Vanishing behaviors

Tim Caro[1] & Paul W. Sherman[2]

[1] Department of Wildlife, Fish and Conservation Biology and Center for Population Biology, University of California, Davis, CA 95616, USA
[2] Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

Abstract

Unique patterns of animal behavior and life histories are not regarded as serious targets in making conservation and management decisions. Here we highlight the conceptual and practical conservation value of preserving such variations, review recent declines in behavioral diversity in wild populations, and encourage conservation biologists, animal behaviorists, and wildlife managers to document and protect behavioral diversity in the wild.

Introduction

Preserving biodiversity is one of the principal goals of conservation. Informally, biodiversity often refers to species richness or species numbers but its formal definition also encompasses diversity of populations, communities, ecosystems and biomes (Groom *et al.* 2005; Hunter & Gibbs 2006). It is well accepted that genetically unique populations and subspecies of wild organisms, and even breeds of domestic animals, are worthy of conservation efforts (e.g., Soule *et al.* 1986; Lauvie *et al.* 2011). However, the outcomes of gene–environment interactions, namely morphological, physiological, and behavioral traits, have been relatively neglected. We believe these components of biological variation should be conservation targets too.

Here we focus on behavioral diversity, which we define as *the total number of species- or population-specific behavioral and life history variants in the wild*. Preserving behavioral diversity is a worthy conservation goal for several conceptual reasons (Ryan 2006; Caro & Sherman 2011). First, loss of behavioral diversity may prevent a popula-

tion from adapting to future environmental changes; and loss of behavioral flexibility within an individual may prevent it from adapting to sudden habitat alterations. For example, bird species with large brains and high propensities for behavioral innovation (flexibility) survive better in novel environments than less innovative, smaller brained species (Sol *et al.* 2005). Second, when behaviors disappear it may signal the loss of mechanisms (due to altered allelic frequencies, hormonal pathways, and so on) that predispose individuals to behave in a certain way; or absence of environmental conditions that allow a particular behavior to develop or to be manifested; or, in the case of population extinction, loss of all individuals that behave in a particular manner. For example, the spatial distribution of songbird dialects can be a marker for subpopulation structure (Laiolo 2008) and bird song diversity can predict the size and productivity of subpopulations, and thus their likelihood of persistence (Laiolo *et al.* 2008). Third, behavioral diversity provides a window on which social and ecological challenges were important enough in a population's evolutionary history to result in presently observable behavioral responses. For example,

antipredator behaviors of prey species are matched closely to particular predators (Seyfarth *et al.* 1980; Sherman 1985), and life history characteristics are matched to particular environments (Dobson 1992). Therefore, rather than being a nebulous, transient entity, unrelated to population or landscape-level concerns, behavioral diversity is likely to be instrumental in promoting population persistence in rapidly changing landscapes.

Several authors have called attention to the importance of preserving behavioral and cultural diversity of animal populations during the current period of rapid anthropogenic change (e.g., Clemmons & Buchholz 1997; Linklater 2004; Whitehead *et al.* 2004; Laiolo & Jovani 2007; Ryan 2006). However, for most species we know very little about whether behavioral diversity is declining, increasing or remaining stable. Neither natural historians of the past nor contemporary animal behaviorists have systematically documented behavioral disappearances among species or populations. Here we draw attention to the phenomenon of behavioral disappearance, suggest which behaviors are likely to vanish next, and encourage scientists and practitioners to become more proactive in retaining behavioral diversity in the wild.

Definition of behavioral disappearance

Behavior is a product of gene–environment interactions. Therefore, behavior provides a window for viewing the outcomes of selection pressures acting in particular ecological contexts. Behaviors that are selectively retained over time are those that enhanced individual fitness, and behaviors that are selectively lost are those which do not help their bearers to cope with environmental conditions (Schlaepfer *et al.* 2010). We define a behavioral disappearance as having occurred when *any population- or species-specific behavior has not been observed in the wild for more than 50 years.*

A few explanations will help justify this definition. First, although behavior patterns can be broadly similar across species, for instance territoriality or defense of offspring, detailed analyses of behaviors always reveal species-specificity. Behavior may also be population-specific, as, for example, in the cultural patterns of bighorn sheep (*Ovis canadensis*) (Berger 1979), chimpanzees (*Pan troglodytes*) (Whiten *et al.* 1999), orangutans (*Pongo pygmaeus*) (van Schaik *et al.* 2003), capuchin monkeys (*Cebus*) (Perry 2011), whales and dolphins (Whitehead *et al.* 2004), and humans (Nettle 2009). Second, we restrict our definition to the wild because unusual or aberrant behaviors can develop and spread in captive populations and domesticated species. Our definition can also be applied to human cultural

attributes if *wild* is broadly defined as preindustrial society (Sutherland 2003). Third, we chose 50 years to be in line with widely accepted definitions of species extinctions (see Brook *et al.* 2003).

