Animal Personality and Conservation Biology

The Importance of Behavioral Diversity

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Introduction

There is significant concern regarding the widespread loss of biodiversity and the destructive effects of human activity on the natural environment (Carson 1962; Wilson 2002). Over 500 extinctions of animal species have been recorded since 1600 (Frankham et al. 2002), with this rate significantly increasing over the past 150 years (Primack 1998). Furthermore, the International Union for Conservation of Nature (IUCN) has over 9,000 species of animals on their Red List of Threatened Species, representing 22% of the total species evaluated (IUCN 2010). This current extinction rate is 100–1,000 times greater than the estimated natural rate of extinction based on the fossil record (Primack 1998), indicating we are in the midst of the Earth's sixth massive extinction.

Conservation biology is a crisis-oriented discipline designed to minimize human impacts on and sustain biodiversity (Primack 1998). The goals of conservation biology include preserving genetic variability to maintain the evolutionary potential of populations (Moritz 2002), sustaining habitats and ecosystem processes, minimizing the effects of habitat disturbance on populations, and maintaining an adequate number of reproductive individuals (Gilpin and Soulé 1986; Hedrick and Kalinowski 2000).

The study and management of animal personalities can play a key role in conservation biology because the variability of personalities within a population may be related to the genetic diversity of that population. Fluctuating selection pressures maintain personality variation (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; chapters 7 and 9) and thus preserve higher levels of genetic diversity, which allows populations to adapt to changing environmental conditions and reduces their risk of extinction. Anthropogenic factors are now, however, altering the nature of selection (Stockwell et al. 2003; Carroll 2008; Fenberg and Roy 2008; Hendry et al. 2008), which

may lead to a reduction in behavioral variation and exacerbate the current conservation crisis.

In this chapter, we first discuss how personality and, in particular, behavioral diversity are important determinants of genetic diversity and the long-term persistence of populations. We then discuss the anthropogenic factors that can reduce behavioral diversity, both in the wild and in captivity, and follow with a discussion on the role of personality research in identifying potentially invasive species. We conclude with a list of recommendations to managers and evolutionary ecologists for understanding and maintaining behavioral diversity in the face of these novel evolutionary pressures.

Personality and genetic diversity

When natural selection acts on phenotypes, the underlying genotypes are where changes take place and genes are, therefore, considered the fundamental unit of biodiversity (Crozier 1997). Without adequate genetic variation, populations are limited in their ability to respond to environmental stochasticity, thereby increasing extinction risk (Frankham 1995; 1999). Maximizing genetic diversity by increasing heterozygosity and decreasing inbreeding (Frankham et al. 2002) is thus considered a top priority in conservation biology for populations or species to persist indefinitely (Frankel 1974; Allendorf and Leary 1986; Frankham 1999).

Maintaining a sufficient breeding population is an effective strategy to maintain high levels of genetic diversity, and population geneticists use the concept of effective population size (N_e) when calculating the probability of a population persisting and remaining genetically viable over time (Gilpin and Soulé 1986). N_e is the number of individuals breeding and contributing genes to succeeding generations in an idealized population (Frankham et al. 2002; Groom et al. 2006; King et al. 2006). An idealized population is one in which there is no selection and consists of a 1:1 sex ratio with random mating, non-overlapping generations, and roughly equal family size (Groom et al. 2006). Natural populations rarely, if ever, meet all of the assumptions of an idealized population, and N_e is usually an order of magnitude lower than actual census data (Frankham 1995; Frankham et al. 2002; Groom et al. 2006).

Behavioral diversity can impact genetic diversity by being directly linked to this underlying diversity, or by affecting demographic patterns that contribute to N_e (Anthony and Blumstein 2000). Variation in personality, which is defined as consistent differences in behavioral patterns between individuals of the same species or population (e.g., Wilson et al. 1994; Boissy

1995; Gosling 2001; Sih et al. 2004b; see introduction, this volume), can be maintained by fluctuating environmental pressures due to variable resource availability (Dingemanse et al. 2004; 2010; Boon et al. 2007; Wolf et al. 2007; Dingemanse and Wolf 2010; Wolf and Wessing 2010), predation levels (Réale and Festa-Bianchet 2003; Smith and Blumstein 2010), social conditions (Both et al. 2005; Bergmüller and Taborsky 2010; Cote et al. 2010), and micro-habitat niches (Buchholz and Clemmons 1997; Wilson 1998) that balance selection (Futuyma 1998) and maintain alternative phenotypes within and between populations. Changing selection pressures promote high levels of genetic diversity underlying phenotypic traits (Houle 1992; Wilson et al. 1994) and, indeed, low to moderate heritabilities have been found for various personality traits in several species (Benus et al. 1991; Réale et al. 2000; Dingemanse et al. 2002; Drent et al. 2003; Fairbanks et al. 2004b; Bell 2005; Sinn et al. 2006; chapters 6– 9). This suggests a significant amount of genetic variation underlying personality (Frankham et al. 2002; King et al. 2006). Thus, novel directional or stabilizing selection pressures (Futuyma 1998) acting counter to balancing or disruptive selection could lead to a reduction of both behavioral and corresponding genetic diversity.

