these results into more precise models of mobbing behavior will enrich our understanding of the evolution of cooperation, one of the more poorly understood problems in evolutionary biology.

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References

1 Curio, E. (1978) The adaptive significance of avian mobbing. I. Teleonomic hypotheses and predictions. *Z. Tierpsychol.* 48, 175–183
2 Pavey, C.R. and Smyth, A.K. (1998) Effects of avian mobbing on roost use and diet of powerful owls, *Ninox strenua*. *Anim. Behav.* 55, 313–318
3 Flasskamp, A. (1994) The adaptive significance of avian mobbing. V. An experimental test of the 'move on' hypothesis. *Ethology* 96, 322–333
4 Curio, E. and Regelmann, K. (1986) Predator harassment implies a real deadly risk: a reply to Hennessy. *Ethology* 72, 75–78
5 Nowak, M.A. (2006) Five rules for the evolution of cooperation. *Science* 314, 1560–1563
6 Axelrod, R. and Hamilton, W.D. (1981) The evolution of cooperation. *Science* 211, 1390–1396
7 Krams, I. *et al.* (2008) Experimental evidence of reciprocal altruism in the pied flycatcher. *Behav. Ecol. Sociobiol.* 62, 599–605
8 Dugatkin, L.A. (1997) *Cooperation among Animals: An Evolutionary Perspective.* Oxford University Press
9 Connor, R.C. (1996) Partner preferences in by-product mutualisms and the case of predator inspection in fish. *Anim. Behav.* 51, 451–454
10 Stevens, J.R. and Hauser, M.D. (2004) Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn. Sci.* 8, 60–65
11 Stevens, J.R. and Stephens, D.W. (2004) The economic basis of cooperation: tradeoffs between selfishness and generosity. *Behav. Ecol.* 15, 255–261
12 Tebbich, S. *et al.* (2002) Cleaner fish *Labroides dimidiatus* recognise familiar clients. *Anim. Cogn.* 5, 139–145
13 Godard, R. (1991) Long-term memory of individual neighbors in a migratory songbird. *Nature* 350, 228–229
14 Sharp, S.P. and Hatchwell, B.J. (2005) Individuality in the contact calls of cooperatively breeding long-tailed tits (*Aegithalos caudatus*). *Behaviour* 142, 1559–1575
15 Lampe, H.M. and Slagsvold, T. (1998) Female pied flycatchers respond differently to songs of mates, neighbors and strangers. *Behaviour* 135, 269–285
16 Hurd, C.R. (1996) Interspecific attraction to the mobbing calls of black-capped chickadees (*Parus atricapillus*). *Behav. Ecol. Sociobiol.* 38, 287–292
17 Krams, I. and Krama, T. (2002) Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, *Fringilla coelebs*. *Proc. Biol. Sci.* 269, 2345–2350
18 Forsman, J.T. *et al.* (2002) Positive fitness consequences of interspecific interaction with a potential competitor. *Proc. Biol. Sci.* 269, 1619–1623

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Letters

A behavioral perspective on fishing-induced evolution

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The potential for excessive and/or selective fishing to act as an evolutionary force has been emphasized recently. However, most studies have focused on evolution of life-history traits in response to size-selective harvesting. Here we draw attention to fishing-induced evolution of behavioral and underlying physiological traits. We contend that fishing-induced selection directly acting on behavioral rather than on life-history traits *per se* can be expected in all fisheries that operate with passive gears such as trapping, angling and gill-netting. Recent artificial selection experiments in the nest-guarding largemouth bass *Micropterus salmoides* suggest that fishing-induced evolution of behavioral traits that reduce exposure to fishing gear might be maladaptive, potentially reducing natural recruitment. To improve understanding and management of fisheries-induced evolution, we encourage greater application of methods from behavioral ecology, physiological ecology and behavioral genetics.

The potential for fishing-induced evolution (FIE) has been discussed recently [1,2]. Most studies reviewed in Ref. [1] have focused on life-history traits that directly or indirectly determine body size. Under the common scenario of size-selective harvesting, large fish face a fitness disadvantage that might cause rapid evolution toward earlier maturation at smaller sizes, higher reproductive investment and lower intrinsic growth capacity and, collectively, smaller size-at-age [2]. Such evolution can degrade fisheries yield and other ecological services within decades [2].

Many studies on FIE, however, fall short in addressing the selection pathways that drive the observed life-history changes. For example, evolution of small body size can result from direct selection for decreased intrinsic growth capacity or be a consequence of selection on correlated life-history or behavioral traits [3]. Indeed, in some passively operated fishing gears (e.g. trapping, angling, gill-netting), behavioral traits rather than body size *per se* determine a fish's vulnerability to capture, and thus its survival and fitness (Figure 1) [3]. In these situations, direct selection on behavior can drive evolutionary changes in correlated life-history traits such as growth rate [3] because the more active, bold and vulnerable individuals tend to also grow faster [4,5]. Despite the important role of behavior in influencing catchability in various fisheries [3,6–8], the behavioral dimension of FIE has largely been neglected.

