability of failure, and cumulative failure rates are high. Here, we first compare characteristics of failed with successful fishes in the Great Lakes to predict fishes capable of becoming established in the future. To further predict high-risk potential invaders, we then compare characteristics of successful fishes that spread quickly with those that spread slowly and those of fishes that are perceived as a nuisance with those that are not.



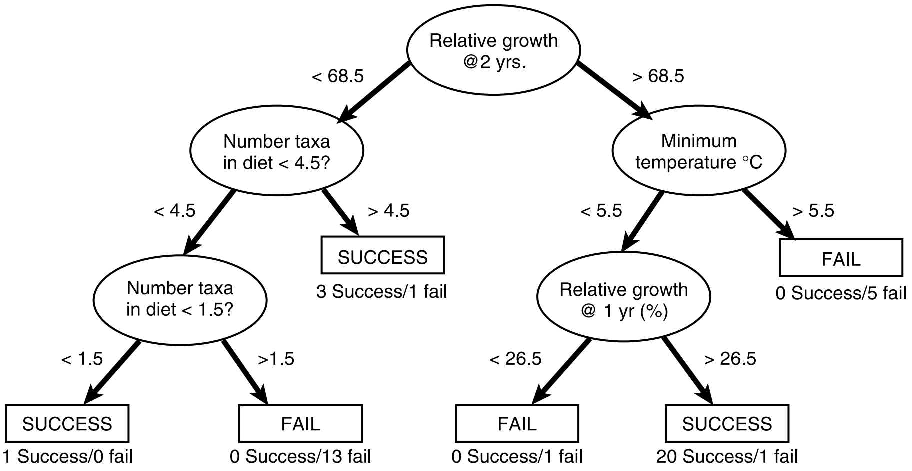


Fig. 2. CART decision tree of successful and failed introduced fishes in the Great Lakes. Ovals represent decision points; rectangles are terminal points in the tree resulting in classification. The numbers of known successful and failed alien species categorized into each terminus are given, illustrating that 2 of 45 species were misclassified.

Discriminant analysis (DA) revealed that successful fishes in the establishment stage (Fig. 1) grew relatively faster, tolerated wider ranges of temperature and salinity, and were more likely to have a history of invasiveness than were failed fishes. A discriminant function using these four characteristics discriminated between failed and successful fishes with 87% accuracy (83% in jackknife validation) (*16*, *17*). Categorical and regression tree analysis (CART), using minimum temperature threshold, diet breadth, and two measures of relative growth, classified failed and successful fishes with 94% accuracy (82% upon cross-validation) (Fig. 2) (*18*).

Quickly spreading fishes had slower relative growth rates, survived poorly in high water temperatures, and tolerated a wider temperature range than did slowly spreading fishes (discriminant function 94% accurate; 90% in jackknife validation) (Fig. 1, spread stage) (*19*) (supporting online text). Nuisance fishes had smaller eggs, had wider salinity tolerances, and survived in lower water temperatures than did nonnuisance fishes (discriminant function 89% accurate; 80% in jackknife validation) (Fig. 1, impact stage) (*20*) (supporting online text). For each stage of the invasion sequence, only three or four characteristics were necessary to correctly classify 87 to 94% of alien fishes documented in the Great Lakes.

Different traits were important for different stages of invasion. For example, relatively fast growth was positively associated with establishment but was negatively associated with quickly spreading species. These patterns confirmed the necessity of invasion stage–specific analyses (supporting online text). Overall, our results demonstrate that quantitative analyses that are ecosystem specific, taxon specific, and stage specific provide a firm quantitative basis for risk assessment.

