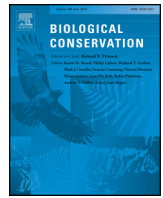




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Review

Should we consider individual behavior differences in applied wildlife conservation studies?



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ABSTRACT

Individually distinctive behavioral traits, or personalities, contribute to population-level processes and ecological interactions important in applied wildlife conservation research. Inter-individual variation in behavioral traits (personality) and correlation among behavioral traits (behavioral syndromes), can influence empirical estimates of population size and structure, models of resource selection and population dynamics, harvest and control in wildlife and fisheries populations, population response to disturbance and novel environments, and the success of reintroductions. Despite the important role that personality and behavioral syndromes play in the ecology and dynamics of wildlife populations, a disconnect between basic and applied research realms continues. While the concept of animal personalities and their role in ecology and evolution is increasingly embraced in the animal behavior, ecology, and evolutionary biology literature, it is less represented in applied wildlife management and conservation literature. We identify 10 research foci, often considered the domain of applied wildlife management and conservation, summarize examples of how these research domains may be influenced by personality and behavioral syndromes, and outline potential implications. We suggest that a focus on individuals in wildlife conservation study can bridge the gap between basic and applied research and incorporate knowledge from both realms towards more effective management, conservation, and recovery of populations.

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1. Introduction

There is increasing recognition of inter-individual behavioral differences within animal populations that are consistent over time and across contexts, known as personalities, behavior types, or behavioral phenotypes (Mittelbach et al., 2014; Réale et al., 2010; Svendsen and Armitage, 1973; Wolf and Weissing, 2012). Behavioral traits commonly measured as components of animal personality include aggression (tendency for agonistic behavior towards conspecifics), exploration-avoidance (how individuals respond to a novel situation), activity (tendency towards movement), shyness–boldness (responses to perceived risk), and sociability (non-agonistic behavior towards conspecifics) (Armitage, 1986; Canestrelli et al., 2015; Réale et al., 2007; Sih et al., 2004b). Behavioral traits that comprise personality are often correlated and suites of correlated behavioral traits are referred to as behavioral syndromes (Sih et al., 2004b). The idea that inter-individual behavioral differences are more than stochastic noise within populations emerged from psychological literature as early as the 1920s (Gosling, 2001), and has received much attention from behavioral ecologists and evolutionary biologists in the last 15–20 years (Réale et al., 2007, 2010; Wolf and Weissing, 2010). Consistent inter-individual behavior differences and correlated behavioral traits have been documented across a variety of taxa and are considered common (Conrad et al., 2011; Gosling, 2001; Réale et al., 2007, 2010; Sih et al., 2004b; Wolf and Weissing, 2012). Further, evidence suggests that behavioral traits and associated syndromes vary in response to environmental conditions (Dingemanse et al., 2010; Sih et al., 2004b). Animal personalities are empirically shown or hypothesized to have impacts on population processes including space use, habitat selection, responses to novel environments, dispersal, species interactions, host–parasite interactions, disease transmission, and other key processes important for wildlife conservation and management (Anthony and Blumstein, 2000; Sih et al., 2012; Smith and Blumstein, 2013; Stamps and Groothuis, 2010; Wolf and Weissing, 2012). Furthermore, behavioral traits and syndromes are shown to be linked to fitness such that individuals will perform better in some circumstances and not others thus maintaining behavioral differences within a population (Dingemanse and Réale, 2013; Sih et al., 2004a, 2004b) and influencing demographic parameters (Anthony and Blumstein, 2000); important considerations for wildlife management.

Wildlife studies often focus on enumeration, correlates of resource use and habitat selection, and demographic processes at the population level (Martin, 1998), yet natural selection operates at the level of individuals (Austin et al., 2004; Lomnicki, 1988). That animal personalities within populations serve to maintain genetic diversity, influence demographic parameters and potentially the results of wildlife research, interpretation of results, and success of conservation or management actions is not often addressed by applied wildlife practitioners (but see Conrad et al., 2011) despite guidelines and reviews that highlight the implications of animal personality in applied wildlife conservation and management practice (Angeloni et al., 2008; Anthony and Blumstein, 2000; Blumstein and Fernández-Juricic, 2010; Caro, 2007; Festa-Bianchet and Apollonio, 2003; Greggor et al., 2016; Smith and Blumstein, 2013; Sutherland, 1998). The presence of animal personalities can bias empirical estimates of population size and structure (Biro, 2013; Biro and Dingemanse, 2008), and which individuals are harvested in managed wildlife and fisheries populations (Biro and Post, 2008). Inclusion of behavioral variability is important in models of animal movement and dispersal (Fraser et al., 2001; Taylor and Cooke, 2014), resource selection, and population dynamics. Personality differences and behavioral syndromes can play a role in how populations will respond to disturbance and novel environments (Atwell et al., 2012; Owen et al., 2016), how individuals will cope with handling, translocation, and reintroduction (Mason, 2010; McDougall et al., 2006), and the success of conservation efforts such as habitat restoration, corridor designs and crossing structures (Caro, 2007). Consideration of animal personalities may be important during all phases of wildlife study. During

the design phase, researchers may consider methods to assess behavioral variability within a population directly, or account for it indirectly via mixed-effects models and alternative sampling methods (e.g. active and passive sampling; Biro, 2013). The presence of animal personalities and context-dependent fitness among them may be important to consider during data collection, analysis, assessment of management implications, and the development of management plans (McDougall et al., 2006).

Published studies that document animal personality and behavioral syndromes and their realized or potential impacts in wildlife conservation are primarily directed towards basic science audiences in animal behavior, ecology, and evolutionary biology, and not towards applied wildlife conservation practitioners. This disconnect mirrors that between animal behavior research in general and its application towards applied conservation (Angeloni et al., 2008; Berger-Tal et al., 2016; Caro, 2007; Sutherland, 1998). The emerging field of conservation behavior (Blumstein and Fernández-Juricic, 2010; Smith and Blumstein, 2013) has facilitated the translation of behavior research to improved wildlife conservation in many areas, yet the connection between animal personality and applied conservation remains underdeveloped (Berger-Tal et al., 2016).