Behaviors can disappear as a result of natural changes, for example, through losses of old individuals with specific behavioral attributes (dialects in birds or language in human populations), or with accumulated wisdom, such as migratory routes or locations of widely scattered food and water sources. But behavior can also disappear as a result of human-induced environmental changes, drift in dwindling populations, or because of population or species extinction. It is the anthropogenically mediated drivers of the latter phenomena that are of increasing concern.

Examples of behavioral disappearance

To illustrate the problem of behavioral disappearances, we have compiled a noncomprehensive list of examples (Table 1). These are drawn primarily from birds and mammals because these taxa have been studied most intensively.

Populations of animals endemic to islands often exhibit little fear of humans or introduced mammalian predators when they are first contacted, making it easy to eradicate them. Examples include Steller's sea cows (*Hydrodamalis gigas*) on the Aleutian Islands and perhaps moas on New Zealand being exterminated by humans, and naïve island endemics being killed off by introduced domestic cats (*Felis domesticus*) and rats (*Rattus*) (Donlan & Wilcox 2008). Strong selection for avoiding unusual, predatory heterospecifics results in rapid loss of behavioral naiveté. Since nearly all islands have been visited and exploited by humans or their commensals, only a few contemporary populations remain behaviorally naive (e.g., those in remote or strictly protected areas such as the Galapagos Islands: Nelson 1968).

Conversely, loss of top predators from ecosystems (Estes *et al.* 2011) results in disappearances of antipredator behaviors. For example, Berger *et al.* (2001) used playbacks and olfactory stimuli to demonstrate that moose (*Alces alces*) lose their ability to distinguish predators where important carnivores such as wolves (*Canis lupus*) have been eliminated. Following reintroduction of wolves and loss of moose calves to these predators, mothers redeveloped hypersensitivity to wolf howls. In long-lived species in which old individuals have superior knowledge of predation threats, selective hunting of larger, older animals by humans can result in losses of social knowledge (e.g., in elephants *Loxodonta africana*, Mc-Comb *et al.* 2011).

Despite decimation of migratory bird (Terborgh 1989) and butterfly populations (Brower & Malcolm 1991) due

Table 1 Aspects of behavior that are known to have disappeared as a result of human causes

Type of disappearance	Causes	Documentation[a]	Reference
Loss of behavioral naiveté			
African ungulates	Hunting by people	Good	Caro (2005)
Loss of predator recognition			
Moose	Extirpation of wolves	Good	Berger et al. (2001)
Loss of migratory routes			
Elephants	Agriculture, hunting, dams, roads	Poor	Pamo & Tchamba (2001)
Bison	Conversion of prairie to crops and fencing	Poor	Seton (1909)
Springbok	Fences, livestock farming, shooting	Fair	Roche (2008)
Malayan sun bears and bearded pigs	Forest fragmentation caused by logging	Poor	Wong et al. (2005)
Loss of song dialects			
White-crowned sparrows	Urban noise	Good	Luther & Baptista (2010)
Interacting in very large groups			
Green turtles	Hunting	Poor	Jackson et al. 2001

[a]Good refers to quantitative documentation; fair to written historical accounts; poor to anecdote or supposition.

to habitat alteration, hunting and pollution, populations continue to migrate. Migrations by nonflying mammals, by contrast, can be curtailed by land conversion and urbanization (reviewed by Bolger et al. 2008; Harris et al. 2009). For example, during the 1700s and 1800s huge herds of springbok (*Antidorcas marsupialis*) irregularly moved across parts of South Africa. Today these movements have been blocked by large-scale fencing and competition with livestock, as well as hunting and drought (Roche 2008). Other examples of thwarted migratory behavior of African mammals include gazelles being prevented from traveling north and south through the Sahel because of human settlement and livestock grazing (Sinclair & Fryxell 1985), restriction of many large mammals to increasingly isolated national parks due to agriculture and fencing outside (e.g., Williamson et al. 1988), and anthropogenic blocks to migratory routes of elephants on many parts of the continent (Loarie et al. 2009). If migrations are thwarted long enough, knowledge of migratory routes to seasonally separated resources will be lost as old individuals die off; eventually, migratory behavior itself may disappear.

