

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.

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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

Mountains. We conducted fieldwork in BNP from January to April of both 2010 and 2011, and in JNP from December to April 2012. Our study areas encompassed the towns of Banff, Alberta, Canada (population 7000) and Jasper, Alberta (population 4500). These areas of high human disturbance created areas of reduced occurrence of the two year-round predators, wolves, *Canis lupus*, and cougars, *Puma concolor*, in both Banff (Goldberg et al., 2014; Ham, 2010; Paquet, Wierczowski, & Callaghan, 1996) and Jasper (Beschta & Ripple, 2007; John Wilmshurst, personal communication, 10 March 2010). Excluding groups of elk comprising only males, the total population of elk overwintering in the Bow Valley during this study was 200–240 each year. This population is composed of adult females and subadults of both sexes, some of which migrate to higher elevations each spring and some of which remain in the winter range year round. Elk using the Jasper town site region numbered 90–100 adult females and subadults and formed three discrete herds we labelled ‘Palisades’, ‘Whistlers’ and ‘Central’. We quantified all behaviours in winter, when elk form large overwintering herds composed of both residents and migrants.

Captive population

Studies of captive-born elk were conducted on an elk ranch near Leduc, Alberta, Canada, during May–September 2011 and January–March 2013. The elk enclosures separated groups of adult females and their calves into three adjacent pens averaging 2.7 ha, with 20–40 elk in each. Coyote, *Canis latrans*, presence was detected adjacent and occasionally inside the pens, but there were no incidences of predation during the study period.

Elk Locations

We followed a general definition of migration as being a seasonal shift from one defined range to another (Lack, 1954, pp. 243–254). We used radiotelemetry and snow tracking to record the locations of wild elk each morning and used minimum convex polygons around the pooled 2010–2012 locations to define winter ranges for the Banff elk herd and three Jasper herds. Based on aerial and ground telemetry and visual identifications, individuals that were detected outside their winter ranges in July–August were labelled ‘migrants’, while those found within the winter range were labelled ‘residents’. The proportion of migrants to residents was stable throughout the study, although up to nine residents were culled, for the purpose of population control, from the Banff population each winter. Of the three herds in JNP, only the ‘Central’ herd entered the town site and was almost entirely nonmigratory, while the two non-town herds were almost entirely migratory.

Predation

We obtained predator activity data post hoc from snow-tracking surveys that were conducted each winter by Parks Canada in BNP, which recorded unique track detections of both wolves and cougars, along linear transects throughout the Bow Valley (methodology described by Ham, 2010). Tracking methods tended to detect tracks made within the past 24 h, although the exact time period between predator occurrence and detection could not be known. Based on the number of snow-track detections, wolf and cougar occurrence was low along transects bisecting most areas used by elk in the winter of 2010, and declined even further in 2011. There were just three depredated elk in 2010, and none in 2011. We expected predation to have some influence on elk behaviour, but we could not incorporate these infrequent events into our multivariate behavioural metrics. Instead, we assessed the potential effect of predator presence by comparing the mean elk flight responses in

locations and during periods with and without evidence of predator activity. This evidence consisted of the occurrence of wolf or cougar tracks on nearby monitoring transects during any of the previous 3 days.

Behavioural Assays

Our assays focused on adult female elk that were individually marked with eartags, VHF radiocollars, or both. We did not include male elk for two reasons; none were marked in our study populations, and these animals tend to be more dispersed on the landscape, which reduces their relevance to conflict in towns stemming from habituation. Capturing and marking was done by Parks Canada as part of its separate, ongoing research. Sample sizes varied among populations and/or years; 22 (JNP), 35 (BNP 2010), 47 (captive) and 51 (BNP 2011). Among the animals sampled in Banff in 2011, 33 were also used in 2010. We observed elk opportunistically throughout the day, but locations and types of data collected during each observation session were chosen nonrandomly to ensure all individuals were assayed in a wide diversity of temporal and spatial contexts. We collected noninvasive data before conducting necessarily disruptive stimulus testing, and targeted no elk more than once per day. All observations and stimulus testing of elk were conducted under the approval of the University of Alberta Ethics for Animal Use Protocol No. 7121112.

Individual position within herd

At the start each observation session, we recorded the location of focal individuals relative to other elk in their discrete group, which was most typically only a fragment of the entire herd (e.g. Altmann, 1974; Dalmau, Ferret, & Manteca, 2010). We rank-ordered and assigned a numerical score for ‘peripheral’, ‘intermediate’ and ‘interior’ positions. We considered elk part of the same group if they appeared to be foraging together, sharing the same space. Elk that were alone or otherwise not part of an identifiable group were considered peripheral. Elk in groups of three or fewer individuals were all considered peripheral, since no individual could be within the others in the group, and elk in groups of six or fewer individuals were considered peripheral or intermediate only. Using these criteria, we calculated a mean ‘position’ score for each individual that was not dependent on group size, with higher values indicating more peripheral positioning. Elk choosing solitude or small groups will thus have higher scores, but this choice is part of what this ‘position’ metric is recording.

Flight response distance

Starting from between 75 and 125 m away, an observer approached individual elk at a normal walking speed and recorded the distance at which the elk responded by moving at least 5 m. In addition to standardizing the starting distance, the same observer conducted all flight response trials in order to minimize the potential influence of speed, body size and gait of an approaching human. We conducted multiple flight trials on each elk to account for seasonal, spatial and temporal variation, and calculated mean individual values for ‘flight’.

Response to novel sound playback

To measure the responses of elk to novel sounds, we hid a speaker in vegetation and waited until marked elk were in its vicinity while facing towards the sound source, and approximately equidistant from it. Sound stimuli were chosen haphazardly without replacement within sample sessions from a wide variety of novel sounds (e.g. machine gun, drum solo, power saw) by a hidden observer. A large variety of sounds were used to lessen potential for habituation to the sounds themselves. In each trial, we recorded the

rank order in which individuals were displaced in response to the sound, considering the first to be displaced as the most responsive. In all cases there were no obstacles (including other elk) inhibiting this displacement. Where we could not directly compare two individuals, we inferred the rank of their responsiveness using results from trials where each individual could be compared separately to elk present in each trial. We then combined the results from all trials and dyadic inferences to create a complete ranking of the relative responsiveness of all individuals. If all individuals responded simultaneously, or not at all, the trial was eliminated from further analyses. We collected data on sound stimuli only in Banff to avoid interfering with another study in Jasper, and because unpredictable responses near fencing presented a potential injury risk to the captive elk.

Exploration of novel objects

We selected as novel objects items that were foreign to wild elk habitat and were expected to elicit a range of individual behavioural responses from neophobia to neophilia (see [Supplementary Fig. S1](#)). We placed these objects throughout our study area, each positioned 7 m away from a motion-activated camera, and changed both the camera site and the novel object after each visit by any group of elk. We categorized each individual elk visit along a gradient of exploratory behaviour: 1 = visited the site and looked at but did not approach the object; 2 = approached object; 3 = investigated object to within one head length of object; 4 = physically interacted with the object. We used the means of these scores to calculate an 'exploration' value for each individual (higher score = more exploratory). As for the sound stimuli, we changed objects after each use (measured by elk visits) to maintain their novelty and prevent habituation.

Social hierarchy

We recorded the results of all dyadic encounters between marked adult females where overt aggression resulted in the displacement of one elk. We categorized the displacing elk as 'dominant' and the displaced animals as 'submissive', and used the collective results to delineate a dominance hierarchy for all marked elk, where higher scores indicate higher ranking. We decided ties between marked elk by using their respective dyadic outcomes with unmarked elk. If direct encounters between two elk had opposite outcomes, we assigned the same rank to both individuals.