Here, we review literature on how animal personality and behavioral syndromes may influence population processes important to wildlife conservation and management and affect outcomes of wildlife research within the following research foci: detection probability and trappability, stress response, animal movement and dispersal, habitat selection, mate choice and reproductive success, parasite infection, human harvest, urbanization and disturbance, invasibility, and captivity and reintroduction. We provide examples of how these foci may be influenced by animal personalities and behavioral syndromes, outline potential implications, and offer recommendations (Table 1).

2. Material and methods

We conducted literature reviews in Thomson Reuters Web of Science™ Core Collection to identify research related to behavior traits, personality, and behavioral syndromes relevant to wildlife conservation and management. We specified a time period between 1900 and March 2016 and searched for primary literature with the terms “animal personality”, “behav* syndrome”, “behav* type”, and “behav* phenotype” listed as a research topic, with results refined by Ecology (to include Zoology, Biology, Behavioral Sciences, Evolutionary Biology, Biodiversity Conservation, Environmental Science, and Marine Freshwater Biology). From our preliminary search of published literature, we identified studies with results and implications directly relevant to applied wildlife conservation and management, and organized our search results by 10 research foci: detection probability and trappability, stress response, animal movement and dispersal, habitat selection, mate choice and reproductive success, parasite infection, human harvest, urbanization and disturbance, invasibility, and captivity and reintroduction.

3. Results

Behav* type was the most commonly used term (behavior type = 3193 hits; behav* phenotype = 722 hits; animal personality = 329 hits; behav* syndrome = 350 hits). Animal personality and associated behavior terms continue to be topics of exponentially increasing interest over the last 15 years (Réale et al., 2010; Fig. 1, personality example), including conservation (animal personality AND conservation = 45 hits), but publications remain largely restricted to the domains of animal behavior and evolutionary biology (Supplementary material Table 1A), and are not well represented in applied literature. Our searches returned minimal hits for “animal personality” or similar terms in applied wildlife management and conservation outlets such as *Journal of Wildlife Management* (animal personality: 1; behav* phenotype: 0; behav* syndrome: 0), *Wildlife Biology* (animal personality: 1; behav*

Table 1
Applied wildlife conservation and management research domains, mechanisms for how individually distinct behavioral traits may influence the outcome of wildlife research, associated implications, and recommendations for dealing with individual behavior differences in wildlife ecology. Note that the list of selected references provided is not exhaustive.

Applied wildlife domain	Mechanisms	Implications for research and management	Recommendations & considerations	Selected references
1 Detection probability and capture success	Bold, active, exploratory individuals most detected and explore novel objects	Detection probability, estimates of population parameters, life history traits, physiology, and variability in behavioral traits may be biased based upon individuals trapped; individual variation in trappability can hinder estimates of population density, social structure, and the efficacy of management actions	Augment studies with non-invasive sampling such as scat, hair, eDNA, and camera traps to better estimate population size	Réale et al. (2000), Biro and Dingemanse (2008), Boon et al. (2008), Marescot et al. (2011), Byrne et al. (2012), Carter et al. (2012), Biro (2013) and Foote et al. (2012)
2 Stress response	Physiology and neurobiology differences among individuals result in different “coping styles” for handling stress	Some individuals more susceptible to negative effects from handling, and can include trap mortality, and long-term effects of increased cortisol and other stress hormones	Implement protocols to monitor captured individuals during handling that account for individual variation in response to handling stress such as monitoring heart or breathing rate, struggle rate, and potentially releasing individuals if a threshold is exceeded.	Koolhaas et al. (1999), von der Ohe and Servheen (2002), Montané et al. (2003), Lupien et al. (2009), Carere et al. (2010), Brommer and Klunen (2012) and Raoult et al. (2012)
3 Movement and space use	Individuals differ in behaviors related to movement and dispersal, exploration, and tendency for risk taking, and these can vary in response to environmental conditions	Many animal movement models simplify inter-individual variability in movement and foraging behavior, leading to over- or under-prediction of actual movement patterns. Models of population dynamics, probability of colonization, and range shift predictions may be limited by overly simplistic representations of natal dispersal distances	Recognize individuals vary in movement behavior and perception of landscape permeability and incorporate inter-individual variability in models of movement, population dynamics, and landscape connectivity	Fraser et al. (2001), Austin et al. (2004) del Mar Delgado and Penteriani (2008), Duckworth (2008), Hawkes (2009), Armitage et al. (2011), Fordham et al. (2014), Taylor and Cooke (2014), Spiegel et al. (2015), Thorlacius et al. (2015) and Canestrelli et al. (2015)
4 Habitat selection	Individuals with particular behavioral traits may occur more frequently in certain environmental contexts compared to others	Habitat alterations, restoration efforts, or disturbance may select for certain behavior traits over others. If some personalities are more attracted to a habitat treatment than others, but are less trappable, erroneous management conclusions may be drawn.	Studies of habitat selection or that aim to compare effects of habitat management actions should consider the potential for habitat preferences to differ among individuals, account for individual heterogeneity in models, and acknowledge that personality-dependent heterogeneity in detection probability and trappability could bias conclusions.	Wilson et al. (1993), Boon et al. (2008), Stamps and Groothuis (2010), Pearish et al. (2013) and Alcalay et al. (2014)
5 Mate choice and reproductive success	Behavioral traits are correlated with mate choice, probability of extra pair copulations, mating success, and offspring personality	Assessment of mate preferences and frequency of extra pair mating may be biased by the behavioral traits of individuals sampled in a study	Incorporate behaviorally heterogeneous individuals for inclusion in mate choice studies; include individuals as covariates in selection models.	Armitage (1986), van Oers et al. (2008), Schuett et al. (2010), David and Cézilly (2011), Sih et al. (2014), Teyssier et al. (2014) and Bierbach et al. (2015)
6 Parasite infections	Some personalities are more susceptible to parasite infection and parasites can alter host behavior to increase opportunities for transmission	Individual behavior traits and fluctuations in parasite density, population density, resources, and predation risk may interact to influence rates of parasite infection and spread, the spatial distribution of individuals, habitat selection, reaction to predators, individual fitness, and population dynamics	Studies of population or behavioral responses may consider inclusion of some estimate of parasite load as an environmental covariate – particularly parasites documented to alter individual behavior. Increased surveillance of endo- and ecto-parasites, either directly or molecularly, may aid in understanding the role parasites play in behavior variation and population regulation	Dobson (1988), Barber and Dingemanse (2010), Thompson et al. (2010), Avilés and Parejo (2011), Dunn et al. (2011), Poulin (2013), Marinov et al. (2015)
7 Harvest success and population implications	Bold, active, fast-growing individuals may be more likely to be depredated, harvested	Non-random mortality from hunting and fishing can select for small, slow growing, secretive individuals that can lead to decreased body/ornament size and fecundity, and reduce the apparent number of individuals available to hunters and anglers. Behavioral traits related to harvest vulnerability may be independent of age, size, or sex.	In heavily harvested populations of conservation or management concern experiencing declines, management plans should be flexible and adaptive to promote and maintain diversity in physical and behavioral traits.	Biro et al. (2004), Biro and Post (2008), Conrad et al. (2011), Ciuti et al. (2012), Monteith et al. (2013), Smith and Blumstein (2013), Hessebauer et al. (2015) and Härkönen et al. (2015)
8 Effects of anthropogenic disturbance	Anthropogenic disturbances may impact individuals in a population differently: Bold, active, exploratory individuals tend to be associated with fast learning, reduced neophobia, increased tolerance for	Disturbance-tolerant individuals may be more likely to use structures such as crossing structures, nest boxes, artificial roosts, enter traps, and potentially accept vaccine baits; disturbance-tolerant individuals are	In recognition that disturbed areas may reduce inter-individual behavior variation and select for certain behavior traits over others, managers could incorporate buffers proportional to the flight initiation	Blumstein et al. (2003); Parker and Nilon (2008), Guillette et al. (2009), Atwell et al. (2012), Titulaer et al. (2012), Lowry et al. (2013), Naguib et al. (2013) and Sol et al. (2013)