Furthermore, direct links have been found between personality and fitness correlates in many species (for reviews see Dingemanse and Réale 2005; Smith and Blumstein 2008; chapters 6–9). Variation in behavioral types may be shaped by trade-offs between current and future fitness so that individuals that adopt more risk-taking behaviors may experience more reproductive and foraging opportunities in the short-term, but also suffer increased mortality, compared with risk-adverse individuals (Stamps 2007; Wolf et al. 2007; Smith and Blumstein 2008). In some cases, conditions favoring the development of an optimum strategy for a particular individual may depend on the proportion of individuals adopting alternative strategies, and stability in behavioral traits may therefore be maintained in a frequency-dependent manner (Wilson et al. 1994; Dall et al. 2004; Bergmüller and Taborsky 2010).

Thus, differential reproduction and mortality within populations appear to be based, at least in part, on interindividual differences in personality or behavioral types (e.g., more or less bold or aggressive—Sih et al. 2004b). Reproductive and survival skew can have significant effects on many aspects of ecology and evolution in animal populations, including decreasing N_e (Anthony and Blumstein 2000), and environmental changes that increase skew can result in increased inbreeding and hasten the loss of heterozygosity. In the following sections, we discuss the anthropogenic changes to the

environment that may alter selection pressures maintaining behavioral and genetic diversity and therefore further exacerbate the current biodiversity crisis.

Anthropogenic factors influencing behavioral diversity in the wild

Animal populations impacted by human activities often suffer from reduced genetic diversity (Gillespie and Guttman 1989; Caizergues et al. 2003; DiBattista 2008). Mechanisms cited for this phenomenon include reduced population sizes and isolated populations, which increase the effect of genetic drift (Frankham et al. 2002; DiBattista 2008). A reduction in behavioral diversity may also be a factor driving the decrease in genetic diversity. Although selection for and against particular behavioral types may vary in the short-term depending on ecological pressures such as predation (Réale and Festa-Bianchet 2003; Smith and Blumstein 2010), food availability (Dingemanse et al. 2004), and social conditions (Both et al. 2005; Bergmüller and Taborsky 2010), shifting environmental conditions may lead to balancing selection on varying life-history strategies and equalize fitness long-term (Dall et al. 2004; Stamps 2007; Wolf et al. 2007; chapter 9). Selective pressures acting for and against particular behavioral types, however, could be significantly altered by anthropogenic activities. In this section, we discuss how personality variation in populations may shape the level of threat caused by habitat fragmentation, pollution, overharvesting, and general human presence and activity in wilderness areas. Particular behavioral types may be more vulnerable to the effects of human activity, disproportionately reducing individual fitness within certain segments of populations and leading to an overall shift in behavioral patterns that reduces behavioral diversity.

HABITAT FRAGMENTATION

The top threat to biodiversity worldwide is habitat loss and degradation, which affects 88% of threatened amphibians and 86% of threatened birds and mammals (Baillie et al. 2004). The building of roads and the clearing of habitat isolate populations and create dispersal barriers limiting the ability of animals to migrate (Andrén 1994; St. Clair 2003; McDonald and St. Clair 2004). Population fragmentation leads to reduced gene flow and increased inbreeding and thus decreases genetic diversity (Wilcox and Murphy 1985; Caizergues et al. 2003; DiBattista 2008). However, negative fitness consequences due to habitat loss may not be generalized throughout a population but, instead, may be distributed on the basis of variability in behavioral responses to fragmentation, such as willingness to disperse to new habitats.

Dispersal strategies between individuals appears to be nonrandom with respect to phenotype (Bélisle and St. Clair 2001; Garant et al. 2005), and personality may be important in determining the effects of fragmentation on species and populations.

Generalist species, for example, do better than more specialized species in fragmented landscapes because of the ability to exploit disturbed areas (Andrén 1994). Generalists exhibit higher rates of dispersal across degraded habitats and anthropogenic barriers (McDonald and St. Clair 2004; Castellón and Sieving 2006), and studies of birds indicate that generalists are less neophobic and more exploratory than specialized species (Greenberg 1983; 1989; Webster and Lefebvre 2001). These behavioral traits may provide generalists with increased flexibility in adapting to novel environments (Greenberg and Mettke-Hofmann 2001; Sol et al. 2002), and skew selection pressures to favor generalist species in fragmented landscapes.

Variability in personality traits may, therefore, shape how individuals respond to and are affected by habitat fragmentation. For example, exploratory behavior in a novel environment or open field, which is a commonly used measure of animal personality (Réale et al. 2007), has been linked with dispersal patterns. Trinidad killifish (*Rivulus hartii*) that ranked higher in exploration of a test tank dispersed further when released back into streams than individuals ranked lower in exploration (Fraser et al. 2001). In great tits (*Parus major*), fast-exploring parents had offspring that dispersed the furthest, fast-exploring females moved farther in the initial stages of natal dispersal than slower ones, and immigrants into the population were faster explorers than locally born birds (Dingemanse et al. 2003). Exploration in great tits is heritable (Dingemanse et al. 2002; Drent et al. 2003) and correlates with other personality traits, including boldness toward a novel object (Verbeek et al. 1994) and aggression (Verbeek et al. 1996). Individuals with differing genotypes may thus differ in their dispersal strategies, leading to skewed mortality among behavioral types in fragmented habitats.

