

Island tameness and the repeatability of flight initiation distance in a large herbivore

Doreen Cabrera, Daniel Andres, Philip D. McLoughlin, Lucie Debeffe, Sarah A. Medill, Alastair J. Wilson, and Jocelyn Poissant

Abstract: Antipredator behaviours can be lost relatively quickly in populations that are relieved of predation, as is known for several species inhabiting islands. Flight initiation distance (FID) is often studied in the context of island tameness; however, little is known about the factors that influence and maintain FID variation in predation-free populations. Here, we studied FID in foals of an isolated predator-free population of feral horses (*Equus caballus* L., 1758) on Sable Island, Canada, to determine if FID could be used for research on consistent individual differences in risk aversion and island tameness. In addition to testing for temporal, spatial, and sex effects on FID, we compared repeatability estimates at two temporal scales (within and among days). Similar FID for measurements obtained on the same day and for males and females indicated an absence of short-term desensitization and sex effects. In contrast, FID decreased for measurements made on subsequent days and from east to west, which could reflect habituation to human presence and (or) other temporal and spatial processes. Repeatability was high (0.42 ± 0.06), but tended to decrease with increasing time intervals. This study highlights the potential of FID for individual-based research on the ecology and evolutionary dynamics of risk aversion in predation-free populations.

Key words: boldness, *Equus caballus*, fear, horse, personality, risk aversion, temperament.

Résumé : Les comportements anti-prédateurs peuvent disparaître assez rapidement dans les populations ne faisant plus l'objet de prédation, comme cela est le cas pour plusieurs espèces habitant des îles. La distance de fuite (DF) est souvent étudiée dans le contexte de la docilité insulaire; cependant, les connaissances sur les facteurs qui influencent et maintiennent les variations de la DF dans les populations sans prédateurs sont toutefois limitées. Nous avons étudié la DF chez des poulains d'une population de chevaux feraux (*Equus caballus* L., 1758) isolée et sans prédateurs à l'île de Sable (Canada) pour déterminer si la DF peut être utilisée pour étudier les différences individuelles sur le plan de l'aversion au risque et de la docilité insulaire. En plus de vérifier la présence d'effets temporels, spatiaux et du sexe sur la DF, nous avons comparé des estimations de la répétabilité à deux échelles temporelles (durant une même journée et sur plusieurs jours). Des DF semblables pour des mesures obtenues le même jour et pour les mâles et les femelles indiquent l'absence de désensibilisation à court terme et d'effets du sexe. Par contre, la DF diminuait pour des mesures prises sur plusieurs jours et de l'est vers l'ouest, ce qui pourrait refléter une habituation à la présence d'humains ou d'autres processus temporels ou spatiaux. La répétabilité était élevée ($0,42 \pm 0,06$), mais tendait à diminuer pour des intervalles de temps plus grands. L'étude fait ressortir le potentiel que présente la DF pour l'étude reposant sur les individus de l'écologie et la dynamique de l'évolution de l'aversion au risque dans les populations sans prédateurs. [Traduit par la Rédaction]

Mots-clés : hardiesse, *Equus caballus*, peur, cheval, personnalité, aversion au risque, tempérament.

Introduction

Although it may be beneficial for animals to adjust their behaviour to cope with dynamic environments (Dall et al. 2004), not all variation within populations can be explained by flexibility alone (Nussey et al. 2007). Individuals often display consistent differences in behaviour across time or contexts, which is generally referred to as personality (Gosling 2001; Réale et al. 2010) or temperament (Réale et al. 2007). For example, studies in animals have documented permanent among-individual variation in aggressiveness (Bell and Sih 2007), boldness (Réale et al. 2009), sociality (Müller and von Keyserlingk 2006), activity (Wilson et al. 1976),

and exploratory behaviour (Dingemanse et al. 2002). Understanding the evolution and maintenance of variation in personality traits in natural populations has become an important focus of evolutionary biology (Smith and Blumstein 2008; Réale et al. 2010; Dingemanse and Dochtermann 2014).

Flight initiation distance (FID), the distance at which an individual flees from an approaching threat (Blumstein 2003), is commonly used by wildlife managers to quantify disturbance effects and establish buffer zones to minimize anthropogenic impacts. According to Ydenberg and Dill's (1986) optimal escape theory, FID should vary as a function of the costs and benefits of fleeing from an approaching threat. More specifically, individuals should

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initiate flight when the costs of remaining exceed those of finding safety. For example, upon detection of a predator, prey may benefit from delaying flight to engage in other fitness-enhancing activities such as foraging and mating. Because risk is dependent on an individual's immediate circumstances (e.g., prey group size: van Schaik et al. 1983; distance to refuge: Lagos et al. 2009), FID is expected to be context-specific. However, as the costs and benefits of leaving also depend on an individual's state (e.g., sex, body condition, social status), persistent differences in FID among individuals are also expected. Although few studies have estimated the repeatability of FID, consistent among-individual differences have been documented, for example, in Burrowing Owls (*Athene cucularia* (Molina, 1782)) (Carrete and Tella 2010), Namib Rock Agamas (*Agama planiceps* Peters, 1862) (Carter et al. 2010), yellow-bellied marmots (*Marmota flaviventris* (Audubon and Bachman, 1841)) (Petelle et al. 2013), and roe deer (*Capreolus capreolus* (L., 1758)) (Bonnot et al. 2015). Among-individual variation in FID has also been shown to have a genetic basis and to be related to life-history differences (Møller 2014; Carrete et al. 2016). Therefore, FID can be seen as a personality trait reflecting an individual's propensity to take risks, or boldness, with the potential to play an important role in ecology and evolution.

Recently, research on the evolution of personality traits has turned toward understanding the phenomenon of island tameness (Cooper et al. 2014; Brock et al. 2015). The concept is relatively old, however. Island tameness and the possible reasons for it was commented on by authors such as Darwin (1839), who observed that animals on remote oceanic islands can be unafraid of people. Antipredator behaviours have obvious benefits in the presence of predators, but where predation risk is reduced or eliminated, maintaining those behaviours is predicted to exert a cost on prey and lead to a selective disadvantage (Blázquez et al. 1997). This is particularly well known from isolated, island populations where individuals are free from predation. In such predator-free environments, the antipredator traits that are commonly displayed in populations subject to predation are diminished or absent. For example, Brock et al. (2015) recently showed that for Aegean Wall Lizards (*Podarcis erhardii* (Bedriaga, 1882)) inhabiting island environments, antipredator behaviours like FID generally decline in tandem with predator diversity across an archipelago, but also increased duration of isolation from predators. Using a phylogeny-controlled analysis, Cooper et al. (2014) showed that FID in 66 lizard species decreases as distance from mainland increases and is shorter in island than mainland populations, concluding that island tameness is a real phenomenon in lizards. Although the evolution of island tameness implies selection on personality traits, no study has yet quantified selection on FID (covariance with fitness components) in this context. A first step in the process would be to identify a candidate population in which prey have been isolated from predation and to determine if FID represents a repeatable trait.