Table 1 (continued)

Applied wildlife domain	Mechanisms	Implications for research and management	Recommendations & considerations	Selected references
	humans, noise, and other disturbances	more likely to become human commensals or pests that increase human-wildlife conflicts, transmit zoonotic diseases, colonize new areas, or become invasive	distance of a species of concern around disturbed, highly urbanized, or rapidly changing areas to maintain as much behavioral variation as possible. Results from studies conducted in highly disturbed areas may not be relevant to populations in less disturbed areas and vice versa.	
9 Wildlife control and invasive species	Individuals at the invasion front often exhibit increased aggression, activity, and boldness, traits considered together as an “invasion syndrome”	Resource availability, temperature, predation risk, and behavioral traits of native and invasive species can influence invasion success and intensity of competition; behaviors associated with invasibility may aid trapping and control efforts initially, however culling programs may select for trap shy individuals, reducing efficacy of eradication programs as efforts continue	Consider how resource availability and other environmental variables impact behavior and competitive interactions between native and invasive species; multiple capture or control methods could be employed simultaneously to reduce behavioral biases	Tuytens et al. (1999), Pintor et al. (2008), Chapple et al. (2012), Brodin and Drotz (2014), Juette et al. (2014), Thorlacius et al. (2015), Zhao and Peishan (2015) and Winandy and Denoël (2015)
10 Reintroduction, translocation, and captivity	Individuals respond differently to captivity, translocation, and reintroduction; some behavioral traits are better suited to captivity, reintroduction, and translocation	Captive breeding programs drive contemporary evolutionary change in animal temperament by selecting for docility, decreased activity, and boldness; these individuals may fare poorly upon release into natural environments	Make efforts to promote and conserve behavioral diversity in captive populations and select a behaviorally diverse group of individuals for each reintroduction attempt.	Shepherdson (1994), McDougall et al. (2006), Mason (2010), Watters and Powell (2012) and Reading et al. (2013)

phenotype: 0; behav* syndrome: 0), *Wildlife Research* (animal personality: 1; behav* phenotype: 1; behav* syndrome: 1), *Conservation Biology* (animal personality: 0; behav* phenotype: 0; behav* syndrome: 1), or *Biological Conservation* (animal personality: 0; behav* phenotype: 0; behav* syndrome: 1).

3.1. Detection probability and capture success

Estimating the size of wildlife populations based upon repeated, random samples of marked or unmarked individuals is common (Silvy, 2012). Despite efforts to obtain systematic random samples of individuals and use of models to account for differences in detection probability, animal personalities can present hidden biases in wildlife sampling protocols and influence the probability of detection and capture (Biro,

2013; Biro and Dingemane, 2008). Personality and behavioral syndromes within a population affect sampling because bold, active, exploratory individuals might be more likely to be sampled (Biro, 2013; Biro and Dingemane, 2008; Carter et al., 2012). Unless the entire population is known, detection probability estimates are necessarily based upon a random sample of the population, a sample that could itself be biased based upon how different personalities relate to detectability (Biro, 2013; Carter et al., 2012). True detection probability could be higher or lower, which in turn affects estimates of population size (Biro, 2013).

In lakes stocked with equal densities of slow, intermediate, and fast growing rainbow trout (*Onchorhynchus mykiss*), fast growing individuals were twice as likely to be sampled despite random sampling methods, likely due to the fact that fast growing individuals were more active and less wary (Biro, 2013). Population size of wolves (*Canis lupus*) in France was underestimated by 27% when individual detection heterogeneity was ignored (Marescot et al., 2011). Biases in detectability due to personality differences may be reduced by inclusion of non-invasive sampling techniques such as DNA extraction from hair or feces, environmental DNA (Foote et al., 2012), or detection via camera traps (Luikart et al., 2010; Mills et al., 2000) to augment sampling methods such as live trapping or netting and distance sampling (Biro, 2013).