As global climate change shifts ecosystem boundaries, animals are expected to respond by attempting to migrate with these shifts (Walther et al. 2002). As habitats are fragmented, however, populations may be forced to reside in islands of habitat surrounded by disturbed areas (Andrén 1994). Areas around fragmented habitats often consist of unsuitable open habitat (Saunders et al. 1991), which may increase the risk of predation for individuals traveling through them. Furthermore, cleared areas between optimal habitats may consist of low-quality food patches, which could compromise condition, or may be filled with anthropogenic risks, such as power lines or automobiles, which can directly injure or kill individuals (Clevenger et al.

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2003). If bolder and more exploratory individuals are more likely to disperse out of fragmented habitats and into open areas between habitats, this could significantly reduce the fitness of those behavioral types and select for a population of shy and nonexploratory individuals. Alternatively, if dispersers are able to migrate into larger, higher-quality habitat than that found in fragmented islands where nondispersers remain, bolder individuals could be selected for over shyer ones. Either of these scenarios could hasten the loss of genetic diversity by biasing the population toward one behavioral type, and effective population size would be significantly reduced if reproductive success is strongly skewed toward either bold or shy individuals (Smith and Blumstein 2008). Other selective processes, however, such as negative frequency-dependent selection, could counteract this process of diversity reduction and contribute to the maintenance of personality variation (see chapters 7 and 9).

POLLUTION

Toxins and chemical pollutants from agricultural, industrial, and municipal activities have become ubiquitous in the environment as they are often carried by abiotic factors around the world far from emission sources (Simonich and Hites 1995; Wilkening et al. 2000; Ikonomou et al. 2002). Many of these compounds, including organochlorine pesticides, polychlorinated biphenyls (PCBs), and heavy metals (Colborn et al. 1993; Zala and Penn 2004), are lipid soluble and therefore accumulate in the tissues of wildlife and increase in concentration at higher trophic levels (Norstrom et al. 1998; Ross et al. 2000; Kannan et al. 2001a, b). Exposure to pollutants, particularly in the early stages of development (Bergeron et al. 1999), can interfere with normal endocrine functions by causing overproduction or underproduction of hormones and can lead to sexual abnormalities and reproductive impairment (Howell et al. 1980; Spearow et al. 1999; Baatrup and Junge 2001; Hayes et al. 2002), altered growth patterns (Relyea and Mills 2001; Bell 2004), decreased cognitive abilities (Schantz et al. 1995; Rice 2000; Schantz and Widholm 2001), and increased mortality (Relyea and Mills 2001).

Behavior is the end point of many developmental and physiological pathways and has, therefore, proved to be a useful indicator of the presence of chemical contaminants (for reviews see Clotfelter et al. 2004; Zala and Penn 2004). Assays that are now standardized for use in the study of animal personality (Réale et al. 2007), including behavioral responses to conspecific intruders (Palanza et al. 1999; Bell 2001), potential mates (Haegele and Hudson 1977; Bayley et al. 1999), potential predators (Bell 2004), novel ob-

jects (Erhard and Rhind 2004), and open fields (Palanza et al. 1999; Erhard and Rhind 2004), have all been used to document changes in aggression, courtship, risky behavior, and general activity levels following exposure to pollutants. These studies indicate that behavioral responses of individuals exposed to contaminants may increase or decrease in frequency and intensity depending on the species and contaminant in question (Clotfelter et al. 2004; Zala and Penn 2004), indicating changes in axes of behavioral variation associated with personality. As anthropogenic contaminants create novel selection pressures in environments, resulting shifts in personality traits not only may impact individual fitness by creating less than optimum phenotypes, but also may lead to demographic and social changes and affect population dynamics that maintain personality variation (Bergmüller and Taborsky 2010; Stamps and Groothuis 2010).

Furthermore, the effects of persistent organic and chemical pollutants are not distributed equally throughout a population, and overall phenotypic variation may decrease owing to novel selection pressures associated with environmental contaminants (Medina et al. 2007). In a wide range of organisms, differences have been found in susceptibility to the effects of pollutants in relation to genotypic differences between strains (Parmigiani et al. 1999; Spearow et al. 1999; 2001) and between individuals within single populations (Chagnon and Guttman 1989; Diamond et al. 1989; Schlueter et al. 1997; Kolok et al. 2004). Moreover, selection for more tolerant individuals has led to reduced genetic diversity in contaminated populations (Gillespie and Guttman 1989; Keklak et al. 1994; Schlueter et al. 1995; Matson et al. 2006). In addition to genetic differences in vulnerability or resistance to the effects of pollutants, nongenetic factors may be important as well (Kolok 2001). Bell (2004), for example, found that threespined stickleback (*Gasterosteus aculeatus*) females exposed to environmentally relevant levels of ethinyl estradiol (an active ingredient of birth control pills and postmenopausal hormone replacement therapy) exhibited increased growth and risky behavior, as well as higher mortality. Subjects originating from a population that evolved under high predation levels were particularly affected (Bell 2004). This result suggests that selection by predators favoring particular phenotypes (Magurran 1990) may have led to individuals that are highly sensitive to predator-induced stress and are therefore more susceptible to the detrimental effects of environmental contaminants (Relyea and Mills 2001).

