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Scale-Dependent Effects of Density and Habitat on Foal Survival

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ABSTRACT Identifying the most appropriate scale to study factors influencing life history is important to evolutionary ecology and wildlife management. For example, the scale at which density is assessed and explains variation in survival can affect how biologists observe and interpret population dynamics, which can influence plans for managing populations. Feral horses (Equus ferus caballus) contrast with most ungulates by exhibiting a mating system characterized

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by female-defense polygyny with persistent, non-territorial breeding groups (bands) and female-biased initial (natal) and subsequent (breeding) dispersal. We predicted that for horses, offspring movements coupled with female-biased breeding dispersal would increase the scale at which density best related to juvenile survival compared to species with greater female philopatry. From 2008 to 2013, we censused the population of feral horses on Sable Island, Canada. We annually computed individual-specific local densities for 442 foals (horses/km² in radii of 2,000 m, 4,000 m, and 8,000 m fixed to a band’s centroid of movements) and whole-island (total) population density, group (band) size, and local access to surface freshwater, which affected movement patterns and selection of vegetation by females. The population of feral horses increased from 380 in 2008 to 559 in 2013. Overwinter survival of foals averaged 82.8%. Island-wide density was the most important predictor of foal mortality and was negatively associated with survival, with a lesser negative effect from local density. Increased access to surface freshwater (ponds) was an important predictor of foal survival but only at certain scales. Our study emphasizes the relevance of a multi-scale approach when analyzing the response of fitness components to changes in habitat and population processes, which may be influenced by the particular social organization of the species.

KEY WORDS density dependence, Equus ferus caballus, feral horse, foal, habitat, population dynamics, Sable Island, scale, survival.
In ecology, scale refers to “…several concepts, including the physical extent of the processes (the ‘range’) and the spatial and temporal resolution of the data (‘grain’)” (Fortin and Dale 2005:9). Scale affects interpretation of ecological processes, including resource selection (Anderson et al. 2005, Boyce et al. 2003, Leblond et al. 2011, Laforge et al. 2015b), sexual segregation (Bowyer et al. 1996), and interspecific (Whittaker and Lindzey, 2004) and intraspecific competition (Mayor and Schaefer 2005). It is important to use the most appropriate scale, or at least develop models that bridge across scales, to understand an ecological system (Chave 2013).

Juvenile survival decreases with increasing intraspecific competition (population density) in many species of wildlife, including Soay sheep (*Ovis aries*; Milner et al. 1999), bighorn sheep (*Ovis canadensis*; Portier et al. 1998), and mallard ducks (*Anas platyrhynchos*; Gunnarsson et al. 2006). In examining how an organism might experience effects of intraspecific competition through exposure to conspecific density, Coulson et al. (1997) reported that it was not at the largest spatial scale of population density (total population size) that the greatest amount of variation in juvenile survival was explained for red deer (*Cervus elaphus*). Rather, the most statistically explanatory scale isolated a population substructure of intermediate local scales of individual experience related to spatial heterogeneity in high quality food resources (grasslands). The link between use of grasslands and a female’s lifetime reproductive success was subsequently reported to interact with its local experience of density (McLoughlin et al. 2006), and adaptive use of habitat depended on how far the local (as opposed to total) population was from reaching carrying capacity (Fortin et al. 2008). A similar situation was reported for juvenile survival of Atlantic salmon (*Salmon solar*), where fine-scale local density was most important in explaining juvenile mortality (Einum and Nislow 2005).

There are many factors that may dictate how and why a life-history trait like density-dependent juvenile survival may vary with scale. Mating systems and social organization can be
important to fine-scale, spatial effects on inbreeding (Chesser 1991) and underpin relationships leading to intraspecific competition (Clutton-Brock 1989) affecting distribution, and hence heterogeneity in population and evolutionary processes (e.g., by affecting reproductive success or sex ratio and dispersal; Dobson 1982, Leturque and Rousset 2004). We might therefore expect social system to play a role in density-dependent phenomena and factor into scale-related questions of density dependence. Little is known, however, about how something like an animal’s social system might affect scale dependence in ecological interactions. One reason for this is the paucity of multi-scale, individual-based analyses of population dynamics for continuously distributed organisms (i.e., where each individual possesses a unique perspective of density, as opposed being grouped into a discrete subpopulation).