Differences in trappability among individuals are documented across many taxa and include mammals, birds, and reptiles and observed differences are associated with personality traits (Carter et al., 2012; Guillette et al., 2010; Réale et al., 2000; Tuytens et al., 1999). Bold, active, exploratory individuals tend to enter live traps or nets more frequently (Biro, 2013; Boon et al., 2008; Boyer et al., 2010; Carter et al., 2012), and the tendency for increased trappability can affect the types of individuals that are incorporated into wildlife studies, potentially leading to behaviorally, physiologically, and physically biased estimates of population characteristics and parameters (Biro and Dingemane, 2008). Further, sampling individuals via live trapping to document personalities and behavioral syndromes may underestimate

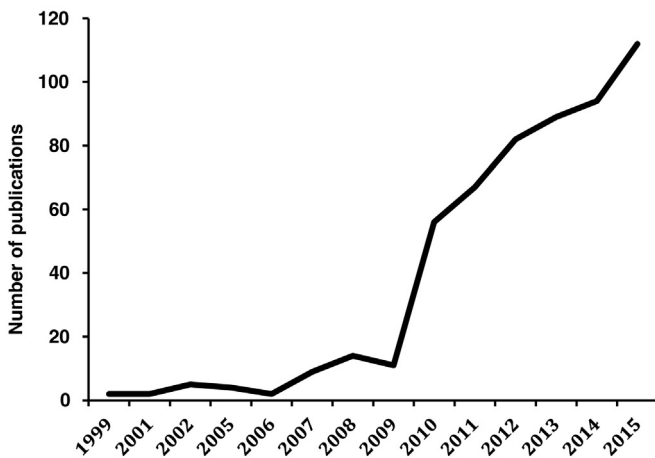


Fig. 1. The frequency of publications that refer to “animal personality” in organismal research between 1996 and 2015. Data accessed from Thomson Reuters Web of Science™ Core Collection, March 2016.

the actual amount of variation in and correlation among behavioral traits (Carter et al., 2012). Consideration of inter-individual variation in trappability is important to adjust estimates of population density, characterize social structure, and to assess the efficacy of management actions. For example, estimates of variation in trappability among European badgers (*Meles meles*) was key to estimate population size and inform how many individuals required vaccination against tuberculosis annually and which vaccination delivery method would be most effective (Byrne et al., 2012).

For wildlife studies that involve the capture of individuals, trapping methodology, gear, and population models may be reviewed in an effort to reduce bias from differential trappability and detectability among individuals. Some individuals may be more wary of particular types of traps, thus incorporating different trap types (e.g. restraints and cage-like traps) in a study may serve to capture different types of individuals and reduce bias (Byrne et al., 2012). Passive trapping methods that rely upon individual investigation and contact with the device or novel food baits may fail to sample individuals that are less active, neophobic, or too wary to approach (Biro, 2013) and methods that do not require investigation, such as pitfall traps may be preferred (Michelangeli et al., 2016). However, it is important to note that even passive sampling methods may fail to sample all individuals due to individual heterogeneity in movement and subsequent probability of trap encounter. Active capture methods that involve hand netting and noosing may bias samples towards individuals whose personality allows researchers to approach within a particular distance (Biro, 2013; Carter et al., 2012). Researchers can improve sampling of wary, less active individuals by allowing animals to habituate to trap presence prior to actual trapping efforts, increase the duration of each trapping session, and employ trapping methods that are robust to behavioral biases such as electrofishing, large set nets, pitfall traps, and driving herding animals towards large nets or corrals (Biro, 2013; Michelangeli et al., 2016). Individual heterogeneity in detection and capture can be accounted for in two widely used platforms for modeling population parameters via mark-recapture data and include Pledger Mixture Models and Individual Random Effects Models in Program MARK (White and Burnham, 1999) and Behavioral Response (*Mb*), Individual Heterogeneity in Capture Probability (*Mh*), models in the R package “unmarked” (Fiske and Chandler, 2011), and Spatial Capture Recapture models via R packages “secr” (Efford, 2016) and “oSCR” (Sutherland et al., 2016). By taking into account inter-individual heterogeneity in detection and trappability due to animal personalities, conservation practitioners can improve estimates of abundance and density.

3.2. Stress response

Behavioral traits are correlated with different stress physiologies that include the hypothalamic-pituitary-adrenal axis reactivity, oxidative status, and underlying neurobiology (Biro and Stamps, 2010; Brommer and Klun, 2012; Carere et al., 2010; Koolhaas et al., 1999; Raoult et al., 2012). Correlations among physiological characteristics and behavioral traits, known as coping styles, include 2 main strategies: 1) proactive strategies characterized by sympathetic and noradrenergic response to stress and a bold, aggressive fight-or-flight behavioral response, and 2) reactive strategies characterized by high parasympathetic activation and hypothalamic-pituitary-adrenal response and low aggression, risk aversion, and a freezing behavioral response (Carere et al., 2010; Koolhaas et al., 1999). Coping styles are documented in a diversity of taxa and are heritable (Brommer and Klun, 2012; Carere et al., 2010; Raoult et al., 2012). Stress response traits are among those commonly measured to define animal personalities (Fucikova et al., 2009; Goldstein and Lawton, 2014) and screen individuals for translocation success (May et al., 2016). Different coping styles within a population have been linked to longevity, propensity to disperse, and reproductive success (Carere et al., 2010; Hall et al., 2015) under different socio-environmental conditions.

Some individuals may be more susceptible to negative impacts of capture stress and trap mortality. Capture and handling are considered among the most stressful events that wild ungulates, and likely many other taxa, experience (Montané et al., 2003). Increased sympathetic activation and circulating levels of testosterone and cortisol, as observed in bold, aggressive individuals (Carere et al., 2010), are associated with increased risk of cardiovascular problems, decreased immune response, potential for lowered reproductive success, body mass, and growth (Carere et al., 2010; Lupien et al., 2009; von der Ohe and Servheen, 2002), exhaustion, hyperthermia, muscle myopathy, rhabdomyolysis, and necrosis (Montané et al., 2003). Because coping styles will confer fitness advantages in some situations and disadvantages in others, there may be an interaction between coping style and demographic parameters (similar to those reviewed in Anthony and Blumstein, 2000). It is therefore important for conservation practitioners to consider how external stressors, including the actions of researchers, may differentially impact individuals under study, and exert selective forces that benefit some individuals and adversely affect others.