In the 1800s in North America, millions of American bison (*Bison bison*) emigrated from woodlands to grasslands in the early Spring, and herds would continue to wander throughout the Spring and Summer months in search of forage (Seton 1909). Some western populations of bison migrated north into Canada in summer and then back to the Great Plains in the USA in winter. Today, the ~20,000 extant bison are restricted to large fenced ranches or to unfenced national parks where annual movements are severely limited by adjacent human activities. Fences and roads associated with oil and gas exploration may likewise sever the last remaining

pronghorn antelope (*Antilocapra americana*) migration on the continent (Berger 2004).

Vocal dialects change over time in birds (e.g., Catchpole & Slater 1995) and mammals (e.g., Rendell & Whitehead 2003) and in some species dialect extinction has occurred. In a 30-year study of white crowned sparrows (*Zonotrichia leucophrys*) in urban San Francisco, USA, Luther and Baptista (2010) showed considerable dialect turnover, with one dialect declining from 64% to 0% between 1969/1970 and 1998, and another declining from 93% to 32%. These changes were attributed to low frequency ambient noise pollution, with dialects being replaced by songs with higher minimum frequencies. In a natural example, male field crickets (*Teleogryllus oceanicus*) on Kauai Island of Hawaii have stopping singing altogether in response to parasitism by flies (*Ormia ochracea*) that are attracted to calling males (Zuk et al. 2006).

Many species consumed by humans once attained far greater population sizes than occur today. Examples from the marine environment include abalone, shrimp, crabs, lobsters, tuna, anchovies, salmon, great whales, and sea turtles (Jackson et al. 2001), and from terrestrial habitats include ungulates such as the Saiga antelope (*Saiga tatarica*) (Singh & Milner-Gulland 2011) and American bison (Insenberg 2000). Individuals that collected in foraging areas or moved together in large schools, herds or flocks required a suite of social skills to maintain contact with conspecifics, and cope with challenges over food, shelter, or mates. However, we know little about the social interactions within such groups, because populations living under native conditions are becoming increasingly rare. Unfortunately, these behaviors will gradually disappear as populations dwindle and interindividual contact is reduced.

The foregoing examples illustrate that not all behavioral disappearances adversely affect populations or species. Indeed, behavioral disappearances can result in both positive and negative consequences. On the one hand, failure to express a behavior may be adaptive, resulting in greater survival and reproductive success. Thus, loss of naiveté toward humans and their commensals and failure of Kauai field crickets to sing increase fitness because they result in avoidance of predators and parasites, respectively. On the other hand, failure to express a behavior may have negative fitness consequences. For example, loss of migratory behavior or knowledge of traditional migratory routes may prevent populations from making latitudinal shifts in response to local resource depletion or rapid climatic changes.

Losses of adaptive components of behavioral diversity resulting from anthropogenic habitat alterations are of greatest concern from the conservation perspective. Losses of nonadaptive behaviors are lower priority for two reasons. First, nonadaptive behaviors are expected to disappear naturally over time due to selection, whereas losses of adaptive behaviors should occur infrequently unless the habitat changes suddenly. Far more adaptive behaviors than nonadaptive behaviors are being lost as the climate changes, native habitats are destroyed, and invasive species are introduced. Second, adaptive behaviors represent long histories of selection for matches between organisms and their environments and are therefore worthy of conservation; nonadaptive behaviors are not finely tuned in this way. Of course, which behaviors are adaptive will change in changing landscapes, but evolutionarily such changes occur gradually, and one adaptive behavior will be substituted for another.

Behavioral change over time

Novel behaviors can arise in undisturbed animal populations in several ways including vocal imitation of other groups (Janik & Slater 1997), incorrect copying (Lemon 1975), cultural drift (Mundinger 1980), and a variety of social learning mechanisms (Whiten 2011), as well as through selection arising from living in different habitats (Seddon 2005). However, new behaviors often attract more immediate attention when free-living populations begin to interact with people and their artefacts. Japanese macaques (*Macaca fuscata*) washing potatoes before consumption is a famous example (Itani 1965). Similarly, certain behavior patterns may become more prevalent following disturbance, such as fear of humans in exploited ungulates (Caro 2005), or birds singing at a lower frequencies in urban contexts (Slabbekoorn & Peet 2003). Although comparative rates of behavioral appearances and disappearances in natural and disturbed
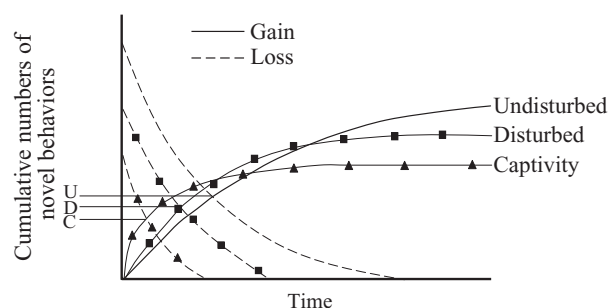