The feral horse (*Equus caballus* (L., 1758)) population of Sable Island National Park Reserve, Nova Scotia, Canada, presents an exceptional opportunity to study the causes and consequences of variation in FID in a natural system, as well as the phenomenon of island tameness. The population, which has been unmanaged and protected from human interference since 1961 (Christie 1995), has been the subject of a long-term, individual-based monitoring program since 2007 (see, e.g., Contasti et al. 2012; Marjamäki et al. 2013; van Beest et al. 2014). Each year between July and September, all individuals are censused and most are measured for a variety of phenotypic traits including dispersal (Debeffe et al. 2015a), morphology (Weisgerber et al. 2015), parasite burden (Debeffe et al. 2016), and life history (Richard et al. 2014). The relatively small size of the island, combined with an absence of trees, makes locating individuals and obtaining repeated FID measurements rather easy. Furthermore, the absence of predators (the horses are currently the only terrestrial mammals on the island, apart from very

minimal human presence) reduces the number of confounding variables that may influence FID and presents a direct opportunity to test if FID is under negative directional selection as predicted for populations inhabiting predator-free islands. Recording FID has been easily incorporated into long-term monitoring activities; however, to consider FID in studies on the evolutionary dynamics of personality including testing for the presence of selection, we must first determine whether it is indeed a repeatable trait in the population (Dingemanse and Dochtermann 2013).

Here, we report on a study of variation in FID in foals (young of the year) of Sable Island horses. We aimed to determine if FID is a repeatable trait with the potential to form the basis of future research on the evolution and maintenance of risk aversion and island tameness. Because animals are known to habituate (become desensitized) to behavioural assays (e.g., Beckmann and Biro 2013) and generally assumed to occur for FID (Rodríguez-Prieto et al. 2009), we tested if FID decreased over successive measurements made on the same day or on successive days. In addition, because risk-taking can vary between the sexes (Samia et al. 2015), we tested if FID varied between males and females. Sable Island is characterized by important west–east biological gradients that could impact FID, including human activity but also horse habitat quality (Contasti et al. 2012), horse social environment (Manning et al. 2015), and genetics (Lucas et al. 2009); thus, we also tested whether FID varied along the length of the 49 km long and narrow (1.5 km at its widest) island. Finally, we tested for the repeatability of FID. Repeatability of behavioural traits have a tendency to decrease with increasing time intervals between measurements (Bell et al. 2009; David et al. 2012); therefore, we tested if repeatability estimates obtained from measurements made on the same day were larger than those made using measurements made on separate days.

Materials and methods

Study area and subjects

The study was conducted on Sable Island National Park Reserve (43°55'N, 60°00'W), a sand bar located approximately 275 km southeast of Halifax, Nova Scotia, Canada (Fig. 1). Sable Island is characterized by large, vegetated sand dunes with heights up to 30 m above sea level. Vegetation associations have been recorded by several authors (Catling et al. 1984; Stalter and Lamont 2006; Tissier et al. 2013) indicating American beachgrass, or marram (*Ammophila breviligulata* Fernald), as a dominant perennial species throughout the island. The island's climate is temperate with milder temperatures than the mainland, but is subject to strong winds and dense fog. The horses were introduced to the island in the 18th century and they have persisted in a feral state since. Captures and periodic rounding up by humans has been legally prohibited since 1961 (Christie 1995). The horses are the only terrestrial mammal on the island and have neither guild competitors nor predators. The social system of the feral horse is described by female-defence polygyny, with horses on Sable Island living year-round in breeding bands (a dominant male (stallion) and harem of females (mares), as well as their offspring) or bachelor groups (unmated males) distributed across the island and generally remain in the same area for the majority of their lives (Welsh 1975). As noted earlier, the population has been the focus of a comprehensive population-wide individual-based study (see, e.g., Contasti et al. 2012; Marjamäki et al. 2013; van Beest et al. 2014; Debeffe et al. 2016). Since the beginning of the study, population size has ranged between 380 individuals in 2008 and 559 individuals in 2013.

Data collection

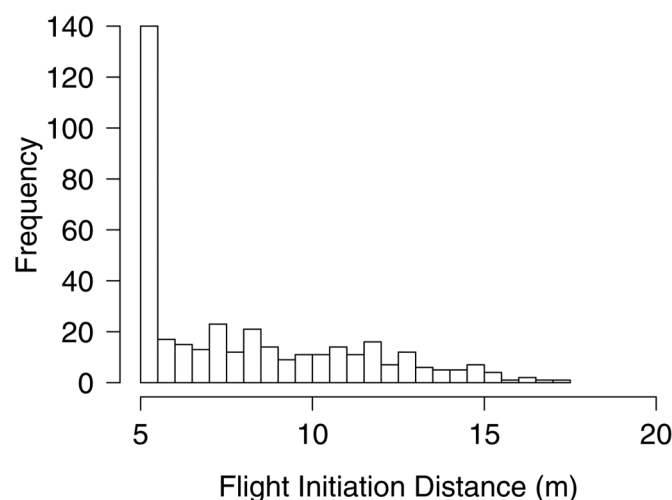
Each year since 2007, the horses have been censused during the mid- to late-breeding season (July–September). The island was divided into seven sections for population monitoring purposes,

Fig. 1. Map of Sable Island, Nova Scotia, Canada.

and daily ground censuses were conducted in one of the sections, resulting in a complete coverage of the island during the course of a week (weather permitting). Observers approached groups on foot and recorded horse age, sex, presence of distinct morphological features (e.g., body and facial markings, scars), female reproductive status (presence or absence of nursing foal), and band membership. Locations were recorded within 5 m of each band or individual using a hand-held global positioning system (GPS). Photographs of each horse were taken to add to a comprehensive population directory and allow subsequent identification.

FID measurements

We obtained FID on two cohorts of foals in 2014 (14 August – 6 September) and 2015 (24 July – 11 August). Foals are born in late spring to mid-summer on Sable Island. Age of foals at the time of measurement therefore ranged from a few days to a few months. Foals on Sable Island are generally found in close proximity of their mother (within a few metres), as is typically the case for horses during their first months of life (Crowell-Davis 1986). We focused on foals primarily because older horses on Sable Island tend to be less responsive to human approach (J. Poissant, personal observation). A similar decline in reactivity to human approach with age has been observed in domestic (nonferal) horses (Søndergaard and Halekoh 2003). Approaches to record FID were performed primarily by one observer (D. Andres; $n = 369$), with contribution from a second observer (S.A. Medill; $n = 9$). After locating a foal, we allowed a delay of 5 min prior to measuring FID to re-establish normal behaviour. Based on pilot data collected at the beginning of the 2014 field season, it was determined that foals generally did not retreat at distances greater than 16 m; hence, we standardized subsequent starting distances at 18.3 m (20 yards). After having been noticed by the foal, observers approached the animal in a direct trajectory at a pace of ~ 1 m/s. Care was taken to conduct approaches on a relatively flat and unobstructed path, and to avoid starting approaches when another horse (including the mother) was present between the target foal and the observer. We recorded the distance at which each foal fled using a handheld laser rangefinder (TruPulse® 360; Laser Technology Inc., Centennial, Colorado, USA) accurate to ± 30 cm.