3.3. Movement and space use

Movements such as foraging, space use, and dispersal are behaviors that vary among individuals (Taylor and Cooke, 2014) and are often correlated with other consistent behavioral traits. Individuals differ in the magnitude of their movements, movement patterns, and propensity to disperse from the natal area. Such heterogeneity in movement pattern and capacity contributes to variability in conspecific and heterospecific interactions, resource use, and competition (Austin et al., 2004; Spiegel et al., 2015) and can influence gene flow, population dynamics, and the distribution and colonization potential of species (Bowler and Benton, 2005; Canestrelli et al., 2015; Cote et al., 2010). Tendency to disperse from the natal area is associated with behavioral traits that include boldness, activity, exploration, aggression, and decreased sociability across many taxa, with activity and exploration most influential in all stages (Armitage et al., 2011; Duckworth and Badyaev, 2007; Duckworth and Kruuk, 2009; Merrick and Koprowski, 2016; Thorlacius et al., 2015). Further, personalities may contribute to the maintenance of leptokurtic distributions of dispersal distances within a population, whereby a few individuals each generation disperse very long distances (Fraser et al., 2001). Natal dispersal is often treated simplistically in population models in which a single fixed dispersal strategy (e.g. random walks) is used to characterize dispersal movements (Bowler and Benton, 2005; del Mar Delgado and Penteriani, 2008; Hawkes, 2009), when in reality there is an underlying distribution of dispersal probabilities and distances. Further, if dispersal is tied to behavioral or physiological traits under selection via predation or harvest (see Section 3.7 below), altered selective pressure could have implications for population dynamics, and species' ability to track shifts in habitat distribution and colonize new areas.

Animal personality, individual physical condition, resource availability, conspecifics, and habitat can interact to influence perceptions of habitat quality, landscape permeability, and how individuals move on the landscape (Bakker and Van Vuren, 2004; Bélisle, 2005; Clobert et al., 2009; Debeffe et al., 2012; Spiegel et al., 2015; Wey et al., 2015). In Roe deer (*Capreolus capreolus*), individual condition and habitat influenced dispersal movements and perceived landscape connectivity. Heavier individuals tended to inhabit rich, heterogeneous habitats and were more likely to disperse and move farther compared to animals in forested habitat, which tended to be lighter. Conversely, red squirrels (*Tamiasciurus hudsonicus*) of low body mass were more likely to cross large clear cuts allowing them to save energy and avoid conspecific aggression (Bakker and Van Vuren, 2004). Behavioral traits (boldness and aggressiveness), sex, social information via conspecific space use intensity, and availability of food, cover, and refuge influenced movement patterns of sleepy lizards (*Tiliqua rugosa*), and interactions among

these factors became more intense when resource availability was low (Spiegel et al., 2015).

Spatially explicit demographic models that account for inter-individual differences in movement behavior and propensity to interact with landscape features may more reliably estimate species range dynamics and extinction risk (Fordham et al., 2014). In northern snake-necked turtles (*Chelodina rugosa*), models that accounted for interactions between individual movement behavior and landscape structure (functional connectivity) resulted in elevated rates of local extinction risk and slower rates of range contraction compared to models that only incorporated structural connectivity (Fordham et al., 2014). The influence of personalities on space use and other movements can be accounted for in spatially explicit models by inclusion of individuals as random effects in linear mixed-effects models, allowing researchers to assess the influence of individual heterogeneity on the process of interest (e.g. Börger et al., 2006).

3.4. Habitat selection

Personalities and individual states can be associated with preferences for particular components of habitat or niches (Boon et al., 2008; Pearish et al., 2013; Wilson et al., 1993), and observed habitat preferences are repeatable (Alcalay et al., 2014). Personality-dependent habitat selection can influence the density and dispersion of individuals, promote the maintenance of personality variation within a population (Stamps and Groothuis, 2010), and may represent a mechanism for sympatric speciation. Such behavior–environment correlations develop when individuals with particular behavioral traits occur more frequently in certain environmental contexts compared to others (Dingemanse et al., 2009; Stamps and Groothuis, 2010), and such contexts could include risk of predation (Bonnot et al., 2015; Boon et al., 2008), microclimates (Cerqueira et al., 2016), habitat, and social structure (Pearish et al., 2013). Increased exploration, use of open areas, and tendency for increased predation were observed in active and bold North American red squirrels (*Tamiasciurus hudsonicus*; Boon et al., 2008) and pumpkinseed sunfish (*Lepomis gibbosus*; Wilson et al., 1993), and risk-tolerant roe deer (*Capreolus capreolus*; Bonnot et al., 2015). Bold Nile tilapia (*Oreochromis niloticus*) consistently prefer warmer thermal microclimates such that temperature preference can be used as a proxy to screen for other behavior traits (Cerqueira et al., 2016). Three-spined sticklebacks (*Gasterosteus aculeatus*) exhibit consistent inter-individual differences in microhabitat use: solitary exploratory individuals prefer open habitat and solitary less exploratory individuals prefer more cover (Pearish et al., 2013).

Considerable variability in structure and quality may exist within habitat types, and spatial heterogeneity in habitat may in turn contribute to spatial heterogeneity in behavior and other traits observed in wildlife species. The relationship between diversity in habitat and behavioral traits could have important implications for management of wildlife and habitats (Boon et al., 2008; Pearish et al., 2013). Habitat modifications and restoration efforts may confer fitness advantages for some individuals, and disadvantages for others based upon individual state and personality. Conservation practitioners can benefit from considering how habitat alterations may differentially impact individuals in a population and provide sufficient heterogeneity to support diversity in individual states and behavioral traits (Smith and Blumstein, 2013).

3.5. Mate choice and reproductive success

Just as individual behavioral trait variation provides a substrate for natural selection (Sih et al., 2004a; van Oers et al., 2005), evidence accumulates to suggest that behavioral traits associated with animal personality play a role in sexual selection and partner compatibility, influence mating success and fitness in heterogeneous environments, and reinforce the maintenance of inter-individual behavior variation (Gabriel and Black, 2012; Schuett et al., 2010; Sih et al., 2014; van Oers et al.,

2008). Sex differences in mean behavior intensity or variability can result in sexual selection for assortative and disassortative behavioral traits (see Schuett et al., 2010 for a thorough review). Boldness, docility, and other behavioral traits may be honest signals of mate quality and reflect information about a potential mate's physiology, natal environment (including parental phenotypes), and life history strategy (Teyssier et al., 2014). Selection of preferred behavioral traits may also be context specific, revealing one mechanism for mate choice variation within a population. In common lizards (*Zootoca vivipara*), individuals vary consistently in sociability and activity and mate preference is dependent on predation risk. Females reared in the absence of predator cues chose active males as mates. When presented with predator cues prior to mating, females exhibited no mate preference (Teyssier et al., 2014). Because male activity level is heritable, females may select mates that will confer offspring behavioral traits with the best prospects for survival depending upon predation risk (Teyssier et al., 2014). Male Atlantic mollies (*Poecilia mexicana*), differ consistently in activity level and boldness, and the intensity of both behavioral traits is reduced when more males are present (i.e. sperm competition is high; Bierbach et al., 2015). The strength of male preference for larger females was both personality and context dependent: bold, active males housed with other males had stronger preference for large females (Bierbach et al., 2015).

