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2 Dr. Antonio Uzal
3 School of Animal Rural and Environmental Sciences
4 Nottingham Trent University
5 Southwell NG25 0QF, UK
6 Phone +44 (0)115 848 5338
7 antonio.uzal@ntu.ac.uk

8 RH: Laforge et al. • Effects of Density on Foal Survival

9 **Scale-Dependent Effects of Density and Habitat on Foal Survival**

10 MICHEL P. LAFORGE,¹ *Department of Biology, University of Saskatchewan, 112 Science*
11 *Place, Saskatoon, SK S7N 5E2, Canada*

12 ANTONIO UZAL,^{2,3} *Department of Biology, University of Saskatchewan, 112 Science Place,*
13 *Saskatoon, SK S7N 5E2, Canada*

14 SARAH A. MEDILL, *Department of Biology, University of Saskatchewan, 112 Science Place,*
15 *Saskatoon, SK S7N 5E2, Canada*

16 PHILIP D. MCLOUGHLIN, *Department of Biology, University of Saskatchewan, 112 Science*
17 *Place, Saskatoon, SK S7N 5E2, Canada*

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

¹ Present affiliation and address: *Department of Animal and Poultry Science, College of Agriculture and Bioresources, University of Saskatchewan, Saskatoon SK, S7N 5A8 Canada*

² Corresponding author's email address: antonio.uzal@ntu.ac.uk

³ Present affiliation and address: *School of Animal Rural and Environmental Sciences, Nottingham Trent University, Southwell NG25 0QF, United Kingdom*

23 by female-defense polygyny with persistent, non-territorial breeding groups (bands) and female-
24 biased initial (natal) and subsequent (breeding) dispersal. We predicted that for horses, offspring
25 movements coupled with female-biased breeding dispersal would increase the scale at which
26 density best related to juvenile survival compared to species with greater female philopatry. From
27 2008 to 2013, we censused the population of feral horses on Sable Island, Canada. We annually
28 computed individual-specific local densities for 442 foals (horses/km² in radii of 2,000 m, 4,000
29 m, and 8,000 m fixed to a band's centroid of movements) and whole-island (total) population
30 density, group (band) size, and local access to surface freshwater, which affected movement
31 patterns and selection of vegetation by females. The population of feral horses increased from
32 380 in 2008 to 559 in 2013. Overwinter survival of foals averaged 82.8%. Island-wide density
33 was the most important predictor of foal mortality and was negatively associated with survival,
34 with a lesser negative effect from local density. Increased access to surface freshwater (ponds)
35 was an important predictor of foal survival but only at certain scales. Our study emphasizes the
36 relevance of a multi-scale approach when analyzing the response of fitness components to
37 changes in habitat and population processes, which may be influenced by the particular social
38 organization of the species.

39 **KEY WORDS** density dependence, *Equus ferus caballus*, feral horse, foal, habitat, population
40 dynamics, Sable Island, scale, survival.

41 In ecology, scale refers to “...several concepts, including the physical extent of the processes (the
42 ‘range’) and the spatial and temporal resolution of the data (‘grain’)” (Fortin and Dale 2005:9).
43 Scale affects interpretation of ecological processes, including resource selection (Anderson et al.
44 2005, Boyce et al. 2003, Leblond et al. 2011, Laforge et al. 2015b), sexual segregation (Bowyer
45 et al. 1996), and interspecific (Whittaker and Lindzey, 2004) and intraspecific competition
46 (Mayor and Schaefer 2005). It is important to use the most appropriate scale, or at least develop
47 models that bridge across scales, to understand an ecological system (Chave 2013).