Fig. 2. Distribution of flight initiation distances (m) measured in Sable Island foals (*Equus caballus*) in 2014 and 2015.

We defined flight as any sudden movement away from the observer (which normally ended with the foal retreating alongside its mother). In nearly all cases, the targeted foal was the first member of the band to react to the approach, and was therefore not startled by the reaction of another horse. Some foals allowed observers to approach to 5 m without signs of flight. Following Parks Canada Agency guidelines and our animal care protocol (University of Saskatchewan Animal Use Protocol 20090032), these approaches were terminated at 5 m and a FID of 5 m was designated for the trial. Usually, at each individual encounter, multiple trials (2–5) were conducted on that individual within minutes to allow testing for short-term repeatability and habituation. On two occasions, FID were obtained on the same individual during two different encounters on the same day (a few hours apart). In these cases, data were considered to come from successive trials from a single encounter. For example, if a foal was

Table 1. Model selection table for determinants of flight initiation distance (FID) in Sable Island foals (*Equus caballus*) ($n_{\text{observations}} = 378$, $n_{\text{foals}} = 105$).

Model	df	Log-likelihood	AIC _c	ΔAIC _c	AIC _c weight
Location + trial day + year	6	−918.88	1849.99	0	0.37
Location + trial day + year + trial number	7	−918.77	1851.85	1.85	0.15
Location + trial day + year + sex	7	−918.88	1852.07	2.08	0.13
Location + trial day + year + sex + sex × location	8	−918.73	1853.85	3.86	0.05
Location + trial day + year + sex + sex × trial day	8	−918.74	1853.88	3.88	0.05
Location + trial day + year + sex + trial number	8	−918.77	1853.94	3.94	0.05
Location + trial day + year + sex + trial number + sex × trial number	9	−917.84	1854.17	4.17	0.05

Note: The full model included the effects of trial number, trial day, summer median location (location), year, sex, and two-way interactions between sex and trial number and between location and trial day. Foal identity was included as a random effect in all models. The log-likelihood, corrected Akaike's information criterion for small sample size (AIC_c), AIC_c difference (ΔAIC_c), and AIC_c weights are presented for top models (models with a ΔAIC_c < 5), and the selected model is in boldface type.

trialed twice at both encounters, then the data were recoded as coming from four consecutive trials performed during a single encounter. At each encounter, we obtained multiple photographs of the foal and other band members to allow subsequent identification. Over the 2 years of data collection, a total of 378 FID measurements were obtained from 105 identified individuals.

Data analysis

Testing for correlates of FID

We used linear mixed models implemented in the R package lme4 (Bates et al. 2015) to test for the influence of several variables on FID. Although FID measurements were not normally distributed (Fig. 2), residuals from mixed models (described below) did not deviate substantially from normality, and Gaussian errors were therefore assumed. We modelled FID as a function of median summer location along a west–east axis (Universal Transverse Mercator (UTM) coordinates, standardized by subtracting mean and dividing by the standard deviation) because Sable Island is characterized by important longitudinal gradients that could impact FID, including greater year-round human presence in the west. Main Station, the facility where all visitors reside and work, is located in the western part of the island. Horses living in the west often (sometimes daily) travel to permanent freshwater ponds located near Main Station (Contasti et al. 2012), and may therefore become habituated to human presence. In contrast, very few people travel to the eastern half of the island due to its relative inaccessibility, meaning that horses in that area, which rely on excavated wells to access freshwater (Contasti et al. 2012), have much less contact with humans. We also included as predictors trial number (successive measurements during the same encounter, ranging from 1 to 5, to test for short-term desensitization to the assay) and trial day (number of days on which FID has been measured on an individual, ranging from 1 to 4, to test for long-term habituation to the assay and (or) human presence). We fitted sex, as well as its two-way interactions with trial number, trial day, and location, to test for a difference in mean FID between males and females and sex-specific temporal and spatial patterns. Finally, the model included year as a fixed effect to account for any difference between years and foal identity as a random effect to account for repeated measurements.

We fitted the model described above, as well as all simpler models, in R using the AICcmodavg package (Mazerolle 2015). The best model was selected using Akaike's information criterion corrected for small sample size (AIC_c), which reflects the best compromise between model precision and model accuracy (Burnham and Anderson 2002; Symonds and Moussalli 2011). According to the rule of parsimony, we selected the simplest model within 2.0 AIC_c of the top model (Burnham and Anderson 2002).

Repeatability of FID

We tested for the repeatability of FID using linear mixed models and restricted maximum likelihood implemented in ASReml release 3.0 (Gilmour et al. 2009). Phenotypic variance (V_p) was parti-

Table 2. Parameter estimates for the selected linear mixed model describing flight initiation distance (FID) in Sable Island foals (*Equus caballus*).

Parameter	Coefficient	SE	df	<i>t</i>	<i>p</i>
Intercept	8.329	0.425	279.2	19.58	<0.001
Trial day	−0.797	0.233	351.5	−3.42	<0.001
Location	0.867	0.222	107.6	3.90	<0.001
Year (2015)	1.382	0.455	103.6	3.04	0.003

Note: Horse identity was included as a random effect.

tioned into variation attributed to differences among (V_{ind}) and within (V_e) individuals by fitting horse identity as a random effect. Repeatability was then calculated as V_{ind}/V_p , where $V_p = V_{\text{ind}} + V_e$. To allow comparing variation with other studies (Houle 1992), we also calculated coefficients of variation as

