University of Nebraska - Lincoln
DigitalCommons@University of Nebraska - Lincoln

USDA National Wildlife Research Center - Staff Publications | Wildlife Damage Management, Internet Center for

1-1-2010

Behavioral flexibility and species invasions: the adaptive flexibility hypothesis

Timothy F. Wright
New Mexico State University, wright@nmsu.edu

J.R. Eberhard
Louisiana State University

E.A. Hobson
New Mexico State University

Michael L. Avery
USDA APHIS National Wildlife Research Center, Gainesville, FL, michael.l.avery@aphis.usda.gov

M.A. Russello
University of British Columbia Okanagan

Follow this and additional works at: http://digitalcommons.unl.edu/icwdm_usdanwrc

Wright, Timothy F.; Eberhard, J.R.; Hobson, E.A.; Avery, Michael L.; and Russello, M.A., "Behavioral flexibility and species invasions: the adaptive flexibility hypothesis" (2010). *USDA National Wildlife Research Center - Staff Publications.* Paper 1258.
http://digitalcommons.unl.edu/icwdm_usdanwrc/1258

This Article is brought to you for free and open access by the Wildlife Damage Management, Internet Center for at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA National Wildlife Research Center - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Ethology Ecology & Evolution 22: 393–404, 2010

Behavioral flexibility and species invasions: the adaptive flexibility hypothesis

T.F. Wright [1,5]*, J.R. Eberhard [2]*, E.A. Hobson [1], M.L. Avery [3] and M.A. Russello [4]

[1] *Department of Biology MSC 3AF, New Mexico State University, Las Cruces, NM 88003, USA*
[2] *Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA*
[3] *USDA/APHIS/WS, National Wildlife Research Center, Florida Field Station, Gainesville, FL 32641, USA*
[4] *Department of Biology, University of British Columbia Okanagan, Kelowna, BC, V1V 1V7, Canada*

Received 15 January 2010, accepted 31 March 2010

Behavioral flexibility is an important adaptive response to changing environments for many animal species. Such plasticity may also promote the invasion of novel habitats by introduced species by providing them with the ability to expand or change their ecological niche, a longstanding idea with recent empirical support. At the individual level, flexibility may arise through innovation, in which an individual invents a new behavior, or through social learning, in which an individual adopts a behavior used by others. There is increasing evidence that the adaptive value of these two modes of learning, and the overall expression of behavioral flexibility, may vary with social and environmental context. In this paper, we propose that invasive species may change the degree to which they express behavioral flexibility in an adaptive manner during the different stages of invasion. Specifically, the "adaptive flexibility hypothesis" predicts that the expression of behavioral flexibility, and thus the diversity of behaviors observed in a population, will be high during the initial stage of introduction into a novel environment due to innovation, followed by a decline in behavioral diversity during the establishment and growth of a founding population due to social learning of successful behavioral variants. We discuss several alternatives to this hypothesis and suggest empirical and theoretical tests of these hypotheses. This "adaptive flexibility hypothesis" suggests that a more nuanced approach to the study of the behaviors employed by individuals in populations at different invasion stages could generate new insight into the importance of such flexibility during species invasions, and the evolution of behavioral plasticity in general.

KEY WORDS: behavioral flexibility, copying, ecological niche, innovation, invasive species, neophobia, plasticity, social learning.

[5] Corresponding author: Timothy F. Wright, Department of Biology MSC 3AF, New Mexico State University, Las Cruces, NM 88003, USA (E-mail: wright@nmsu.edu).

*These authors contributed equally to this paper.

ISSN 0394-9370 print/ISSN 1828-7131 online
© 2010 Dipartimento di Biologia Evoluzionistica dell'Università, Firenze, Italia
DOI: 10.1080/03949370.2010.505580
http://www.informaworld.com

This article is a U.S. government work, and is not subject to copyright in the United States.

INTRODUCTION

Behavioral flexibility is employed by many species as an adaptive response to changing environments. Flexibility in behavior lies at one end of a continuum of plastic responses that includes developmental plasticity in individual physiology and anatomy, and genetic responses to selection over generations (DUKAS 1998b; PIGLIUCCI 2001; WEST-EBERHARD 2003). Of these forms of response, behavioral changes can generally occur most quickly and thus are best suited for rapid responses to changes in the external environment. An organism may face such changes due to naturally occurring events or to human activities that alter its native habitat. It may also face rapid changes when introduced into a novel habitat by human activities. A variety of factors determine whether an introduced species will be successful in establishing a breeding population in its new habitat, and whether it will become invasive (RICHARDSON et al. 2000; KOLAR & LODGE 2001; COLAUTTI & MACISAAC 2004, REJMÁEK et al. 2005). In this paper we discuss the role of behavioral flexibility in mediating the establishment success of an organism introduced into a novel environment, and propose a new model that describes how the expression of behavioral flexibility may be expected to change through the successive stages of establishment, population growth, and invasion.