Figure 1 Schematic graph showing the expected cumulative number of behaviors gained or lost over time in a single species in three different environments: captivity (C), disturbed habitats (D), and undisturbed habitats (U). Points of intersection between acquisition and loss curves extrapolate to the equilibrium number of behaviors on the *y*-axis. At equilibrium, we expect numbers of different behaviors to decrease in the order U > D > C.

habitats are known in only a few cases (e.g., Nishida *et al.* 2009), we can nonetheless prognosticate about the balance between appearances and disappearances of behaviors in natural undisturbed environments, in anthropogenically perturbed environments, and in captivity (Figure 1).

We hypothesize that when free-living individuals are brought into captivity they will acquire a small number of new behavior patterns rapidly as they settle into the narrow confines of their radically altered enclosures. Free-living populations in newly disturbed wild settings may also acquire new behaviors but more slowly due to less severe habitat modification. Eventually they will acquire more behaviors than in captivity due to the greater complexity of even disturbed natural habitats. We expect populations in undisturbed highly complex habitats will acquire a greater number of behaviors in total but far more slowly. Figure 1 also illustrates that captive populations may quickly lose many of their natural behaviors due to habitat simplification and small population sizes. Populations living in disturbed habitats also should lose behaviors because anthropogenic disturbance often results in habitat simplification and loss of heterospecific pressures. Undisturbed populations, the "null model" in Figure 1, will lose behaviors at the slowest rate due to selective maintenance of adaptive responses and occasional losses due to gradually changing selection pressures.

Our hypothetical curves bear on the issue of how to maintain populations during the demographic bottleneck that is envisioned by conservation biologists to occur in the next ~100 years. Figure 1 illustrates that the number of behaviors in populations living in captivity is likely to be lower than in free-living populations; and that behavioral diversity is likely to be more depauperate in disturbed than in undisturbed habitats. Assuming these

curves are roughly correct, in situ conservation in un-altered habitats is preferable to ex situ conservation if our goal is to preserve evolved behavior and life history patterns; preventing behavioral extinctions is yet another reason for preserving native habitats.

Where might we see the next wave of behavioral disappearances? Some attempts have been made to predict future species extinctions based on life history characteristics and behaviors of related threatened species. For example, large-brained, behaviorally innovative species, which tend to be habitat generalists (Overington *et al.* 2011) and live socially (Schultz & Dunbar 2006), survive better than small-brained species in novel environments (Sol *et al.* 2005); carnivores with large home ranges are particularly prone to population extirpation due to hunting outside protected areas (Woodroffe & Ginsberg 1998); and primates that exhibit low reproductive rates are prone to extinction due to anthropogenic causes (Purvis *et al.* 2000). This suggests that other vertebrates which are solitary, habitat specialists, and have extensive ranging behavior or low reproductive rates are at risk too. In a similar fashion, we may be able to foretell future behavioral disappearances by examining regions of the behavioral landscape where behavior is vanishing. As illustrations, we predict disappearances of antipredator behaviors in larger herbivorous mammals due to loss of apex carnivores (Berger *et al.* 2001); continued loss of migratory routes and perhaps migratory behaviors among terrestrial mammals due to habitat fragmentation (Berger 2004); reduction in escalated fighting in species where males are shot for their weaponry (Jachmann *et al.* 1995; Coltman *et al.* 2003); and a parallel lowering of criteria acceptable to females when choosing mates due to reduced variance in male ornamentation (Anthony & Blumstein 2000); breakdown in territoriality in rodents when individuals are crowded into urban and fragmented populations (Berdoy & Drickamer 2007); increased behavioral Allee effects where behavior cannot be manifested in overly small group or population sizes (Courchamp *et al.* 1999); and even reduced cultural diversity in human populations due to globalization and the internet (Maffi 2001).