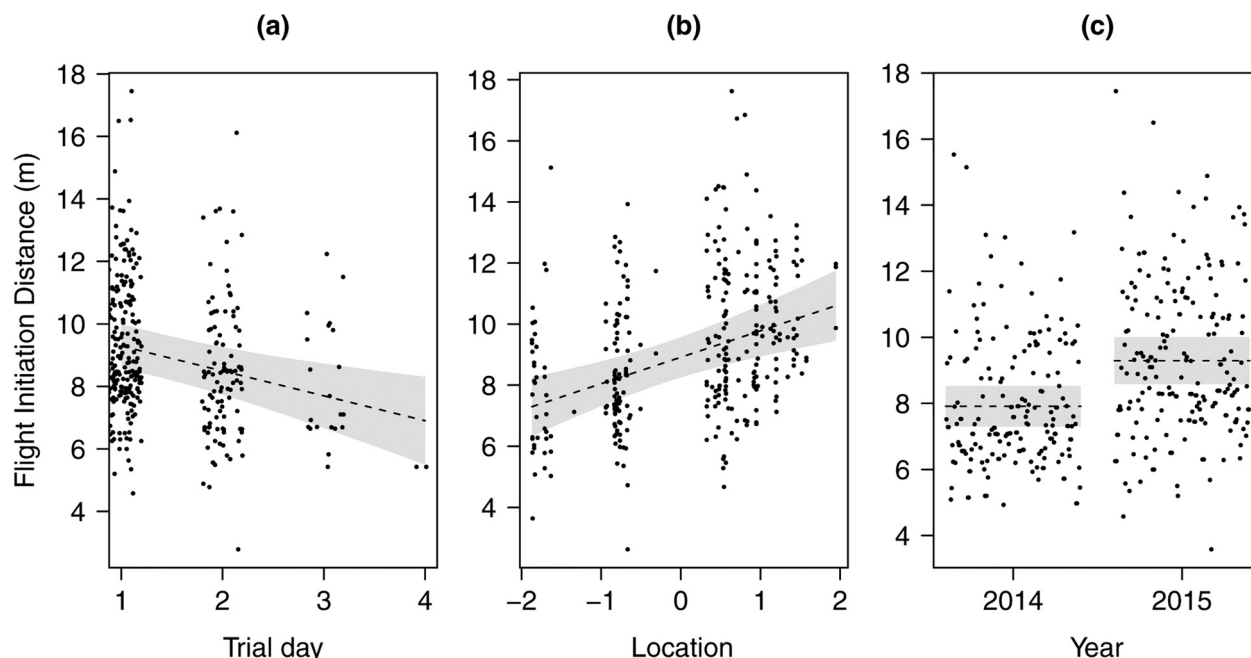
(1)
$$CV = 100 \times \frac{\sqrt{V}}{\bar{X}}$$

where V is the variance of interest (i.e., V_p , V_{ind} , or V_e) and \bar{X} is the trait mean. Standard errors for variance components and ratios were generated by ASReml, whereas standard errors for CV were obtained using eq. 6 of Garcia-Gonzalez et al. (2012).

The initial model included all FID measurements. However, because repeatability of behavioural traits can decrease with increasing time intervals between measurements (e.g., David et al. 2012), we also tested if repeatability estimates differed when only considering measurements made within or among days. To calculate within-day repeatability, horses measured on multiple days were given a unique ID for each day on which they were measured. To estimate among-day repeatability, we used the mean of FID values obtained on the same day as phenotypes. Finally, we also estimated repeatability while accounting for known sources of variation identified through model selection (i.e., location, trial day, and year) by including these as fixed effects in the mixed models. We refer to such repeatability estimates as “conditional” repeatability. Sample sizes for repeatability analyses are presented in Table 3.

The significance of V_{ind} was tested using likelihood ratio tests. For hypotheses involving parameters on the boundary of parameter space, such as variances, the theoretical asymptotic distribution of the likelihood ratio is a mixture of χ^2 variates, where the mixing probabilities are 0.5, one with 0 degrees of freedom and the other with 1 degree of freedom (Self and Liang 1987; Gilmour et al. 2009). The p values from χ^2 tests with 1 degree of freedom were therefore divided by 2. To test for the significance of differences between different repeatability estimates (i.e., within-day vs. among-days, and while including vs. not including fixed effects), we generated 95% confidence intervals of the difference between repeatability estimates using 1 million bootstrap-like replicates by drawing random samples from the sampling variance–

Fig. 3. Predicted relationships between flight initiation distance (FID) and (a) trial day, (b) standardized median summer location (from west to east), and (c) year in Sable Island foals (*Equus caballus*) from a linear mixed model including individual ID as a random effect. Plots were generated using the R visreg function. Values for trial day were jittered to ease visualization. Points show changes in response while holding other all variables constant and grey areas depict 95% confidence intervals of predicted relationships.



covariance matrix of REML estimate of V_{ind} and V_e (available in the ASReml vnp output file) using the R mvnrm function from the package mvtnorm (Grenz et al. 2008).

Ethical note

Permission to perform this study was granted by Parks Canada Agency Research and Collections (permit SINP-2013-14314). Following permit restrictions set by Parks Canada Agency, horses were not approached closer than 5 m. Sampling methods were achieved under the approval of the University of Saskatchewan Animal Use Protocol 20090032.

Results

FID measurements

A total of 378 FID measurements were obtained from 105 foals (58 in 2014 and 47 in 2015) during 159 encounters (Fig. 2). Mean (± 1 standard deviation (SD)) FID was 8.01 ± 3.18 (median = 7.1). Of the 378 trials, 111 (29%) were terminated at 5 m, whereas the remainder were greater than 5 m ($n = 267$; 71%). At each encounter, foals were, on average, submitted to 2.38 trials (1 trial = 3; 2 trials = 110; 3 trials = 36; 4 trials = 10; 5 trials = 3). Sixty-one foals were only measured on a single day, whereas 44 foals were measured on multiple days (2 days = 35; 3 days = 8; 4 days = 1) for a mean of 1.51 days per horse. In cases where the same horse was measured on different days, the number of days between measurements ranged from 2 to 22 days (10.2 ± 5.5 days).

Model selection

Variation in foal FID was best described by a model including location, trial day, and year (Table 1). FIDs were shorter in the west than in the east, decreased over days, and were overall shorter in 2014 than in 2015 (Table 2, Figs. 3a–3c). There was no evidence of short-term desensitization to the assay, or sex effects.

Repeatability of FID

Repeatability of FID was estimated by partitioning phenotypic variation into among- and within-individual components using linear mixed models and REML (Table 3). When considering the

entire data set (i.e., measurements made within and among days), repeatability was estimated at 0.42 ± 0.06 ($ind^2 \pm SE$). Point estimates were larger for repeatability estimates obtained from measurements made on the same day relative to measurements made on separate days (within-day repeatability = 0.55 ± 0.05 vs. among-days repeatability = 0.39 ± 0.12), which is consistent with expectations, but the difference was not statistically significant ($\Delta V_{ind} = 0.16$; 95% CI = $-0.08, 0.45$). Finally, repeatability estimates conditioned on known sources of variation were only marginally reduced (and not significantly so) compared with unconditioned ones (Table 3).