48 Juvenile survival decreases with increasing intraspecific competition (population density)
49 in many species of wildlife, including Soay sheep (*Ovis aries*; Milner et al. 1999), bighorn sheep
50 (*Ovis canadensis*; Portier et al. 1998), and mallard ducks (*Anas platyrhynchos*; Gunnarsson et al.
51 2006). In examining how an organism might experience effects of intraspecific competition
52 through exposure to conspecific density, Coulson et al. (1997) reported that it was not at the
53 largest spatial scale of population density (total population size) that the greatest amount of
54 variation in juvenile survival was explained for red deer (*Cervus elaphus*). Rather, the most
55 statistically explanatory scale isolated a population substructure of intermediate local scales of
56 individual experience related to spatial heterogeneity in high quality food resources (grasslands).
57 The link between use of grasslands and a female’s lifetime reproductive success was
58 subsequently reported to interact with its local experience of density (McLoughlin et al. 2006),
59 and adaptive use of habitat depended on how far the local (as opposed to total) population was
60 from reaching carrying capacity (Fortin et al. 2008). A similar situation was reported for juvenile
61 survival of Atlantic salmon (*Salmon solar*), where fine-scale local density was most important in
62 explaining juvenile mortality (Einum and Nislow 2005).

63 There are many factors that may dictate how and why a life-history trait like density-
64 dependent juvenile survival may vary with scale. Mating systems and social organization can be

65 important to fine-scale, spatial effects on inbreeding (Chesser 1991) and underpin relationships
66 leading to intraspecific competition (Clutton-Brock 1989) affecting distribution, and hence
67 heterogeneity in population and evolutionary processes (e.g., by affecting reproductive success or
68 sex ratio and dispersal; Dobson 1982, Leturque and Rousset 2004). We might therefore expect
69 social system to play a role in density-dependent phenomena and factor into scale-related
70 questions of density dependence. Little is known, however, about how something like an
71 animal's social system might affect scale dependence in ecological interactions. One reason for
72 this is the paucity of multi-scale, individual-based analyses of population dynamics for
73 continuously distributed organisms (i.e., where each individual possesses a unique perspective of
74 density, as opposed being grouped into a discrete subpopulation).

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

89 categories; Richard et al. 2014). Horses on Sable Island provide an opportunity to compare scale-
90 dependent population dynamics against what has been reported for ungulates with different social
91 systems.

92 Originally introduced sometime in the mid-1700s, Sable Island's feral horses have always
93 been free-ranging with minimal interference by humans (Christie 1995). The horses of Sable
94 Island present a markedly distinct genetic structure from other horse breeds but are most closely
95 related to the Nordic breeds of horses and ponies (Plante et al. 2007, Prystupa 2012). Though
96 introduced, the horses are treated by Parks Canada Agency as a naturalized species constituting
97 an important part of the ecosystem. Over the course of our study (2008–2013), total population
98 size increased from 380 individuals to 559, an increase of 47%. Foals dispersed from their natal
99 band 33.4% of the time, with approximately a third of foals (10.2% of all foals) dispersing on
100 their own (without their mother). Natal dispersal distance of female foals over winter averaged
101 $3,572 \text{ m} \pm 1,546 \text{ m}$ (SD; Contasti 2011). Female dispersal to different bands was common (30.5%
102 of mothers).

103 Following Coulson et al. (1997), we examined density feedbacks on juvenile overwinter
104 survival at multiple spatial scales for horses on Sable Island, using an individual-based approach.
105 Horses on Sable Island exist in a natural though simplified system without predation, human
106 interference, or interspecific competition (the horses are the island's only terrestrial mammal). As
107 part of a long-term, individual-based monitoring program for this population (Contasti et al.
108 2012, Marjamäki et al. 2013, Richard et al. 2014, van Beest et al. 2014, Rozen-Rechels et al.
109 2015), we tracked the overwinter fates of all foals alive on the island at the end of each summer
110 ($n = 442$). We quantified each animal's unique experience of the environment including attributes
111 of social group (band size) and a foal's (and its mother's) access to freshwater and exposure to
112 population density at 4 spatial scales of increasing size (2,000-m, 4,000-m, and 8,000-m buffers

113 around median band centroid locations and total population density). We chose these scales to
114 reflect different percentiles of mean annual horse movement relating to the intensity of use of
115 their home ranges.