Proactive attempts to save behavior

From a practical standpoint, why should we be concerned if behaviors disappear? There are at least five reasons:

(1) Behavioral variation gives populations the opportunity to escape from environmental stressors now and in the future.

(2) Preservation of behavioral diversity allows us to seed wild populations with behaviors that may prevent

Table 2 Examples of human interventions to restore animal behavior in the wild

Training captive marsupials to recognize nonnative predators prior to their release	Griffin *et al.* (2000)
Teaching whooping cranes (*Grus canadensis*) to undergo annual migrations following an ultra-light plane	Langenberg *et al.* (2002)
Removing of dams to allow salmon to migrate upstream	Stanley & Doyle (2003)
Taking down fences that prevent large mammal movements	Bartlam-Brooks *et al.* (2011)
Feeding California condor chicks (*Gymnogyps californianus*) destined for release using puppets	Utt *et al.* (2008)
Teaching black-footed ferrets (*Nustela nigripes*) to hunt their prey	Tresz (2007)

their extermination by invasive species ("behavioral rescue:" Schlaepfer *et al.* 2005).

(3) A wide suite of behaviors can provide us with a toolkit for tutoring captive born individuals for reintroduction into the wild giving them the survival tools necessary to live in a novel environment (Moore *et al.* 2008).

(4) Variations in behavior can unlock evolutionary puzzles and teach us about the power of natural selection to mold adaptation. Studies of behavioral variants are essential to testing many central hypotheses in behavioral ecology (Caro & Sherman 2011).

(5) Animal behavior and population-specific variations in behavior are important conservation tools for raising public awareness as witnessed, for example, in the popular David Attenborough and Steve Irwin TV series.

In regard to points 2 and 3, Table 2 outlines some well-known examples of behavioral rehabilitation. All were expensive, and they were conducted with the intent of bolstering animal populations in the wild; however, they additionally serve to maintain species- and population-specific behaviors. Some of these efforts would have been facilitated if behaviors could have been copied from other individuals (Lefebvre 1995). Many species of free-living and captive mammals quickly learn to imitate behaviors of conspecifics that result in rewards of food or avoidance of predators (Galef 2007). Use of these novel conservation approaches depends on the existence of behavioral variants that can serve as tutors for the population that is being reinforced (Schlaepfer *et al.* 2005).

In essence, however, these (see Table 2) and other conservation management techniques, informed by studies of animal behavior (Blumstein & Fernandez-Juricic

2010), are last ditch attempts to reinstigate behavior in discrete populations. Instead, we suggest a more proactive conservation strategy: that field behaviorists document and share information necessary to compare behaviors among study populations and identify where consistent similarities and differences in behavior are found. A beautiful example comes from comparison of seven chimpanzee populations where only seven out of 65 behavior patterns were common to all sites (Whiten *et al.* 1999). Perry (2011) and van Schaik *et al.* (2003) provided similar data on cultural uniqueness among free-living populations of capuchins and orangutans, respectively. As a start, we suggest that zoologists identify aspects of behavioral and life history variation in the population(s) on which they work, focusing first on behaviors that affect Ne, the effective population size (e.g., reproductive suppression, dispersal, mating systems: Anthony & Blumstein 2000), as well as traditional themes such as territoriality, hunting, and foraging behavior, and social systems, and then collaborate to assess whether any are unique (i.e., occur only in that population) and hence merit special consideration for preservation. Such collaboration would be facilitated by developing a web-based data depository with uniform reporting formats. Next, we encourage conservation and management agencies to use behavioral uniqueness as a criterion for deciding which populations of a species deserve special protection. Whereas there are many criteria currently employed in targeting conservation efforts including identifying areas of species richness (e.g., Conroy & Noon 1996), endemic species (e.g., Loyola *et al.* 2007), and evolutionary uniqueness (e.g., Crozier 1992), to our knowledge none has used unique behaviors or life history characteristics of species or populations as a conservation goal despite their being an organism's best solution to ecological pressures and hence an important product of natural selection (i.e., another type of evolutionary uniqueness). Of course population-specific behaviors—just like population-specific genetic characteristics—can change naturally or even disappear over time. Since we cannot predict the course of such changes, however, the prudent approach is to document and protect all forms of population uniqueness, including in the behavioral realm.

We hope to elevate the status of behavior as a criterion for protection of a species or population. To help achieve this end, granting agencies should encourage well-planned comparative studies of populations of the same species in habitats that differ in ways predicted to affect behavioral traits of interest, rather than discouraging such studies just because one or a few studies of that species already have been done. We also urge conservation decision-makers to adopt policies to protect uniquely behaving populations when they are discovered.