We next used our models to predict the risk to the Great Lakes from potential unintentional introductions through ballast water from the Ponto Caspian basin (Black Sea, Caspian Sea, and surrounding watersheds), a recent source of alien species in the Great Lakes (*21*). We found sufficient species characteristics for 66 (out of 110) of these fishes (*22*). DA predicted that 24 species could become established; CART predicted 36. The predictions of DA and CART were 57% similar [Jaccard's similarity coefficient (*23*)]. We suggest that the 22 fishes common to both predictive models (Table 1) pose the greatest risk of establishment in the Great Lakes. Sixteen of these species were predicted to be able to spread through the Great Lakes quickly (Table 1). Of these, five were predicted to become nuisance species (Table 1) and would therefore be the least desirable additions to the Great Lakes. A previous study based on a qualitative assessment also predicted that the tyulka (*Clupeonella cultriventris*) and monkey goby (*Neogobius fluviatilis*) would be detrimental to the Great Lakes if introduced (*24*). From greatest to least risk to the Great Lakes, these five species are followed by the remaining 17 species listed in Table 1, the 15 species predicted by only one of the establishment models to be able to colonize the Great Lakes (*17*), and finally the 29 fishes predicted by both models to fail in the Great Lakes (*17*).

High-risk fishes from the Ponto Caspian may also be introduced into the Great Lakes by intentional introduction. The Ponto Caspian natie rudd, *Scardinius erythrophthalmus*, became established in the United States by the live-bait industry, for example (*25*). Three high-risk species not yet established would also be appealing bait species, and seven are already in the coolwater aquaria and water garden trades in Europe (Table 1). Efforts to educate consumers and industries and/or the mandatory application of legally binding species-specific risk assessments could greatly reduce the risks from intentional pathways.

We also compiled a list of 14 additional fishes that are potential aquaculture, bait, sport, or pet fishes and used our models to assess their risk of establishment, spread, and impact in the Great Lakes if introduced. Four of these species were predicted by both the DA and CART to become established in the Great Lakes (Table 1) (supporting online text). None were predicted to spread quickly and to be perceived as a nuisance in the Great Lakes. All but redear sunfish (*Lepomis microlophus*) were predicted to have a low impact; two were predicted to spread slowly (Table 1).

Our predictions about two fishes, in particular, should be interpreted with caution. Our models predict that the controversial black carp, *Mylopharyngodon piceus*, now being considered for listing as an injurious species in the Lacey Act because of potential negative impacts (*26*), would not become established in the Great Lakes if introduced. Our models also predict that the silver carp, *Hypopthalmichthys molitrix*, which has quickly spread through the upper Mississippi-Illinois river systems and sometimes hurts boaters as the fish leap from the water (*27*), would neither spread quickly nor be perceived as a nuisance in the Great Lakes. These species exhibit characteristics (diet specialization of black carp on abundant molluscan resources in the Great Lakes, and rare leaping behavior in silver carp) that differ substantially from those of species on which the models were developed, and our models may not be robust to such deviations. In addition, all our predictions are applicable to the Great Lakes proper, not to tributaries and large river systems in which these carp species, for example, are already established and causing strongly negative consequences.

Recent history suggests that unless appropriate changes occur in education, policy, and management, there is a high likelihood that some of the high-risk fishes listed in Table 1 will be introduced into the Great Lakes region. The utility of identifying species at a high risk of becoming established, spreading, or impacting an ecosystem is most apparent for intentional pathways. If the perceived risk of allowing these species into the Great Lakes basin is greater than the perceived benefit, then their entry into particular states, the region, or the country could be controlled. Unintentional pathways, especially the ballast water and hulls of ships, are also important pathways for some species we identify as high risk (Table 1). Since 1985, ruffe (*Gymnocephalus cernuus*), round goby (*Neogobius melanostomus*), and tubenose goby (*Proterorhinus marmoratus*) have become established in the Great Lakes by the shipping industry. Changes in the seasonal timing and location of ballasting could reduce the risk of introducing high-risk species not yet in the Great Lakes (Table 1). For example, to reduce the risk of transporting bottom-dwelling monkey gobies, ballast water could be drawn from the upper regions of the water column or could be treated (e.g., with filtration or short-lived toxins) during times of peak larval goby abundance. Our analyses provide the basis for targeting such education, policy, and management efforts directed toward high-risk species and the pathways that are most likely to transport them.