SOURCES AND CONSEQUENCES OF BEHAVIORAL FLEXIBILITY

The ability of an organism to selectively modify behaviors in response to changing circumstances may arise from a number of sources. Innate behaviors, or those independent of experience, may allow individuals to respond to a variety of different stimuli, but these reactions, although perhaps highly tuned, are non-modifiable. Such flexibility is predicted to be beneficial to the degree that either the cues for, or the timing of, changes are predictable across generations, such as diurnal or seasonal changes in the environment, or developmental changes of the animal itself (STEPHENS 1991; DUKAS 1998b; SHETTLEWORTH 1998). Most discussions of behavioral flexibility, however, focus on situations where the behavior of individuals is modified by experience (DUKAS 1998a; SHETTLEWORTH 1998; READER & LALAND 2003a). In this conception of behavioral plasticity, changes in the behavioral repertoire can result from individual learning in which an individual either modifies an existing behavior or invents a new one, termed "innovation" (READER & LALAND 2003b). Changes in behavior can also result from "copying" or other forms of social learning, in which new behavioral variants are learned from others (BOYD & RICHERSON 1985; LALAND et al. 1996; READER & LALAND 2003b). Behavioral flexibility through either type of learning is predicted to be beneficial when environments change, although social learning may be less advantageous when environments vary so rapidly or unpredictably that the information acquired from others is unreliable or outdated (DAWKINS 1980; HARLEY 1981; STEPHENS 1991; DUKAS 1998b; SOL 2003).

Individual and social learning differ in their propensity to introduce new behavioral variants into the repertoire of individuals and populations. Individual learning can produce innovative behaviors that are novel for an individual or a population, and increase the behavioral flexibility of the former and the behavioral diversity of the latter (READER & LALAND 2003b). In contrast, social learning involves, by definition, the adoption of a behavior already performed by others (GALEF & LALAND 2005). Thus social learning can lead to increased behavioral flexibility in the individual that adopts new behavioral variants, but generally does not increase behavioral diversity, where behavioral diversity is analogous to species diversity within ecological communities. This is because

social learning does not introduce new variants into a population, unless the model for the behavior is new to the population, and may reduce the frequency of many existing variants (Reader & Laland 2003b). Furthermore, when social learning is focused on only a few models or behavioral variants, it can lead to the establishment of learned cultural traditions that supplant behaviors acquired through innovation, and thus lead to an overall reduction in the number of behavioral variants expressed by individuals and the population (Boyd & Richerson 1985; Laland et al. 1996). Thus social learning may have contrasting effects on behavioral flexibility and diversity at the individual and population levels depending on which individuals learn and adopt new behaviors, which individuals model behaviors that are incorporated by others, and the relative frequency of the behavioral variant being learned. These contrasting effects are reflected in historical views of social learning and culture, which have been considered by some workers as conservative forces, and by others as sources of novel behaviors (Galef 2003).

In recent years there has been an increase in the number of empirical studies of the causes and consequences of behavioral flexibility. Many studies take a comparative approach to examine environmental, neuroanatomical and social correlates of behavioral flexibility across species. Comparative studies of primates have found associations between brain size and innovation, social learning and tool use (Reader & Laland 2002); between innovation and sex, age and social rank (Reader & Laland 2001); between innovation and neophilia (Day et al. 2003); and between innovation and neocortex size, diet breadth, and laboratory measures of learning but not with geographic range or climatic variability (Reader & Macdonald 2003). Comparative studies of birds have found similar trends, with associations between the size of the hyperstriatum ventrale and feeding innovation (Timmermans et al. 2000); neophilia and learning (Greenberg 2003); brain size and mortality rates (Sol et al. 2007); brain size and climatic variability (Schuck-Paim et al. 2008); brain size and social complexity (Burish et al. 2004); and between brain size and both propensity to innovate and success in novel habitats (Sol et al. 2005).

A complementary line of investigation conducted largely with captive populations has focused on inter-individual variation in flexibility and its costs, benefits and consequences. In guppies, *Poecilia reticulata*, innovation ability, as measured by completing a novel foraging task, was found to vary with sex, body size and degree of food deprivation (Laland & Reader 1999a), and innovation rate was correlated with competitive ability in males but not females (Laland & Reader 1999b). These results suggest that innovation may be state dependent and triggered by metabolic needs. Further studies demonstrated that specific behavioral innovations could increase in frequency in populations via social learning (Lachlan et al. 1998; Reader & Laland 2000). In some cases this process led to a potentially maladaptive conformity to a specific behavior (Laland & Williams 1998; Day et al. 2003) that was subsequently released in the absence of demonstrators (Brown & Laland 2002). In starlings, *Sturnus vulgaris*, individual learning rates were correlated with neophilia, dominance and speed of solving a novel foraging task (Boogert et al. 2006). Surprisingly, social associations in starlings did not predict the path by which foraging innovations spread through groups, perhaps because of artificially small and confined groups (Boogert et al. 2008). Likewise, in both rooks, *Corvus frugilegus,* and ravens, *Corvus corax,* neophobia to novel foods is reduced in the presence of conspecifics (Stowe et al. 2006a; Dally et al. 2008); in ravens the degree of neophobia, and of social learning, is further modified by the social relationships among individuals (Stowe et al. 2006b; Schwab et al. 2008). Wild Carib grackles, *Quiscalus lugubris,* were found to vary their expression of a novel foraging behavior with food type and risk of kleptoparasitism, suggesting that individuals may vary their behavioral

repertoire with social context (MORAND-FERRON et al. 2004). Additional avian examples of variation in neophobia and exploratory behavior with age and social context are reviewed in GREENBERG & METTKE-HOFMANN (2001). Overall these studies suggest that (i) behavioral flexibility sometimes confers fitness advantages, (ii) these benefits vary with social context, individual state and the external environment, and thus (iii) the expression of flexibility can vary over time in potentially adaptive ways.