References

Anthony, L.L., Blumstein, D.T. (2000) Integrating behaviour into wildlife conservation: the multiple ways that behaviour can reduce N_e. *Biol Conserv* **95,** 303–315.

Bartlam-Brooks, H.L.A., Bonyongo, M.C., Harris, S. (2011) Will reconnecting ecosystems allow long-distance mammal migrations to resume? A case study of zebra *Equus burchelli* migration in Botswana. *Oryx* **45,** 210–216.

Berdoy, M., Drickamer, L.C. (2007) Comparative social organization and life history of *Rattus* and *Mus*. Pages 380–392 in Wolff, J.O., Sherman, P.W., editors. *Rodent Societies*. University of Chicago Press, Chicago.

Berger, J. (1979) Social ontogeny and behavioral diversity: consequences for bighorn sheep *Ovis canadensis* inhabiting desert and mountain environments. *J Zool Lond* **188,** 251–266.

Berger, J. (2004) The last mile: how to sustain long-distance migration in mammals. *Conserv Biol* **18,** 320–331.

Berger, J., Swenson, J.E., Persson, I.-L. (2001) Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* **291,** 1036–1039.

Blumstein, D.T., Fernandez-Juricic, E. (2010) *A primer of conservation behavior*. Sunderland, Mass, Sinaeur.

Bolger, D.T., Newmark, W.D., Morrison, T.A., Doak, D.F. (2008) The need for integrative approaches to understand and conserve migratory ungulates. *Ecol Lett* **11,** 63–77.

Brook, N.W., Sodhi, N.S., Ng, P.K.L. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature* **424,** 420–423.

Brower, L.P., Malcolm, S.B. (1991). Animal migrations: endangered phenomena. *Am Zool* **31,** 265–276.

Catchpole, C.K., Slater, P.J.B. (1995) *Bird song: biological themes and variations*. Cambridge University Press, Cambridge.

Caro, T.M. (2005) Behavioural indicators of exploitation. *Ethol Ecol Evol* **17,** 189–194.

Caro, T., Sherman, P.W. (2011) Endangered species and a threatened discipline: behavioural ecology. *Trends Ecol Evol* **26,** 111–118.

Clemmons, J.R., Buchholz, R. (1997) Linking conservation and behavior. Pages 3–22 in Clemmons, J.R., Buccholz, R., editors. *Behavioral approaches to conservation in the wild*. Cambridge University Press, Cambridge.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C., Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature* **426,** 655–658.

Conroy, M.J., Noon, B.R. (1996) Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. *Ecol Appl* **6,** 763–773.

Courchamp, F., Clutton-Brock, T.H., Grenfell, B. (1999) Inverse density dependence and the Allee effect. *Trends Ecol Evol* **14,** 405–410.

Crozier, R.H. (1992) Genetic diversity and the agony of choice. *Biol Conserv* **61,** 11–15.

Dobson, F.S. (1992) Body mass, structural size, and life history patterns of the Columbian ground squirrel. *Am Nat* **140,** 109–125.

Donlan, C.J., Wilcox, C. (2008) Diversity, invasive species and extinctions in insular ecosystems. *J Appl Ecol* **45,** 1114–1123.

Estes, J.A., Terborgh, J., Brashares, J.S. *et al.* (2011) Trophic downgrading of planet earth. *Science* **333,** 301–306.

Galef, B.G. Jr. (2007) Social learning by rodents. Pages 207–215 in Wolff, J.O., Sherman, P.W., editors. *Rodent Societies.* University of Chicago Press, Chicago.

Griffin, A.S., Blumstein, D.T., Evans, C.S. (2000) Training capitive-bred or translocated animals to avoid predators. *Conserv Biol* **14,** 1317–1326.

Groom, M.J., Meffe, G.K., Carroll, R.C. (2005) *Principles of conservation biology,* 3rd edition. Sinaeur, Sunderland, MA.

Harris, G., Thirgood, S., Hopcraft, J.G.C., Cromisigt, J.P.G.M., Berger, J. (2009) Global decline in aggregated migrations of large terrestrial mammals. *Endang Species Res* **7,** 55–76.

Hunter, M.L., Gibbs, J.P. (2006) *Fundamentals of conservation biology,* 3rd edition. Blackwell. Malden, MA.