Feral horses (*Equus ferus caballus*) contrast with most other ungulates by exhibiting a mating system that more resembles that of primates (Cameron et al. 2009), being characterized by year-round, female-defense polygyny that results in non-territorial breeding groups (bands) consisting of a harem of females and 1 or 2 adult males (stallions), and other groups of non-reproducing males (bachelors) and adolescents (Berger 1986, Linklater et al. 2000). In horses, both sexes disperse and will move among bands (Berger 1986, Clutton-Brock 1989), although natal (initial) and secondary (breeding) dispersal from bands is generally female-biased (Marjamäki et al. 2013). Dispersal rate in feral horses on Sable Island, Nova Scotia (Fig. 1), was previously reported to result in compensatory and depensatory density feedbacks (Herrando-Pérez et al. 2012), contingent on the state of individuals and the spatial scale at which density acted on individuals (Marjamäki et al. 2013, van Beest et al. 2014). Density affects the ecology of horses on Sable Island, including behaviors such as density-dependent habitat selection (van Beest et al. 2014, Rozen-Rechels et al. 2015) and dispersal (Marjamäki et al. 2013), and rates of survival and reproduction (with density negatively affecting survival for all age and sex
categories; Richard et al. 2014). Horses on Sable Island provide an opportunity to compare scale-dependent population dynamics against what has been reported for ungulates with different social systems.

Originally introduced sometime in the mid-1700s, Sable Island’s feral horses have always been free-ranging with minimal interference by humans (Christie 1995). The horses of Sable Island present a markedly distinct genetic structure from other horse breeds but are most closely related to the Nordic breeds of horses and ponies (Plante et al. 2007, Prystupa 2012). Though introduced, the horses are treated by Parks Canada Agency as a naturalized species constituting an important part of the ecosystem. Over the course of our study (2008–2013), total population size increased from 380 individuals to 559, an increase of 47%. Foals dispersed from their natal band 33.4% of the time, with approximately a third of foals (10.2% of all foals) dispersing on their own (without their mother). Natal dispersal distance of female foals over winter averaged 3,572 m ± 1,546 m (SD; Contasti 2011). Female dispersal to different bands was common (30.5% of mothers).

Following Coulson et al. (1997), we examined density feedbacks on juvenile overwinter survival at multiple spatial scales for horses on Sable Island, using an individual-based approach. Horses on Sable Island exist in a natural though simplified system without predation, human interference, or interspecific competition (the horses are the island’s only terrestrial mammal). As part of a long-term, individual-based monitoring program for this population (Contasti et al. 2012, Marjamäki et al. 2013, Richard et al. 2014, van Beest et al. 2014, Rozen-Rechels et al. 2015), we tracked the overwinter fates of all foals alive on the island at the end of each summer (n = 442). We quantified each animal’s unique experience of the environment including attributes of social group (band size) and a foal’s (and its mother’s) access to freshwater and exposure to population density at 4 spatial scales of increasing size (2,000-m, 4,000-m, and 8,000-m buffers
around median band centroid locations and total population density). We chose these scales to reflect different percentiles of mean annual horse movement relating to the intensity of use of their home ranges.

We generated 2 competing hypotheses for how density may affect foal survival. Our first hypothesis was that the scale at which foal mortality would be detected in relation to density would mirror that for red deer fawns in Coulson et al. (1997), where local density in a defined area around the focal individual would best predict foal mortality due to local competition for resources. By contrast, social system and trends in philopatry may play an important role in determining the most appropriate scale at which to examine density dependence in population processes, including juvenile survival. Horses on Sable Island show female-biased natal and breeding dispersal (social dispersal), and females with accompanying offspring can and do leave bands in response to increases in band size and conspecific density (Marjamäki et al. 2013). Dispersal events largely occur during winter (Marjamäki et al. 2013, Debeffe et al. 2015).