Vigilance behaviour

We used a high-definition video camera to film groups of grazing elk for focal samples of 10 min, and then watched the videos to determine precise time budgets for individuals. We differentiated multiple forms of vigilance or potentially vigilant behaviour, such as 'pseudovigilance' (i.e. multitasking vigilance with eating; [Fortin, Boyce, & Merrill, 2004](#)) and 'apparent vigilant behaviour', which video analysis later revealed to be social or rumination behaviour. We identified vigilance where individuals held their head stiffly above the height of their shoulders and were clearly attentive either visually or with erect and focused ears. We used this method only on the wild elk where the presence of predators increased its relevance and where uninterrupted 10 min observation was more feasible because of the absence of fences disrupting sight-lines, animal density was lower and radiocollars improved sightability. We calculated the proportion of time spent vigilant out of total observation time, where a higher value indicates more time spent vigilant.

Lead elk

As in many ungulate species, herd movements are often dictated by lead elk cows, which are followed by the remainder of the herd

([Geist, 1982](#)). These lead elk thus probably also influence the migratory decisions of other elk. In BNP (2010 only), when large enough groups of elk moved from one discrete habitat patch to another, the herd typically formed in single or double file with clear leaders at the heads of these lines. We could easily distinguish these travel bouts from regular foraging events, in which elk move independently without leadership. We identified leaders by their position in front of a linear group of elk and a movement trajectory that was followed by the others. Each time we observed such movement, we recorded the identity of the lead elk and summed these events as individual scores for leading behaviour. We considered this sum to be a reliable relative metric because our daily tracking data caused us to observe all elk similar numbers of times.

Data Analyses

We used principal component analysis (PCA) to quantify elk behavioural syndromes, using eigenvectors to demonstrate the relationships between each of the personality traits we measured, and reducing this information to two orthogonal axes upon which we could plot the relative positions of each individual elk within two dimensions of any existing behavioural syndromes. PCA was preferred over nonmetric dimensional scaling (NMDS) for this step, but non-normality in some behavioural metrics discouraged the use of the PCA axes as independent variables for further analysis, and so we employed NMDS for the purpose of creating a single dimension defining a gradient of personality types. Not all behavioural metrics could be recorded in each study area (above), which resulted in variation among locations and years in the number of metrics used to derive personality types (BNP 2010 = all 7 behaviours, BNP 2011 = 6 behaviours, JNP = 5 behaviours, captive = 4 behaviours). We derived separate gradients for each population and year. We assessed the consistency of behavioural types by comparing our personality metric to elk age for the captive population and by comparing annual metrics for the 33 animals measured in both years in the BNP population. We did not have information on individual ages of wild elk. When using *t* tests, we report all possible comparisons (see Results); thus, *P* values are not adjusted for multiple comparisons (following: [Rothman, 1990](#); [Saville, 1990](#)). We set $\alpha = 0.05$ and performed all statistics using Stata 11.1 (StataCorp, College Station, TX, U.S.A.).

RESULTS

Behavioural Correlations

In BNP (2010), we recorded 5–18 flight response trials per elk ($\bar{x} = 9.4$), 239 total sound stimulus dyads, 158 dominance interactions, 51 incidents of leading behaviour, 5–16 time budgets and positions in herd per elk ($\bar{x} = 9.6$) and presented 66 unique novel objects that were visited by at least one elk. Because vigilance and pseudovigilance behaviours were correlated, our final vigilance metric combined the two. In BNP (2011), we recorded 4–19 flight response trials per elk ($\bar{x} = 13.1$), 333 total sound stimulus dyads, 334 dominance interactions, 4–20 time budgets and individual positions ($\bar{x} = 10.6$) and presented 144 novel objects. In JNP we recorded 6–15 flight trials per elk ($\bar{x} = 11.1$), 90 dominance interactions, 4–30 time budgets and individual positions ($\bar{x} = 21.3$) and presented 61 novel objects. On the elk farm, we recorded 6–16 flight response trials and positions in herd per elk ($\bar{x} = 11.9$) and 101 dominance interactions and presented 27 novel objects.

Application of PCA reduced the data to orthogonal axes that accounted for 72.0% (BNP 2010), 80.2% (BNP 2011), 83.4% (JNP) and 91.5% (captive) of the variation in each behavioural data set ([Figs 1, 2](#)).

In BNP and JNP, all behaviours loaded most heavily onto the first factor (F1, horizontal axis) except for vigilance, which loaded most heavily onto F2. The correlations between pairs of behaviours (Table 1) elucidated a behavioural syndrome in which a single dimension (F1) could be interpreted as a personality gradient that ranged from negative values we equated with ‘shy’ to positive values we deemed to be ‘bold’. We considered vigilance to be part of a secondary personality dimension. Eigenvalues depicting the relationships between the factors and behaviours showed that elk with the higher scores on the boldness axis were more dominant, more exploratory, adopted more peripheral positions within the herd, had lower flight response distance, were less responsive to novel sounds and were more likely to lead groups of elk (Figs 1, 2). The correlations among our behavioural metrics were consistent across our study populations.

Consistency of Personality across Contexts

To demonstrate that these behavioural correlations were consistent across contexts, and thus constituted a true behavioural

syndrome gradient, we used NMDS to reduce the data to a single dimension we termed ‘personality’ (BNP 2010: $N = 35$, loss criterion = 0.011; BNP 2011: $N = 50$, loss criterion = 0.0075; JNP: $N = 22$, loss criterion = 0.0076; captive: $N = 70$, loss criterion = 0.0071). Scree plots and ordination stress tests show that little information was lost by using just one dimension compared to two, so we used these single personality scores as a dependent variable in two further analyses. We assessed the effect of age in the captive population for which we found no relationship for individuals that ranged from 3 to 14 years old ($F_{1,69} = 0.43$, $R^2 = 0.006$, $P = 0.52$; Fig. 3). In BNP, personality values were highly correlated for the 33 individuals that were measured in both years ($F_{1,32} = 263$, $R^2 = 0.79$, $P < 0.001$; Fig. 3).

As a measure of the effect of predator presence, we compared average elk flight response distances within specified areas for 3-day periods with and without evidence of predator activity. When wolf tracks were detected, flight response distances increased from 40.4 m to 46.3 m (SE = ±8.7 m; two-tailed t test: $t_{1,50} = 2.75$, $P < 0.01$), but the presence of cougar tracks caused a slighter increase (to 42.5 m) that was not statistically different from days