Discussion

Our results indicate that FID is highly repeatable in foals of Sable Island horses, at least for measurements made either on the same day or up to a few weeks apart, with approximately 40% of the phenotypic variation explained by permanent differences among individuals. This adds to the limited (but rapidly growing) evidence for the presence of consistent individual differences in FID in wild vertebrate populations (see, e.g., Carrete and Tella 2010; Carter et al. 2010; Evans et al. 2010; Selmann et al. 2012; Petelle et al. 2013; Bonnot et al. 2015), and highlights the potential of FID as a candidate trait for future research on the ecology and evolution of differences in behaviour in Sable Island horses. Although FID is typically considered in the context of predator–prey interactions and human–wildlife disturbance, research in wild vertebrates, including the present study, indicate that it may find wider applications as a way to quantify consistent individual differences in risk aversion or boldness.

Repeatability estimates can decline with increasing time intervals between measurements due to temporal decoupling of environmental and (or) genetic influences. We observed such a tendency in this study, but the difference was not statistically significant. This is comparable to the results of Debeffe et al. (2015b) in roe deer, where a similar nonsignificant trend in the repeatability of another behavioural trait (docility) was observed. Power to detect biologically meaningful differences in repeatability in wild populations such as in the current study is arguably low. Since the

Table 3. Variation and repeatability of flight initiation distance (FID) in Sable Island foals (*Equus caballus*).

Data set	Fixed effects	n (obs)	Mean ± SD	V_p	V_{ind}	V_e	ind^2	e^2	CV_p	CV_{ind}	CV_e
Within + among days	Mean	103 (376)	8.03±3.18	10.09 (0.92)	4.20 (0.86)***	5.88 (0.50)	0.42 (0.06)	0.58 (0.06)	39.57 (1.80)	25.55 (2.61)	30.22 (1.29)
Within days	Mean	156 (375)	8.03±3.18	10.06 (0.89)	5.55 (0.87)***	4.51 (0.43)	0.55 (0.05)	0.45 (0.05)	39.49 (1.74)	29.34 (2.30)	26.43 (1.26)
Among days	Mean	45 (99)	7.86±2.83	8.01 (1.26)	3.15 (1.22)***	4.86 (0.93)	0.39 (0.12)	0.61 (0.12)	36.02 (2.82)	22.58 (4.38)	28.07 (2.69)
Within + among days	Mean + trial day + location + year	103 (376)	8.03±3.18	9.14 (0.82)	3.50 (0.76)***	5.64 (0.48)	0.38 (0.06)	0.62 (0.06)	37.67 (1.68)	23.32 (2.52)	29.58 (1.26)
Within days	Mean + trial day + location + year	156 (375)	8.03±3.18	9.06 (0.78)	4.56 (0.77)***	4.50 (0.43)	0.50 (0.05)	0.50 (0.05)	37.48 (1.62)	26.60 (2.23)	26.41 (1.26)
Among days	Mean + trial day + location + year	45 (99)	7.86±2.83	6.71 (1.06)	2.42 (1.03)**	4.29 (0.83)	0.36 (0.12)	0.64 (0.12)	32.97 (2.60)	19.79 (4.20)	26.38 (2.54)

Note: **, $p < 0.01$; ***, $p < 0.001$. Horse identity was included as a random effect. Sample size, total number of observations (in parenthesis), and raw trait means and standard deviations (SD) are presented. Phenotypic variance (V_p), as well as variance attributed to variation among individuals (V_{ind}) and variation within individuals (V_e), were estimated using linear mixed models and REML. The proportion of phenotypic variation attributed to permanent variation among (repeatability, $ind^2 = V_{ind}/V_p$) and within ($e^2 = V_e/V_p$) individuals, as well as corresponding coefficients of variation (CV_p , CV_{ind} , CV_e), are also presented. Results are from models only including trait mean as a fixed effect and models including known sources of variation (trial day, location, and year). Standard errors are presented in parentheses. Statistical significance of V_{ind} was tested using likelihood ratio tests.

observed trend is in line with expectations and because time intervals were short relative to a horse's expected lifetime, the potential for time interval to affect repeatability estimates should not be discounted. Nevertheless, in a study of domestic horses, [Lansade and Bouissou \(2008\)](#) found that a horse's response to approaching humans was similar at 8 months, 1.5 years, and 2.5 years of age. It would therefore be interesting, in future research, to determine if trends documented here hold once more individuals are measured for a longer period of time, and in particular whether among-individual differences in FID persist across ontogeny.

Repeatability of FID was only marginally reduced once conditioned on sources of variation considered in this study (year, trial day, and location). This indicates that variation among individuals is primarily due to other factors, which could be environmental or genetic in origin ([Dingemanse and Dochtermann 2014](#); [Wilson and Poissant 2016](#)). For example, variation in FID could be due to social variables not considered here, such as group size and composition. Foal behaviour could also be influenced by local adult sex ratio and stallion characteristics if FID is related to the risk of maternal separation when mothers are being harassed by competing adult males, or perhaps infanticide ([Gray et al. 2012](#)). In addition to considering additional variables, our understanding of within- and among-individual variation in FID in the study system could be improved by increasing the number of traits measured in foals. In particular, FID could be related to the distance between a foal and its mother at the time of measurement. Interestingly, mother-foal distance is known to vary among foals in horses ([Wolff and Hausberger 1994](#)), and could therefore represent a trait of its own potentially phenotypically and (or) genetically correlated to FID as part of a behavioural syndrome.

We did not find evidence for short-term desensitization to repeated approaches performed within minutes on the same day. Although consistent with results from a study of FID in semiferal Welsh Mountain ponies ([Birke et al. 2011](#)), this result is nonetheless surprising given that short-term desensitization has been documented for a number of behavioural assays (e.g., [Bell et al. 2009](#); [Beckmann and Biro 2013](#)) and is widely assumed to occur for FID ([Rodríguez-Prieto et al. 2009](#)). In contrast, there are two lines of evidence for long-term habituation to people. First, FID was shorter for foals that had already been assayed on previous days ([Fig. 3a](#)). This is similar to findings in domestic horses, where FID was found to be lower in foals exposed to human presence in early life ([Henry et al. 2006](#)). Second, FID was shorter in the western half of the island, where human activity is concentrated.