FLEXIBILITY AND SPECIES INVASIONS

While an interest in the adaptive nature of behavioral responses to environmental change has long been an integral part of the study of animal behavior, there is an increasing interest in the role played by behavioral flexibility in species invasions (SOL 2003; PRICE & SOL 2008). Invasion by exotic species is one of the largest threats to native species worldwide (WILCOVE et al. 1998; SALA et al. 2000; CLAVERO & GARCÍA-BERTHOU 2005; but see GUREVITCH & PADILLA 2004). Invasive species can modify habitats, reduce species diversity through competition and predation, facilitate disease emergence and adversely affect ecosystem functions (MOONEY et al. 2005; PIMENTEL et al. 2005; SALO et al. 2007). Successful invasion of a new habitat involves several successive stages (RICHARDSON et al. 2000; KOLAR & LODGE 2001; COLAUTTI & MACISAAC 2004): transport from native habitat (generally human-mediated), introduction to new habitat, establishment and growth of a self-sustaining population at the original introduction site (also termed "naturalization"; RICHARDSON et al. 2000), and invasion to new sites (see Fig. 1 in KOLAR & LODGE 2001). At present there are gaps in our understanding of the invasion process and the factors that facilitate or inhibit transition between one stage and another (RICHARDSON et al. 2000; KOLAR & LODGE 2001; PUTH & POST 2005). An improved knowledge of the behavioral characteristics that facilitate species invasions should aid in the control and mitigation of their detrimental effects (KOLAR & LODGE 2001; SOL 2003; CASSEY et al. 2004).

Behavioral flexibility is thought to aid introduced species during invasion by providing them with the ability to expand or even change their ecological niche by exploiting new foods, shelters, or habitats (DUNCAN et al. 2003; PRICE et al. 2008). It may also provide a mechanism for avoiding ecological and evolutionary traps, which may result from rapid environmental changes that alter the reliability of cues used in behavioral or life-history decisions (SCHLAEPFER et al. 2002). Such plasticity is distinct from considerations of species as "generalists" or "specialists"; these classifications are static concepts based on physiological constraints and overlook the potentially rapid responses to environmental changes that can occur through innovation or social learning of novel behaviors (GREENBERG 1990). The idea that more flexible species are more likely to be successful invaders is a longstanding one (MAYR 1965; ROUGHGARDEN 1972; MORSE 1980). Recent comparative studies have supported this hypothesis, with more innovative bird species (as measured by feeding innovations) being more successful invaders of New Zealand (SOL & LEFEBVRE 2000) and worldwide (SOL et al. 2002, 2005); similar patterns are seen in mammals (SOL et al. 2008). The combination of innovation with social learning, as documented in a number of primate species (READER & LALAND 2002), is likely to be especially advantageous for species in novel habitats, as it could allow copying exploratory behavior *per se* as well as permitting the rapid transmission of successful strategies.

On the other hand, there may be benefits in limiting the degree of flexibility and exploratory behavior expressed by an individual. For example, neophobia, or the avoidance of novel objects, could reduce an organism's exposure to the deleterious effects of unfamiliar resources such as novel foods, nesting sites or shelter, and by doing so could

minimize an organism's exposure to dangerous predators, diseases or toxic foods, and reduce expenditures on energetically costly activities like antiparasite behaviors (Greenberg 1990, 2003; Greenberg & Mettke-Hofmann 2001; Hughes & Cremer 2007). Greenberg's "neophobia threshold hypothesis" suggests that neophobia regulates an animal's degree of ecological plasticity, since the response to novelty plays a role in ecologically important behaviors such as food and habitat choice (Greenberg 1990). Neophobia may be modulated by neophilia, or a tendency toward exploratory behavior; these two behavioral drives were hypothesized by Greenberg & Mettke-Hofmann (2001) to vary independently with the degree of environmental complexity and the degree of danger or competition in a given environment to produce differing levels of exploratory behavior under different ecological conditions. Limited behavioral flexibility may also be advantageous when behaviors that are beneficial in a new habitat are linked with dispersal strategies, at least during natural range expansions (Duckworth & Badyaev 2007).

While much of the work to date regarding invasion success has examined interspecific patterns of invasion and correlates of success, recent studies of several taxa provide evidence that behavioral flexibility may be an important mechanism involved in the invasion of new habitats. Martin & Fitzgerald (2005) found that under controlled captive conditions, individual house sparrows, *Passer domesticus*, from an actively invading population (Colón, Panama) were more likely to approach and consume novel foods than were sparrows from a long-established population (Princeton, New Jersey). A comparison of introduced versus native populations of the rusty crayfish, *Oronectes rusticus*, found that foraging behavior varied depending on the competitor species present in native vs introduced habitats, and this behavioral flexibility may explain the higher growth rates, and invasiveness, of *O. rusticus* in its introduced range (Pintor & Sih 2009). Field and laboratory studies of the invasive Argentine ant, *Linepithema humile*, show that colonies are able to modify their aggressive behavior depending on their size and the presence of competitors, and this behavioral flexibility could allow even small colonies to persist and thrive in a new environment (Sagata & Lester 2009). Based on these findings, Sagata & Lester (2009) point out that propagule size, which is thought to be a fundamental driver of invasions (Lockwood et al. 2005; Simberloff 2009), may have limited power to predict invasion success in species with behavioral flexibility. Furthermore, a spatially explicit individual-based model has shown that learning can facilitate the expansion into a novel habitat by allowing the persistence of locally (genetically) maladapted populations (Sutter & Kawecki 2009). These model-based findings are supported by field and experimental studies of crayfish (Hazlett et al. 2002) and crabs (Roudez et al. 2008), which have found significantly greater learning abilities for invasive species when compared with native relatives. Finally, a well-documented example of a behavioral innovation facilitating the invasion of a new habitat is provided by black rats, *Rattus rattus*, that have successfully invaded the Jerusalem pine forest as a result of a feeding innovation (stripping pine cones to obtain seeds) that is transmitted via social learning (Terkel 1994, 1995).