Departure of foals with females during dispersal increases foal overwinter survival (Debeffe et al. 2015), suggesting a role for dispersal to affect variation in foal survival. Therefore, our alternate hypothesis was that dispersal of females and foals would result in a situation where individuals are better able to exploit resources evenly across the island, leading to population density at larger scales being a better predictor of overwinter survival than measurements taken at smaller scales.

STUDY AREA

Sable Island National Park Reserve, located 275 km southeast of Halifax, Nova Scotia, Canada (43° 55′ N, 60° 00′ W), is a crescent-shaped sand bar home to a population of free-ranging feral horses (Fig. 1). It is approximately 49 km long and 1.25 km in width at its widest point, and is comprised of sandy beaches and vegetated and bare sand dunes ≥30 m high. The island’s climate
was temperate oceanic with cool summers and wet winters. Catling et al. (1984), Freedman et al. (2011), and Tissier et al. (2013) detailed the flora present. Sable Island was treeless, and the vegetation community was dominated by American beach grass, or marram (*Ammophila breviligulata*), which occurred throughout most of the vegetated parts of the island. Shrub-dominated heath (*Empetrum nigrum, Juniperus communis, Myrica pensylvanica, Rosa virginiana, Vaccinium angustifolium*) was the climax vegetation association found on Sable Island. The west end of the island contained patches of sandwort (*Honckenya peploides*) and beach pea (*Lathyrus japonicus* var. *maritimus*). Several permanent freshwater ponds covering approximately 20 ha were used by horses and confined to western and central areas of the island (Contasti 2011, Contasti et al. 2012). Ephemeral melt- and rain-water ponds occurred on the east half of the island but generally disappeared in summer, and horses on east Sable Island had to excavate drinking holes to access freshwater (Contasti 2011). This environmental gradient underlaid density-dependent habitat selection processes with major consequences for population and social dynamics across the length of the island (Marjamäki et al. 2013, Richard et al. 2014, Manning et al. 2015). Aside from a small human presence (researchers and tourists), feral horses were the only terrestrial mammals on the island.

**METHODS**

**Data Collection and GIS Analysis**

We obtained direct observations of individual horses via systematic ground censuses on Sable Island (weekly observations from Jul–Sep), including 21,392 individual observations encompassing the entire population ($N = 380, 437, 503, 448, 534, and 559$ individuals, respectively, between 2008 and 2013, including 442 foals alive in Sep 2008 through 2013; counts updated from Richard et al. [2014]). Each daily sampling effort included 1 of 7 sections of the island, stratified to allow complete coverage of a section in 1 day and roughly complete coverage
of the island in 1 week. We approached horses on foot (which were largely indifferent to our
presence) and recorded the location of an individual using a hand-held global positioning system
(GPS) with location error to within 5 m. We determined the horse’s identity (to determine
survival status and band membership from year to year) from facial features and other
distinguishing marks (verified using digital photographs at every sampling event), sex,
reproductive status, and group membership. Our photography-based approach to cataloguing
each individual is described in Contasti (2011). If a horse was not observed during an entire
season, we assumed that it had died. We evaluated whether our censuses were adequate by
comparing, for 2010 data, our summer counts of non-foals with that obtained from high-
resolution aerial photography in January 2010 (prior to births). The latter was flown by aircraft at
an altitude of approximately 450 m as part of a census of the population of grey seals
(*Halichoerus grypus*) on Sable Island, which also proved excellent for counting horses (Bowen et
al. 2011). This confirmed that our 2010 census accounted for >99% of the horses present as
expected. A previous study (Welsh 1975) reported that horses have small home ranges on Sable
Island (2.8 ± 1.2 km$^2$ [̅$x$ ± SD], $n = 32$ bands), which generally range from one end of the island
to the other and are compressed along its length.