116 We generated 2 competing hypotheses for how density may affect foal survival. Our first
117 hypothesis was that the scale at which foal mortality would be detected in relation to density
118 would mirror that for red deer fawns in Coulson et al. (1997), where local density in a defined
119 area around the focal individual would best predict foal mortality due to local competition for
120 resources. By contrast, social system and trends in philopatry may play an important role in
121 determining the most appropriate scale at which to examine density dependence in population
122 processes, including juvenile survival. Horses on Sable Island show female-biased natal and
123 breeding dispersal (social dispersal), and females with accompanying offspring can and do leave
124 bands in response to increases in band size and conspecific density (Marjamäki et al. 2013).
125 Dispersal events largely occur during winter (Marjamäki et al. 2013, Debeffe et al. 2015).
126 Departure of foals with females during dispersal increases foal overwinter survival (Debeffe et al.
127 2015), suggesting a role for dispersal to affect variation in foal survival. Therefore, our alternate
128 hypothesis was that dispersal of females and foals would result in a situation where individuals
129 are better able to exploit resources evenly across the island, leading to population density at
130 larger scales being a better predictor of overwinter survival than measurements taken at smaller
131 scales.

132 **STUDY AREA**

133 Sable Island National Park Reserve, located 275 km southeast of Halifax, Nova Scotia, Canada
134 ($43^{\circ} 55' N$, $60^{\circ} 00' W$), is a crescent-shaped sand bar home to a population of free-ranging feral
135 horses (Fig. 1). It is approximately 49 km long and 1.25 km in width at its widest point, and is
136 comprised of sandy beaches and vegetated and bare sand dunes ≥ 30 m high. The island's climate

137 was temperate oceanic with cool summers and wet winters. Catling et al. (1984), Freedman et al.
138 (2011), and Tissier et al. (2013) detailed the flora present. Sable Island was treeless, and the
139 vegetation community was dominated by American beach grass, or marram (*Ammophila*
140 *breviligulata*), which occurred throughout most of the vegetated parts of the island. Shrub-
141 dominated heath (*Empetrum nigrum*, *Juniperus communis*, *Myrica pensylvanica*, *Rosa*
142 *virginiana*, *Vaccinium angustifolium*) was the climax vegetation association found on Sable
143 Island. The west end of the island contained patches of sandwort (*Honckenya peploides*) and
144 beach pea (*Lathyrus japonicus* var. *maritimus*). Several permanent freshwater ponds covering
145 approximately 20 ha were used by horses and confined to western and central areas of the island
146 (Contasti 2011, Contasti et al. 2012). Ephemeral melt- and rain-water ponds occurred on the east
147 half of the island but generally disappeared in summer, and horses on east Sable Island had to
148 excavate drinking holes to access freshwater (Contasti 2011). This environmental gradient
149 underlaid density-dependent habitat selection processes with major consequences for population
150 and social dynamics across the length of the island (Marjamäki et al. 2013, Richard et al. 2014,
151 Manning et al. 2015). Aside from a small human presence (researchers and tourists), feral horses
152 were the only terrestrial mammals on the island.

153 **METHODS**

154 **Data Collection and GIS Analysis**

155 We obtained direct observations of individual horses via systematic ground censuses on Sable
156 Island (weekly observations from Jul–Sep), including 21,392 individual observations
157 encompassing the entire population ($N = 380, 437, 503, 448, 534,$ and 559 individuals,
158 respectively, between 2008 and 2013, including 442 foals alive in Sep 2008 through 2013; counts
159 updated from Richard et al. [2014]). Each daily sampling effort included 1 of 7 sections of the
160 island, stratified to allow complete coverage of a section in 1 day and roughly complete coverage

161 of the island in 1 week. We approached horses on foot (which were largely indifferent to our
162 presence) and recorded the location of an individual using a hand-held global positioning system
163 (GPS) with location error to within 5 m. We determined the horse's identity (to determine
164 survival status and band membership from year to year) from facial features and other
165 distinguishing marks (verified using digital photographs at every sampling event), sex,
166 reproductive status, and group membership. Our photography-based approach to cataloguing
167 each individual is described in Contasti (2011). If a horse was not observed during an entire
168 season, we assumed that it had died. We evaluated whether our censuses were adequate by
169 comparing, for 2010 data, our summer counts of non-foals with that obtained from high-
170 resolution aerial photography in January 2010 (prior to births). The latter was flown by aircraft at
171 an altitude of approximately 450 m as part of a census of the population of grey seals
172 (*Halichoerus grypus*) on Sable Island, which also proved excellent for counting horses (Bowen et
173 al. 2011). This confirmed that our 2010 census accounted for >99% of the horses present as
174 expected. A previous study (Welsh 1975) reported that horses have small home ranges on Sable
175 Island ($2.8 \pm 1.2 \text{ km}^2$ [$\bar{x} \pm \text{SD}$], $n = 32$ bands), which generally range from one end of the island
176 to the other and are compressed along its length.