Insenberg, A.C. (2000) *The Destruction of the Bison, an environmental history, 1750–1920.* Cambridge University Press, Cambridge.

Itani, J. (1965) On the acquisition and propagation of a new food habit in the troop of Japanese monkeys at Takasakiyama. Pages 52–65 in Imanishi, K., Altmann, S.A., editors. *Japanese monkeys: a collection of translations.* University of Alberta Press, Edmonton, Canada.

Jachmann, H., Berry, P.S.M., Imae, H. (1995) Tusklessness in African elephants: a future trend. *Afr J Ecol* **33,** 230–235.

Jackson, J.B.C., Kirby, M.X., Berger, W.H. *et al.* (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293,** 629–638.

Janik, V.M., Slater, P.J.B. (1997) Vocal learning in mammals. *Adv Study Behav* **26,** 59–99.

Laiolo, P. (2008) Characterizing the spatial structure of songbird cultures. *Ecol Appl.* **18,** 1774–1780.

Laiolo, P., Jovani, R. (2007) The emergence of animal culture conservation. *Trends Ecol Evol* **22,** 5.

Laiolo, P., Vogeli, M., Serrano, D., Tella, J.L. (2008) Song diversity predicts the viability of fragmented bird populations. *PLoS ONE* **3,** e1822

Langenberg, J., Hartup, B., Olson, G., Spalding, M., Miller, K. (2002) Health management for the reintroduction of whooping cranes (*Grus americana*) using ultra-light guided migration. 2002 *Proc Am Ass Zoo Vet* 246–248.

Lauvie, A., Audiot, A., Couix, N., Casabianca, F., Brives, H., Verrier, E. (2011) Diversity of rare breed management programs: between conservation and development. *Livestock Sci* **140,** 161–170.

Lefebvre, L. (1995) Culturally-transmitted feeding behaviour in primates: evidence for accelerating learning rates. *Primates* **36,** 227–239.

Lemon, R.E. (1975) How birds develop song dialects. *Condor* **77,** 385–406.

Linklater, W.L. (2004) Wanted for conservation research: behavioral ecologists with a broader perspective. *BioScience* **54,** 352–360.

Loarie, S.R., Van Aarde, R.J., Pimm, S.L. (2009) Fences and artificial water affect African savannah elephant movement patterns. *Biol Conserv* **142,** 3086–3098.

Loyola, R.D., Kubota, U., Lewinsohn, T.M. (2007) Endemic vertebrates are the most effective surrogates for identifying conservation priorities among Brazilian ecoregions. *Divers Distrib* **13,** 389–396.

Luther, D., Baptista, L. (2010) Urban noise and the cultural evolution of bird songs. *Proc Roy Soc Lond B* **277,** 469–473.

Maffi, L., editor. (2001) *On biocultural diversity: linking language, knowledge, and the environment.* Smithsonian Institution Press, Washington, DC.

McComb, K., Shannon, G., Durant, S.M. *et al.* (2011) Leadership in elephants: the adaptive value of age. *Proc Roy Soc Lond B* **278,** 3270–3276.

Moore, J.A., Bell, B.D., Linklater, W.L. (2008) The debate on behavior in conservation: New Zealand integrates theory with practice. *BioScience* **58,** 454–459.

Mundinger, P.C. (1980) Animal cultures and a general theory of cultural evolution. *Ethol Sociobiol* **1,** 183–223.

Nelson, B. (1968) *Galapagos: islands of birds.* Willam Morrow and Company, New York.

Nettle, D. (2009) Ecological influences on human behavioural diversity: a review of recent findings. *Trends Ecol Evol* **24,** 618–624.

Nishida, T., Matsusaka, T., McGrew, W.C. (2009) Emergence, propagation or disappearance of novel behavioral patterns in the habituated chimpanzees of Mahale: a review. *Primates* **50,** 23–36.

Overington, S.E., Griffin, A.S., Sol, D., Lefebvre, L. 2011. Are innovative species ecological generalists? A test in North American birds. *Behav Ecol* **22,** 1286–1293.

Pamo, E.T., Tchamba, M.N. (2001) Elephants and vegetation change in the Sahelo-Soudanian region of Cameroon. *J Arid Environ* **48,** 243–253.

Perry, S. (2011) Social traditions and social learning in capuchin monkeys (*Cebus*). *Phil Trans Roy Soc B* **366,** 988–996.

Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M. (2000) Predicting extinction risk in declining populations. *Proc Roy Soc Lond B* **267,** 1947–1952.