All collection and sampling methods (strictly behavioral observation) were approved
by the University of Saskatchewan’s Animal Research and Ethics Board, under University of
Saskatchewan Animal Care Protocol 20090032 and guidance of the Canada Council on Animal
Care. Access to Sable Island for this research project was granted by written permission of M.
Voigt, Canada Coast Guard for years 2008–2012; however, in the year of 2012, as management
of the island transitioned from Coast Guard to Parks Canada Agency, we also obtained and
followed conditions of a Research License (14668) provided by Parks Canada Agency 2012–
2014.
We used ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA) to compute conspecific densities and proportion of freshwater in 3 buffers of increasing radius (2,000 m, 4,000 m, and 8,000 m) centered on each band’s median centroid location. Buffer radii generally corresponded to the 80th, 95th, and 99th percentile of annual movements of all horses and were selected to reflect a continuum of scales. We selected the 99th percentile (8,000-m buffer) to reflect the annual movement rate of nearly all horses in the population. We selected the 95th percentile (4,000-m buffer) to eliminate outliers of extraordinary dispersal, and the 2,000-m buffer (80th percentile) to approximate the core area used by individuals. Within each buffer, we calculated the density of conspecifics as a function of vegetated area (km$^2$; hereafter local density) because horses used beaches primarily for transitory movements or resting. We also calculated the proportion of freshwater in each buffer and total population density over the whole island as a function of horses/km$^2$ of vegetated area (hereafter total density). We included vegetation availability implicitly in the density term as horses/km$^2$ of vegetated area; therefore, we did not include any other explicit vegetation terms in our models; therefore we did not include any other explicit vegetation terms in our models. We obtained habitat and vegetation data from high-resolution aerial photography and a Light Detection and Ranging (LIDAR) map (2009) classified and ground-truthed by the Applied Geomatics Research Group (AGRG) at Nova Scotia Community College, Middleton, Nova Scotia, Canada.

**Statistical Analyses**

Foal overwinter survival was a binary response variable, with 0 representing animals that died between 1 August of the birth year ($t$) and 15 July of the following year ($t + 1$), and 1 describing those that survived. We used generalized linear mixed effects models (GLMM) with a binomial error structure in R Version 3.2.1 (R Core Team 2015) to model survival as a function of local density and habitat variables at the 3 local scales measured and total island density. Our maximal
model included as covariates local density and proportion of freshwater (computed at 1 of the 3
identified scales), band size, and total density. We used Z-scores to compare effect sizes between
different parameters and to facilitate convergence of models. We tested for collinearity between
predictors at all scales and ensured no pair of variables had a Pearson’s correlation coefficient of
\( r > |0.7| \) (Dormann et al. 2013) and that no variable had a variance inflation factor >5 (Menard
1995). Unlike population density, surface freshwater availability did not vary among years
because we used 1 map (dated 2009); hence, we could not generate a variable for the whole-
 island scale. Marjamäki et al. (2013) noted significant collinearity between local density (at the
8,000-m scale) and distance of overwinter movements, and so we also did not include distance of
dispersal (if it occurred) as a covariate in our models. We tested our final models for trends in
average residuals versus expected values using binned residuals (Gelman and Hill 2007) with the
R package arm (Gelman and Su 2015) because plotting raw residuals versus fitted values are
generally not useful after logistic regression (we did not detect any serious anomalies). We tested
3 model structures for random effects: band identification (ID), maternal ID, and both (not
nested). We were not able to test maternal ID nested within band ID because of dispersal of
mothers to different bands.

Following Burnham and Anderson (2002), we developed a set of candidate models (Table
1) that we evaluated using small sample size adjusted Akaike’s Information Criterion (AIC\(_c\)). We
employed a hierarchical method of model selection, first determining the optimal random effect
structure and then performing model selection on the fixed effects. We tested the 3 random effect
structures using the maximal (fully parametrized) model with local density and proportion
freshwater modeled at each of our 3 scales using a GLMM using the R package lme4 (Bates et al.
2015) and selected the model with the lowest AIC\(_c\) (Zuur et al. 2009), which resulted in our using
models with maternal ID only. Once we had determined the most informative random term
structure, we ran each model in our candidate model set at each of our 3 scales and ranked each model by AIC$_c$. We used model-averaging techniques using the R package AICcmodavg (Mazerolle 2015) to generate model-averaged parameter estimates for all models that had an AIC$_c < 10$ from the top model at each scale. To evaluate predictive capacity of our final GLMM, we adopted the approach of Boyce et al. (2002), which applies to this situation. We evaluated this model using $k$-fold cross-validation (test-to-training ratio of 5 data subsets), whereby we tested predictive capacity of partitioned models against withheld training data using the mean Spearman’s rank correlation ($\bar{r}_s$) between training and test data, grouped within 10 bins (Boyce et al. 2002). In a separate analysis, we re-ran all models replacing total island density with year, to determine whether other inter-annual effects besides density may have had an impact on foal survival.