177 All collection and sampling methods (strictly behavioral observation) were approved
178 by the University of Saskatchewan's Animal Research and Ethics Board, under University of
179 Saskatchewan Animal Care Protocol 20090032 and guidance of the Canada Council on Animal
180 Care. Access to Sable Island for this research project was granted by written permission of M.
181 Voigt, Canada Coast Guard for years 2008–2012; however, in the year of 2012, as management
182 of the island transitioned from Coast Guard to Parks Canada Agency, we also obtained and
183 followed conditions of a Research License (14668) provided by Parks Canada Agency 2012–
184 2014.

185 We used ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA) to
186 compute conspecific densities and proportion of freshwater in 3 buffers of increasing radius
187 (2,000 m, 4,000 m, and 8,000 m) centered on each band's median centroid location. Buffer radii
188 generally corresponded to the 80th, 95th, and 99th percentile of annual movements of all horses
189 and were selected to reflect a continuum of scales. We selected the 99th percentile (8,000-m
190 buffer) to reflect the annual movement rate of nearly all horses in the population. We selected the
191 95th percentile (4,000-m buffer) to eliminate outliers of extraordinary dispersal, and the 2,000-m
192 buffer (80th percentile) to approximate the core area used by individuals. Within each buffer, we
193 calculated the density of conspecifics as a function of vegetated area (km^2 ; hereafter local
194 density) because horses used beaches primarily for transitory movements or resting. We also
195 calculated the proportion of freshwater in each buffer and total population density over the whole
196 island as a function of horses/ km^2 of vegetated area (hereafter total density). We included
197 vegetation availability implicitly in the density term as horses/ km^2 of vegetated area; therefore,
198 we did not include any other explicit vegetation terms in our models; therefore we did not include
199 any other explicit vegetation terms in our models. We obtained habitat and vegetation data from
200 high-resolution aerial photography and a Light Detection and Ranging (LIDAR) map (2009)
201 classified and ground-truthed by the Applied Geomatics Research Group (AGRG) at Nova Scotia
202 Community College, Middleton, Nova Scotia, Canada.

203 **Statistical Analyses**

204 Foal overwinter survival was a binary response variable, with 0 representing animals that died
205 between 1 August of the birth year (t) and 15 July of the following year ($t + 1$), and 1 describing
206 those that survived. We used generalized linear mixed effects models (GLMM) with a binomial
207 error structure in R Version 3.2.1 (R Core Team 2015) to model survival as a function of local
208 density and habitat variables at the 3 local scales measured and total island density. Our maximal

209 model included as covariates local density and proportion of freshwater (computed at 1 of the 3
210 identified scales), band size, and total density. We used *Z*-scores to compare effect sizes between
211 different parameters and to facilitate convergence of models. We tested for collinearity between
212 predictors at all scales and ensured no pair of variables had a Pearson's correlation coefficient of
213 $r > |0.7|$ (Dormann et al. 2013) and that no variable had a variance inflation factor >5 (Menard
214 1995). Unlike population density, surface freshwater availability did not vary among years
215 because we used 1 map (dated 2009); hence, we could not generate a variable for the whole-
216 island scale. Marjamäki et al. (2013) noted significant collinearity between local density (at the
217 8,000-m scale) and distance of overwinter movements, and so we also did not include distance of
218 dispersal (if it occurred) as a covariate in our models. We tested our final models for trends in
219 average residuals versus expected values using binned residuals (Gelman and Hill 2007) with the
220 R package *arm* (Gelman and Su 2015) because plotting raw residuals versus fitted values are
221 generally not useful after logistic regression (we did not detect any serious anomalies). We tested
222 3 model structures for random effects: band identification (ID), maternal ID, and both (not
223 nested). We were not able to test maternal ID nested within band ID because of dispersal of
224 mothers to different bands.

