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# Behavioural syndromes predict loss of migration in wild elk

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Despite rapid growth in the literature on personality in wild animals, personality has seldom been explored as a tool for wildlife management in human-altered landscapes. That context frequently involves the habituation of wildlife to people, which can alter predator–prey relationships, contribute to ecosystem damage and result in human–wildlife conflict. For many ungulate species, habituation is also associated with changes to facultative behaviours, such as migration, which may also be related to individual variation. We studied these relationships by identifying behavioural types in two wild populations of elk, *Cervus canadensis*, within which habituation is prevalent, and in one captive population. We defined behavioural types by the relative position of each individual along a shy–bold gradient that we derived for each population from seven behavioural metrics. Those metrics included repeated measures of reactions to three stimuli (approaching humans, novel objects and novel sounds), two state variables measured with scan samples (position within herd and vigilance) and two all-occurrence records of specific behaviours (outcome of dominance interactions and herd leading). Boldness scores were more similar within than among individuals in all three populations, consistent between years, and unrelated to age. In the wild, the shyer half of each population was three times more likely to exhibit migratory behaviour, whereas the bolder half was just as likely (3:1) to express year-round residency. Our results suggest that personality could be an important tool for managing habituated wildlife. By identifying behavioural types and their associations with particular tendencies, managers could proactively target specific individuals for behavioural modification to foster greater coexistence of people and wildlife.


The management of animals in protected areas around the world is challenged by the process of habituation, whereby an individual reduces responses to stimuli that lack negative consequences (Messmer, 2009). Habituation to humans and their infrastructure is often related to food conditioning (i.e. association of food with humans, e.g. Bounds & Shaw, 1994), but it can also occur wherever encounters are consistently benign (Bejder, Samuels, Whitehead, Finn, & Allen, 2009). Habituation is more likely when animals are naturally tolerant (e.g. Smith, Herrero, & DeBruyn, 2005) or when people occupy wildlife habitat (e.g. Strum, 2010), create refuges from predators (e.g. Washburn & Seamans, 2012), or displace wildlife via habitat loss (e.g. Morano et al., 2012). Habituation can also threaten the security of people for species that are large (e.g. Chakraborty & Mondal, 2013), carnivorous (e.g. Rauer, Kaczensky, & Knauer, 2003; Shivik, Treves, & Callahan, 2003), or susceptible to zoonotic diseases (e.g. Plowright et al., 2011). In some species, particularly ungulates, habituation has been linked to declines in migratory behaviour (Middleton et al., 2013; White, Barten, Crouse, & Crouse, 2014), which, in turn, can cause hyperabundant local populations and subsequent habitat degradation (Walter et al., 2010) that erodes ecosystem functions (e.g. Beschta & Ripple, 2009). All of these changes create intense challenges for wildlife managers in protected areas worldwide (Thompson & Henderson, 1998; Whittaker & Knight, 1998).

Solutions to the many problems associated with wildlife habituation are challenged by the fact that wildlife management and conservation generally target populations, whereas habituation, like all behaviours, is an intrinsic attribute of individuals. Consequently, preventative approaches to manage habituated animals are typically applied to entire populations, even though the resulting problems usually begin with a subset of individuals. For example, most protected areas have extensive prohibitions to prevent animals from accessing anthropogenic food as a means of preventing food conditioning and associated conflict (Spencer, Beausoleil, & Martorello, 2007), but if those measures fail and conflict arises, specific individuals may be targeted for intervention by hazing or aversive conditioning (e.g. Honeyman, 2008; Kloppers, St. Clair, & Hurd, 2005; Mazur, 2010). According to

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learning theory (e.g. reviewed by Domjan, 2010), this reactive approach to behavioural adjustment is more difficult, labour intensive and, ultimately, less successful than a more proactive approach. As with other early intervention programmes (e.g. behavioural modification of young children showing early signs of developmental problems; Einfield, Tonge, & Clarke, 2013), a proactive approach to the management of habituation-prone wildlife is likely to increase success while reducing associated costs.

Historically, managers were unable to address habituated animals proactively, waiting instead until the emergence of conflict behaviours, because there was little awareness of individual variation in behavioural tendencies among wild animals, and no metrics for measuring it. That has changed with the emergence of extensive literature that has quantified individual variation as personality (Gosling, 2001), behavioural syndromes (reviewed by Dingemanse, Dochtermann, & Nakagawa, 2012; Sih, Bell, & Johnson, 2004), coping styles (Koolhaas, de Boer, Buwalda, & van Reenan, 2007), or temperament (Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Within these constructs, individuals are typically categorized along one or more gradients. The shy–bold axis was one of the first examples of this approach to be generalized (Wilson, Clark, Coleman, & Dearstyne, 1994), and it continues to be used extensively (reviewed by Carter, Feeney, Marshall, Cowlishaw, & Heinsohn, 2013) and is relevant to the process of habituation (Oosten, Magnhagen, & Hemelrijk, 2010). A boldness score for an individual is usually derived from one or more specific behavioural metrics such as aggression, exploration of novel objects or environments, acceptance of predation risk, and others (reviewed by Stamps, 2007). Although hundreds of studies of personality have been applied to diverse taxa in the past two decades, a minority addressed free-living animals, and we are unaware of any that attempt to classify wild mammals by personality as a tool for their management.