**RESULTS**

Of 442 foals entering their first winter from 2008 to 2013, 82.8% survived to the next census period. A foal’s exposure to conspecific density in the year it was born ($t$) had a larger mean and standard deviation at small scales than at large ones (Table 2). Using maternal ID only as a random effect provided the best fit for our models as determined by AIC$_c$. Using a model structure with band ID or band ID and maternal ID raised the AIC$_c$ of our fully parametrized model by between 1.6 and 3.0 (see Table S1, available online at www.onlinelibrary.wiley.com). Our results suggested that no single model was clearly superior in describing foal overwinter survival; the top 6 models all had a $\Delta$AIC$_c$ from the top model < 2.0 (Table 3). All top models included local density and total density. Proportion of freshwater was important in many of the top models, was retained in our best model at the 8,000-m and the 2,000-m scale (Table 3), and enhanced probability of survival; however, the term was not informative in our model-averaged estimates at any scale (Table 4). Both local density and total density negatively affected survival
in our models at each of our 3 local scales (Table 4); however, the effect was greater for total density than for local density at all 3 scales. Band size was uninformative at all scales (Table 4). The k-fold cross-validation values for the best model at the 2,000-m, 4,000-m, and 8,000-m scales were 0.62, 0.75, and 0.68, respectively.

Models generated using year instead of total island density were better overall predictors of foal overwinter mortality (Table 3). Year as a factor, however, reveals little about the underlying ecological processes in how foal survival changes as a function of year, whereas modeling density allowed us to make meaningful ecological conclusions (we could not include both in our main analysis because of collinearity).

**DISCUSSION**

It has become increasingly recognized that animal life-history traits are influenced differentially across scales (Wiens 1989, Levin 1992, Wheatley and Johnson 2009). Conspecific densities at larger scales were generally more informative than smaller scales in terms of predicting foal overwinter survival for horses on Sable Island, with total density being most explanatory and negatively associated with survival. Both total density and local densities appeared in our top models, suggesting that density at several scales can be important when assessing foal overwinter survival; however, the effect was nearly twice as strong for total island density as for local density. Our study supports previous work that has emphasized the relevance of scale in ecological studies, in particular the response of fitness components to changes in habitat quality or population dynamics (Coulson et al. 1997, Johnson et al. 2001, Maurer and Taper 2002, Leblond et al. 2011, Laforge et al. 2015b).

Our results contrast with numerous other studies that have investigated scalar processes in life-history traits. Studies of roe deer (*Capreolus capreolus*) reported that fine-scale variation in food resources at the home-range scale have the greatest effect on fawn biomass (Pettorelli et al.
and survival (Pettorelli et al. 2005). Einum and Nislow (2005) reported juvenile survival in salmon was density-dependent at small scales and overwinter survival in red deer fawns was reported by Coulson et al. (1997) to be affected by conspecific density at intermediate scales. By contrast, Vreeland et al. (2004) did not find any effect of home-range scale habitat variation in fawn survival and suggested that factors at the landscape level may have been important in their system.

Habitat quality, availability of cover habitat, and predation pressure have been identified as important influences of large herbivore life-history traits for many species (Coulson et al. 1997, Milner-Gulland et al. 2000, Nilsen et al. 2004). For horses on Sable Island, habitat quality is relatively homogeneous, and cover habitat (e.g., trees and shrubs) and predation pressure are non-existent. Cost of dispersal for horses in our study was therefore likely much less than in many other studies. In their study of salmon, Einum and Nislow (2005) suggest that the metabolic costs and risk of predation pressure make dispersal costly in this species, resulting in less dispersal and greater density-dependent mortality at local scales. Similarly, Stuart-Smith et al. (1997) reported that caribou (Rangifer tarandus) calf mortality was higher in fragmented landscapes where individuals had smaller home ranges, suggesting similar barriers to dispersal were responsible for fine-scale juvenile mortality.