225 Following Burnham and Anderson (2002), we developed a set of candidate models (Table
226 1) that we evaluated using small sample size adjusted Akaike's Information Criterion (AIC_c). We
227 employed a hierarchical method of model selection, first determining the optimal random effect
228 structure and then performing model selection on the fixed effects. We tested the 3 random effect
229 structures using the maximal (fully parametrized) model with local density and proportion
230 freshwater modeled at each of our 3 scales using a GLMM using the R package *lme4* (Bates et al.
231 2015) and selected the model with the lowest AIC_c (Zuur et al. 2009), which resulted in our using
232 models with maternal ID only. Once we had determined the most informative random term

233 structure, we ran each model in our candidate model set at each of our 3 scales and ranked each
234 model by AIC_c . We used model-averaging techniques using the R package `AICcmodavg`
235 (Mazerolle 2015) to generate model-averaged parameter estimates for all models that had an
236 $AIC_c < 10$ from the top model at each scale. To evaluate predictive capacity of our final GLMM,
237 we adopted the approach of Boyce et al. (2002), which applies to this situation. We evaluated this
238 model using k -fold cross-validation (test-to-training ratio of 5 data subsets), whereby we tested
239 predictive capacity of partitioned models against withheld training data using the mean
240 Spearman's rank correlation (\bar{r}_s) between training and test data, grouped within 10 bins (Boyce et
241 al. 2002). In a separate analysis, we re-ran all models replacing total island density with year, to
242 determine whether other inter-annual effects besides density may have had an impact on foal
243 survival.

244 **RESULTS**

245 Of 442 foals entering their first winter from 2008 to 2013, 82.8% survived to the next census
246 period. A foal's exposure to conspecific density in the year it was born (t) had a larger mean and
247 standard deviation at small scales than at large ones (Table 2). Using maternal ID only as a
248 random effect provided the best fit for our models as determined by AIC_c . Using a model
249 structure with band ID or band ID and maternal ID raised the AIC_c of our fully parametrized
250 model by between 1.6 and 3.0 (see Table S1, available online at www.onlinelibrary.wiley.com).
251 Our results suggested that no single model was clearly superior in describing foal overwinter
252 survival; the top 6 models all had a ΔAIC_c from the top model < 2.0 (Table 3). All top models
253 included local density and total density. Proportion of freshwater was important in many of the
254 top models, was retained in our best model at the 8,000-m and the 2,000-m scale (Table 3), and
255 enhanced probability of survival; however, the term was not informative in our model-averaged
256 estimates at any scale (Table 4). Both local density and total density negatively affected survival

257 in our models at each of our 3 local scales (Table 4); however, the effect was greater for total
258 density than for local density at all 3 scales. Band size was uninformative at all scales (Table 4).
259 The k -fold cross-validation values for the best model at the 2,000-m, 4,000-m, and 8,000-m
260 scales were 0.62, 0.75, and 0.68, respectively.

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

266 **DISCUSSION**

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

278 Our results contrast with numerous other studies that have investigated scalar processes in
279 life-history traits. Studies of roe deer (*Capreolus capreolus*) reported that fine-scale variation in
280 food resources at the home-range scale have the greatest effect on fawn biomass (Pettorelli et al.

281 2003) and survival (Pettorelli et al. 2005). Einum and Nislow (2005) reported juvenile survival in
282 salmon was density-dependent at small scales and overwinter survival in red deer fawns was
283 reported by Coulson et al. (1997) to be affected by conspecific density at intermediate scales. By
284 contrast, Vreeland et al. (2004) did not find any effect of home-range scale habitat variation in
285 fawn survival and suggested that factors at the landscape level may have been important in their
286 system.

287 Habitat quality, availability of cover habitat, and predation pressure have been identified
288 as important influences of large herbivore life-history traits for many species (Coulson et al.
289 1997, Milner-Gulland et al. 2000, Nilsen et al. 2004). For horses on Sable Island, habitat quality
290 is relatively homogeneous, and cover habitat (e.g., trees and shrubs) and predation pressure are
291 non-existent. Cost of dispersal for horses in our study was therefore likely much less than in
292 many other studies. In their study of salmon, Einum and Nislow (2005) suggest that the
293 metabolic costs and risk of predation pressure make dispersal costly in this species, resulting in
294 less dispersal and greater density-dependent mortality at local scales. Similarly, Stuart-Smith et
295 al. (1997) reported that caribou (*Rangifer tarandus*) calf mortality was higher in fragmented
296 landscapes where individuals had smaller home ranges, suggesting similar barriers to dispersal
297 were responsible for fine-scale juvenile mortality.