Although the above is consistent with what we might expect from habituation to human presence and (or) approach, it could, however, also reflect unrelated biological processes. In particular, the variable "trial day" considered in our study is highly correlated with Julian date, and the effects of these two variables currently cannot be teased apart due to high collinearity. The observed decrease in FID over trial days could therefore be due to natural temporal variation rather than habituation. For example, foal-mother distance, another trait related to risk aversion, is known to increase rapidly in a foal's first few months of life ([Crowell-Davis 1986](#)). It could be that foals perceive risks (including humans) as less of a threat when increasing in size over the summer. Alternatively, changes in behaviour could reflect shifts in physiology, such as a steady decline in plasma cortisol concentrations in early life ([Panzani et al. 2009](#); [Comin et al. 2012](#)). Similarly, spatial variation in FID could be due to important west-east gradients in horse habitat quality ([Contasti et al. 2012](#)), social environment ([Manning et al. 2015](#)), and genetic diversity ([Lucas et al. 2009](#)) that are known to occur along the length of the island, rather than (or in addition to) human presence. For example, FID could be related to spatial variation in band size or local sex ratio (as mentioned earlier) or diet ([Redondo et al. 2009](#); [Han and Dingemanse 2015](#)). In principle,

behavioural differences between east and west could also reflect local adaptation and (or) genetic drift.

Despite thousands of years of co-evolution, naïve horses generally fear humans (Hausberger et al. 2008; Lansade and Bouissou 2008; Birke et al. 2011), as is the case for most livestock species (Rushen et al. 1999). However, the risk perceived by horses when being approached by humans may arguably differ from that of nondomesticated species. Specifically, horses may not associate humans with predation as much as other species do. However, anecdotally, in Alberta, Canada, where feral horse populations are exposed to predation, FID is often over an order of magnitude larger than on Sable Island (>50 m; J. Poissant, personal observation). This suggests that FID in horses, whether directly or indirectly through correlation with other risk aversion traits, could be influenced by predation risk. However, whether this pattern holds across populations, as seen in other species (Cooper et al. 2014), remains to be determined.

This study is one of the first to establish FID as a repeatable behavioural trait. This finding opens the door to a number of additional analyses in the study population, including testing for the presence of additive genetic variance for FID and genetic correlations with other traits (Wilson and Poissant 2016), as well as the presence of negative directional selection as predicted for populations inhabiting predator-free islands (Cooper et al. 2014; Brock et al. 2015). Although additional research will be necessary to confidently identify drivers and consequences of observed temporal and spatial variation in FID, results clearly indicate that foals in the east have greater FIDs than those in the west. This raises the intriguing possibility that even within predator-free islands, the ecology and evolution of antipredator behaviours may be spatially variable.

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References

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Beckmann, C., and Biro, P.A. 2013. On the validity of a single (boldness) assay in personality research. *Ethology*, **119**(11): 937–947. doi:10.1111/eth.12137.

Bell, A.M., and Sih, A. 2007. Exposure to predation generates personality in three-spined sticklebacks (*Gasterosteus aculeatus*). *Ecol. Lett.* **10**(9): 828–834. doi:10.1111/j.1461-0248.2007.01081.x. PMID:17663716.

Bell, A.-M., Hankison, S.J., and Laskowski, K.L. 2009. The repeatability of behaviour: a meta-analysis. *Anim. Behav.* **77**(4): 771–783. doi:10.1016/j.anbehav.2008.12.022. PMID:24707058.

Birke, L., Hockenhull, J., Creighton, E., Pinno, L., Mee, J., and Mills, D. 2011. Horses' responses to variation in human approach. *Appl. Anim. Behav. Sci.* **134**(1–2): 56–63. doi:10.1016/j.applanim.2011.06.002.

Blázquez, M.C., Rodríguez-Estrella, R., and Delibes, M. 1997. Escape behavior and predation risk of mainland and island spiny-tailed Iguanas (*Ctenosaura hemilopha*). *Ethology*, **103**(12): 990–998. doi:10.1111/j.1439-0310.1997.tb00141.x.

Blumstein, D.T. 2003. Flight-initiation distance in birds is dependent on intruder starting distance. *J. Wildl. Manage.* **67**(4): 852–857. doi:10.2307/3802692.

Bonnot, N., Verheyden, H., Blanchard, P., Cote, J., Debeffe, L., Cargnelutti, B., Klein, F., Hewison, A.J.M., and Morellet, N. 2015. Interindividual variability in

habitat use: evidence for a risk management syndrome in roe deer? *Behav. Ecol.* **26**(1): 105–114. doi:10.1093/beheco/aru169.

Brock, K.M., Bednekoff, P.A., Pafilis, P., and Foutopoulos, J. 2015. Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears? *Evolution*, **69**(1): 216–231. doi:10.1111/evo.12555. PMID:25346210.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Carrete, M., and Tella, J.L. 2010. Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance-induced habitat selection. *Biol. Lett.* **6**(2): 167–170. doi:10.1098/rsbl.2009.0739. PMID:19864278.

Carrete, M., Martínez-Padilla, J., Rodríguez-Martínez, S., Rebolo-Ifrán, N., Palma, A., and Tella, J.L. 2016. Heritability of fear of humans in urban and rural populations of a bird species. *Sci. Rep.* **6**: 31060. doi:10.1038/srep31060. PMID:27499420.

Carter, A.J., Goldizen, A.W., and Tromp, S.A. 2010. Agamas exhibit behavioral syndromes: bolder males bask and feed more but may suffer higher predation. *Behav. Ecol.* **21**(3): 655–661. doi:10.1093/beheco/arq036.

Catling, P.M., Freedman, B., and Lucas, Z. 1984. The vegetation and phytogeography of Sable Island, Nova Scotia. *Proc. N.S. Inst. Sci.* **34**(3–4): 180–247.

Christie, B.J. 1995. The horses of Sable Island. Pottersfield Press, Lawrencetown Beach, N.S.

Comin, A., Veronesi, M.C., Montillo, M., Faustini, M., Valentini, S., Cairolì, F., and Prandi, A. 2012. Hair cortisol level as a retrospective marker of hypothalamic-pituitary-adrenal axis activity in horse foals. *Vet. J.* **194**(1): 131–132. doi:10.1016/j.tvjl.2012.04.006. PMID:22633175.

Contasti, A.L., Tissier, E.J., Johnstone, J.F., and McLoughlin, P.D. 2012. Explaining spatial heterogeneity in population dynamics and genetics from spatial variation in resources for a large herbivore. *PLoS ONE*, **7**(10): e47858. doi:10.1371/journal.pone.0047858. PMID:23118900.

Cooper, W.E., Pyron, R.A., and Garland, T. 2014. Island tameness: living on islands reduces flight initiation distance. *Proc. R. Soc. B Biol. Sci.* **281**: 20133019. doi:10.1098/rspb.2013.3019.

Crowell-Davis, S.L. 1986. Spatial relations between mares and foals of the Welsh pony (*Equus caballus*). *Anim. Behav.* **34**(4): 1007–1015. doi:10.1016/S0003-3472(86)80159-2.

Dall, S.R.X., Houston, A.I., and McNamara, J.M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecol. Lett.* **7**(8): 734–739. doi:10.1111/j.1461-0248.2004.00618.x.

Darwin, C. 1839. Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle, under the command of captain Fitzroy, R.N. from 1832–1836. Henry Colburn, London, UK.