Studies have shown that environmental stress (e.g., predator-induced stress) increases the negative impacts of pollutants (Relyea and Mills 2001).

It is possible that shyer and more reactive individuals are especially vulnerable to pollutants because they respond more strongly to stress than bolder individuals with increased activity in the hypothalamic-pituitary-adrenal (HPA) axis (Uhde et al. 1984; Kagen et al. 1988; Sapolsky 1990), leading to higher corticosteroid levels (Beuving et al. 1989; Koolhaas et al. 1999; Ruis et al. 2000; Cavigelli and McClintock 2003; Cavigelli 2005). The physiological response of sticklebacks to confinement stress varies depending on an individual's boldness and aggression level (Bell et al. 2010), suggesting that particular behavioral phenotypes may be more sensitive to environmental challenges. Behavioral diversity within populations may, therefore, be directly reduced by novel selection pressures associated with pollution acting against more sensitive phenotypes.

OVERHARVESTING

Throughout the world, humans use wildlife as a natural resource for consumption, sport, and profit (Festa-Bianchet 2003; Hutchings and Fraser 2008). Increasing global demand and improved harvesting techniques have led to the overexploitation of many of these resources, however, and overharvesting is now a major threat to a significant proportion of species threatened with extinction; including 55% of threatened fishes, 33% of threatened mammals, 30% of threatened birds, and 6% of threatened amphibians are threatened with extinction (Baillie et al. 2004). Furthermore, harvesting pressures are often not distributed randomly within populations but, instead, are skewed toward individuals possessing targeted phenotypes (Hutchings and Fraser 2008). Trophy hunting in mammals, for example, typically focuses on the largest individuals or those with the most elaborate ornaments (Milner et al. 2007). Fishing practices also bias catches through management regulations imposing minimum size limits (Conover and Munch 2002) and equipment that tends to selectively harvest larger fish (Bohnsack et al. 1989; Dahm 2000; Law 2000). Anthropogenic selection overriding natural selection on heritable phenotypic traits (Carlson et al. 2007; Edeline et al. 2007; Darimont et al. 2009) may, therefore, lead to the rapid removal of specific alleles or genotypes from a population, reducing variation, and hindering population recovery once harvesting pressures subside (Law 2000; Conover and Munch 2002; Allendorf and Hard 2009).

Studies of exploited species have documented several life-history and demographic changes within populations related to harvesting pressures (Law 2000; Festa-Bianchet 2003; Milner et al. 2007; Fenberg and Roy 2008; Darimont et al. 2009; Wolak et al. 2010). Trophy hunting in mammals has

been followed by decreases in body weight and ornament size over time (Jachmann et al. 1995; Coltman et al. 2003; Garel et al. 2007; Proaktor et al. 2007), while periods of intense fishing have been correlated with decreases in body size and age at maturity (Law 2000; Sinclair et al. 2002; Olsen et al. 2004; Hutchings 2005; Edeline et al. 2007). Laboratory experiments with a commercially exploited fish species (*Menidia menidia*) have also shown that selective harvesting for large individuals over as little as four generations leads to lower harvested biomass and mean body weight due to selection for slow-growing genotypes (Conover and Munch 2002). Size-selective harvesting has thus been hypothesized to indirectly select against fast growth because individuals possessing this trait attain harvestable size at a younger age and may have less of an opportunity to reproduce (Law 2000; Olsen et al. 2004; Proaktor et al. 2007).

An alternative explanation, however, is that growth rate may be reduced due to correlational selection of both personality and growth rate. Bolder and more active individuals forage and grow at higher rates (Mangel and Stamps 2001; Sih et al. 2003; Ward et al. 2004; Biro et al. 2006; Stamps 2007), but may also be more vulnerable to harvesting because they take more risks (Dugatkin 1992; Sih et al. 2003; Biro et al. 2004; Stamps 2007). In one of the best examples to date of anthropogenic selection acting directly on animal personality traits, Biro and Post (2008) simulated an intensive gillnet fishery of rainbow trout (*Oncorhynchus mykiss*) and found that fast-growing genotypes were harvested at three times the rate of slow-growing genotypes independent of body size. They attributed these results to fast-growing individuals increasing their encounter rate with fishing equipment by behaving more boldly and actively.

Additional studies are needed to determine whether this same pattern is found in other harvested species. If so, this may be an indication that overharvesting can unintentionally select for slower-growing and more neophobic populations, including practices that do not target specific sizes, such as fur trapping (Coltman 2008), waterfowl hunting (Fox and Madsen 1997), and predator control (Sacks et al. 1999; Mettler and Shivik 2007).