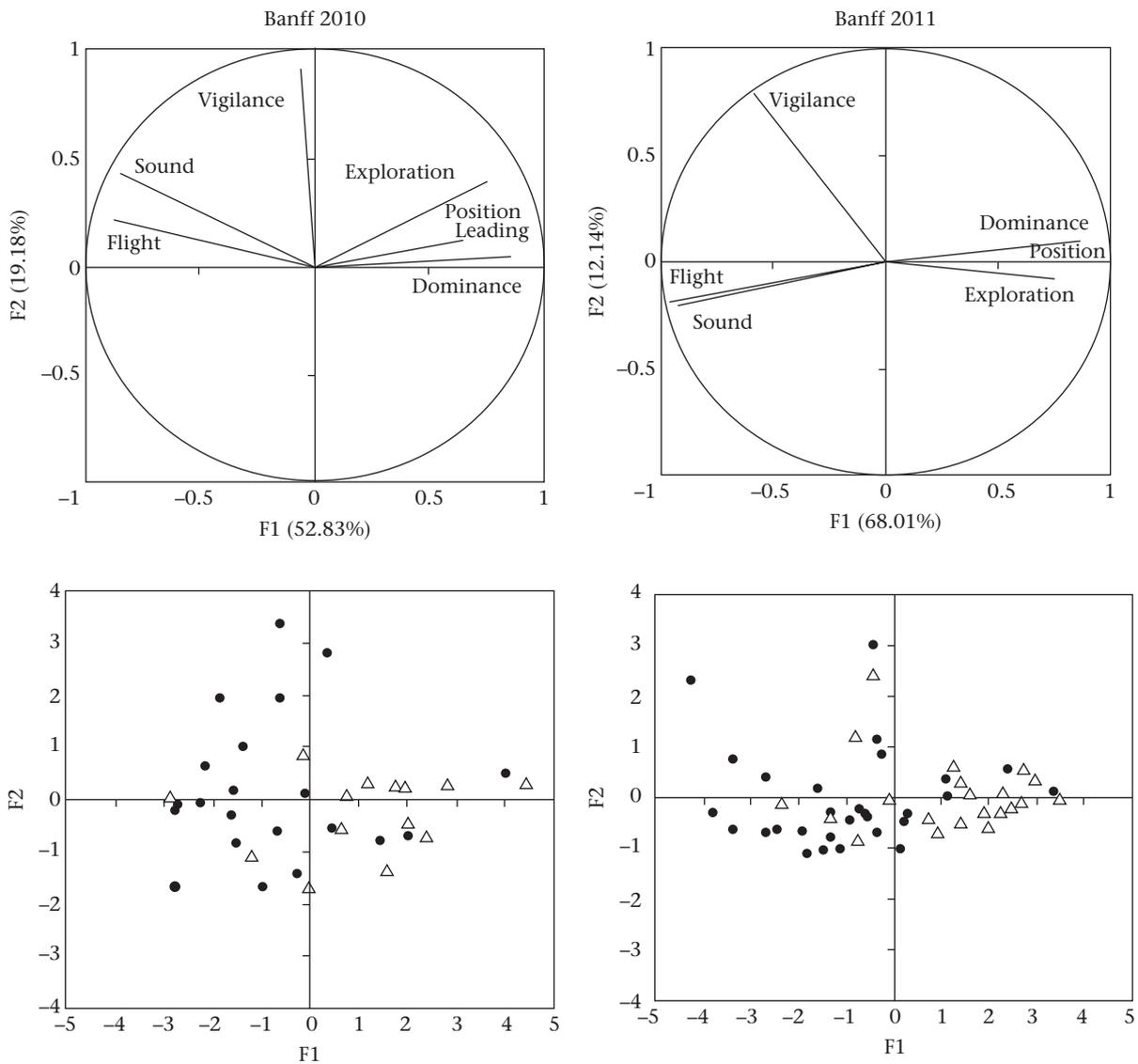


Figure 1. PCA results for personality traits composing behavioural syndromes in wild elk in Banff National Park, Alberta, Canada. Top panels show eigenvectors for each personality trait. Bottom panels show positions of individual elk along factor axes (open triangles: residents; solid circles: migrants).

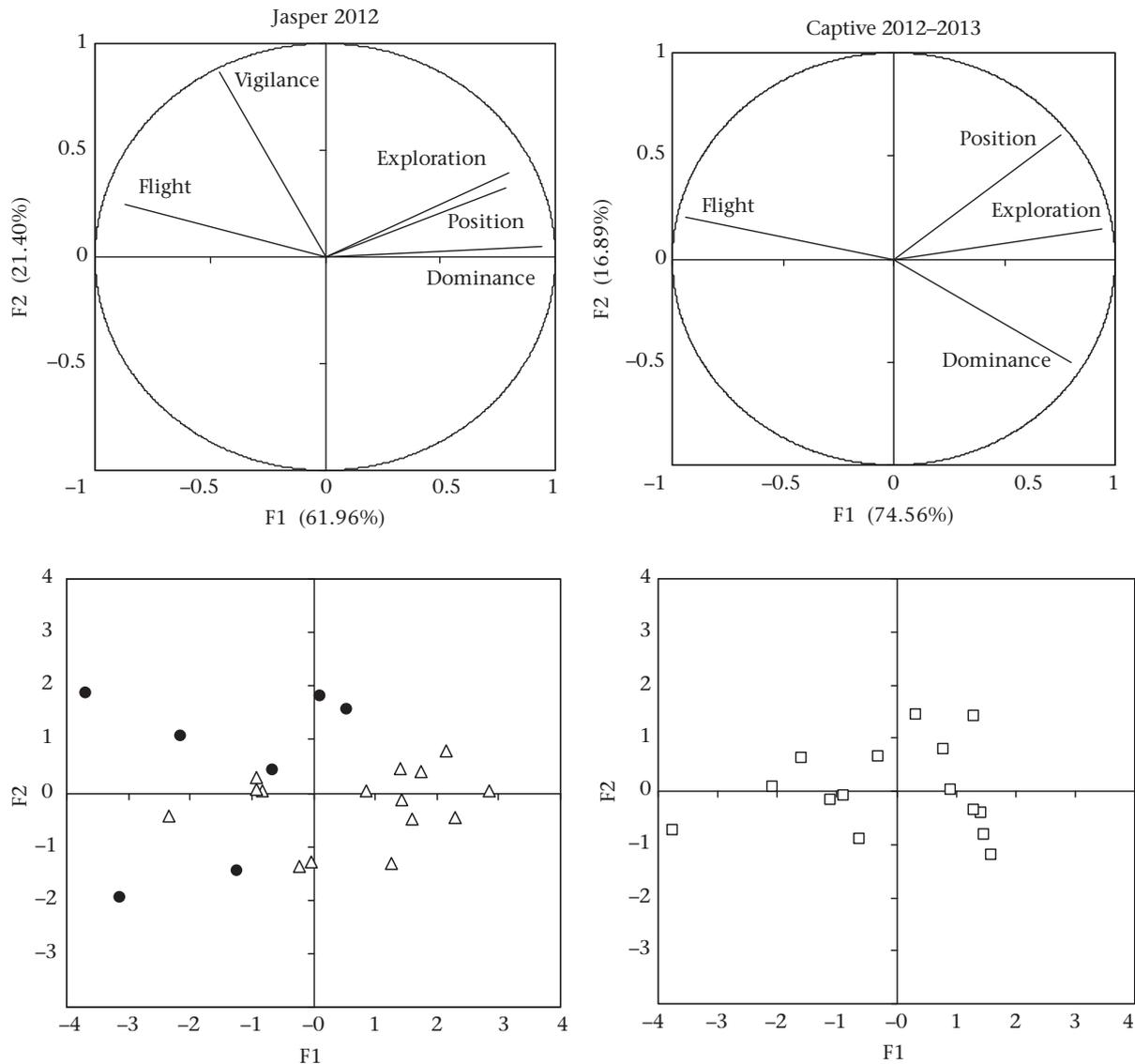


Figure 2. PCA results for personality traits composing behavioural syndromes in wild elk in Jasper National Park, Alberta, and in a captive population of elk near Wetaskiwin, Alberta. Top panels show eigenvectors for each personality trait. Bottom panels show positions of individual elk along factor axes (open triangles: residents; solid circles: migrants).

without predators ($t_{1,28} = 0.69$, $P = 0.49$). When measured for single days, the effect of wolf activity was more slight and diminished over time, when measured 1 day after (± 5.1 m; $t_{1,40} = 1.73$, $P = 0.092$), 2 days after (± 3.9 m; $t_{1,37} = 1.45$, $P = 0.16$) or 3 days after (± 0.6 m; $t_{1,35} = 0.31$, $P = 0.76$) a wolf track was detected.

Personality and Migratory Strategies

In the Banff population, migrant elk ($N = 29$) had 40% higher mean flight responses (two-tailed t test: $t_{48} = 4.05$, $P < 0.001$) and 67% higher mean ranking in response to novel sounds ($t_{48} = 3.35$, $P < 0.01$) compared to resident elk ($N = 21$). Resident elk had 50% higher exploration scores ($t_{48} = 3.01$, $P < 0.01$), 9% higher position scores ($t_{48} = 3.02$, $P < 0.01$) and a mean dominance ranking that was 61% higher than migrant elk ($t_{48} = 3.11$, $P < 0.01$; Fig. 4). Mean vigilance scores were 36% higher in migrants than in residents ($t_{48} = 1.72$, $P = 0.092$). Factor loadings for personality in migrants were larger for behaviours relating to anthropogenic and novel stimuli (i.e. flight from humans, novel objects and sounds), whereas residents had higher factor loadings for nonanthropogenic and

non-novel stimuli (i.e. vigilance, position in herd, social hierarchy; Table 2). While we could not determine whether these differences were statistically significant, they are potentially ecologically significant. As descriptive variables, these factor loadings suggest that resident elk were less variable in behaviours related to anthropogenic stimuli whereas migrants were less variable in behaviours that related to nonanthropogenic contexts.