Personalities may influence the rate of extrapair copulations, partner compatibility, number of successful matings, and offspring survival and recruitment. In great tits (*Parus major*), males and females vary consistently in exploratory behavior; the probability of being cuckolded (broods with extrapair offspring) was highest in extreme fast-exploring and slow-exploring pairs (van Oers et al., 2008). Male water striders (*Aquarius remigis*) differ consistently in levels of activity and aggression; active-aggressive males spent the most time searching for females and had the highest mating success and this relationship was consistent across social contexts (Sih et al., 2014). In yellow-bellied marmots, females differ in levels of amicability and social behaviors; adult female sociability was positively correlated with reproductive success, and subsequent recruitment of yearling female into the population (Armitage, 1986). Steller's jays (*Cyanocitta stelleri*) vary consistently in exploration and risk-taking behavior; individuals paired with behaviorally similar partners experienced increased reproductive success and behavioral matching may be most important in poor years (Gabriel and Black, 2012). Studies of mate choice may be biased by the behavioral traits of individuals sampled (David and Cézilly, 2011) and associated social context. Personality-dependent heterogeneity in mate choice and reproductive success may be an important consideration for increasing success of captive breeding programs (Greggor et al., 2016), conservation of species with complex mating and social systems, and populations that are in decline or threatened due in part to low reproductive success.

3.6. Parasite infections

Some behavioral traits may increase exposure and susceptibility to parasites, with implications for the conservation of host species and the maintenance of imperfect levels of host defense observed in wild populations (Avilés and Parejo, 2011). Individuals may differ in their exposure to parasites based upon their behavioral tendencies, and once infected, parasites can alter host behavior in a manner conducive to parasite transmission (Barber and Dingemanse, 2010; Poulin, 2013). Host behavior manipulation by parasites influences many factors associated with wildlife research to include habitat use, risk taking, trappability, and population dynamics, and is considered another mechanism that can influence inter-individual behavior differences in wildlife populations (Barber and Dingemanse, 2010; Dobson, 1988). Malaria (*Plasmodium* and *Leucocytozoon*) infection affected problem solving ability, exploration, and risk taking in great tits (Dunn et al., 2011). Similarly, malaria-infected common nightingales (*Luscinia*

megarhynchos) exhibited increased neophilia and risk taking behavior (Marinov et al., 2015).

Behavioral traits that make individuals more susceptible to parasite infection include increased sociability and social behaviors such as allogrooming, foraging behavior, increased exploration, and neophilia (Barber and Dingemanse, 2010). The interplay among parasites, parasite avoidance, individual behavior, and fitness is complex (Barber and Dingemanse, 2010) and can play a role in population dynamics. Parasites can contribute to the regulation of host populations (Tompkins and Begon, 1999), and their role in host population dynamics is a key issue in the conservation and management of threatened wildlife species (Thompson et al., 2010). How parasites influence individual behaviors and the extent to which personalities contribute to parasite infection and transmission in wildlife populations can provide insight into the prediction and potential mitigation of outbreaks, associated fitness costs, and transmission to humans. This is particularly relevant for imperiled or endemic species faced with non-native species and associated exposure to novel parasites via spillover (e.g. Thompson et al., 2010). Studies designed to quantify behavioral traits within a population should consider assessing parasite infection as an environmental covariate (Dunn et al., 2011). Increased surveillance of parasites in wildlife populations via non-invasive molecular tools (Thompson et al., 2010) can enhance our understanding of the relationships among parasite infections, infection intensity, animal personality, and population dynamics.

3.7. Harvest success and population implications

Individuals in a population vary in detection and capture probabilities (see Section 3.1 above), and may differ in the likelihood of being depredated by natural predators or harvested via hunting and fishing, with the likelihood of being depredated or harvested dependent upon interactions between behavior and environment. In both wildlife and fisheries, larger, older, or faster-growing individuals tend to be selected for harvest both for cultural reasons (e.g. trophy size) and due to regulations on minimum size limits (Biro and Post, 2008; Coltman et al., 2003; Monteith et al., 2013). Artificial selection for phenotypic traits via harvest is shown to influence both the demographic and phenotypic composition of populations, resulting in decreased abundance of desirable individuals (Coltman et al., 2003; Festa-Bianchet, 2003), and desirable phenotypic traits are often correlated with behavior. In fishes, bold, aggressive exploratory behavioral traits are correlated with faster growth rates (Biro, 2013; Biro and Post, 2008), and in natural populations, growth rate and size are maintained below maximum levels by negative selection from predators as the boldest, fastest growing individuals are most likely to forage in risky open water habitats (Biro et al., 2004). Commercial and recreational fisheries impose similar, often more intense negative selection (Biro and Post, 2008; Hessenauer et al., 2015; Mittelbach et al., 2014). In a simulated intensive commercial gillnet fishery on trout, fast-growing, active, bold individuals were harvested at three times the rate of slow-growing, shy individuals independent of body size, an example of fisheries-induced evolution of a life history trait (growth rate; Biro and Post, 2008). Because certain personalities are more vulnerable to harvest, minimum size limit regulations will not reduce negative selection and loss of fast-growing genotypes from the population, which leads to slower-growing, less fecund fisheries with lower yields – an important consideration for the recovery of threatened fisheries (Biro and Post, 2008). Recreational angling is also shown to impose artificial selection on heritable, correlated behaviors including boldness, exploration, activity, foraging behavior, resting metabolic rate, and nest defense in bass (*Micropterus* spp.) (Hessenauer et al., 2015) and Eurasian perch (*Perca fluviatilis*) (Härkönen et al., 2015). In species where nest defense is essential for increasing egg and larval survival, angling may be detrimental to population recovery and persistence as bold, aggressive individuals may be the best nest defenders, but also the most likely to be caught (Mittelbach et al., 2014).