HUMAN PRESENCE AND ACTIVITY IN WILDERNESS AREAS

As human population expands, more areas formerly considered unoccupied wilderness are being developed and used for economic and recreational activities. Even national parks, which are considered prime habitat for wildlife, were visited by over 281 million people in 2010 in the United States alone. With such a significant human presence, even benign activi-

ties can have large impacts on animal populations. Evidence suggests that animals are altering their behavior in these anthropogenically affected environments, with some tolerating, and even taking advantage of, the presence of humans. Pregnant moose (*Alces alces*) within and surrounding Grand Teton National Park have redistributed birth sites closer to paved roads as brown bears (*Ursus arctos*), a potential predator of neonates, are becoming reestablished within the ecosystem (Berger 2007). Brown bears avoid paved roads, so birthing females are able to use roads as protection from potential predation. Personality may be playing a role in such behavioral shifts and conferring fitness advantages to individuals more tolerant of and habituating more rapidly to human activity. It has been shown that personality traits play a significant role in the behavioral and physiological responses of animals to stress (Uhde et al. 1984; Carere et al. 2001; Carere et al. 2003; Fairbanks et al. 2004a; chapter 12), with shy or more inhibited individuals responding more strongly to novel or stressful situations than bold or more proactive individuals (Koolhaas et al. 1999; Ruis et al. 2000; Cavigelli and McClintock 2003; chapter 12 and 15). Elevated stress levels over a prolonged time can compromise body condition and immune system functions and cause individuals to be more susceptible to disease and the negative effects of environmental fluctuation (Capitanio et al. 1998; Cavigelli and McClintock 2003; López et al. 2005; chapter 15). Such a scenario could give individuals with bolder and less inhibited personalities a fitness advantage and could alter selection pressures maintaining personality variation.

Studies are just now beginning to investigate the role of personality in shaping patterns of differential response and tolerance to human presence and activity. In Gault Nature Reserve in Québec, Canada, Martin and Réale (2008) found a higher frequency of explorative and docile eastern chipmunks (*Tamias striatus*) in areas with high human activity, while less explorative and docile individuals maintained home ranges in less frequented areas. The population thus distributed themselves in a nonrandom manner according to personality type and human presence. Such human effects of distribution could potentially lead to patchy, fragmented populations and reduce overall effective population sizes if interbreeding between subpopulations is reduced. To avoid stressful situations, individuals less tolerant and more wary of humans may also be forced into suboptimal areas with lower-quality food patches and a higher quantity of predators (Berger 2007) and suffer reduced fitness. Differential selection on personality types from human pressures may therefore lead to changes in the relative frequency of personality types within a population resulting in reduced behavioral diversity.

Behavioral diversity in captive environments

Two major issues concerning animal populations in captivity are loss of genetic diversity and adaptation to captive environments. Loss of genetic diversity reduces the capacity of populations to cope with environmental change, and adaptation to captivity may select for phenotypes maladaptive in the wild (Frankham 1999; Reed and Frankham 2003; Frankham 2008). Either of these factors can seriously compromise the ultimate goal of many captive-breeding programs, which is to release individuals back into their historic ranges and reestablish populations that have been extirpated or severely reduced (Griffith et al. 1989; Kleiman 1989; Frankham 1999; Seddon et al. 2007). In this section we discuss how selection in captivity for particular personality traits can lead to behavioral types ill-suited for survival in the wild. We also discuss how behavioral diversity can be affected by the reintroduction strategy employed.

SELECTING FOR TAMENESS

The success rate of reintroduction projects has historically been low (Beck et al. 1994; Wolf et al. 1996), and a review found that projects using wild-caught animals were twice as likely to succeed as those using captive-reared animals (Griffith et al. 1989). Research on animal domestication indicates that individuals differ in their ability to cope with and reproduce in captivity (Berry 1969; Price 1984), which can lead to selection of phenotypes more tolerant of humans. Changes in morphology, physiology, behavior, and genetics take place with the selective breeding of tame animals (Price 1970; Belyaev 1979; Belyaev et al. 1985; Marliave et al. 1993; Künzl et al. 2003) and can lead to populations ill-equipped to survive in the wild. Thus, unintentional selection for tame and more risk-taking behavioral types in captivity may be partially to blame for reintroduction failures.

Enclosure characteristics and husbandry procedures, for example, can increase stress levels and select for behavioral types that allow individuals to better cope with these conditions (McDougall et al. 2006; Clubb and Mason 2007; Peng et al. 2007). A study of black rhinoceros (*Diceros bicornis*) in zoos throughout the United States found that reproductive success and mortality correlated respectively with the size of the enclosure in which animals were housed and the amount of viewing area to which the public had access (Carlstead et al. 1999a). Keepers also rated subjects on several different behavioral attributes and found that enclosure design affected levels of dominance, fearfulness, and agitation (Carlstead et al. 1999a), all traits that have been shown to affect reproductive success in captive rhinoceros (Carlstead

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et al. 1999b). Cheetahs (*Acinonyx jubatus*) in North American breeding facilities also exhibit differential reproductive success depending on their assayed behavioral type, with nonbreeders rated as being more fearful than breeders independent of sex, age, and facility where individuals are housed (Wielebnowski 1999). Thus, selection pressures maintaining personality variation in the wild may be replaced in captivity by selection for more docile and tolerant individuals.