The mean positions along the F1 personality gradient, which we interpreted approximately as a shy–bold gradient, were significantly higher for residents than for migrants in both populations and, in BNP, in both years (BNP 2010: residents: 1.10 ± 0.48 ; migrants: -0.73 ± 0.37 ; $t_{1,33} = 3.03$, $P = 0.005$; BNP 2011: residents: 1.16 ± 0.34 ; migrants: -0.84 ± 0.36 ; $t_{1,48} = 3.89$, $P < 0.001$; JNP: residents: 0.68 ± 0.47 ; migrants: -1.43 ± 0.46 ; $t_{1,20} = 3.08$, $P < 0.01$). There were no similar differences between the mean values for F2 between migrants and residents in either population or year (BNP 2010: $t_{1,33} = 0.97$, $P = 0.39$; BNP 2011: $t_{1,48} = -0.41$, $P = 0.68$; JNP: $t_{1,20} = 1.51$, $P = 0.15$). In BNP, migratory choices in the summer following data collection were significantly predicted by personality values in each of 2010 (logistic regression: LL = -18.54,

Table 1

Correlation matrix for behavioural traits comprising behavioural syndromes in wild elk (Banff National Park, BNP; Jasper National Park, JNP) and captive elk (Amberlane)

	Flight	Vigilance	Position	Exploration	Sound	Dominance	Leading
BNP 2010							
Flight	1						
Vigilance	0.151	1					
Position	-0.522	-0.221	1				
Exploration	-0.415	-0.100	0.452	1			
Sound	0.867	0.344	-0.436	-0.281	1		
Dominance	-0.757	-0.003	0.617	0.583	-0.693	1	
Leading	-0.528	0.076	0.512	0.238	-0.490	0.521	1
BNP 2011							
Flight	1						
Vigilance	0.423	1					
Position	-0.716	-0.440	1				
Exploration	-0.666	-0.408	0.422	1			
Sound	0.920	0.414	-0.783	-0.576	1		
Dominance	-0.832	-0.437	0.597	0.625	-0.765	1	
JNP 2012							
Flight	1						
Vigilance	0.534	1					
Position	-0.567	-0.102	1				
Exploration	-0.579	-0.049	0.551	1			
Dominance	-0.722	-0.399	0.710	0.757		1	
Amberlane							
Flight	1						
Position	-0.541		1				
Exploration	-0.878		0.726	1			
Dominance	-0.777		0.383	0.612		1	

Significant outcomes ($P < 0.050$) are shown in bold.

$\chi^2_1 = 7.17$, $N = 33$, $P < 0.01$) and 2011 (LL = -28.95, $\chi^2_1 = 10.13.30$, $N = 50$, $P < 0.01$), but similar information was not available in JNP. Based on the median personality value along the F1 (shy–bold) gradient, the shyer half of the population migrated at approximately a 3:1 ratio in both 2010 and 2011, whereas the bolder half of the population were residents, again at a 3:1 ratio (Fig. 5). At the end of our study we learned that the boldest and most dominant individual that we identified in the Banff population had been reported repeatedly in public safety incidents, one of which required hospitalization of a person.

DISCUSSION

In this study, we explored the potential to apply the concept of behavioural syndromes (sensu Sih et al., 2004) to wild, but habituated elk and to demonstrate how personality might apply to wildlife management and conservation. Our first objective was to determine whether elk show covarying suites of behaviours that are consistent across contexts, a necessary condition for categorizing this variation as behavioural types (Sih et al., 2004). Based on values from up to seven different behavioural metrics, we used multivariate statistics to identify a gradient of personality types in each population that could be interpreted along a shy–bold axis (Wilson et al., 1994). Bolder elk in each population were characterized by lower flight distances, lesser responsiveness to sounds, occupancy of more peripheral positions within groups, greater exploration of novel objects, social dominance over shyer conspecifics and a greater tendency to lead other elk to new locations. The presence of similar tendencies in two wild populations and one captive population suggests that this suite of behavioural traits is conserved across contexts and through ecological time. Further evidence of their permanence was provided by the lack of dependence of behavioural type on animal age in our captive population and the consistency of values measured for 33 wild individuals between years. We confirmed the presence of consistent and recognizable behavioural types in elk and identified several

behavioural metrics with which these behavioural types might be identified for other wild animals and management purposes.

Our second objective was to determine whether variation in personality among individuals could predict migratory choices. We emphasized migration as a management outcome because it is already known to vary among individuals within ungulate populations (Boyce, 1991; Geist, 1971; Naidoo, Du Preez, Stuart-Hill, Jago, & Wegmann, 2012) and is declining in ungulate populations worldwide (reviewed by: Berger, 2004; Bolger, Newmark, Morrison, & Doak, 2008). It also appears to be related to habituation (sensu Fynn & Bonyongo, 2011; Hebblewhite & Merrill, 2009; Muhly, Semeniuk, Massolo, Hickman, & Musiani, 2011), which creates further management issues. We found remarkable consistency between the two wild populations for the bolder half of the population to adopt a resident strategy with a 3:1 ratio. Correspondingly, the shyer halves of the elk in each population were three times more likely to migrate. This tendency applied in both Banff, where migrants and residents mixed seasonally, and Jasper, where the groups appeared to be separate year round. Interestingly, migratory strategies were not completely separable by personality scores. Our classification designated a quarter of the animals in each population as bold migrants or shy residents, indicating that migratory choices were influenced by additional factors, which may have acted independently or as an interaction with personality. This variation and several other aspects of our results have important implications for wildlife managers with additional insights for basic research concerning animal personality and the evolution of behavioural types.

The first of these insights may be the consistency with which a single gradient of bold to shy behavioural types was evident in three different study populations, under captive and wild conditions, and among years. The additional consistency within individuals and the lack of an effect of age both support the existence of a genetic basis to animal personality as emphasized for species ranging from wild bighorn sheep, *Ovis canadensis* (Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009) to humans (Caspi,

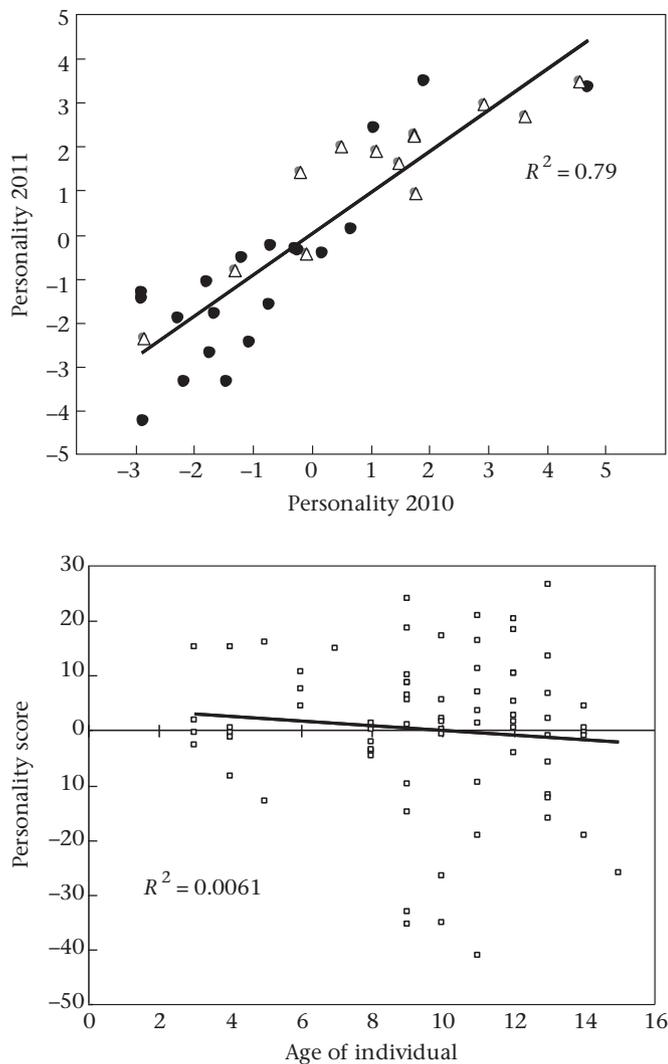


Figure 3. (a) Comparison of wild elk personality in 2010 and those same individuals in 2011. Open triangles: residents; solid circles: migrants. (b) Effect of age on personality in captive elk. Personality gradients are dimension 1 from NMDS analysis.