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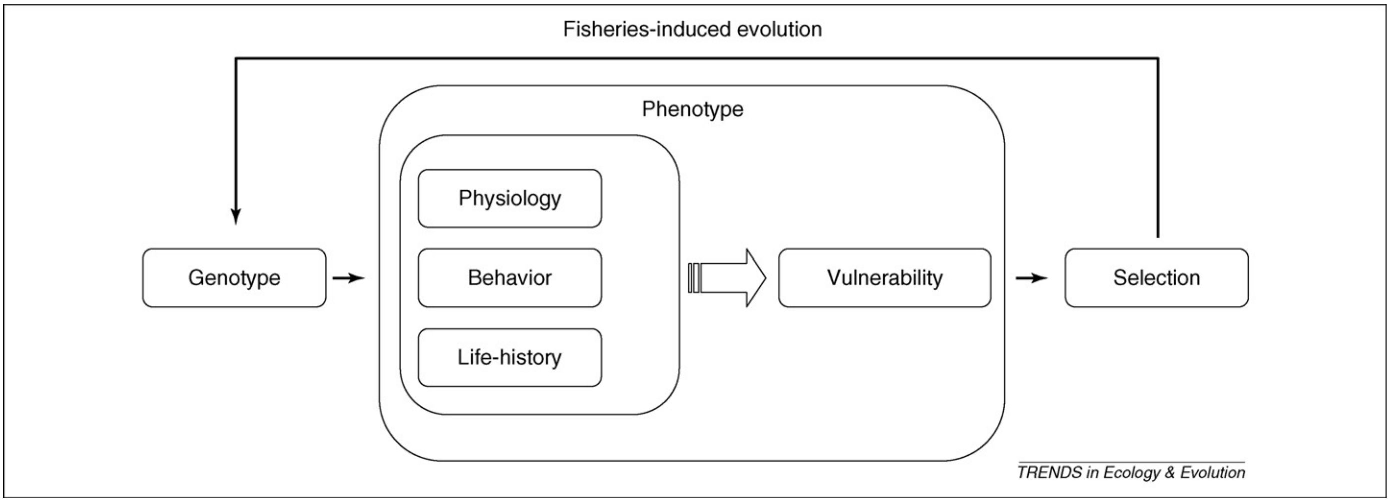

Figure 1. Mechanistic pathway of fishing-induced evolution by selection on fishing vulnerability. In this scheme, vulnerability to capture is considered a heritable trait as part of the fish's phenotype. Vulnerability to capture comprises a bundle of physiological, behavioral and life-history traits that jointly determine vulnerability to capture. In passive fisheries, vulnerability to capture is largely determined by specific behavioral patterns rather than by body size-related life-history traits *per se*. Due to genetic correlations between behavioral, physiological and life-history traits, fisheries-induced selection on behavioral traits might alter physiologies and life histories, but behavior might also change in response to selection on correlated life-history or other traits.

Evolutionary responses to fisheries-induced selection depend on the selection differential and the heritability of the trait [1]. Large selection pressures on behavioral traits can be expected when specific behavioral patterns increase the encounter probability with the fishing gear, thus influencing survival and fitness. For example, vulnerability to capture by gill-nets not only depends on body size and shape but is also strongly related to an individual's activity level [3,7]. Similarly, in recreational angling, vulnerability to capture can be size related, but most importantly depends on a fish's decision to attack and/or ingest baited hooks [7–9]. In this context, bold and aggressive personalities, individuals with lower cognitive abilities and those with higher metabolism and growth capacity often take more risks and hide less in structured habitat, rendering these fish more vulnerable to capture [3,7,8]. Thus, behavior-driven vulnerability to fishing might constitute an underappreciated mechanism for selection on growth rate [3] or other life-history traits [5]. Alternatively, due to genetic correlations between physiological, behavioral and life-history traits (Figure 1), evolution of behavioral traits might be an indirect consequence of selection on body size under strongly size-selective harvesting. Collectively, if exploitation directly or indirectly induces a large selection differential on particular heritable behavioral traits, evolving fish stocks will not only become less abundant and smaller [2] but also harder to catch [3,6–9], which diminishes the quality of the fishery.

Selection responses of behavioral traits to fishing can be rapid because heritabilities of behavioral traits are often larger than those of life-history traits [10,11]. Indeed, in largemouth bass (*Micropterus salmoides*), artificial selection for vulnerability to recreational angling induced evolutionary changes in various physiological and behavioral traits after only four generations [8]. Vulnerable individuals had higher metabolic rates and resting cardiac activity, and provided more intense parental care than invulnerable fish of the same body size [8]. Vulnerability to capture therefore was primarily determined by physiological and behavioral traits rather than by body size. This suggests that selective harvest of highly vulnerable largemouth bass could impact the population in the long term by altering parental care activity and level of aggression [8]. Moreover, in nest-guarding species, FIE is conceivable even in the absence of fishing mortality, for example when recreational anglers practice catch-and-release during the reproductive period [8]. In these situations, the fitness of more aggressive and vulnerable individuals is reduced when they are temporarily removed from their nests, leaving the brood susceptible to rapid egg predation [12]. Over time, this might favor more wary and less vulnerable genotypes that happen to also be inferior nest guarders.