Studies do indicate that captive-bred animals are behaviorally distinct from their wild counterparts for several different personality traits. Individuals bred in captivity over several generations exhibit reduced levels of aggression (Mathews et al. 2005), increased boldness (Yoerg and Shier 1997; McPhee 2003b), and increased exploratory behavior (Price 1970; McPhee 2003a). Captive conditions may thus cause shyer and more neophobic individuals to experience prolonged elevated stress levels (Koolhaas et al. 1999; Carere et al. 2003; Cavigelli and McClintock 2003), which may reduce their fitness relative to bolder individuals. Not only might this lead to a captive population maladapted to fluctuating environmental conditions found in the wild, but also selecting for reduced behavioral variation in heritable traits will reduce genetic diversity.

PERSONALITY AND REINTRODUCTION

High levels of mortality are often seen in the initial stages of reintroduction projects (Seddon et al. 2007; Teixeira et al. 2007). Reintroductions can be costly and time-consuming, particularly those employing soft-release techniques (Kleiman 1989) in which released animals are provided with supplemental food or shelter, and each individual is a valuable commodity. Predation (Short et al. 1992; Miller et al. 1994; Banks et al. 2002) and possibly stress (Teixeira et al. 2007) are major causes of mortality for reintroduced animals, which can significantly delay the reestablishment of populations and remove potentially valuable alleles from the gene pool. Several studies have therefore tested the efficacy of predicting release success of individuals on the basis of pre-release behavioral screening (Van Heezik et al. 1999; Munkwitz et al. 2005) for the purpose of selective release: those behavioral types that respond most appropriately to potentially risky and stressful situations are more likely to survive following reintroduction (Mathews et al. 2005). Supporting this idea is a study with swift foxes (*Vulpes velox*), which found that those individuals that died following reintroduction into the wild were bolder toward novel objects in captivity than those that survived (Bremner-Harrison et al. 2004).

Bolder individuals have higher reproductive success, however, across a number of species (for a review see Smith and Blumstein 2008). Thus, releasing only shy individuals may increase survival in the short-term, but could have negative impacts on reproduction. Furthermore, selectively releasing particular behavioral types would reduce overall behavioral diversity, which may limit the variety of microhabitats available for reintroduced populations to exploit (Watters and Meehan 2007).

A reintroduction study of brown trout (*Salmo trutta*) found that individuals identified as dominant and more aggressive in captivity grew faster in the wild than subordinates, suggesting higher fitness levels (Höjesjö et al. 2002). Smaller fish were more mobile, however, when released back into the wild and exploited faster-flowing habitats closer to the shore than the larger fish. These findings indicate that individuals possessing behavioral types deemed "less suitable" for release by behavioral screening can be successful in heterogeneous natural habitats and allow for the establishment of populations over broader environmental gradients.

An alternative pre-release strategy is to train individuals in the appropriate skills and behavioral responses needed for survival (Biggins et al. 1999; Vargas and Anderson 1999; Griffin et al. 2000). Predator training, for example, involves enhancing antipredator behavior by pairing the sight of a predator with an aversive experience (Chivers and Smith 1994; McLean et al. 2000) or, as is often done with fish, pairing conspecific alarm cues with either predatory visual or chemical cues (Chivers and Smith 1994; Korpi and Wisenden 2001).

Research into the underlying mechanisms of behavioral syndromes suggest that personality traits including boldness and aggression (Huntingford 1976; Riechert and Hedrick 1993; Bell and Stamps 2004) and boldness and exploratory behavior (Van Oers et al. 2004) may be tightly linked owing to underlying physiological (Ketterson and Nolan 1999; chapter 12) or genetic mechanisms (Van Oers et al. 2004; Bell 2005; chapter 12). In populations possessing such rigid syndromes, behaviors may not be able to change independently of each other (Bell and Stamps 2004), and training individuals to be more fearful of predators could unintentionally lead to suboptimal behavior in other contexts (e.g., less aggression when competing with conspecifics for food or potential mates) (Sih et al. 2004a, b).

Tight correlations across population are not always found, however, and varying environmental pressures appear to select for the presence or absence of rigid syndromes (Bell 2005; Dingemanse et al. 2007). Without the necessary evolutionary pressures selecting for genetically linked behaviors

(Bell and Stamps 2004; Bell 2005), populations may evolve more plastic personalities and individuals may not exhibit multicontext behavioral changes following predator training.

Personality and invasion biology: identifying potential threats

Globalization of human activity has promoted both the intentional and accidental spread of species across natural dispersal barriers. Exotic and invasive species can disrupt ecological processes by causing the extinction of native species through competition, predation, and disease (for reviews see Mack et al. 2000; Pimentel et al. 2000). Among the most well-known and notorious examples of invasive animals are the cane toad (*Bufo marinus*) in Australia, the zebra mussel (*Dreissena polymorpha*) in North America, and the brown tree snake (*Boiga irregularis*) in Guam (Lowe et al. 2000). Introduced pests and predators have led to the collapse of agricultural, forestry, and fishery resources in some areas (Mack et al. 2000), and economic losses due to exotic species are in excess of $137 billion per year in the United States alone (Pimentel et al. 2000). A long-standing goal of ecologists has been to identify the biological characteristics that define successful colonists (Lodge 1993; Kolar and Lodge 2001), and personality research may be useful in this regard.