These studies are evidence of a growing recognition that learning and behavioral flexibility are key factors in the success of invasive species. To our knowledge, however, there have been no longitudinal studies of behavioral flexibility during invasion; it remains to be determined exactly how behavioral flexibility enhances invasion success, whether the benefits of flexibility are constant over all stages of invasion, and to what degree the expression of behavioral flexibility might vary adaptively during different invasion stages (Sol 2003).

THE ADAPTIVE FLEXIBILITY HYPOTHESIS

We propose that individuals in invasive populations will change the degree to which they express behavioral flexibility during different stages of invasion in an adaptive manner (Fig. 1). Specifically, we hypothesize that during the initial introduction stage, when founding individuals are exploring a new environment, innovation will be favored and the expression of flexibility, as measured by the number of behavioral variants present in a population, will be high. Populations in which these individuals survive and reproduce sufficiently to create a self-sustaining population would enter the establishment stage of species invasions. Copying more successful behavioral variants will be favored over exploration and innovation in established populations due to the time costs associated with exploration and the opportunity costs of foregoing behavioral alternatives that others have demonstrated to be successful. These processes would lead to a gradual decrease in the number of behavioral variants observed. If the founding population continues to grow to a sufficient degree, it will enter the invasion stage in which overcrowding favors dispersal and the founding of daughter populations. Where these new populations occupy novel environments that offer new resources to be exploited and new dangers to be avoided, behavioral flexibility will again be favored in dispersers, leading to a transitory rise in the number of behavioral variants. Successful daughter populations would in turn enter an established stage in which behavioral diversity would be reduced by copying of the most successful behavioral variants; this suite of variants may well differ from those persisting in the founding population. We term this hypothesis the "adaptive flexibility hypothesis" (Fig. 1a).

There are several alternatives to the adaptive flexibility hypothesis (Fig. 1b–d). One alternative is that the expression of behavioral flexibility is constant regardless of invasion stage. Levels of behavioral flexibility may remain constant through time and uniform across individuals because a species' inherent propensity for flexibility is relatively fixed. Alternatively, behavioral flexibility may be fixed at different levels in different individuals or classes of individuals due to consistent personality differences or behavioral syndromes (Sih et al. 2004). Consistent individual differences have been documented for exploratory behavior in great tits, *Parus major*, in which individuals can be sorted into fast or slow explorers by the latency to which they approached a novel object or explored a novel habitat (Verbeek et al. 1994). Such differences have been shown to be both repeatable within an adult individual and heritable in wild birds (Dingemanse et al. 2002), but are less repeatable within an individual in lines artificially selected for either fast or slow exploratory behavior (Carere et al. 2005). A second alternative is, that after an initial rise, the number of behavioral variants in a population remains relatively constant over time due to a "skill pool effect" (Giraldeau 1994) in which individuals remain specialized on a few behavioral variants rather than copying the successful variants of others. A third alternative is that copying of successful variants does occur during the establishment phase, resulting in a reduced suite of behavioral variants in a population, but that the cultural traditions formed through copying are sufficiently strong that dispersing individuals do not exhibit an increased diversity of behaviors upon founding daughter populations. Low diversity of behavioral variants may also be expected if dispersers selectively settle in environments that best match their learned behavioral repertoire. All of these alternatives, and the adaptive flexibility hypothesis itself, are amenable to testing as discussed below.

The adaptive flexibility hypothesis is primarily applicable to behaviors with a significant learned component, and incorporates several behavioral processes related to learning. These include neophobia, innovation, individual learning and social learning. Evaluating the relative importance of these various processes is critical to testing and refining the hypothesis. We predict that where novel behaviors are rewarded, individual