Fewer data demonstrate direct correlations between behavioral traits and vulnerability to anthropogenic hunting, but evidence suggests that some behavioral traits may increase susceptibility to hunter harvest. Bighorn sheep (*Ovis canadensis*) ewes that were more likely to be trapped were considered bold, reproduced earlier, and had higher weaning success (Réale et al., 2000). However, during years of high predation from mountain lions (*Puma concolor*), bold, less docile ewes were less likely to be depredated by a natural predator (Réale and Festa-Bianchet, 2003). Bold, active elk (*Cervus elaphus*) males and females exhibited increased use of open areas and were most likely to be harvested by hunters (Ciuti et al., 2012). Similarly, some individual black bears (*Ursus americanus*) were more likely to be trapped, observed in camera traps, and shot by hunters irrespective of sex, age, or time spent in the study area (Noyce et al., 2001). Recommendations to counteract the effects of hunter harvest on decreased antler size, reduced male age structure, and associated life history traits include less selective pressure on large, fast growing males, and increased harvest of females (Monteith et al., 2013). However, if certain individuals are behaviorally vulnerable to harvest independent of age, size, and sex (Biro and Post, 2008), harvest may continue to exert negative selective pressure on fast-growing, bold, active individuals, with potential to increase the frequency of small, shy animals with decreased fecundity in the population (exploitation-induced evolutionary change; Ciuti et al., 2012). Artificial selection for shy, less active, slower growing individuals in fish and wildlife populations can result in decreased detection of individuals by researchers, and yield by hunters and anglers. Thus management recommendations should address ways to maintain diversity in physical and behavioral phenotypes via flexible adaptive management of harvested populations (Smith and Blumstein, 2013).

3.8. Effects of anthropogenic disturbance

Human-induced changes to earth's ecosystems are pervasive and drive observable evolutionary change in fish and wildlife populations (Smith and Bernatchez, 2008). Selective pressures exerted by urbanization, landscape fragmentation, and climate change are generally beyond the scope of environmental conditions under which species have evolved (Lowry et al., 2013; Sih, 2013; Sol et al., 2013). Individuals vary in their ability to tolerate such disturbances, with population-level implications. Bold, aggressive, exploratory individuals have reduced neophobia to objects and food and are more likely to tolerate anthropogenic disturbances, move through human-modified landscapes, and colonize new areas (Duckworth and Badyaev, 2007; Sol et al., 2013; Tuomainen and Candolin, 2011). The tendency for increased density and aggression and decreased wariness and fear of humans in urbanized environments, has been termed the “urban wildlife syndrome” documented in many synurbic species such as gray squirrels (*Sciurus carolinensis*) and coyote (*Canis latrans*) (Parker and Nilon, 2008 and references therein).

How adaptive particular behavioral traits are in response to anthropogenically created novel situations and environments is context dependent (Sih, 2013; Tuomainen and Candolin, 2011), but in general bold, docile, active, explorers tend to be innovative and quick learners (Guillette et al., 2009; Titulaer et al., 2012), exhibit more behavioral flexibility (Frost et al., 2007), are less stressed by human presence, and are more successful in the face of urbanization and disturbance (see reviews by Lowry et al., 2013; Sol et al., 2013). In great tits (*Parus major*), nestling provisioning behavior and nest success in the face of anthropogenic noise depended upon the personality of both parents, where active, exploratory males and less active, slow exploring females were more tolerant of noise and visited nests more frequently (Naguib et al., 2013). Rapid phenotypic divergences were observed between urban and rural dark-eyed junco (*Junco hyemalis thurberi*) populations in their native montane breeding range and a newly colonized (c.a. 1983) urban population (Atwell et al., 2012). Urban colonists exhibited consistently higher levels of corticosterone, bold, exploratory behavior

traits, and lower flight initiation compared to individuals in the native montane population (Atwell et al., 2012).

How individual behaviors, life history traits, and associated population parameters change in response to anthropogenically-altered environments has positive and negative implications for wildlife management and conservation (Lowry et al., 2013; Thompson and Henderson, 1998). Disturbance-adapted individuals may be more likely to utilize novel, conservation-oriented structures such as wildlife crossings, nest boxes, artificial roosts, enter traps for the purposes of marking, radio-collaring, collection of biophysical samples, or translocation, and accept vaccine baits. Conversely, disturbance-adapted individuals are more likely to become human commensals or pests that increase human-wildlife conflicts, transmit zoonotic diseases, colonize new areas (Duckworth, 2008), or become invasive. The maintenance of less-disturbed buffers around highly disturbed areas may promote utilization by and continued survival of individuals that are less behaviorally suited to anthropogenically altered environments (Blumstein et al., 2003; Richardson and Miller, 1997).

3.9. Wildlife control and invasive species

Propagule pressure alone may not sufficiently predict successful invasion and establishment of non-native species (Chapple et al., 2012). The behavioral traits of non-native individuals that colonize new areas at the invasion front tend to differ from the source population mean and are characterized by increased aggression (Duckworth and Badyaev, 2007; Winandy and Denoël, 2015), boldness, and activity (Brodin and Drotz, 2014; Thorlacius et al., 2015); correlated traits often considered together as an ‘invasion syndrome’ (Chapple et al., 2012). Different personalities and behavioral syndromes may be favored at various stages of invasion or colonization (Chapple et al., 2012; Wolf and Weissing, 2012) and have consequences for management and control efforts (Juetter et al., 2014). Behavioral traits of invading individuals can impact native residents via increased competition, agonistic interactions, and disease transmission. The extent to which invading individuals negatively impact residents, in turn, depends upon the behavioral traits of individual residents.