Behavioral attributes are increasingly recognized as useful predictors in identifying the proximate causes of invasion success (Holway and Suarez 1999). Dispersal tendency (Rehage and Sih 2004; Bubb et al. 2006), behavioral flexibility (Sol and Lefebvre 2000; Hughes and Cremer 2007), and competitive ability (Rehage et al. 2005; Duckworth and Badyaev 2007; Maestripieri 2007) have been identified as traits common to successful invaders. Variation in these traits has also been linked to animal personality. High dispersal rates are seen in more exploratory individuals (Fraser et al. 2001; Dingemanse et al. 2003), more aggressive individuals outcompete less aggressive ones (Riechert and Hedrick 1993; Civantos 2000), and increased plasticity has been associated with boldness (Greenberg 1983; 1989). Invasion success depends on the ability to colonize, establish, and spread (Holway and Suarez 1999) and may therefore favor species exhibiting syndromes for boldness, aggression, and exploration (Sih et al. 2004a; b; Maestripieri 2007). For example, populations of the signal crayfish (*Pacifastasus leniusculus*), which is a successful invader in many parts of the world, exhibit an aggression/activity/boldness syndrome that may contribute to their ability to outcompete native species (Pintor et al. 2008).

Therefore, to assess potential threats, natural and life-history traits that

are correlated with high levels of boldness, aggression, and exploratory behavior should be identified (Bell and Sih 2007; Johnson and Sih 2007; Polo-Cavia et al. 2008). Such an approach would then allow managers to prioritize control efforts for the multiple exotics often found in single ecosystems. Tame species, for example, may be bigger threats because animals that live in close association with humans are often successful invaders (Newsome and Noble 1986; Sol et al. 2002; Jeschke and Strayer 2006; Maestripieri 2007). Invasive species also tend to grow faster than outcompeted natives (Newsome and Noble 1986; Hill and Lodge 1999; Sakai et al. 2001), which may favor more bold or aggressive behavioral types in the invaders (Stamps 2007).

Within-species personality variation may also account for changes in behavior and demography in invasive populations that affect expansion rate and the probability of reestablishing natives. Once exotics colonize, it's expected that a subset of the bolder and more exploratory individuals within the population would lead the invasion. Selection pressures for more competitive and flexible individuals along the invasion front may lead to the evolution of bolder and more aggressive personality traits, relative to the initial colonizing population, and rapidly increase the rate of expansion (Phillips et al. 2006). Birds that have recently invaded are, indeed, bolder (Martin and Fitzgerald 2005) and more aggressive (Duckworth and Badyaev 2007) than more established populations of the same species. Once the invasion front moves through, however, selection pressures may change and traits adaptive on the invasion front may be selected against in stable environments (Brown et al. 2007). Western bluebirds (*Sialia mexicana*) in newly colonized areas are more aggressive, but overall aggression decreases in only a few generations because aggressive males provide little to no parental care (Duckworth and Badyaev 2007). The intensity of behavioral traits indicative of aggressive invaders may therefore be reduced in more established populations, and it may be more feasible to reestablish native animals in these areas than to slow the invasion front.

Recommendations for managing behavioral diversity

Additional research is needed to further elucidate the effects of human activity on shaping and changing personality traits, and periodic assays of personality will allow managers to monitor for effects in the wild and incorporate personality measurements into captive studbooks to track the breeding success rate of varying behavioral types. What further techniques should be employed, however, to maintain variation, and what else do we need to know to better understand the evolutionary ecology of personality?

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We have five recommendations to managers. First, to maintain behavioral diversity, environmental heterogeneity should be preserved when designing reserves (e.g., Smith et al. 1997; 2001). Selection acts in different directions in heterogeneous environments (Frankham et al. 2002), which is the basis for some hypotheses explaining personality variation (Réale and Festa-Bianchet 2003; Dall et al. 2004; Dingemanse et al. 2004; Both et al. 2005; Boon et al. 2007; Wolf et al. 2007; chapters 7 and 9). Thus, by conserving different habitat types and not just those most optimal for a particular species or population, the evolutionary processes shaping behavioral and genetic diversity will be maintained (Schneider et al. 1999; Moritz 2002; Watters et al. 2003; Rocha et al. 2005). Heterogeneous habitats with varying selection pressures may then allow recurrent selection to restore variation and phenotypes previously diminished (Moritz 1999; 2002; Bell and Sih 2007).

Second, for harvested populations, management strategies should be developed that preserve natural variation to maintain long-term sustainable yields (e.g., Conover and Munch 2002). Bolder and more active individuals may be more vulnerable to harvesting because they take more risks (Biro and Post 2008). Minimum-size limits for harvesting would therefore be ineffective in preventing population shifts toward slow-growing genotypes if selection on behavioral vulnerability is the evolutionary mechanism driving this response (Biro and Post 2008). Adaptive management strategies therefore need to be implemented that update patterns of harvesting as stocks evolve to maintain and rebuild behavioral and genetic diversity (Law 2000; Allendorf and Hard 2009). Establishing no-take zones and marine protected areas, for example, may act to maintain variation by allowing a portion of populations to express unconstrained ranges of sizes, growth rates, and behavioral types (Trexler and Travis 2000).