The potential for evolution of behavioral and physiological traits and its consequences for life history, demography and fishing quality constitutes a fascinating, yet largely overlooked research area within the emerging field of FIE. To improve understanding and management of FIE, we encourage collaboration between fishery scientists and evolutionary ecologists (*sensu* [1]), and greater application of methods from behavioral ecology, physiological ecology and behavioral genetics.

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References

1 Kuparinen, A. and Merilä, J. (2007) Detecting and managing fisheries-induced evolution. *Trends Ecol. Evol.* 22, 652–659
2 Jørgensen, C. *et al.* (2007) Managing evolving fish stocks. *Science* 318, 1247–1248
3 Biro, P.A. and Post, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc. Natl. Acad. Sci. U. S. A.* 105, 2919–2922

4 Biro, P.A. and Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* 23, 361–368
5 Walsh, M.R. *et al.* (2006) Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9, 142–148
6 Wohlfart, G. *et al.* (1975) Genetic variation in seine escapability of the common carp. *Aquaculture* 5, 375–387
7 Brauhn, J.L. and Kincaid, H. (1982) Survival, growth, and catchability of rainbow trout of four strains. *North Am. J. Fish. Manage.* 2, 1–10
8 Cooke, S.J. *et al.* (2007) Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiol. Biochem. Zool.* 80, 480–490
9 Askey, P.J. *et al.* (2006) Linking angling catch rates and fish learning under catch-and-release regulations. *North Am. J. Fish. Manage.* 26, 1020–1029
10 Mousseau, T.A. and Roff, D.A. (1987) Natural selection and the heritability of fitness components. *Heredity* 59, 181–197
11 Merilä, J. and Sheldon, B.C. (2000) Lifetime reproductive success and heritability in nature. *Am. Nat.* 155, 301–310
12 Suski, C.D. *et al.* (2003) The effect of catch-and-release angling on parental care behavior of male smallmouth bass. *Trans. Am. Fish. Soc.* 132, 210–218

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Book Review

Birds without boundaries

The Migration Ecology of Birds by Ian Newton, Academic Press, 2007. £42.99, hbk (984 pages) ISBN 9780125173674

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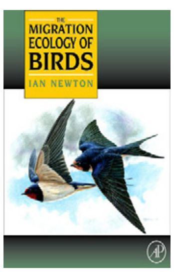

In a world of instant electronic access to the latest published research, it is all too easy to be unaware of the great wealth of information contained within printed books and journals. This is particularly important for a subject such as bird migration, for which our understanding has developed from published accounts of observations and experiments spanning centuries. *The Migration Ecology of Birds* is a remarkably detailed and highly readable account of this vast literature.

As is clear from the quotations that begin each chapter of this book, the subject of bird migration has always fascinated humans. The astonishing annual journeys undertaken by migrants, the skills necessary to navigate across oceans and continents and return to the same patch of woodland or wetland, and the intricate adaptations that underpin these feats have been the subject of huge numbers of studies. The focus of this book is on ecological aspects of migration, but this requires an understanding of disciplines including flight mechanics, large-scale weather patterns, bird physiology, behavior, evolution and population dynamics. The 28 chapters of this book cover topics including physiological adaptations for migratory flight, global variation in patterns of migration, the evolution of migration routes and types, environmental impacts on migration, mechanisms of population limitation in migrants and many more. The whole book is packed with clearly described examples, many of which are presented in fully referenced summary tables which will prove invaluable to researchers.

Modern techniques such as satellite transmitters, geolocator tags and stable isotope analyses have greatly enhanced our ability to measure key aspects of bird migration, particularly at the level of the individual. This book describes many of these developments but sets them within a much broader historical context of published studies of bird migration. This context is both highly informative and provides a powerful basis for understanding current and future changes to migratory populations. For example, the book contains fascinating accounts of recent shifts in migration and their causes, allowing insights into how different species might respond to future changes.

Having to cope with conditions in different parts of the world within each year might make migratory species particularly vulnerable to recent rapid changes in land-use and climatic conditions, and population sizes of many migratory bird species are currently declining. By contrast, their mobility and greater geographical knowledge could allow them to respond to changing conditions more rapidly than other species. The opening chapters of this book describe the hazards with which birds contend during migration, the often extraordinary energetic requirements for fuelling these flights and the diverse array of mechanisms they employ to aid navigation. On reading these chapters it would be easy to imagine how relatively small changes in environmental conditions could have drastic impacts on these species. However, migratory birds have persisted through successive periods of glaciation when high-latitude habitats were not available, and migratory routes are therefore likely to have repeatedly reestablished during interglacial periods. Will this flexibility benefit migratory species or are current rates of change in climatic conditions, land-use patterns and habitat availability so fast that migrants are in fact more vulnerable than sedentary species? In the final chapters of this book, Ian Newton takes a measured and thorough approach to these issues, describing in detail the range of processes that influence population change in migratory birds, assessing the evidence for each and highlighting the many areas in which we do not yet have enough understanding to predict how these species might fare in the future.

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