

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

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Abstract: Anti-predator 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 (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

Introduction

While 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 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 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, 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. While few studies have estimated the repeatability of FID, consistent among-individual differences have been documented, for example in burrowing owls *Athene cunicularia* 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 (Brock et al. 2014; Cooper et al. 2014). 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. Anti-predator 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 anti-predator traits that are commonly displayed in populations subject to predation are diminished or absent. For example, Brock et al. (2014) recently showed that for Aegean wall lizards *Podarcis erhardii* Bedriaga, 1882, inhabiting island environments, anti-predator 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. While 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 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, and 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. 2015), 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. Further, 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 which 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. Beckman 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 which 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 (Figure 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 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], and 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 (in 2008) and 559 (in 2013) individuals.

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 7 sections for population monitoring purposes, 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/absence of nursing foal), and band membership. Locations were recorded within 5 m of each band/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 (August 14–September 6) and 2015 (July 24–August 11). 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 meters), 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, pers. obs.). A similar decline in reactivity to human approach with age has been observed in domestic (non-feral) horses (Søndergaards et al. 2003). Approaches to record FID were performed primarily by one observer (D. Andres, $n = 369$), with contribution from a second observer (S. Medill, $n = 9$). After locating a foal, we allowed a delay of 5 minutes 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 meter per second. 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., Colorado, USA) accurate to ± 30 cm.

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 AUP 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 was considered to come from successive trials from a single encounter. For example, if a foal was trialled twice at both encounters, the data was recoded as coming from 4 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 two 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. While FID measurements were not normally distributed (Figure 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 standard deviation) because Sable island is characterised by important longitudinal gradients which 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 1–5, 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 1–4, 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 the Akaike Information Criterion corrected for small sample size (AIC_c), which reflects the best compromise

between model precision and 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 3.0 (Gilmour et al. 2009). Phenotypic variance (V_p) was partitioned into variation attributed to differences among (V_{ind}) and within individuals (V_e) by fitting horse identity as a random effect. Repeatability was then calculated as V_{ind} / V_p , where $V_p = V_{ind} + V_e$. To allow comparing variation with other studies (Houle 1992), we also calculated coefficients of variation as:

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

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 equation 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 average 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). 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-covariance matrix of REML estimate of V_{ind} and V_e (available in the ASReml vvp output file) using the R `rmvnorm` function from the package `mvtnorm` (Genz et al. 2009).

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 (Saskatoon, Canada) Animal Care 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 (Figure 2). Mean FID \pm 1 standard deviation (SD) was 8.01 ± 3.18 (median = 7.1). Of the 378 trials, 111 (29%) were terminated at 5 m while 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). 61 foals were only

measured on a single day while 44 were measured on multiple days (2 days = 35, 3 days = 8, 4 days = 1), for an average 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 (mean = 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, Figure 3a-c). 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 dataset (i.e. measurements made within and among days), repeatability was estimated at 0.42 ± 0.07 ($\text{ind}^2 \pm \text{SE}$). 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 ($\Delta V_{\text{ind}} = 0.16$, 95 % CI = -0.08, 0.45). Finally, repeatability estimates conditioned on known sources of variation were only marginally reduced (and not significantly so) compared to 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; Seltmann 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. While 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. (2015) in roe deer, where a similar non-significant 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 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 month, 1.5 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. While consistent with results from a study of FID in semi-feral 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; Beckman 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 (Figure 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.

While 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 non-domesticated 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, pers. obs.). 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 (Brock et al. 2014; Cooper et al. 2014). While 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 anti-predator behaviours may be spatially variable.