2005; Penney, David, & Witt, 2011). In addition to consistency across sites and context (captive versus wild), behavioural types appeared to be consistent through time despite stochasticity in human disturbances, weather variables, forage availability, and even predator activity. Of these temporal variables, the presence of predators appeared to exert an effect on elk behaviour as measured by flight response distances. This effect was most apparent when measured for several days at a time and it appeared to decline rapidly in the days following predator detection. Elk responses to predators appeared to be temporary and relative; the average herd flight responses in BNP were actually lower in the year with greater predator activity (as reported by Ham, 2011). Even so, captive elk that had never known predators, migration, or even variation in food supply showed a range of personality scores comparable to the two wild populations. Together, these results support the assertion by Sih, Cote, Evans, Fogarty, and Pruitt (2012) that personality traits (e.g. bold–shy; neophobic–neophilic) are relatively hardwired from an early age and do not change much in response to environmental influences. The further implication is that personality predicts migration, and not the other way around.

The relative permanence of behavioural types in our study animals lends additional insights to the phenomenon of facultative

migration in ungulates, which others have suggested is an adaptation to variable environments (reviewed by Fynn & Bonyongo, 2011). Our results also suggest that variation in predation pressure is especially relevant; a subpopulation of animals in JNP residing in an area with more predators contained mostly migratory individuals. However, our results also suggest that the advantage of migration (or residency) is partially dependent on animal personality, which must limit the consistency and speed of adaptation at the level of populations. Indeed, the gradual increase in residency that appears to occur with increasing habituation in some elk populations would be expected if (1) bold behavioural types are more likely to habituate than shy animals, but (2) bold types are strongly, but not completely, correlated with the resident strategy. Some mismatches in the optimal alignment of personality and migratory strategy would occur if, for example, animals are more likely to adopt the migratory strategy shown by their mothers, regardless of personality tendencies inherited from their fathers. Such situations may be the reason that individual elk are sometimes known to switch from a migratory to resident strategy or vice versa.

The prevalence of facultative migration in ungulates provides, in turn, a potential insight for the broader study of animal personality. As prey species, ungulates may be especially prone to the loss of migration if their habituation to people occurs more rapidly and completely than their habituation to predators (sensu Berger, 2004; Clutton-Brock, 1992). This effect is likely widespread for ungulates in protected areas without hunting (e.g. Ciuti et al., 2011), where they would be expected to benefit from a closer association with people than can be tolerated for or by predators (sensu Conover, 2002). The effect of refuge from predators on migration may generalize well beyond ungulates. For example, a year-round resident warbler species (*Sylvia melanocephala*) shows more exploratory behaviour than a closely related migratory species (*Sylvia borin*; Mettke-Hoffman, Ebert, Schmidt, Steiger, & Stieb, 2005). Among roach fish (*Rutilus rutilus*), bolder animals migrate more often, but they do so to reach refuge from predation (Chapman et al., 2011). Together, these findings refine the suggestion that personality, determined early in life through a combination of genes and developmental environment, constrains the subsequent behavioural choices of individuals (sensu Dochtermann & Dingemans, 2013). Further study may reveal that personality is a mechanism primarily for behavioural adaptations that relate to self-preservation.

Notwithstanding the insights we propose above, we do not mean to suggest that personality is the only or most important factor affecting recent changes to animal migration. Habitat loss, degradation and fragmentation impact all migratory species. Physical barriers that increase movement costs impede the migration of wildebeest, *Connochaetes taurinus* (Morrison & Bolger, 2012) and Mongolian gazelles, *Procapra gutturosa* (Ito et al., 2005). Migratory barriers for monarch butterflies, *Danaus plexippus*, are caused by human management of milkweed (*Asclepias* spp.) and cause population declines (Satterfield, Maerz, & Altizer, 2015). Similar declines afflict populations of northern right whales, *Eubalaena glacialis*, which migrate through a gauntlet of shipping lanes and fishing equipment (Morano et al., 2012). Even in our study, elk experienced impediments to migration from human infrastructure, which was one of the reasons for the creation of crossing structures on the Trans Canada highway that bisects Banff National Park (e.g. Clevenger & Wierzchowski, 2006).

Despite these caveats, we suggest that more attention to animal personality could provide wildlife managers and conservationists with an important tool for interpreting and managing habituation. In essence, the same personality types that evolved to exploit different or changing environments over evolutionary time (sensu

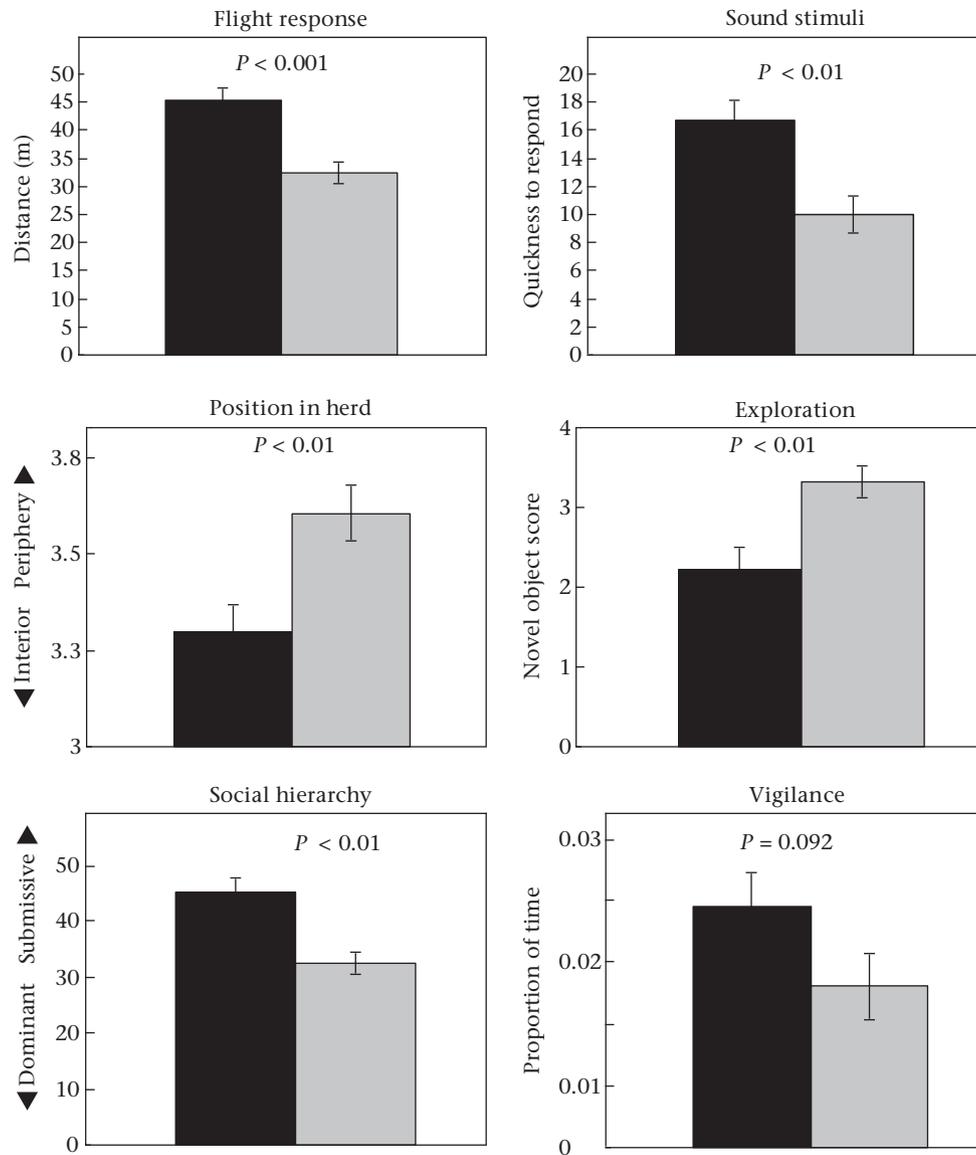


Figure 4. Mean scores for correlated individual behavioural traits composing elk behavioural syndromes, for each migrant (black bars) and resident (grey bars) adult female elk in Banff National Park, Alberta, Canada. All measures were taken when residents and migrants form a single overwintering herd. Y axes for sound stimuli and social hierarchy represent rank ordination. Y axes for position in herd and exploration represent average scored values for those behaviours. P values are for two-tailed *t* test results with $df = 48$. Error bars are SE.