Most risk-assessment protocols, such as the Weed Risk Assessment (*7*) and the Ge-

Table 1. Ponto Caspian fishes and pet, sport, aquaculture, and bait species predicted by both DA and CART models to become established in the Laurentian Great Lakes if introduced. Bold indicates species predicted to pose the highest risk to the Great Lakes. Fishes are listed by family from the most ancestral to the most derived.

Predicted successful fishes	Predicted rate of spread	Predicted level of impact
Unintentional introductions: Ponto Caspian fishes		
Family Clupeidae		
Caspian shad (*Caspialosa caspia*)	Fast	Nonnuisance
Pontic shad (*Caspialosa pontica*)	Fast	Nonnuisance
Tyulka (*Clupeonella cultriventris*)	**Fast**	**Nuisance**
Family Cyprinidae		
Roach (*Rutilus rutilus*)*	Fast	Nonnuisance
Sunbleak (*Leucaspius delineatus*)*	Slow	Nonnuisance
Chub (*Leuciscus cephalus*)*†	Slow	Nonnuisance
Common dace (*Leuciscus leuciscus*)†	Fast	Nonnuisance
Eurasian minnow (*Phoxinus phoxinus*)*†	**Fast**	**Nuisance**
Tench (*Tinca tinca*)*	Slow	Nonnuisance
Bleak (*Alburnus alburnus*)	Fast	Nonnuisance
Family Cyprinidontidae		
Toothed carp (*Aphanius fasciatus*)	Slow	Nonnuisance
Black Sea silverside (*Aphanius boyeri*)	**Fast**	**Nuisance**
Family Percidae		
European perch (*Perca fluviatilis*)*	**Fast**	**Nuisance**
Zander (*Stizostedion lucioperca*)	Slow	Nonnuisance
Family Gobiidae		
Caucasian goby (*Knipowitschia caucasica*)	Fast	Nonnuisance
Longtail goby (*Knipowitschia longecaudatus*)	Fast	Nonnuisance
Monkey goby (*Neogobius fluviatilis*)*	**Fast**	**Nuisance**
Racer goby (*Neogobius gymnotrachelus*)	Fast	Nonnuisance
Sand goby (*Pomatoschistus minutus*)	Slow	Nonnuisance
Starry goby (*Benthophilus stellatus*)	Fast	Nonnuisance
Family Cottidae		
Bullhead (*Cottus gobio*)	Fast	Nonnuisance
Family Gasterosteidae		
Ukranian stickleback (*Pungitius platygaster*)	Fast	Nonnuisance
Intentional introductions: aquaculture, sport, pet, and bait fishes		
Family Cyprinidae		
Silver carp (*Hypopthalmichthys molitrix*)	Slow	Nonnuisance
Family Salmonidae		
European whitefish (*Coregonus albula*)	Fast	Nonnuisance
Chum salmon (*Onchorhynchus keta*)	Fast	Nonnuisance
Family Centrarchidae		
Redear sunfish (*Lepomis microlophus*)	Slow	Nuisance

*Currently in water garden or aquarium trade in Europe. †Potential use as live bait.

neric Nonindigenous Aquatic Organisms Risk Analysis Review Process recently updated in the United States (*28*), are based on expert opinion or qualitative assessments, and not on rigorously quantitative statistics. In contrast, the approach illustrated here is quantitative, repeatable, and transparent—characteristics a recent National Research Council report urges should apply to the next generation of risk assessments (*11*).