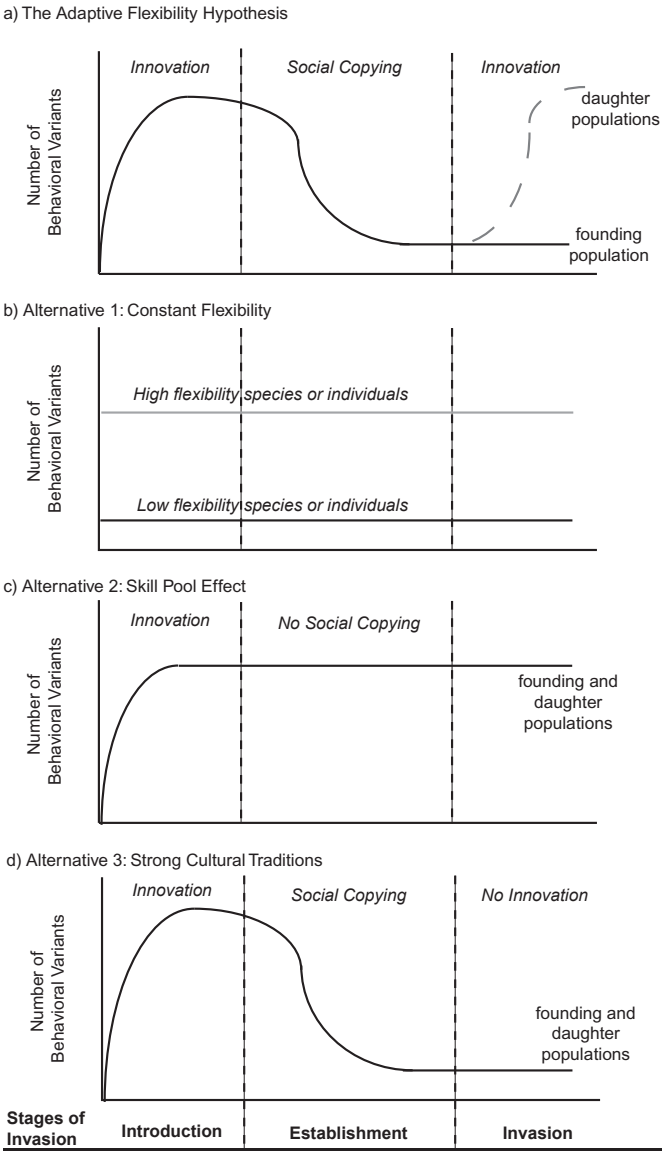

Fig. 1. — Conceptual models of different alternatives for changes in the expression of behavioral flexibility through successive stages of a species invasion. Behavioral flexibility is measured by the number of behavioral variants in a population (solid line). Vertical dashed lines denote the various stages of species invasion listed across the bottom of the figure. The introduction stage represents the initial period that follows the movement of a species into a novel habitat via human actions, the establishment stage represents the period when this initial introduced population becomes self-sustaining, and the invasion stage represents the period when this population spreads beyond the initial point of introduction and becomes abundant (Richardson et al. 2000; Kolar & Lodge 2001). (a) The adaptive flexibility hypothesis predicts that the number of behavioral variants in a population will rise due to innovation and exploration during the population introduction stage then decline as the population becomes established and

learning and innovation could quickly lead to the expression of a large variety of alternative behaviors expressed by different individuals in a recently introduced population. Subsequently, biased social learning of successful variants is key to the decline in behavioral variants predicted by the hypothesis. Although we have emphasized copying behavior as the most obvious form of social learning that would produce this effect, it is likely that other forms of social learning, such as local enhancement, stimulus enhancement, or social facilitation, would also reduce the diversity of behaviors. In these types of social learning, individuals would be acquiring behavior patterns in the same context as the model, which would often result in the same behavioral outcome. It will be important to test this prediction that all forms of social learning would have similar effects, since copying is generally thought to be less taxonomically widespread than other forms of social learning (DUKAS 1998a; SHETTLEWORTH 1998).

The adaptive flexibility hypothesis focuses on how individuals and populations might change in their expression of behavioral plasticity on relatively short timescales through learning. The predicted decline in behavioral flexibility could occur over successive generations or even within a single generation, depending on how frequently individuals learned new variants and whether transmission of learned variants was vertical (between generations) or horizontal (within generations). It is also possible that selection might lead to adaptive changes over many generations in the genetic mechanisms underlying behavior; such changes might lead to an increased capacity (rather than the propensity) to express behavioral flexibility, or they might lead to a reduction of the capacity for social learning through genetic accommodation of successful variants (WEST-EBERHARD 2003).

Learned behaviors that might be expected to show adaptive flexibility include foraging strategies, diet choice, nesting or burrowing site choice, roosting or sleeping site choice, anti-predator responses, preferred group sizes, mate choice and anti-parasite strategies. Not all learned behaviors are expected to follow this model; for example, learned vocal signals may be under a different selection regime than many other learned behaviors (SLATER & LACHLAN 2003). Where shared vocal patterns are used to denote group membership (NOWICKI 1983; BOUGHMAN 1998), convergence to a single vocal variant may occur quickly in newly established populations without any intermediate rise in the number of variants expressed by individuals. In species where learned vocal signals are used as honest indicators of individual quality in social competition for resources or in gaining access to mates (WEST-EBERHARD 1983; SEARCY & NOWICKI 2005), selection may either favor diversification or homogeneity of vocal signals independent of invasion stage.

The adaptive flexibility hypothesis and its alternatives are testable given multiple populations of a behaviorally flexible introduced species. The most direct test would be provided by longitudinal studies that track the changes in the number of variants of a particular class of behavior (e.g. foraging methods) used by known individuals within a single founding population and its daughter populations as they pass through different stages of invasion. An alternative approach would be to catalog behavioral variants of different

---

copying of successful variants leads to cultural traditions. The dotted line represents the rise in behavioral variants predicted in newly established daughter populations due to innovation in a new environment. (b) Alternative hypothesis 1 suggests that the degree of behavioral flexibility expressed by a species (or classes of individuals within species) is stable, leading to a constant number of variants across stages. (c) Alternative hypothesis 2 is based on the "skill pool effect" (GIRALDEAU 1994), which suggests that individuals would maintain specialized subsets of the behavioral variants present in a population rather than copying successful variants, leading to a constant number of behavioral variants in a population after an initial rise due to innovation. (d) Alternative hypothesis 3 suggests that the cultural traditions formed through social copying could be sufficiently strong to suppress innovation in daughter populations founded during the invasion stage.