Rendell, L.E., Whitehead, H. (2003) Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc Roy Soc Lond B* **270,** 225–231.

Roche, C. (2008) 'The fertile brain and inventive power of man': anthropogenic factors in the cessation of springbok treks and the disruption of the Karoo ecosystem, 1865–1908. *Africa* **78,** 157–188.

Ryan, S.J. (2006) The role of culture in conservation planning for small or endangered populations. *Conserv Biol* **20,** 1321–1324.

Schlaepfer, M.A., Sherman, P.W., Blossey, B., Runge, M.C. (2005) Introduced species as evolutionary traps. *Ecol Lett* **8,** 241–246.

Schlaepfer, M.A., Sherman, P.W., Runge, M.C. (2010) Decision making, environmental change, and population persistence. Pages 506–515 in Westneat, D.F., Fox, C.W., editors. *Evolutionary behavioral ecology*. Oxford University Press, Oxford.

Seddon, N. (2005) Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* **59,** 200–215.

Seton, E.T. (1909) *Life-histories of northern animals: an account of the mammals of Manitoba. Vol 1, Grass eaters*. Charles Scribner's Sons, New York.

Seyfarth, R.M., Cheney, D.L., Marler, P. (1980) Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* **210,** 801–803.

Sherman, P.W. (1985) Alarm calls of Belding's ground squirrels to aerial predators—nepotism or self-preservation? *Behav Ecol Sociobiol* **17,** 313–323.

Shultz, S., Dunbar, R.I.M. (2006) Both social and ecological factors predict ungulate brain size. *Proc Roy Soc Lond B* **273,** 207–215.

Sinclair, A.R.E., Fryxell, J.M. (1985) The Sahel of Africa: ecology of a disaster. *Can J Zool* **63,** 987–994.

Singh, N.J., Milner-Gulland, E.J. (2011) Conserving a moving target: planning protection for a migratory species as its distribution changes. *J Appl Ecol* **48,** 35–46.

Slabbekoorn, H., Peet, M. (2003) Birds sing at a higher pitch in urban noise. *Nature* **424,** 267.

Sol, D., Duncan, R.P., Blackburn, T.M., Cassey, P., Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proc Natl Acad Sci USA* **102,** 5460–5465.

Soule, M.E., Gilpin, M., Conway, W.G., Foose, T.J. (1986) The millennium ark: how long a voyage, how many staterooms, how many passengers? *Zoo Biology* **5,** 101–113.

Stanley, E.H., Doyle, M.W. (2003) Trading off: the ecological effects of dam removal. *Front Ecol Environ* **1,** 15–22.

Sutherland, W.J. (2003) Parallel extinction risk and global distribution of languages and species. *Nature* **423,** 276–279.

Terborgh, J. (1989) *Where have all the birds gone? Essays on the biology and conservation of birds that migrate to the American tropics*. Princeton University Press, Princeton, NJ.

Tresz, H. (2007) Providing enrichment in highly controlled environments: black-footed ferret (*Mustela nigripes*) enrichment program at the Phoenix zoo. *Int Zoo News* **54**(6), 324–331.

Utt, A.C., Harvey, N.C., Hayes, W.K., Carter, R.L. (2008) The effects of rearing method on social behaviors of mentored, captive-reared juvenile California condors. *Zoo Biol* **27,** 1–18.

Van Schaik, C.P, Ancrenaz, M., Borgen, G. *et al.* (2003) Orangutan cultures and the evolution of material culture. *Science* **299,** 102–105.

Whitehead, H., Rendell L., Osborne, R.W. Wursig, B. (2004) Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol Conserv* **120,** 427–437

Whiten, A. (2011) The scope of culture in chimpanzees, humans and ancestral apes. *Phil Trans Roy Soc B* **366,** 997–1007.

Whiten, A., Goodall, J., McGrew, W.C. *et al.* (1999) Cultures in chimpanzees. *Nature* **399,** 682–683.

Williamson, D., Williamson, J., Ngwamotsoko, K.T. (1988) Wildebeest migration in the Kalahari. *Afr J Ecol* **26,** 269–280.

Wong, S.T., Servheen, C., Ambu, L., Norhayati, A. (2005) Impacts of fruit production cycles on Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian Borneo. *J Trop Ecol* **21,** 627–639.

Woodroffe, R., Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas. *Science* **280,** 2126–2128.

Zuk, M., Rotenberry, J.T., Tinghitella, R.M. (2006) Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biol Lett* **2,** 521–524.