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

305 al. 2013) and we suspect that this process may increase variability in local density effects on the
306 overwinter survival of accompanying foals.

307 Availability of freshwater appeared to be a lesser (compared to local density) but still
308 important influence of foal survival across most scales of observation. Heterogeneity in
309 freshwater as a resource influences spatial distribution and movement patterns for horses on
310 Sable Island (Rozen-Rechels et al. 2015), other populations of feral horses (Rubenstein 1981,
311 Berger 1986), and other large herbivores such as springbok (*Antidorcas marsupialis*; Ritter and
312 Bednekoff 1995) and African elephants (*Loxodonta africana*; Chamaillé-Jammes et al. 2007).
313 Freshwater availability was a positive predictor of foal survival, which we suspect is mainly
314 manifest through effects on body condition and resources for lactation in mothers. Contasti et al.
315 (2012) noted that body condition in female horses significantly declined from west to east on
316 Sable Island (2008–2010) in accordance with the west to east reduction in availability of surface
317 freshwater on the island. Heterogeneity in fixed, high quality resources, like ponds including
318 freshwater and their associated vegetation, may act to explain survival similar to the case in red
319 deer (Coulson et al. 1997). Density-related associations on high-nutrition grasslands (*Agrostis*-
320 *Festuca*) were attributed to small-scale influences on red deer calf survival; high-resolution scales
321 were good descriptors of population substructure during summer, when good grazing was
322 distributed heterogeneously. Small-scale effects of density aggregations, which were likely linked
323 to sources of permanent freshwater, did translate directly into density effects on survival in our
324 study, however, not to the extent that larger-scale density effects predicted mortality (Table 4).

325 Many studies reported inter-annual, density-independent processes (or processes interacting
326 with density) acting on population dynamics to affect juvenile survival. Spring temperatures have
327 been correlated with juvenile survival in bighorn sheep lambs (Portier et al. 1998) and red deer
328 (Albon et al. 1987). Soay sheep juvenile overwinter survival appears to be driven by a

329 combination of both density and weather effects (Grenfell et al. 1998, Milner et al. 1999). Our
330 results suggest a similar situation in horses on Sable Island; models using year instead of total
331 density improved our models, suggesting density-dependent and density-independent effects are
332 at play in juvenile survival. It is likely that greater total island densities are associated with
333 overwinter resource depletion, which is likely exacerbated by extreme weather effects leading to
334 increased mortality (Manning et al. 2015).

335 **MANAGEMENT IMPLICATIONS**

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

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534 **Figure Caption**

535 Figure 1. Sable Island, Nova Scotia, Canada. Sable Island National Park Reserve (43° 55' N; 60°
536 00' W), located approximately 275 km east-southeast of Halifax, Nova Scotia, Canada. The
537 island is a crescent shaped sand bar 49 km long and 1.25 km at its widest (vegetation in grey).

538

539 Table 1: List of a priori candidate models for linear regression analysis of foal survival, Sable
540 Island, Nova Scotia, Canada, 2008–2013. Each model was evaluated with local density and
541 proportion water computed at each of 3 scales: 2,000 m, 4,000 m, and 8,000 m.

Local density + total density + proportion freshwater + band size

Local density + total density + band size

Local density + total density + proportion freshwater

Local density + total density

Local density

Total density

Local density + proportion freshwater

Null

542 Table 2: Distribution of density (horses/km² of vegetated area) in summer of birth across 4 spatial scales for foals born into bands of
 543 feral horses on Sable Island, Nova Scotia, Canada, 2008–2013. Presented is the mean (\bar{x}), standard deviation (SD), and coefficient of
 544 variation (c_v) for increasing scales of individual experience, each metric centered on the median centroid of a band’s movements in the
 545 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
 546 divided by vegetated area on the island (without SD or c_v).