populations to quantify the expression of behavioral flexibility in a particular class of behavior. If these populations vary in their invasion stage then the numbers of variants can be compared across populations as a measure of the degree of behavioral flexibility expressed by individuals during different stages of invasion; here behavioral variation at the population level would serve as a proxy measure of behavioral flexibility at the individual level based on the testable assumption that population diversity was not produced by individual specialization. A third approach would be to compare introduced populations with ones from the native range. The latter are likely to represent established populations to which behavioral variants within invading populations at different stages may be compared. A fourth approach would be experiments with captive individuals to assess a species' general propensity for innovation, copying, neophobia and flexibility, and to test the critical assumption that individuals will preferentially copy variants that are more successful in a particular environment. Finally, quantitative modeling approaches would be useful to determine the range of conditions under which the temporal changes in behavioral flexibility predicted by the adaptive flexibility hypothesis might occur, and to disentangle the relative importance of the various underlying behavioral processes.

CONCLUSIONS

There is considerable evidence from a range of species suggesting that behavioral flexibility can benefit those individuals that employ it. These advantages may vary with social context, individual state and external environment, suggesting that the expression of flexibility might be expected to vary over time even within an individual. There is increasing evidence that behavioral flexibility plays an important role in facilitating invasions by species, particularly in species capable of both individual and social learning. Our proposed adaptive flexibility hypothesis predicts that the expression of behavioral flexibility might change with stage of invasion, with high flexibility observed early in invasions followed by decreases as some individuals identify locally adaptive behavioral strategies and these innovations spread through social learning. Studies focusing on the number of variants expressed in a population and the degree of flexibility expressed by individuals should provide more insight into the causes and consequences of species invasions and the evolution of behavioral flexibility in general.

ACKNOWLEDGEMENTS

We thank C. Dahlin, A. Young, E. Schirtzinger, K. Petren and M.J. West-Eberhard for their helpful comments on the manuscript. TFW was supported by National Science Foundation grant IOS-0725032.

REFERENCES

Boogert N.J., Reader S.M., Hoppitt W. & Laland K.N. 2008. The origin and spread of innovations in starlings. *Animal Behaviour* 75: 1509–1518.

Boogert N.J., Reader S.M. & Laland K.N. 2006. The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour* 72: 1229–1239.

Boughman J.W. 1998. Vocal learning by greater spear-nosed bats. *Proceedings of the Royal Society (B)* 265: 227–233.

Boyd R. & Richerson P.J. 1985. Culture and the evolutionary process. *Chicago*: *Chicago University Press*.

BROWN C. & LALAND K.N. 2002. Social learning of a novel avoidance task in the guppy: conformity and social release. *Animal Behaviour* 64: 41–47.

BURISH M.J., KUEH H.Y. & WANG S.S.-H. 2004. Brain architecture and social complexity in modern and ancient birds. *Brain Behavior and Evolution* 63: 107–124.

CARERE C., DREN P.J., PRIVITERA L., KOOLHAAS J.M. & GROOTHUIS T.G.G. 2005. Personalities in great tits, *Parus major*: stability and consistency. *Behavioral Ecology* 70: 795–805.

CASSEY P., BLACKBURN T., JONES K.E. & LOCKWOOD J.L. 2004. Mistakes in the analysis of exotic species establishment: source pool designation and correlates of introduction success among parrots (Aves: Psittaciformes) of the world. *Journal of Biogeography* 31: 277–284.

CLAVERO M. & GARCÍA-BERTHOU E. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology & Evolution* 20: 110.

COLAUTTI R.I. & MACISAAC H.J. 2004. A neutral terminology to define 'invasive' species. *Diversity and Distributions* 10: 135–141.

DALLY J.M., CLAYTON N.S. & EMERY N.J. 2008. Social influences on foraging by rooks (*Corvus frugilegus*). *Behaviour* 145: 1101–1124.

DAWKINS R. 1980. Good strategy or evolutionarily stable strategy?, pp. 331–367. In: Barlow G.W. & Silverberg J., Eds. AAAS Selected Symposium 35. *Boulder, CO*: *Westview Press*.

DAY R.L., COE R.L., KENDAL J.R. & LALAND K.N. 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour* 65: 559–571.

DINGEMANSE N.J., BOTH C., DRENT P.J., VAN OERS K. & VAN NOORDWIJK A.J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* 64: 929–938.

DUCKWORTH, R.A. & BADYAEV A.V. 2007. Coupling Of dispersal and aggression facilitates the rapid range expansion of a passerine birds. *Proceedings of the National Academy of Sciences of the United States of America* 104: 15017–15022.

DUKAS R. 1998a. Cognitive ecology: the evolutionary ecology of information processing and decision making. *Chicago*: *Chicago University Press*.

DUKAS R. 1998b. Evolutionary ecology of learning, pp. 129–174. In: Dukas R., Ed. Cognitive ecology: the evolutionary ecology of information processing and decision making. *Chicago*: *Chicago University Press*.

DUNCAN R.P., BLACKBURN T. & SOL D. 2003. The ecology of bird introductions. *Annual Review of Ecology and Systematics* 34: 71–98.