David, M., Auclair, Y., and Cezilly, F. 2012. Assessing short- and long-term repeatability and stability of personality in captive zebra finches using longitudinal data. *Ethology*, **118**(10): 932–942. doi:10.1111/j.1439-0310.2012.02085.x.

Debeffe, L., Richard, E., Medill, S.A., Weisgerber, J.N., and McLoughlin, P.D. 2015a. Costs of social dispersal in a polygynous mammal. *Behav. Ecol.* **26**(6): 1476–1485. doi:10.1093/beheco/arv092.

Debeffe, L., Lemaître, J.F., Bergvall, U.A., Hewison, A.J.M., Gaillard, J.M., Morellet, N., Goulard, M., Monestier, C., David, M., Verheyden-Tixier, H., Jäderberg, L., Vanpé, C., and Kjellander, P. 2015b. Short- and long-term repeatability of docility in the roe deer: sex and age matter. *Anim. Behav.* **109**: 53–63. doi:10.1016/j.anbehav.2015.08.003.

Debeffe, L., McLoughlin, P.D., Medill, S.A., Stewart, K., Andres, D., Shury, T., Wagner, B., Jenkins, E., Gilleard, J.S., and Poissant, J. 2016. Negative covariance between parasite load and body condition in a population of feral horses. *Parasitology*, **143**(8): 983–997. doi:10.1017/S0033182016000408. PMID:27046508.

Dingemanse, N.J., and Dochtermann, N.A. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J. Anim. Ecol.* **82**(1): 39–54. doi:10.1111/1365-2656.12013. PMID:23171297.

Dingemanse, N.J., and Dochtermann, N.A. 2014. Individual behaviour: behavioural ecology meets quantitative genetics. In *Quantitative genetics in the wild*. Edited by A. Charmantier, D. Garant, and L.E.B. Kruuk. Oxford University Press, Oxford, UK. pp. 54–67.

Dingemanse, N.J., Both, C., Drent, P.J., Van Oers, K., and Van Noordwijk, A.J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim. Behav.* **64**(6): 929–938. doi:10.1006/anbe.2002.2006.

Evans, J., Boudreau, K., and Hyman, J. 2010. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, **116**(7): 588–595. doi:10.1111/j.1439-0310.2010.01771.x.

García-González, F., Simmons, L.W., Tomkins, J.L., Kotiaho, J.S., and Evans, J.P. 2012. Comparing evolvabilities: common errors surrounding the calculation and use of coefficients of additive genetic variation. *Evolution*, **66**(8): 2341–2349. doi:10.1111/j.1558-5646.2011.01565.x. PMID:22834736.

Genz, A., Bretz, F., Hothorn, T., Miwa, T., Mi, X., Leisch, F., and Scheipl, F. 2008. mvtnorm: Multivariate normal and t distribution. R package version 0.9-0 [computer program]. Available from <https://cran.r-project.org/web/packages/mvtnorm/index.html>.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Thompson, R., and Butler, D. 2009. ASReml user guide release 3.0. VSN International Ltd., Hemel Hempstead, UK.