Our results suggest that differences in social system and juvenile dispersal ability may play a role in the scale at which density affects juvenile mortality. For example, in red deer, female dispersal is rare (Clutton-Brock and Albon 1989, Albon et al. 1992), which may explain why intermediate scales were clearly best at describing overwinter survival in juvenile red deer (Coulson et al. 1997). This contrasts to the situation on Sable Island, where natal dispersal of female foals overwinter can be several kilometers (Contasti 2011). Female horses are generally accompanied by their offspring when leaving social groups in response to density (Marjamäki et
al. 2013) and we suspect that this process may increase variability in local density effects on the overwinter survival of accompanying foals.

Availability of freshwater appeared to be a lesser (compared to local density) but still important influence of foal survival across most scales of observation. Heterogeneity in freshwater as a resource influences spatial distribution and movement patterns for horses on Sable Island (Rozen-Rechels et al. 2015), other populations of feral horses (Rubenstein 1981, Berger 1986), and other large herbivores such as springbok (*Antidorcas marsupialis*; Ritter and Bednekoff 1995) and African elephants (*Loxodonta africana*; Chamaillé-Jammes et al. 2007).

Freshwater availability was a positive predictor of foal survival, which we suspect is mainly manifest through effects on body condition and resources for lactation in mothers. Contasti et al. (2012) noted that body condition in female horses significantly declined from west to east on Sable Island (2008–2010) in accordance with the west to east reduction in availability of surface freshwater on the island. Heterogeneity in fixed, high quality resources, like ponds including freshwater and their associated vegetation, may act to explain survival similar to the case in red deer (Coulson et al. 1997). Density-related associations on high-nutrition grasslands (*Agrostis-Festuca*) were attributed to small-scale influences on red deer calf survival; high-resolution scales were good descriptors of population substructure during summer, when good grazing was distributed heterogeneously. Small-scale effects of density aggregations, which were likely linked to sources of permanent freshwater, did translate directly into density effects on survival in our study, however, not to the extent that larger-scale density effects predicted mortality (Table 4).

Many studies reported inter-annual, density-independent processes (or processes interacting with density) acting on population dynamics to affect juvenile survival. Spring temperatures have been correlated with juvenile survival in bighorn sheep lambs (Portier et al. 1998) and red deer (Albon et al. 1987). Soay sheep juvenile overwinter survival appears to be driven by a
combination of both density and weather effects (Grenfell et al. 1998, Milner et al. 1999). Our results suggest a similar situation in horses on Sable Island; models using year instead of total density improved our models, suggesting density-dependent and density-independent effects are at play in juvenile survival. It is likely that greater total island densities are associated with overwinter resource depletion, which is likely exacerbated by extreme weather effects leading to increased mortality (Manning et al. 2015).

**MANAGEMENT IMPLICATIONS**

Managers of wide-ranging, long-lived species (e.g., large mammals) may be at particular risk of making prior assumptions about the scale at which population dynamics should be monitored or studied. In light of our findings, a more reliable methodology to analyse the response of fitness components to changes in habitat and population processes (in particular early survival) may involve a multi-scale approach in which an understanding of the social system plays a role. In species that exhibit strong dispersal responses such as horses, management efforts should be focussed on broad scales. Using a framework of multiple grains in animal habitat selection studies (Laforge et al. 2015a, b), informed by knowledge of the species’ social system, will provide valuable insight into selection and dispersal patterns. Following such a protocol will assist in the development of more effective and directed conservation and management plans, which is especially critical for the viability of isolated species and populations.

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LITERATURE CITED


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Figure Caption

Figure 1. Sable Island, Nova Scotia, Canada. Sable Island National Park Reserve (43° 55′ N; 60° 00′ W), located approximately 275 km east-southeast of Halifax, Nova Scotia, Canada. The island is a crescent shaped sand bar 49 km long and 1.25 km at its widest (vegetation in grey).
Table 1: List of a priori candidate models for linear regression analysis of foal survival, Sable Island, Nova Scotia, Canada, 2008–2013. Each model was evaluated with local density and proportion water computed at each of 3 scales: 2,000 m, 4,000 m, and 8,000 m.