GALEF B.G. 2003. Social learning: promoter or inhibitor of innovation?, pp. 137–152. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York*: *Oxford University Press*.

GALEF B.G. & LALAND K.N. 2005. Social learning in animals: empirical studies and theoretical models. *Bioscience* 55: 489–499.

GIRALDEAU L.-A. 1994. Group foraging: the skill pool effect and frequency-dependent learning. *The American Naturalist* 124: 72–79.

GREENBERG R. 1990. Ecological plasticity, neophobia, and resource use in birds. *Studies in Avian Biology* 13: 431–437.

GREENBERG R. 2003. The role of neophobia and neophilia in the development of innovative behavior in birds, pp. 175–196. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York*: *Oxford University Press*.

GREENBERG R. & METTKE-HOFMANN C. 2001. Ecological aspects of neophobia and neophilia in birds, pp. 119–178. In: Nolan V. Jr & Thompson C.F., Eds. Current ornithology. *New York*: *Kluwer Academic/Plenum Publishers*.

GUREVITCH J. & PADILLA D.K. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution* 19: 470–474.

HARLEY C.B. 1981. Learning the evolutionarily stable strategy. *Journal of Theoretical Biology* 89: 611–633.

HAZLETT B.A., ACQUISTAPACE P. & GHERARDI F. 2002. Differences in memory capabilities in invasive and native crayfish. *Journal of Crustacean Biology* 22: 439–448.

HUGHES D.P. & CREMER S. 2007. Plasticity in antiparasite behaviours and its suggested role in invasion biology. *Animal Behaviour* 74: 1593–1599.

KOLAR C.S. & LODGE D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16: 199–204.

LACHLAN R.F., CROOKS L. & LALAND K.N. 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. *Animal Behaviour* 56: 270–274.

LALAND K.N. & READER S.M. 1999a. Foraging innovation in the guppy. *Animal Behaviour* 57: 331–340.
LALAND K.N. & READER S.M. 1999b. Foraging innovation is inversely related to competitive ability in male but not in female guppies. *Behavioral Ecology* 10: 270–274.
LALAND K.N., RICHERSON P.J. & BOYD R. 1996. Developing a theory of animal social learning, pp. 129–154. In: Heyes C.M. & Galef B.G. Jr, Eds. Social learning in animals: the roots of culture. *San Diego*: *Academic Press*.
LALAND K.N. & WILLIAMS K. 1998. Social transmission of maladaptive information in the guppy. *Behavioral Ecology* 9: 493–499.
LOCKWOOD J.L., CASSEY P. & BLACKBURN T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20: 223–228.
MARTIN L.B. & FITZGERALD L. 2005. A taste for novelty in invading house sparrows, *Passer domesticus*. *Behavioral Ecology* 16: 702–707.
MAYR E. 1965. The nature of colonising birds, pp. 29–43. In: Baker E.G. & Stebbins G.L., Eds. The genetics of colonizing species. *New York*: *Academic Press*.
MOONEY H.A., MACK R.N., MCNEELY J.A., NEVILLE L.E., SCHEI P.J. & WAAGE J.K. 2005. Invasive alien species: a new synthesis. *Washington DC: Island Press*.
MORAND-FERRON J., LEFEBVRE L., READER S.M., SOL D. & ELVIN S. 2004. Dunking behaviour in carib grackles. *Animal Behaviour* 68: 1267–1274.
MORSE D.H. 1980. Behavioral mechanisms in ecology. *Cambridge*, *MA*: *Harvard University Press*.
NOWICKI S. 1983. Flock-specific recognition of chickadee calls. *Behavioral Ecology and Sociobiology* 12: 317–320.
PIGLIUCCI M. 2001. Phenotypic plasticity: beyond nature and nurture. *Baltimore*: *Johns Hopkins Press*.
PIMENTEL D., ZUNIGA R. & MORRISON D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273–288.
PINTOR L.M. & SIH A. 2009. Differences in growth and foraging behavior of native and introduced populations of an invasive crayfish. *Biological Invasions* 11: 1895–1902.
PRICE T. & SOL D. 2008. Introduction: genetics of colonizing species. *The American Naturalist* 172: S1–S3.
PRICE T., YEH P.J. & HARR B. 2008. Phenotypic plasticity and the evolution of a socially selected trait following colonization of a novel environment. *The American Naturalist* 172: S49–S62.
PUTH L.M. & POST D.M. 2005. Studying invasion: have we missed the boat? *Ecology Letters* 8: 715–721.
READER S.M. & LALAND K.N. 2000. Diffusion of foraging innovations in the guppy. *Animal Behaviour* 60: 175–180.
READER S.M. & LALAND K.N. 2001. Primate innovation: sex, age and social rank differences. *International Journal of Primatology* 22: 787–805.
READER S.M. & LALAND K.N. 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America* 99: 4436–4441.
READER S.M. & LALAND K.N. 2003a. Animal innovation. *New York*: *Oxford University Press*.
READER S.M. & LALAND K.N. 2003b. Animal innovation: an introduction, pp. 3–35. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York*: *Oxford University Press*.
READER S.M. & MACDONALD K. 2003. Environmental variability and primate behavioral flexibility, pp. 83–116. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York*: *Oxford University Press*.
REJMÁNEK M., RICHARDSON D.M., HIGGINS S.I., PITCAIRN M.J. & GROTKOPP E. 2005. Ecology of invasive plants: state of the art. In: Mooney H.A. et al., Eds. Invasive alien species: a new synthesis. *Washington DC*: *Island Press*.
RICHARDSON D.M., PYSEK P., REJMÁNEK M., BARBOUR M.G., PANETTA F.D. & WEST C.J. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107.
ROUDEZ R.J., GLOVER T. & WEIS J.S. 2008. Learning in an invasive and a native predatory crab. *Biological Invasions* 10: 1191–1196.
ROUGHGARDEN J. 1972. Evolution of niche width. *The American Naturalist* 106: 683–718.
SAGATA K. & LESTER P.J. 2009. Behavioural plasticity associated with propagule size, resources, and the invasion success of the Argentine ant *Linepithema humile*. *Journal of Applied Ecology* 46: 19–27.
SALA O.E., CHAPIN III S., ARMESTO J.J., BERLOW E., BLOOMFIELD J., RODOLFO DIRZO E.H.-S., HUENNEKE L.F., JACKSON R.B., KINZIG A., LEEMANS R., LODGE D.M., MOONEY H.A., OESTERHELD M., POFF N.L., SYKES M.T., WALKER B.H., WALKER M. & WALL D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.