Table 2

Percentage contribution of each variable to F1 and F2 PCA axes, for migrant and resident elk

	Migrants		Residents	
	F1	F2	F1	F2
Anthropogenic/novel stimuli				
Flight	23.489	3.894	21.965	1.600
Exploration	14.744	2.178	7.158	58.298
Sound	22.485	1.520	20.957	8.332
Nonanthropogenic/non-novel stimuli				
Vigilance	6.460	84.770	11.107	23.485
Position	14.775	3.080	17.286	5.610
Dominance	18.047	4.558	21.527	2.676

Individual behaviours composing elk behavioural syndromes are grouped in relation to anthropogenic and novel stimuli versus nonanthropogenic and non-novel stimuli, including predation detection and social interactions. Significant personality factors for migrants and residents are shown in bold.

Smith & Blumstein, 2008) can now be exploited by managers. An obvious application may be to proactively treat invasive, urban-exploiting species that are prone to conflict following the loss of migration, such as Canada geese, *Branta canadensis* (Washburn & Seamans, 2012) and fruit bats (*Pteropus* spp.; Plowright et al., 2011). If these populations stem from a few bold pioneers, managers could intensively target the first few individuals that arrive in new areas and avoid waiting for the population to grow and problems to develop. Likewise, it could be as important to reduce habituation in rare species, as occurred when managers realized, and then carefully prevented, the contagion effect of bold, captive-bred whooping cranes, *Grus americana*, that habituated to people, abandoned migration and reduced flock-level survival in the wild (Urbanek, Szyszkowski, & Zimorski, 2014). For other threatened species, such as caribou (*Rangifer* spp.), it could be helpful to manipulate bolder individuals to facilitate greater habituation to human-dominated areas (Johnson & Russell, 2014), thereby

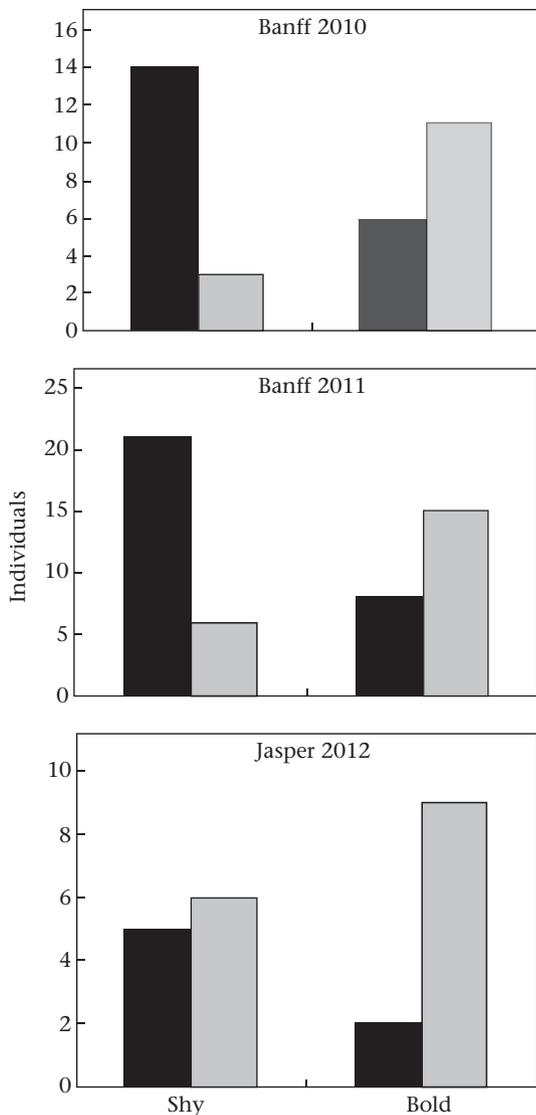


Figure 5. Population proportions of migrant (black bars) and resident (grey bars) elk with shy or bold personality types, in Banff National Park, Alberta, Canada, in 2010 and 2011, and Jasper National Park, Alberta, in 2012. Global medians of personality scores for each population were used to divide each population into shy and bold halves.

compensating for their relative shyness in the complex, multipredator, multiprey systems in which they reside (e.g. Gustine, Parker, Lay, Gillingham, & Heard, 2006). This benefit probably explains why migration is declining in moose, *Alces alces*, which have higher calf survival in areas near people (White et al., 2014), and nyala, *Tragelaphus angasii*, which seek out human-disturbed areas (Atickem et al., 2014).

A likely and recurrent challenge to using animal personality for the conservation and management of wildlife will be the frequency with which humans unintentionally select for compatible individuals of many species (e.g. Agnvall, Jongren, Strandberg, & Jensen, 2012; Ciuti et al., 2011; Ramkumar, Ramakrishnan, & Saravanamuthu, 2014; Shivik et al., 2003). Humans do this without anticipating how these bold, habituating pioneers facilitate the arrival of shy individuals via conspecific attraction (sensu Michelena, Jeanson, Deneubourg, & Sibbal, 2010) to produce burgeoning populations that are sedentary, increasingly bold, and eventually problematic. In some cases, that inadvertent selection may only cause inconvenience, but considerable risk to public

safety occurs when carnivores are habituated. For example, cougars are returning to their former ranges across North America, often living in close proximity to humans who are unaware of their presence (e.g. Knopff, Webb, & Boyce, 2013). Such seemingly adaptive responses to anthropogenic change by predators may also produce ecological traps, as has been described for threatened grizzly bears, *Ursus arctos horribilis*, foraging in productive roadside habitat (e.g. Neilson, Stenhouse, & Boyce, 2006). To use animal personality as a management tool, it will be necessary to anticipate and recognize complex behavioural adaptations, which will often occur as frequency-dependent interactions among individuals (sensu Smith, 1974), both within and among species. Because personality itself is presumed to result from frequency-dependent selection in the context of mixed evolutionarily stable strategies (e.g. Brodersen et al., 2014; Patrick, Charmantier, & Weimerskirch, 2013; Wolf & Weissing, 2012), greater use of animal personality by wildlife managers is as likely to contribute to as benefit from the burgeoning basic literature on behavioural types.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.02.007>.

References

- Agnvall, B., Jongren, M., Strandberg, E., & Jensen, P. (2012). Heritability and genetic correlations of fear-related behaviour in red junglefowl: possible implications for early domestication. *PLoS One*, 7, e35162.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 47, 227–265.
- Atickem, A., Loe, L. E., & Stenseth, N. C. (2014). Individual heterogeneity in use of human shields by mountain nyala. *Ethology*, 120, 715–725.
- Ball, J. P., Nordengren, C., & Wallin, K. (2001). Partial migration by large ungulates: characteristics of seasonal moose (*Alces alces*) ranges in northern Sweden. *Wildlife Biology*, 7, 39–47.
- Bejder, L., Samuels, A., Whitehead, H., Finn, H., & Allen, S. (2009). Impact assessment research: use and misuse of habituation, sensitization and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series*, 395, 177–185.
- Berger, J. (2004). The last mile: how to sustain long-distance migration in mammals. *Conservation Biology*, 18, 320–331.
- Beschta, R. L., & Ripple, W. J. (2007). Wolves, elk, and aspen in the winter range of Jasper National Park, Canada. *Canadian Journal of Forest Research*, 37, 1873–1885.
- Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, 142, 2401–2414.
- Bolger, D. T., Newmark, W. D., Morrison, T. A., & Doak, D. F. (2008). The need for integrative approaches to understand and conserve migratory ungulates. *Ecology Letters*, 11, 63–77.
- Bounds, D. L., & Shaw, W. W. (1994). Managing coyotes in U.S. National Parks: human–coyote interactions. *Natural Areas Journal*, 14, 280–284.