547

Year		Scale (m)			
		2,000	4,000	8,000	Total
2008 ($n = 69$)	\bar{x}	28.2	14.7	7.7	12.7
	SD	17.0	9.0	5.3	
	c_v	0.60	0.61	0.69	
2009 ($n = 62$)	\bar{x}	42.4	20.3	10.2	14.6
	SD	31.2	12.9	6.9	
	c_v	0.74	0.63	0.68	
2010 ($n = 83$)	\bar{x}	37.1	21.4	12.1	16.8
	SD	16.4	13.1	9.2	

	c_v	0.44	0.61	0.76	
2011 ($n = 56$)	\bar{x}	41.7	24.9	15.9	15
	SD	31.6	21.9	16.5	
	c_v	0.76	0.88	1.03	
2012 ($n = 93$)	\bar{x}	37.1	20.6	11	17.8
	SD	13.8	10.9	6.7	
	c_v	0.37	0.53	0.61	
2013 ($n = 79$)	\bar{x}	45.5	25.7	14.1	18.7
	SD	19.7	13.1	7.3	
	c_v	0.43	0.51	0.52	
All years ($n = 442$)	\bar{x}	38.6	33.9	29.8	16.2
	SD	22.2	16.5	12.3	2.1
	c_v	0.57	0.49	0.41	0.13

548 Table 3: Scale, degrees of freedom (df), adjusted Akaike's Information Criterion (AIC_c), log
 549 likelihood (LL) and R^2 for the top models describing foal overwinter survival on Sable Island,
 550 Nova Scotia, Canada, 2008–2013. Scale refers to the size of the buffer around which we
 551 quantified local density and proportion of freshwater. For comparison, we also present in the 2
 552 last columns AIC_c and R^2 values for models with year (factorial) in the model as opposed to total
 553 island density.

Model	Scale (m)	df	AIC_c	LL	R^2	Year AIC_c
Local density + total density (year) + proportion freshwater	8,000	5	391.08	-190.47	0.112	387.60
Local density + total density (year)	8,000	4	391.23	-191.57	0.100	387.24
Local density + total density (year) + proportion freshwater	2,000	5	391.23	-190.55	0.112	387.93
Local density + total density (year)	2,000	4	391.82	-191.87	0.095	388.54
Local density + total density (year) + proportion freshwater + band size	8,000	6	392.93	-190.37	0.113	389.52
Local density + total density (year)	4,000	4	392.93	-192.42	0.093	389.20
Local density + total density (year) + band size	8,000	5	393.15	-191.51	0.101	389.19
Local density + total density (year) + proportion freshwater + band size	2,000	6	393.21	-190.51	0.113	389.99
Local density + total density (year) + band size	2,000	5	393.82	-191.84	0.096	390.61
Null		2	406.75	-201.36	0.000	406.75

554 Table 4. Model-averaged coefficients and 95% confidence intervals of models with difference in
 555 adjusted Akaike's Information Criterion (ΔAIC_c) <10 from the top model at each scale of
 556 observation for foal overwinter survival (t to $t + 1$) for foals of feral horses on Sable Island, Nova
 557 Scotia, Canada, 2008–2013. Density was measured as horses/km² of vegetated area. Scale refers
 558 to the size of the buffer around which we quantified local density and proportion of freshwater.

Scale (m)	Variable	B	95% CI ^a	
			Lower	Upper
2,000	Intercept*	1.92	1.49	2.36
	Local density*	-0.32	-0.60	-0.03
	Island density*	-0.55	-0.87	-0.23
	Proportion freshwater	0.25	-0.06	0.57
	Band size	-0.04	-0.32	0.24
4,000	Intercept*	1.90	1.47	2.33
	Local density	-0.28	-0.57	0.02
	Island density*	-0.55	-0.86	-0.23
	Proportion freshwater	0.14	-0.16	0.44
	Band size	-0.05	-0.32	0.23
8,000	Intercept*	1.89	1.47	2.31
	Local density*	-0.33	-0.61	-0.05
	Island density*	-0.52	-0.84	-0.20
	Proportion freshwater	0.22	-0.08	0.52
	Band size	-0.06	-0.33	0.22

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