SALO P., KORPIMÄKI E., BANKS P.B., NORDSTRÖM. M. & DICKMAN C.R. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society (B)* 274: 1237–1243.

SCHLAEPFER M.A., RUNGE M.C. & SHERMAN P.W. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17: 474–480.

SCHUCK-PAIM C., ALONSO W.J. & OTTONI E.B. 2008. Cognition in an everchanging world: climactic variability is associated with brain size in Neotropical parrots. *Brain, Behavior and Evolution* 71: 200–215.

SCHWAB C., BUGNYAR T., SCHLOEGL C. & KOTRSCHAL K. 2008. Enhanced social learning between siblings in common ravens *Corvus corax*. *Animal Behaviour* 63: 933–942.

SEARCY W.A. & NOWICKI S. 2005. The evolution of animal communication: reliability and deception in signaling systems. *Princeton, NJ: Princeton University Press*.

SHETTLEWORTH S.J. 1998. Cognition, evolution and behavior. *New York: Oxford University Press*.

SIH A., BELL A.M., JOHNSON J.C. & ZIEMBA R.E. 2004. Behavioral syndromes: an integrative overview. *The Quarterly Review of Biology* 79: 241–277.

SIMBERLOFF D. 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution & Systematics* 40: 81–102.

SLATER P.J.B. & LACHLAN R.F. 2003. Is innovation in bird song adaptive?, pp. 117–135. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York: Oxford University Press*.

SOL D. 2003. Behavioural innovation: a neglected issue in the ecological and evolutionary literature? pp. 63–82. In: Reader S.M. & Laland K.N., Eds. Animal innovation. *New York: Oxford University Press*.

SOL D., BACHER S., READER S.M. & LEFEBVRE L. 2008. Brain size predicts the success of mammal species introduced into novel environments. *The American Naturalist* 172: S63–S71.

SOL D., DUNCAN R.P., BLACKBURN T.M., CASSEY P. & LEFEBVRE L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences of the United States of America* 102: 5460–5465.

SOL D. & LEFEBVRE L. 2000. Behavioural flexibility predicts invasion success in birds introduced to New Zealand. *Oikos* 90: 599–605.

SOL D., SZEKELY T., LIKER A. & LEFEBVRE L. 2007. Big-brained birds survive better in nature. *Proceedings of the Royal Society (B)* 274: 763–769.

SOL D., TIMMERMANS S. & LEFEBVRE L. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour* 63: 495–502.

STEPHENS D.W. 1991. Change, regularity and value in the evolution of animal learning. *Behavioral Ecology* 2: 77–89.

STOWE M., BUGNYAR T., HEINRICH B. & KOTRSCHAL K. 2006a. Effects of group size on approach to novel objects in ravens (*Corvus corax*). *Ethology* 112: 1079–1088.

STOWE M., BUGNYAR T., LORETTO M.C., SCHLOEGL C., RANGE F. & KOTRSCHAL K. 2006b. Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behavioural Processes* 73: 68–75.

SUTTER M. & KAWECKI T.J. 2009. Influence of learning on range expansion and adaptation to novel habitats. *Journal of Evolutionary Biology* 22: 2201–2214.

TERKEL J. 1994. Social transmission of pine cone feeding behavior in the black rat, pp. 229–256. In: Galef B.G. Jr et al., Eds. Behavioral aspects of feeding. *Langhorne, PA: Harwood Academic Publishing*.

TERKEL J. 1995. Cultural transmission in the black rat: pine cone feeding. *Advances in the Study of Behavior* 24: 119–154.

TIMMERMANS S., LEFEBVRE L., BOIRE D. & BASU P. 2000. Relative size of the hyperstriatum ventrale in the best predictor of feeding innovation rate in birds. *Brain Behavior and Evolution* 56: 196–203.

VERBEEK M.E., DRENT P.J. & WIEPKE P.R. 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour* 48: 1113–1121.

WEST-EBERHARD M.J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* 58: 155–183.

WEST-EBERHARD M.J. 2003. Developmental plasticity and evolution. *New York: Oxford University Press*.

WILCOVE D.S., ROTHSTEIN D., DUBOW J., PHILLIPS A. & LOSOS E. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48: 607–615.