<table>
<thead>
<tr>
<th>Model Description</th>
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<tbody>
<tr>
<td>Local density + total density + proportion freshwater + band size</td>
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<tr>
<td>Local density + total density + band size</td>
</tr>
<tr>
<td>Local density + total density + proportion freshwater</td>
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<tr>
<td>Local density + total density</td>
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<tr>
<td>Local density</td>
</tr>
<tr>
<td>Total density</td>
</tr>
<tr>
<td>Local density + proportion freshwater</td>
</tr>
<tr>
<td>Null</td>
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</tbody>
</table>
Table 2: Distribution of density (horses/km² of vegetated area) in summer of birth across 4 spatial scales for foals born into bands of feral horses on Sable Island, Nova Scotia, Canada, 2008–2013. Presented is the mean ($\bar{x}$), standard deviation (SD), and coefficient of variation ($c_v$) for increasing scales of individual experience, each metric centered on the median centroid of a band’s movements in the year ($t$) in which a foal was born. Annual means at the whole-island scale (total) are total number of horses on the island that year divided by vegetated area on the island (without SD or $c_v$).

<table>
<thead>
<tr>
<th>Year</th>
<th>Scale (m)</th>
<th>2,000</th>
<th>4,000</th>
<th>8,000</th>
<th>Total</th>
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<tr>
<td>2008 ($n = 69$)</td>
<td>$\bar{x}$</td>
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<td>14.7</td>
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<td>2009 ($n = 62$)</td>
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<td>20.3</td>
<td>10.2</td>
<td>14.6</td>
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<tr>
<td></td>
<td>SD</td>
<td>31.2</td>
<td>12.9</td>
<td>6.9</td>
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<tr>
<td></td>
<td>$c_v$</td>
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<td>0.63</td>
<td>0.68</td>
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<td>2010 ($n = 83$)</td>
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<td>37.1</td>
<td>21.4</td>
<td>12.1</td>
<td>16.8</td>
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<tr>
<td></td>
<td>SD</td>
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<td>13.1</td>
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<tr>
<td>Year</td>
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<td>SD</td>
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<td>----------</td>
<td></td>
</tr>
<tr>
<td>2011 (n = 56)</td>
<td>56</td>
<td>41.7</td>
<td>31.6</td>
<td>0.76</td>
<td></td>
</tr>
<tr>
<td>2012 (n = 93)</td>
<td>93</td>
<td>37.1</td>
<td>13.8</td>
<td>0.37</td>
<td></td>
</tr>
<tr>
<td>2013 (n = 79)</td>
<td>79</td>
<td>45.5</td>
<td>19.7</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>All years (n = 442)</td>
<td>442</td>
<td>38.6</td>
<td>22.2</td>
<td>0.57</td>
<td></td>
</tr>
</tbody>
</table>
Table 3: Scale, degrees of freedom (df), adjusted Akaike’s Information Criterion (AIC<sub>c</sub>), log likelihood (LL) and $R^2$ for the top models describing foal overwinter survival on Sable Island, Nova Scotia, Canada, 2008–2013. Scale refers to the size of the buffer around which we quantified local density and proportion of freshwater. For comparison, we also present in the last columns AIC<sub>c</sub> and $R^2$ values for models with year (factorial) in the model as opposed to total island density.