Much potential now exists to apply the concept of behavioural syndromes to wildlife conservation and management, generally, and to the problem of habituated ungulates in particular. Ungulates are a logical target for several reasons. First, habituated ungulates are both prevalent and problematic in protected areas throughout North America (e.g. Brook, 2009; Schultz & Bailey, 1978; Thompson & Henderson, 1998) and elsewhere in the world (e.g. Atickem, Loe, & Stenseth, 2014; Setsaas, Holmern, Mwakalebe, Stokke, & Roskaft, 2007). Second, wild ungulates play important roles in ecosystems as both herbivores and prey (e.g. Laundre, Hernandez, & Altendorf, 2001), and some species can be tamed enough to be farmed as livestock, where they can provide a reservoir of further behavioural information (sensu Driscoll, MacDonald, & O'Brien, 2009). Finally, most ungulate species exhibit partial migration, meaning that populations contain both resident and migratory individuals in ratios that can change over time (e.g. Ball, Nordengren, & Wallin, 2001; Boyce, 1991; White, Davis, Barnowe-Meyer, Crabtree, & Garrott, 2007). Because migration appears to have evolved more generally to maximize resource acquisition in changing environments (sensu Singland & Greenwood, 1983), the prevalence of partial migration in ungulates and other animals (Lundberg, 2013) is logically related to variation in both risks and rewards.

Elk, *Cervus canadensis*, are among the ungulate species that exhibit partial migration, which appears to be driven primarily by seasonal changes in access to forage (Boyce, 1991). Elk that move to higher elevations in summer appear to offset the cost of migration with access to younger, more nutritious forage and reduced risk of predation (Gates & Hudson, 1978). These benefits may accrue even if predation risk increases during migratory movement (Hebblewhite & Merrill, 2011), but these benefits may be further affected by changing climatic regimes (Middleton et al., 2013). The net benefits of migration can be lost where resident elk can exploit human-dominated areas as refuges from predators (Goldberg, Hebblewhite, & Bardsley, 2014; Hebblewhite & Merrill, 2009; Thompson & Henderson, 1998). These advantages increase in protected areas where hunting by people is prohibited, especially if predators are either absent or show more wariness of humans than their prey do (Conover, 2002; Shannon, Cordes, Hardy, Angeloni, & Crooks, 2014). Habituated, resident elk may also benefit from anthropogenic forage such as lawns, gardens, crops and refuse (Mackenzie, 2001).

Several authors have proposed that increasing habituation in ungulate populations reduces the prevalence of migration (Goldberg et al., 2014; Hebblewhite & Merrill, 2009; Thompson & Henderson, 1998), but no one has anticipated how underlying behavioural types may determine the propensity to habituate in the first place. Such exploration is well warranted if identifying the animals that are prone to habituation could support the development of more effective management actions to retain migratory behaviour, thereby avoiding the resulting detrimental ecological effects and human–wildlife conflict. These problems are prevalent near the towns of Banff and Jasper, in Alberta, Canada, each of which is embedded in a large national park of the same name, in the Canadian Rocky Mountains. In both areas, the proportion of resident elk appears to have increased gradually over the past several decades, with fewer animals migrating to higher elevations (Kloppers et al., 2005; Mackenzie, 2001). Over the same period, increasing human populations and infrastructure have been concentrated at lower elevations where they displace wary predators and overlap with elk wintering ranges. These changes have undoubtedly affected the historic benefits of migration, but likely with differences among individuals in relation to behavioural types.

We addressed the potential to apply behavioural syndromes to the management of habituated ungulates with partial migration by studying wild elk near the towns of Banff and Jasper and evaluating the generality of our metrics with a captive population in central Alberta that knows neither migration nor predation. We studied elk in winter, when resident and migratory individuals overlapped near the towns in valley bottoms. Our objectives were to (1) identify a suite of behavioural traits that could be used to identify a gradient of behavioural types relevant to the process of habituation, and (2) determine the variation in these metrics among versus within both individuals and populations and identify potential associations with migratory behaviour. If behavioural types stem largely from consistent and inherent differences among individuals, we predicted they would be apparent in both wild and captive elk, as well as residents and migrants. If behavioural types affect individual evaluation of the costs and benefits of migration, we predicted that the average boldness of residents and migrants would differ and, specifically, that resident individuals would be bolder than migrants. Combining these predictions, our overarching hypothesis was that elk personality would predict migratory choices, and not the other way around. These results would demonstrate the potential for individual-based management of wildlife. These results could also show that the identification of unique personality types with particular ecological tendencies could allow managers to proactively target specific animals for behavioural modification and other conservation interventions.

## METHODS

### *Study Areas and Focal Elk Herds*

#### *National parks*

Banff National Park (BNP) and Jasper National Park (JNP) are large, neighbouring protected areas within the Canadian Rocky