- Boyce, M. S. (1991). Migratory behavior and management of elk (*Cervus elaphus*). *Applied Animal Behaviour Science*, 29, 239–250.
- Brodersen, J., Chapman, B. B., Nilsson, P. A., Skov, C., Hansson, L.-A., & Bronmark, C. (2014). Fixed and flexible: coexistence of obligate and facultative migratory strategies in a freshwater fish. *PLoS One*, 9(3), e90294. <http://dx.doi.org/10.1371/journal.pone.0090294>.
- Brook, R. K. (2009). Historical review of elk–agriculture conflicts in and around Riding Mountain National Park, Manitoba, Canada. *Human–Wildlife Conflicts*, 3, 72–87.
- Carter, A. J., Feeney, W. E., Marshall, H. H., Cowlshaw, G., & Heinsohn, R. (2013). Animal personality: what are behavioural ecologists measuring? *Biological Reviews*, 88, 465–475.
- Caspi, A. (2005). Personality development: stability and change. *Annual Review of Psychology*, 56, 453–484.
- Chakraborty, K., & Mondal, J. (2013). Perceptions and patterns of human–elephant conflict at Barjora block of Bankura district in West Bengal, India: insights for mitigation and management. *Journal of Environmental Development and Sustainability*, 15, 547–565.
- Chapman, B. B., Hulthen, K., Blomqvist, D. R., Hansson, L. A., Nilson, J. A., Brodersen, J., et al. (2011). To boldly go: individual differences in boldness influence migratory tendency. *Ecology Letters*, 14, 871–876.
- Ciuti, S., Muhly, T. B., Paton, D. G., McDevitt, A. D., Musiani, M., & Boyce, M. S. (2011). Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), 4407–4416. <http://dx.doi.org/10.1098/rspb.2012.1483>.
- Clevenger, A. P., & Wierzchowski, J. (2006). Maintaining and restoring connectivity in landscapes fragmented by roads. In K. Crooks, & M. Sanjayan (Eds.), *Connectivity conservation* (pp. 502–535). Cambridge, U.K.: Cambridge University Press.
- Clutton-Brock, J. (1992). The process of domestication. *Mammal Review*, 22, 79–85.
- Conover, M. (2002). *Resolving human–wildlife conflicts: The science of wildlife damage management*. Boca Raton, FL: Lewis.
- Dalmau, A., Ferret, A., & Manteca, X. (2010). Vigilance behavior of Pyrenean chamois *Rupicapra pyrenaica pyrenaica*: effect of sex and position in the herd. *Current Zoology*, 56, 232–237.
- Dingemans, N. J., Dochtermann, N. A., & Nakagawa, S. (2012). Defining behavioural syndromes and the role of ‘syndrome deviation’ in understanding their evolution. *Behavioral Ecology and Sociobiology*, 66, 1543–1548.
- Dochtermann, N. A., & Dingemans, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, 24(4), 806–811. <http://dx.doi.org/10.1093/beheco/art002>.
- Domjan, M. (2010). *The principles of learning and behavior* (6th ed.). Belmont, CA: Thomson Wadsworth.
- Driscoll, C. A., MacDonald, D. W., & O’Brien, S. J. (2009). From wild animals to domestic pets, an evolutionary view of domestication. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 9971–9978.
- Einfeld, S. L., Tonge, B. J., & Clarke, K. S. (2013). Prevention and early intervention for behaviour problems in children with developmental disabilities. *Current Opinions in Psychiatry*, 26, 263–269.
- Fortin, D., Boyce, M. S., & Merrill, E. H. (2004). Multi-tasking by mammalian herbivores: overlapping processes during foraging. *Ecology*, 85, 2312–2322.
- Fynn, R. W. S., & Bonyongo, M. C. (2011). Functional conservation areas and the future of Africa’s wildlife. *African Journal of Ecology*, 49, 175–188.
- Gates, C., & Hudson, R. J. (1978). Energy costs of locomotion in wapiti. *Acta Theriologica*, 23, 365–370.
- Geist, V. (1971). *Mountain sheep: A study in behaviour and evolution*. Chicago, IL: Chicago University Press.
- Geist, V. (1982). Adaptive behavioural strategies. In J. W. Thomas, & D. E. Towell (Eds.), *Elk of North America: Ecology and management* (pp. 219–278). Harrisburg, PA: Stackpole Books.
- Goldberg, J. F., Hebblewhite, M., & Bardsley, J. (2014). Consequences of a refuge for the predator–prey dynamics of a wolf–elk system in Banff National Park, Alberta, Canada. *PLoS One*, 9(3), e91417. <http://dx.doi.org/10.1371/journal.pone.0091417>.
- Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychology Bulletin*, 127, 45–86.
- Gustine, D. D., Parker, K. L., Lay, R. J., Gillingham, M. P., & Heard, D. C. (2006). Calf survival of woodland caribou in a multi-predator ecosystem. *Wildlife Monographs*, 165, 1–32.
- Ham, S. (2010). *Wildlife corridors around developed areas in Banff National Park, Winter 2009/2010*. Progress report. Banff, Alberta: Parks Canada Banff Warden Service.
- Ham, S. (2011). *Wildlife corridors around developed areas in Banff National Park, Winter 2010/2011*. Progress report. Banff, AB: Parks Canada Banff Warden Service.
- Hebblewhite, M., & Merrill, E. H. (2009). Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology*, 90, 3445–3454.
- Hebblewhite, M., & Merrill, E. H. (2011). Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. *Oikos*, 120, 1860–1870.
- Honeyman, J. (2008). *A retrospective evaluation of the effectiveness of aversive conditioning on grizzly bears in Peter Lougheed Provincial Park, Alberta, Canada* (M.Sc. thesis). Victoria, BC, Canada: Royal Roads University.
- Ito, T. Y., Miura, N., Lhagvasuren, B., Enkhbileg, D., Takatsuki, S., Tsunekawa, A., et al. (2005). Preliminary evidence of a barrier effect of a railroad on the migration of Mongolian gazelles. *Conservation Biology*, 19, 945–948.
- Johnson, C. J., & Russell, D. E. (2014). Long-term distribution responses of a migratory caribou herd to human disturbance. *Biological Conservation*, 177, 52–63.
- Kloppers, E. L., St. Clair, C. C., & Hurd, T. E. (2005). Predator-resembling aversive conditioning for managing habituated wildlife. *Ecology and Society*, 10(1), 31. <http://www.ecologyandsociety.org/vol10/iss1/art31/>.
- Knopff, K. H., Webb, N. F., & Boyce, M. S. (2013). Cougar population status and range expansion in Alberta during 1991–2010. *Wildlife Society Bulletin*, 38(1), 116–121. <http://dx.doi.org/10.1002/wsb.369>.
- Koolhaas, J. M., de Boer, S. F., Buwalda, B., & van Reenan, K. (2007). Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. *Brain, Behavior and Evolution*, 70, 218–226.
- Lack, D. (1954). *The natural regulation of animal numbers*. Oxford, U.K.: Clarendon Press.
- Laundre, J. W., Hernandez, L., & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing the ‘landscape of fear’ in Yellowstone National Park, U.S.A. *Canadian Journal of Zoology*, 79, 1401–1409.
- Lundberg, P. (2013). On the evolutionary stability of partial migration. *Journal of Theoretical Biology*, 321, 36–39.
- Mackenzie, J. (2001). *Movement patterns of elk in response to predation risk and energy gain in Banff National Park* (Masters of Science Thesis). Guelph, Ontario: Department of Zoology, University of Guelph.
- Mazur, R. L. (2010). Does aversive conditioning reduce human–black bear conflict? *Journal of Wildlife Management*, 74, 48–54.
- Messmer, T. A. (2009). Human–wildlife conflicts: emerging opportunities. *Human–Wildlife Conflicts*, 3, 10–17.
- Mettke-Hofmann, C., Ebert, C., Schmidt, T., Steiger, S., & Stieb, S. (2005). Personality traits in resident and migratory warbler species. *Behaviour*, 142, 1357–1375.
- Michelena, P., Jeanson, R., Deneubourg, J. L., & Sibbal, A. M. (2010). Personality and collective decision-making in foraging herbivores. *Proceedings of the Royal Society B: Biological Sciences*, 277, 1093–1099.
- Middleton, A. D., Kauffman, M. J., McWhirter, D. E., Cook, J. G., Cook, R. C., Nelson, A. A., et al. (2013). Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. *Ecology*, 94, 1245–1256.
- Morano, J. L., Rice, A. N., Tielens, J. T., Estabrook, B. J., Murray, A., Roberts, B. L., et al. (2012). Acoustically detected year-round presence of right whales in an urbanized migration corridor. *Conservation Biology*, 26, 698–707.
- Morrison, T. A., & Bolger, D. T. (2012). Wet season range fidelity in a tropical migratory ungulate. *Journal of Animal Ecology*, 81, 543–552.
- Muhly, T. B., Semeniuk, C., Massolo, A., Hickman, L., & Musiani, M. (2011). Human activity helps prey win the predator–prey space race. *PLoS One*, 6(3), e17050.
- Naidoo, R., Du Preez, P., Stuart-Hill, G., Jago, M., & Wegmann, M. (2012). Home on the range: factors explaining partial migration of African buffalo in a tropical environment. *PLoS One*, 7, e36527.
- Neilson, S. E., Stenhouse, G. B., & Boyce, M. S. (2006). A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, 130, 217–229.
- Oosten, J. E., Magnhagen, C., & Hemelrijk, C. K. (2010). Boldness by habituation and social interactions: a model. *Behavioral Ecology and Sociobiology*, 64, 793–802.
- Paquet, P. C., Wierzchowski, J., & Callaghan, C. (1996). *Summary report on the effects of human activity on gray wolves in the Bow river valley, Banff National Park, Alberta*. Prepared for the Banff Bow Valley Study. Ottawa, ON: Department of Canadian Heritage.
- Patrick, S. C., Charmantier, A., & Weimerskirch, H. (2013). Differences in boldness are repeatable and heritable in a long-lived marine predator. *Ecology and Evolution*, 13, 4291–4299.
- Penney, L. M., David, E., & Witt, L. A. (2011). A review of personality and performance: identifying boundaries, contingencies, and future research directions. *Human Resource Management Review*, 21, 297–310.
- Plowright, R. K., Foley, P., Field, H. E., Dobson, A. P., Foley, J. E., Eby, P., et al. (2011). Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). *Proceedings of the Royal Society B: Biological Sciences*, 278(1725), 3703–3712. <http://dx.doi.org/10.1098/rspb.2011.0522>.
- Ramkumar, K., Ramakrishnan, B., & Saravanamuthu, R. (2014). Crop damage by Asian elephants *Elaphus maximus* and effectiveness of mitigating measures in Coimbatore Forest Division, South India. *International Research Journal of Biological Sciences*, 3, 1–11.
- Rauer, G., Kaczensky, P., & Knauer, F. (2003). Experiences with aversive conditioning of habituated brown bears in Austria and other European countries. *Ursus*, 14, 215–224.
- Réale, D., Martin, J., Coltman, D. W., Poissant, J., & Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, 22, 1599–1607.
- Réale, D., Reader, S. M., Sol, D., McDougall, P. T., & Dingemans, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82, 291–318.
- Rothman, K. J. (1990). No adjustments are needed for multiple comparisons. *Epidemiology*, 1, 43–46.
- Satterfield, D. A., Maerz, J. C., & Altizer, S. (2015). Loss of migratory behaviour increases infection risk for butterfly host. *Proceedings of the Royal Society B: Biological Sciences*, 282(1801), 20141734. <http://dx.doi.org/10.1098/rspb.2014.1734>.