Third, for captive animals that may be later released into the wild, heterogeneous environments and enrichment techniques that facilitate the development and maintenance of behavioral diversity should be used (Watters and Meehan 2007). Although there is a limit in the ability to duplicate the heterogeneity of natural environments, maintaining populations under varying environmental (Korhonen and Niemelä 1996; Biggins et al. 1999; Meehan and Mench 2002; Kelley et al. 2005) and social (Goodey and Liley 1986; Chapman et al. 2008) conditions readily achieved in captivity facilitates variation in boldness and aggression.

Fourth, for reintroduction programs, individuals possessing behavioral types identified as most likely to survive following pre-release screening should be the first to be released. Increasing survivorship of the initial in-

dividuals released is key to maximizing the chances of reestablishing a self-sustaining population (Frankham et al. 2002). Shyer individuals may be more likely to evade predation (Dugatkin 1992) and less exploratory individuals are not likely to move far from the release site (Fraser et al. 2001; Dingemanse et al. 2003), which is important when soft-release techniques are being employed.

Fifth, if predator training is conducted before reintroduction, managers should assay multiple behavioral types before and after training to determine how traits across contexts are being shaped. Correlated behaviors across contexts should be able to change independently of each other if they are domain specific (Wilson 1998; Nelson et al. 2008; Sinn et al. 2010). Alternatively, correlated behaviors that are due to underlying physiological (Ketterson and Nolan 1999) or genetic (Van Oers et al. 2004; Bell 2005) mechanisms may be constrained to change together (Bell and Stamps 2004). Populations possessing such rigid behavioral syndromes may exhibit unintended behavioral changes in other ecological contexts following training, which may offset any fitness benefits.

For research biologists, we have two recommendations. First, a formal evolutionary ecology of personality should be developed (see Réale et al. 2010). Differences in behavioral types and behavioral syndromes between related taxa and populations can have major effects on ecology and evolution (Sih et al. 2004b; chapters 6–9), as well as on their susceptibility to anthropogenic threats, and their potential to become invasive species. Predation pressure, for example, is a likely explanation for the presence of a bold-aggression syndrome in some populations of sticklebacks and the lack of one in others (Bell and Stamps 2004; Bell 2005; Bell and Sih 2007; Dingemanse et al. 2007), and species-specific differences in wariness may be based on life history, natural history, and morphological differences (Stankowich and Blumstein 2005; Blumstein 2006). Additional selection pressures shaping personality should, therefore, be identified using techniques developed for measuring selection on quantitative traits and correlated characters (Lande and Arnold 1983; Arnold and Wade 1984a, b; Schluter 1988; Schluter and Nychka 1994). Such approaches may highlight whether particular populations are constrained in their behavioral flexibility. Furthermore, the role of selection for maintaining behavioral variability must be thoroughly studied to understand the potential threats caused by anthropogenic activities. Not only may novel selection pressures arising from such activities overwhelm those mechanisms responsible for shaping and maintaining personality variation, but also, because balancing selection as a mechanism becomes less effective in smaller populations (Wright 1931; Seddon and Baverstock 1999;

Miller and Lambert 2004), endangered species may be particularly at risk of losing behavioral diversity.

Second, a widespread understanding of the fitness consequences of personality is needed. Although few studies exist, evidence does suggest that personality and behavioral types account for differential survival and reproductive success (Smith and Blumstein 2008; 2010; Logue et al. 2009). The strength of these relationships may vary across species and populations, however, owing to potential differences in the mechanisms shaping personality variation (Smith and Blumstein 2008). The effect that personality has on effective population size and, in turn, genetic diversity may be less severe in populations exhibiting a weak link between behavioral type and fitness and more so in populations that show a stronger effect of personality on fitness. Thus, discerning the adaptive mechanisms maintaining personality variation would allow managers and behavioral biologists to identify those populations more at-risk from anthropogenic activities and associated novel selection pressures.

Conclusions

Numerous calls have been made for the incorporation of animal behavior into conservation biology (Clemmons and Buchholz 1997; Caro 1998; Shumway 1999; Gosling and Sutherland 2000), but this desired synthesis remains incomplete (Sutherland 1998; Candland 2005). Recognition that individuals, populations, and species behave in a consistent and variable manner may help bring these disciplines more closely together (e.g., McDougall et al. 2006; Watters and Meehan 2007). Personality is correlated with several life-history traits, and heritability estimates indicate a link to genetic diversity. Consideration of personality traits and of differences in personalities between species may also enhance reintroduction success and help identify potentially invasive species. Evolutionary pressures shaping such personality patterns may be altered, however, by novel anthropogenic pressures and lead to a reduction in behavioral and corresponding genetic diversity. Efficiently managing behavioral diversity should be enhanced by adaptive management (Blumstein 2007; Seddon et al. 2007) and the application of rigorous experimental designs.

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