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Table 1. Model selection table for determinants of flight initiation distance (FID) in Sable Island foals (*Equus caballus*, $n_{\text{observations}} = 378$, $n_{\text{foals}} = 105$). 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, location and trial day. Foal identity was included as a random effect in all models. The LogLikelihood (LogLik), corrected AIC for small sample size (AICc),

AICc difference ($\Delta AICc$) and AICc weights (AICcWt) are presented for top models (models with a $\Delta AICc < 5$), and the selected model is in bold.

| Model | df | logLik | AICc | $\Delta AICc$ | AICcWt |
|---|----------|----------------|----------------|---------------|-------------|
| 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 |

Table 2. Parameter estimates for the selected linear mixed model describing flight initiation distance (FID) in Sable Island foals (*Equus caballus*). Horse identity was included as a random effect.

| Parameter | Coefficient | s.e. | df | t-value | p-value |
|-----------|-------------|-------|-------|---------|---------|
| 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 |

Table 3. Variation and repeatability of flight initiation distance (FID) in Sable Island foals (*Equus caballus*). Sample size, total number of observations (in parenthesis), and raw trait means (with standard deviation) are presented. Phenotypic variance (V_p) as well 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.

| Dataset | 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) |

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure Legends

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

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

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. Trial day values were jittered to ease visualization. Points show changes in response while holding other all variables constant and grey area depict 95% confidence intervals of predicted relationships.

Fig. 1

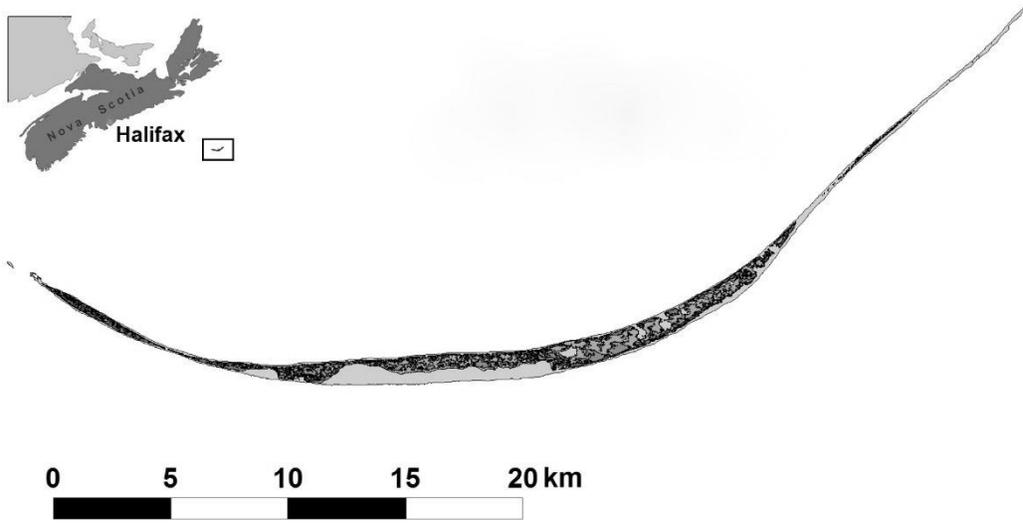


Fig. 2

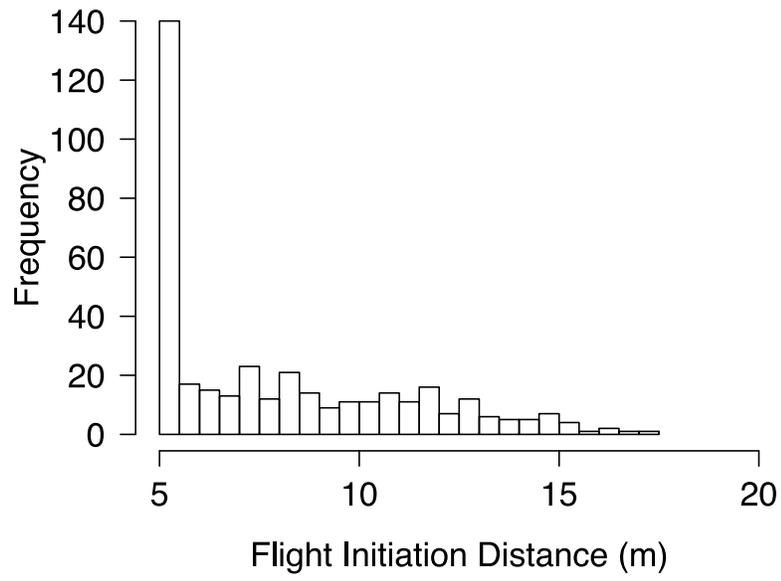


Fig. 3