- Saville, D. J. (1990). Multiple comparison procedures: the practical solution. *American Statistician*, 44, 174–180.
- Schultz, R. D., & Bailey, J. A. (1978). Responses of national park elk to human activity. *Journal of Wildlife Management*, 42, 91–100.
- Setsaas, T. H., Holmern, T., Mwakalebe, G., Stokke, S., & Roskaft, E. (2007). How does human exploitation affect impala populations in protected and partially protected areas? A case study from the Serengeti ecosystem, Tanzania. *Biological Conservation*, 136, 563–570.
- Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. *PLoS One*, 9, e94630. <http://dx.doi.org/10.1371/journal.pone.0094630>.
- Shivik, J. A., Treves, A., & Callahan, P. (2003). Non-lethal techniques for managing predation: primary and secondary repellents. *Conservation Biology*, 17, 1531–1537.
- Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19, 372–378.
- Sih, A., Cote, J., Evans, M., Fogarty, S., & Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15, 278–289.
- Singland, J. R., & Greenwood, P. J. (1983). *The ecology of animal movement*. Oxford, U.K.: Clarendon Press.
- Smith, J. M. (1974). The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology*, 47, 209–221.
- Smith, B. R., & Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, 19(2), 448–455. <http://dx.doi.org/10.1093/beheco/arm144>.
- Smith, T. S., Herrero, S., & DeBruyn, T. D. (2005). Alaskan brown bears, humans, and habituation. *Ursus*, 16, 1–10.
- Spencer, R. D., Beausoleil, R. A., & Martorello, D. A. (2007). How agencies respond to human–black bear conflicts: a survey of wildlife agencies in North America. *Ursus*, 18, 217–229.
- Stamps, J. (2007). Growth–mortality tradeoffs and ‘personality traits’ in animals. *Ecology Letters*, 10, 355–363.
- Strum, S. C. (2010). The development of primate raiding: implications for management and conservation. *International Journal of Primatology*, 31, 133–156.
- Thompson, M. J., & Henderson, R. E. (1998). Elk habituation as a credibility challenge for wildlife professionals. *Wildlife Society Bulletin*, 26, 477–483.
- Urbanek, R. P., Szyszkoski, E. K., & Zimorski, S. E. (2014). Winter distribution dynamics and implications to a reintroduced population of migratory whooping cranes. *Journal of Fish and Wildlife Management*, 5, 340–362.
- Walter, W. D., Lavelle, M. J., Fischer, J. W., Johnson, T. L., Hygnstrom, S. E., & VerCauteren, K. C. (2010). Management of damage by elk (*Cervus elaphus*) in North America: a review. *Wildlife Research*, 37, 630–646.
- Washburn, B. E., & Seamans, T. W. (2012). Foraging preferences of Canada geese among turfgrasses: implications for reducing human–goose conflicts. *Journal of Wildlife Management*, 76, 600–607.
- White, K. S., Barten, N. L., Crouse, S., & Crouse, J. (2014). Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. *Ecology*, 95, 225–237.
- White, P. J., Davis, T. L., Barnowe-Meyer, K. K., Crabtree, R. L., & Garrott, R. A. (2007). Partial migration and philopatry of Yellowstone pronghorn. *Biological Conservation*, 135, 502–510.
- Whittaker, D., & Knight, R. L. (1998). Understanding wildlife responses to humans. *Wildlife Society Bulletin*, 26, 312–317.
- Wilson, D. S., Clark, A. B., Coleman, K., & Dearstyne, T. (1994). Shyness and boldness in humans and other animals. *Trends in Ecology & Evolution*, 9, 442–446.
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27, 452–461.