Gosling, S.D. 2001. From mice to men: what can we learn about personality from

- animal research? *Psychol. Bull.* **127**(1): 45–86. doi:10.1037/0033-2909.127.1.45. PMID:11271756.
- Gray, M., Cameron, E., Peacock, M., Thain, D., and Kirchoff, V. 2012. Are low infidelity rates in feral horses due to infanticide? *Behav. Ecol. Sociobiol.* **66**(4): 529–537. doi:10.1007/s00265-011-1301-4.
- Han, C.S., and Dingemanse, N.J. 2015. Effect of diet on the structure of animal personality. *Front. Zool.* **12**(Suppl. 1): S5. doi:10.1186/1742-9994-12-S1-S5. PMID:28400852.
- Hausberger, M., Roche, H., Henry, S., and Visser, E.K. 2008. A review of the human–horse relationship. *Appl. Anim. Behav. Sci.* **109**(1): 1–24. doi:10.1016/j.applanim.2007.04.015.
- Henry, S., Richard-Yris, M.A., and Hausberger, M. 2006. Influence of various early human–foal interferences on subsequent human–foal relationship. *Dev. Psychobiol.* **48**(8): 712–718. doi:10.1002/dev.20189. PMID:17111402.
- Houle, D. 1992. Comparing evolvability and variability of quantitative traits. *Genetics*, **130**(1): 195–204. PMID:1732160.
- Lagos, P.A., Meier, A., Tolhuysen, L.O., Castro, R.A., Bozinovic, F., and Ebensperger, L.A. 2009. Flight initiation distance is differentially sensitive to the costs of staying and leaving food patches in a small-mammal prey. *Can. J. Zool.* **87**(11): 1016–1023. doi:10.1139/Z09-089.
- Lansade, L., and Bouissou, M.-F. 2008. Reactivity to humans: a temperament trait of horses which is stable across time and situations. *Appl. Anim. Behav. Sci.* **114**(3–4): 492–508. doi:10.1016/j.applanim.2008.04.012.
- Lucas, Z.L., McLoughlin, P.D., Coltman, D.W., and Barber, C. 2009. Multiscale analysis reveals restricted gene flow and a linear gradient in heterozygosity for an island population of feral horses. *Can. J. Zool.* **87**(4): 310–316. doi:10.1139/Z09-019.
- Manning, J.A., Medill, S.A., and McLoughlin, P.D. 2015. Climate fluctuations interact with local demography and resources to predict spatially dynamic adult sex ratios in a megaherbivore. *Oikos*, **124**(9): 1132–1141. doi:10.1111/oik.02273.
- Marjamäki, P.H., Contasti, A.L., Coulson, T.N., and McLoughlin, P.D. 2013. Local density and group size interacts with age and sex to determine direction and rate of social dispersal in a polygynous mammal. *Ecol. Evol.* **3**(9): 3073–3082. doi:10.1002/ece3.694. PMID:24101995.
- Mazerolle, M.J. 2015. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 2.0-3 [computer program]. Available from <https://cran.r-project.org/web/packages/AICcmodavg/index.html>.
- Møller, A.P. 2014. Life history, predation and flight initiation distance in a migratory bird. *J. Evol. Biol.* **27**(6): 1105–1113. doi:10.1111/jeb.12399. PMID:24797579.
- Müller, R., and von Keyserlingk, M.A. 2006. Consistency of flight speed and its correlation to productivity and to personality in *Bos taurus* beef cattle. *Appl. Anim. Behav. Sci.* **99**(3–4): 193–204. doi:10.1016/j.applanim.2005.05.012.
- Nussey, D.H., Wilson, A.J., and Brommer, J.E. 2007. The evolutionary ecology of individual phenotypic plasticity in wild populations. *J. Evol. Biol.* **20**(3): 831–844. doi:10.1111/j.1420-9101.2007.01300.x. PMID:17465894.
- Panzani, S., Villani, M., McGladdery, A., Magri, M., Kindahl, H., Galeati, G., Martino, P.A., and Veronesi, M.C. 2009. Concentrations of 15-ketodihydro-PGF $_{2\alpha}$, cortisol, and progesterone in the plasma of healthy and pathologic newborn foals. *Theriogenology*, **72**(8): 1032–1040. doi:10.1016/j.theriogenology.2009.06.015. PMID:19748663.
- Petelle, M.B., McCoy, D.E., Alejandro, V., Martin, J.G.A., and Blumstein, D.T. 2013. Development of boldness and docility in yellow-bellied marmots. *Anim. Behav.* **86**(6): 1147–1154. doi:10.1016/j.anbehav.2013.09.016.
- Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating animal temperament within ecology and evolution. *Biol. Rev. Camb. Philos. Soc.* **82**(2): 291–318. doi:10.1111/j.1469-185X.2007.00010.x. PMID:17437562.
- Réale, D., Martin, J., Coltman, D.W., Poissant, J., and Festa-Bianchet, M. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. *J. Evol. Biol.* **22**(8): 1599–1607. doi:10.1111/j.1420-9101.2009.01781.x. PMID:19555442.
- Réale, D., Dingemanse, N.J., Kazem, A.J.N., and Wright, J. 2010. Evolutionary and ecological approaches to the study of personality. *Philos. Trans. R. Soc. B Biol. Sci.* **365**: 3937–3946. doi:10.1098/rstb.2010.0222.
- Redondo, A.J., Carranza, J., and Trigo, P. 2009. Fat diet reduces stress and intensity of startle reaction in horses. *Appl. Anim. Behav. Sci.* **118**(1–2): 69–75. doi:10.1016/j.applanim.2009.02.008.
- Richard, E., Simpson, S.E., Medill, S.A., and McLoughlin, P.D. 2014. Interacting effects of age, density, and weather on survival and current reproduction for a large mammal. *Ecol. Evol.* **4**(19): 3851–3860. doi:10.1002/ece3.1250. PMID:25614799.
- Rodríguez-Prieto, I., Fernández-Juricic, E., Martín, J., and Regis, Y. 2009. Anti-predator behavior in blackbirds: habituation complements risk allocation. *Behav. Ecol.* **20**(2): 371–377. doi:10.1093/beheco/arn151.
- Rushen, J., Taylor, A.A., and de Passillé, A.M. 1999. Domestic animals' fear of humans and its effect on their welfare. *Appl. Anim. Behav. Sci.* **65**(3): 285–303. doi:10.1016/S0168-1591(99)00089-1.
- Samia, D.S.M., Möller, A.P., Blumstein, D.T., Stankowich, T., and Cooper, W.E. 2015. Sex differences in lizard escape decisions vary with latitude, but not sexual dimorphism. *Proc. R. Soc. B Biol. Sci.* **282**: 1805. doi:10.1098/rspb.2015.0050.
- Self, S.G., and Liang, K.Y. 1987. Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *J. Am. Stat. Assoc.* **82**(398): 605–610. doi:10.1080/01621459.1987.10478472.
- Seltmann, M.W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., and Hollmén, T. 2012. Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Anim. Behav.* **84**(4): 889–896. doi:10.1016/j.anbehav.2012.07.012.
- Smith, B.R., and Blumstein, D.T. 2008. Fitness consequences of personality: a meta-analysis. *Behav. Ecol.* **19**(2): 448–455. doi:10.1093/beheco/arm144.
- Søndergaard, E., and Halekoh, U. 2003. Young horses' reactions to humans in relation to handling and social environment. *Appl. Anim. Behav. Sci.* **84**(4): 265–280. doi:10.1016/j.applanim.2003.08.011.
- Stalter, R., and Lamont, E.E. 2006. The historical and extant flora of Sable Island, Nova Scotia, Canada. *J. Torr. Bot. Soc.* **133**(2): 362–374. doi:10.3159/1095-5674(2006)133[362:THAEFO]2.0.CO;2.
- Symonds, M.R., and Moussalli, A. 2011. A brief guide to model selection, multi-model inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav. Ecol. Sociobiol.* **65**(1): 13–21. doi:10.1007/s00265-010-1037-6.
- Tissier, E.J., McLoughlin, P.D., Sheard, J.W., and Johnstone, J.F. 2013. Distribution of vegetation along environmental gradients on Sable Island, Nova Scotia. *Ecoscience*, **20**(4): 361–372. doi:10.2980/20-4-3616.
- Van Beest, F.M., Uzal, A., Vander Wal, E., Laforge, M.P., Contasti, A.L., Colville, D., and McLoughlin, P.D. 2014. Increasing density leads to generalization in both coarse-grained habitat selection and fine-grained resource selection in a large mammal. *J. Anim. Ecol.* **83**(1): 147–156. doi:10.1111/1365-2656.12115. PMID:23931034.
- van Schaik, C.P., van Noordwijk, M.A., Warsono, B., and Sutriano, E. 1983. Party size and early detection of predators in Sumatran forest primates. *Primates*, **24**(2): 211–221. doi:10.1007/BF02381083.
- Weisgerber, J.N., Medill, S.A., and McLoughlin, P.D. 2015. Parallel-laser photogrammetry to estimate body size in free-ranging mammals. *Wildl. Soc. Bull.* **39**(2): 422–428. doi:10.1002/wsb.541.
- Welsh, D.A. 1975. Population, behavioural and grazing ecology of horses of Sable Island, Nova Scotia. Ph.D. thesis, Department of Biology, Dalhousie University, Halifax, N.S.
- Wilson, A.J., and Poissant, J. 2016. Quantitative genetics in natural populations. In *The encyclopedia of evolutionary biology*. Vol. 3. Edited by R.M. Kliman. Academic Press, Oxford. pp. 361–371. doi:10.1016/B978-0-12-800049-6.00046-9.
- Wilson, R.C., Vacek, T., Lanier, D.L., and Dewsbury, D.A. 1976. Open-field behavior in muroid rodents. *Behav. Biol.* **17**(4): 495–506. doi:10.1016/S0091-6773(76)90901-9. PMID:788698.
- Wolff, A., and Hausberger, M. 1994. Behaviour of foals before weaning may have some genetic basis. *Ethology*, **96**(1): 1–10. doi:10.1111/j.1439-0310.1994.tb00876.x.
- Ydenberg, R.C., and Dill, L.M. 1986. The economics of fleeing from predators. *Adv. Stud. Behav.* **16**: 229–249. doi:10.1016/S0065-3454(08)60192-8.