The interaction of environmental conditions, behavioral traits, and competitive abilities among native and non-native species may predict the exclusion or persistence of the native species in the presence of an invader (Winandy and Denoël, 2015), particularly when the invader is ecologically similar (Pintor et al., 2008). In palmate newts (*Lissotriton helveticus*), aggression from a non-native predator (goldfish; *Carassius auratus*), individual boldness, and developmental phenotype (metamorphs or paedomorphs) influenced time spent foraging. This interaction among behavioral and physical traits of native and non-native species may explain how non-native goldfish, which do not prey upon newts, contributed to a dramatic decline in newt abundance (Winandy and Denoël, 2015). Resource abundance may modulate behavioral traits such that agonistic interactions and competition among invasive and native species may be intensified in low resource situations. Invasive signal crayfish (*Pacifastacus leniusculus*) were bolder and more aggressive in streams with low prey availability; boldness and aggression were reduced in streams with more prey, even in the presence of a native congener (Pintor et al., 2008). Increased temperatures as a result of global climate change may influence behavioral traits, invasion success, and intensity of competition between native and non-native species. In poikilothermic organisms, environmental temperature can influence behavioral trait expression, metabolic rates, food consumption, and invasion success. A 3 °C increase in water temperature resulted in increased activity, aggression, and boldness in invasive red swamp crayfish (*Procambarus clarkii*; (Zhao and Peishan, 2015).

Once an invasive species is established, control efforts may modify the behavioral composition of the invasive population, complicating complete eradication (Juetter et al., 2014; Tuytens et al., 1999). Behavioral traits that contribute to invasion success (e.g. boldness, activity,

aggression) are also associated with increased trappability and capture success (see Section 3.1 above), and trapping efforts to control invasives may be more effective on bold individuals and inadvertently introduce artificial selection for shy and less trappable individuals (Tuytens et al., 1999) or less dominant individuals (Stuecheli, 1991), making enumeration and eradication more difficult. Multiple capture or control measures may be undertaken simultaneously so as not to bias efforts towards any particular behavioral phenotype.

3.10. Reintroduction, translocation, and captivity

Considerable variation exists in how species and individual animals respond to captive environments (Mason, 2010; McDougall et al., 2006). Bold, docile, less active behavioral traits are associated with increased fitness in captivity compared to shy, aggressive, active types and this fitness dichotomy, in conjunction with artificial, anthropogenic selection, has led to altered behavioral traits in captive populations over relatively short time periods (McDougall et al., 2006). Such contemporary evolutionary shifts in the behavioral traits of captive populations can hamper the success of reintroduction efforts (Reading et al., 2013) by reducing behavioral heterogeneity and associated genetic diversity that is adaptive in the wild (Smith and Blumstein, 2013). Therefore the maintenance of behavioral heterogeneity in captive populations is an important consideration for the management of wildlife in zoos or captive breeding centers, particularly for the implementation of translocation and reintroduction efforts (Reading et al., 2013; Shepherdson, 1994).

Reintroduction success may depend in part upon individual ability to move through and navigate structurally complex environments, avoid predators, forage efficiently, interact socially, respond to stress, select habitat components, and avoid humans (May et al., 2016; Reading et al., 2013). Provision of diverse rearing environments or simulated habitats, skill training, and enrichment activities has aided in development of key behaviors in preparation for reintroduction (McDougall et al., 2006; Reading et al., 2013; Shepherdson, 1994; Watters and Meehan, 2007). Appropriate enrichment and skill training has improved reintroduction success in many threatened and endangered species including black-footed ferrets (*Mustela nigripes*), Columbia Basin pygmy rabbits (*Brachylagus idahoensis*), black-tailed prairie dogs (*Cynomys ludovicianus*), California condors (*Gymnogyps californianus*), and American bison (*Bison bison*) (Reading et al., 2013). Behavioral assays of individuals along several trait axes pre-release allows managers to select a more behaviorally (and presumably physiologically and genetically) diverse group slated for release (May et al., 2016; Reading et al., 2013; Smith and Blumstein, 2013; Watters and Meehan, 2007) and may serve to increase survival and persistence post-release.

4. Conclusions

Animal personalities and behavioral syndromes influence population-level processes and result in ecological interactions important in applied wildlife conservation and management (Smith and Blumstein, 2013). Rather than just noise around a population mean, individually distinct behavioral traits have observable ecological and evolutionary consequences (Réale et al., 2007; Sih et al., 2012; Wolf and Weissing, 2012). That personalities and behavioral syndromes are maintained within populations is testament to their importance, not only as the canvas upon which natural selection acts, but also as the products of natural selection (Réale et al., 2007). Heterogeneity in availability of food, mates, territories, competition intensity, predation risk, and susceptibility to parasites across time and space are examples of selective forces that act to maintain distinct personalities and behavioral syndromes within a population (Wolf and Weissing, 2010). As products of natural selection, observed rapid changes to the frequency of individually distinct behavioral traits within populations facing strong selection (e.g.

from harvest, urbanization, captivity, invasive species) are examples of contemporary evolution and serve as reminders that management actions can have evolutionary consequences (Ashley et al., 2003; Stockwell et al., 2003). Therefore the ecological and evolutionary consequences of anthropogenic disturbance and management actions on personality and behavioral syndromes should be considered along with other ecologically important traits to ensure evolutionary enlightened management (Ashley et al., 2003).

Here we summarize how consideration of animal personality and behavioral syndromes provides important insight into applied wildlife conservation research. Direct measurement of behavioral traits and documenting animal personality can be time consuming, data intensive, and potentially subject individuals to added stress, and may therefore not be feasible in some wildlife conservation studies. However, consideration of animal personality, even without direct measure, may account for unexplained variability in population models and studies of resource and mate selection, reduce bias in, and reduce unintentional selection for particular behavioral traits via wildlife harvest, control, and reintroduction efforts while facilitating improved wildlife conservation in the face of anthropogenic disturbance and changing landscapes. Where possible, we suggest that managers consider the following:

1. Account for inter-individual behavioral heterogeneity by including individuals as random effects in linear mixed-effects models of resource selection (e.g. Duchesne et al., 2010), movement (Börger et al., 2006), and population demographics (e.g. Fiske and Chandler, 2011).
2. Promote the maintenance of diverse behavioral traits in wild and captive populations by retaining environmental heterogeneity and structural complexity (Smith and Blumstein, 2013).
3. Adopt flexible, adaptive management strategies for harvested populations that maintain diversity in physical and behavioral traits (Coltman et al., 2003; Festa-Bianchet, 2003; Smith and Blumstein, 2013).
4. Consider how conservation and management actions may influence ecologically important behavioral traits within wildlife populations based upon what is currently known about the population. Consider what new insights may arise from collecting information on personality variation.

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