Although the results presented here are specific to the Great Lakes, this approach to constructing predictive models could be applied to a diversity of plant and animal taxa inhabiting a variety of terrestrial and aquatic ecosystems. As highlighted by the U.S. National Management Plan on invasive species (*5*), the urgent need to focus attention on prevention requires the development of species risk-assessment protocols. As alien species move along the invasion sequence (from transport to introduction, establishment, spread, and impact), management options become more limited. Even in the rare cases in which the knowledge and technology exist to control an established species, such efforts are expensive and must be practiced in perpetuity (*29*). For example, the United States and Canada jointly spend about U.S. $15 million annually to control sea lamprey (*Petromyzon marinus*) in the Great Lakes (*30*); these costs have been incurred since 1956 and will continue as long as sea lamprey control remains a management goal. Quantitative risk assessments that identify the alien species most likely to establish, spread quickly, and become a nuisance could be the foundation for efforts to prevent future expensive and environmentally damaging invasions.

References and Notes

1. H. A. Mooney, R. J. Hobbs, *Invasive Species in a Changing World* (Island Press, Washington, DC, 2000).
2. F. J. Rahel, *Science* **288**, 854 (2000).
3. O. E. Sala *et al.*, *Science* **287**, 1770 (2000).
4. D. Pimentel, L. Lach, R. Zuniga, D. Morrison, *Bioscience* **50**, 53 (1999).
5. National Invasive Species Council, *National Management Plan: Meeting the Invasive Species Challenge* (National Invasive Species Council, Washington, DC, 2001).
6. D. M. Lodge, *Trends Ecol. Evol.* **8**, 133 (1993).
7. R. H. Groves, F. D. Panetta, J. G. Virtue, *Weed Risk Assessment* (CSIRO Publishing, Collingwood, Victoria, Australia, 2001).
8. Committee on the Scientic Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States, *Predicting Invasions of Nonindigenous Plants and Plant Pests* (National Academy Press, Washington, DC, 2002).
9. M. Enserink, *Science* **285**, 1834 (1999).
10. C. S. Kolar, D. M. Lodge, *Trends Ecol. Evol.* **16**, 199 (2001).
11. Committee on Environment and Natural Resources of the National Science and Technology Council, *Ecological Risk Assessment in the Federal Government*, Report CENR/5-99/001 (May 1999).
12. S. H. Reichard, C. W. Hamilton, *Conserv. Biol.* **11**, 193 (1997).
13. M. Rejmanek, D. M. Richardson, *Ecology* **77**, 1655 (1996).
14. Detailed Materials and Methods are available as supporting material on *Science* Online.
15. Method suggested by A. Grafen, *Philos. Trans. R. Soc. London Ser. B* **326**, 119 (1989). Classification of P. B. Moyle, C. C. Cech Jr., *Introduction to Ichthyology* (Prentice Hall, Upper Saddle River, NJ, ed. 3, 1996).
16. Function coefficients for the establishment DA (signs indicate association with establishment): constant = 9.8025, closer to mature length by 2 years = 0.0704, wide temperature range = 0.1430, wide salinity tolerance = 1.5844, history of invasiveness = 1.4602.
17. The reliability of our models (and all other models) is a function of the accuracy of the prediction and the frequency with which the event occurs at all (i.e., the "base rate," or proportion of introduced species that establish). Low base rate probability inflates the number of "false-positives" identified by the screening tool (species predicted to become established, spread quickly, or be perceived as a nuisance) (*31*). See online material for a discussion of the influence of base rate on our results.
18. CART was performed with CART software (Salford Systems, San Diego, CA).
19. Discriminant function coefficients for the spread DA (signs indicate association with spreading quickly): constant = 24.68635, survive higher temperatures = –1.52543, wide temperature range = 0.95508, closer to mature length by 2 years = –0.0000076.
20. Discriminant function coefficients for the impact DA (signs indicate association with being a nuisance): constant = –1.29465, egg diameter = –2.41764, minimum temperature threshold = –0.17902, salinity range = 0.73598.
21. A. Ricciardi, H. J. MacIsaac, *Trends Ecol. Evol.* **15**, 62 (2000).
22. J. Illies, *Limnofauna Europea* (Fischer Verlag, Stuttgart, Germany, 1978).
23. C. J. Krebs, *Ecological Methodology* (Harper & Row, New York, 1989).
24. A. Ricciardi, J. B. Rasmussen, *Can. J. Fish. Aquat. Sci.* **55**, 1759 (1998).
25. B. Cudmore-Vokey, E. J. Crossman, "Checklists of the fish fauna of the Laurentian Great Lakes and their connecting channels," Canadian Manuscript Report of Fisheries and Aquatic Sciences 2550 (Canadian Department of Fisheries and Oceans, Ottawa, Canada, 2000).
26. *Fed. Regist.* **67**, 49280 (2002).
27. E. Sharp, "Beware big fish: Asian carp are threat to lakes," *Detroit Free Press*, 11 April 2002; available at www.freep.com/sports/outdoors/outcol11_200204411.htm.
28. Risk Assessment and Management Committee, *Generic Nonindigenous Aquatic Organisms Risk Analysis Review Process* (Report to the Aquatic Nuisance Species Task Force, 21 October 1996); available at www.anstaskforce.gov/gennasrev.htm.
29. U.S. Congress, *Harmful Nonindigenous Species in the United States* (Office of Technology Assessment, Washington, DC, 1993).
30. C. I. Goddard, Great Lakes Fishery Commission, circular letter (8 July 1997).
31. C. S. Smith, W. M. Lonsdale, J. Fortune, *Biol. Invas.* **1**, 89 (1999).
32. We thank R. Sparks, E. Marsden, and D. Schneider for thoughtful discussion. We also thank J. Drake, J. Feder, K. Filchak, T. Kreps, B. Leung, and anonymous reviewers for comments on earlier versions of the manuscript. Thanks are also due to the fish managers and exotic species specialists who responded to our nuisance survey. This research is part of a larger project (National Sea Grant 643-1532-04). Additional support was provided by the Great Lakes Fishery Commission, Environmental Protection Agency STAR fellowship (R-82889901-0), the NSF Biocomplexity Initiative, a Clare Boothe Luce Presidential Fellowship (C.S.K.), and the Equal Opportunities Section of the American Fisheries Society (C.S.K.).