<table>
<thead>
<tr>
<th>Model</th>
<th>Scale (m)</th>
<th>df</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>LL</th>
<th>$R^2$</th>
<th>Year AIC&lt;sub&gt;c&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Local density + total density (year) + proportion freshwater</td>
<td>8,000</td>
<td>5</td>
<td>391.08</td>
<td>−190.47</td>
<td>0.112</td>
<td>387.60</td>
</tr>
<tr>
<td>Local density + total density (year)</td>
<td>8,000</td>
<td>4</td>
<td>391.23</td>
<td>−191.57</td>
<td>0.100</td>
<td>387.24</td>
</tr>
<tr>
<td>Local density + total density (year) + proportion freshwater</td>
<td>2,000</td>
<td>5</td>
<td>391.23</td>
<td>−190.55</td>
<td>0.112</td>
<td>387.93</td>
</tr>
<tr>
<td>Local density + total density (year)</td>
<td>2,000</td>
<td>4</td>
<td>391.82</td>
<td>−191.87</td>
<td>0.095</td>
<td>388.54</td>
</tr>
<tr>
<td>Local density + total density (year) + band size</td>
<td>8,000</td>
<td>6</td>
<td>392.93</td>
<td>−190.37</td>
<td>0.113</td>
<td>389.52</td>
</tr>
<tr>
<td>Local density + total density (year) + band size</td>
<td>4,000</td>
<td>4</td>
<td>392.93</td>
<td>−192.42</td>
<td>0.093</td>
<td>389.20</td>
</tr>
<tr>
<td>Local density + total density (year) + band size</td>
<td>8,000</td>
<td>5</td>
<td>393.15</td>
<td>−191.51</td>
<td>0.101</td>
<td>389.19</td>
</tr>
<tr>
<td>Local density + total density (year) + proportion freshwater</td>
<td>2,000</td>
<td>6</td>
<td>393.21</td>
<td>−190.51</td>
<td>0.113</td>
<td>389.99</td>
</tr>
<tr>
<td>Local density + total density (year) + band size</td>
<td>2,000</td>
<td>5</td>
<td>393.82</td>
<td>−191.84</td>
<td>0.096</td>
<td>390.61</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td></td>
<td>406.75</td>
<td>−201.36</td>
<td>0.000</td>
<td>406.75</td>
</tr>
</tbody>
</table>
Table 4. Model-averaged coefficients and 95% confidence intervals of models with difference in adjusted Akaike’s Information Criterion ($\Delta AIC_c$) <10 from the top model at each scale of observation for foal overwinter survival ($t$ to $t + 1$) for foals of feral horses on Sable Island, Nova Scotia, Canada, 2008–2013. Density was measured as horses/km$^2$ of vegetated area. Scale refers to the size of the buffer around which we quantified local density and proportion of freshwater.

<table>
<thead>
<tr>
<th>Scale (m)</th>
<th>Variable</th>
<th>B</th>
<th>95% CI$^a$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Lower</td>
</tr>
<tr>
<td>2,000</td>
<td>Intercept*</td>
<td>1.92</td>
<td>1.49</td>
</tr>
<tr>
<td></td>
<td>Local density*</td>
<td>–0.32</td>
<td>–0.60</td>
</tr>
<tr>
<td></td>
<td>Island density*</td>
<td>–0.55</td>
<td>–0.87</td>
</tr>
<tr>
<td></td>
<td>Proportion freshwater</td>
<td>0.25</td>
<td>–0.06</td>
</tr>
<tr>
<td></td>
<td>Band size</td>
<td>–0.04</td>
<td>–0.32</td>
</tr>
<tr>
<td>4,000</td>
<td>Intercept*</td>
<td>1.90</td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td>Local density</td>
<td>–0.28</td>
<td>–0.57</td>
</tr>
<tr>
<td></td>
<td>Island density*</td>
<td>–0.55</td>
<td>–0.86</td>
</tr>
<tr>
<td></td>
<td>Proportion freshwater</td>
<td>0.14</td>
<td>–0.16</td>
</tr>
<tr>
<td></td>
<td>Band size</td>
<td>–0.05</td>
<td>–0.32</td>
</tr>
<tr>
<td>8,000</td>
<td>Intercept*</td>
<td>1.89</td>
<td>1.47</td>
</tr>
<tr>
<td></td>
<td>Local density*</td>
<td>–0.33</td>
<td>–0.61</td>
</tr>
<tr>
<td></td>
<td>Island density*</td>
<td>–0.52</td>
<td>–0.84</td>
</tr>
<tr>
<td></td>
<td>Proportion freshwater</td>
<td>0.22</td>
<td>–0.08</td>
</tr>
<tr>
<td></td>
<td>Band size</td>
<td>–0.06</td>
<td>–0.33</td>
</tr>
</tbody>
</table>

$^a$ Informative parameters (CIs not overlapping 0).