Supporting Online Material

www.sciencemag.org/cgi/content/full/298/5596/1233/DC1

Materials and Methods

SOM Text

Tables S1 to S9

References and Notes

4 July 2002; accepted 19 September 2002

Avian Persistence in Fragmented Rainforest

Luc Lens,[1,2]* Stefan Van Dongen,[1] Ken Norris,[3] Mwangi Githiru,[2,4] Erik Matthysen[1]

What factors determine the persistence of species in fragmented habitats? To address this question, we studied the relative impacts of forest deterioration and fragmentation on bird species in 12 rainforest fragments in Kenya, combining 6 years of individual capture-recapture data with measurements of current captures and museum specimens. Species mobility, as estimated from species-specific dispersal rates, and tolerance to habitat deterioration, as estimated from change in fluctuating asymmetry with increasing habitat disturbance, explained 88% of the variation in patch occupancy among eight forest bird species. Occupancy increased with mobility and with tolerance to deterioration, where both variables contributed equally to this relationship. We conclude that individual-level study, such as of dispersal behavior and phenotypic development, can predict patterns of persistence at the species level. More generally, for conservation tactics to stand a high chance of success, they should include action both within sites, to minimize habitat deterioration, and across landscapes, to maximize dispersal.

Anthropogenic habitat deterioration is imposing new selection pressures on organisms, increasing local extinction rates (*1*). Simultaneously, reduced movement among remnant patches lowers colonization rates, which further negatively affects demographic and genetic population parameters (*2*). From a conservation perspective, the impacts of habitat deterioration and the impacts of habitat fragmentation might demand different strategies. Whereas the former often requires management of populations within local (protected)