Population Ecology

Identifying Hidden Sinks in Growing Populations From Individual Fates and Movements: The Feral Horses of Sable Island

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ABSTRACT Identifying the existence of population sinks is critical for conservation and management. However, because of density-dependent dispersal, sinks can sometimes be masked by immigration events, especially during phases of population growth. We present a large-scale, empirical demonstration of within-population source-sink dynamics using the feral horses (*Equus ferus caballus*) of Sable Island National Park Reserve, Nova Scotia, Canada, as a model. We tracked the fates and movements of 98.7% of the female population ($n = 190–237$) across 3 demographic clusters (subunits) during a period of rapid population growth (2008–2010; 24.7% increase in density). All subunits experienced increases in population size each year ($\lambda > 1.0$). Our individual-based analysis showed that western Sable Island, where water availability was greatest, behaved as a source and would have grown with or without immigration in all years. However, the central (and fastest growing subunit) would have declined from 2008–2009 ($\lambda = 0.951$) without immigration. Further, the eastern subunit would have declined in 2 intervals ($\lambda = 0.932, 0.999$) without immigration. Our study demonstrates that the propensity of habitat to act as a sink can be masked during a period of population growth because of density-dependent immigration from adjacent habitats. These findings present a caution to managers charged with conserving wide-ranging species with long population cycles for which effects of immigration on local population growth rate can be difficult to isolate using standard methods of enumeration. © 2013 The Wildlife Society.

KEY WORDS apparent survival, demographic connectivity, density dependence, emigration, *Equus ferus caballus*, feral horse, immigration, Sable Island, source-sink dynamics.

Variability in landscape characteristics can lead to spatial population substructure where groups of individuals (subunits or demes) experience different opportunities for recruitment and survival (Amarasekare 1994, Mauritzen et al. 2002, Naranjo and Bodmer 2007, Schwartz et al. 2010). Source-sink theory (Pulliam 1988, Pulliam et al. 1992) predicts that individuals occupying high-quality habitats (sources) tend to have area-specific advantages in Darwinian fitness, compared to those in low-quality habitats (sinks). Differences in rates of survival and recruitment can result in a surplus of individuals in sources and a deficit of individuals in sinks, even if the whole population shows stability. Accurately delineating sources and sinks within a population is critical for species conservation and management (Donovan et al. 1995, Dias 1996, Schwartz et al. 2010, Kerbiriou et al. 2012). However, distinguishing source from sink habitat can be challenging, especially during phases of rapid population growth (Gundersen et al. 2001).

Hidden sinks may arise during temporary population growth or stability when immigrants balance sink-related deaths (compensatory immigration; Turgeon and Kramer 2012). This may occur through a process similar to the rescue effect (Hanski 2001, Robinson et al. 2008) or when individuals select for sink habitat because of incomplete knowledge of the fitness landscape (Delibes et al. 2001). Only by identifying the basis of population growth in sink habitat (immigration vs. births and emigration vs. deaths) can the true status of a subunit be ascertained (Runge et al. 2006). Despite its importance to population ecology and conservation, few empirical studies have documented the details of subunit-specific demography and growth for wild populations (e.g., Watkinson and Sutherland 1995, Virgl and Messier 2000, Peery et al. 2006, Turgeon and Kramer 2012).

We present a large-scale, empirical test of compensatory immigration and the source-sink model using the feral horses of Sable Island National Park Reserve, Nova Scotia, Canada, in which we tracked the fates and movements of females

during a period of rapid population growth (2008–2010). Our analysis was based on a priori identification of 3 spatially distinct, but open (i.e., subject to immigration and emigration) population subunits distributed along a longitudinal gradient (west-central-east) of habitat quality (surface water and forage; Contasti et al. 2012). By tracking all females on the island, we were able to isolate the effects of immigration and emigration versus resident births and deaths on subunit-specific population growth, which allowed us to identify the presence of sources and hidden sinks even though all subunits showed population growth. We predicted source subunits to occur in areas with high surface water availability and forage as these resources are expected to be limiting to feral horses (Rubenstein 1981, Berger 1986), and sinks to occur where resources were less available. We also expected that true sources would maintain positive growth in the absence of immigration and that emigration from these subunits would increase with density (Pulliam 1988, Turgeon and Kramer 2012).

STUDY AREA

Sable Island (43°55′N, 60°00′W) is a 49-km crescent-shaped sand bar located approximately 275 km east of Halifax, Nova Scotia, Canada (Fig. 1). The treeless island is comprised of wide, sandy beaches and vegetated and bare sand dunes up to 30 m in elevation. Vegetation was dominated by American beach grass, or marram (*Ammophila breviligulata*), which occurred throughout most of the vegetated parts of the island. The west side of the island contained high-quality patches of sandwort (*Honckenya peploides*) and beach pea (*Lathyrus japonicus* var. *maritimus*), which were not as abundant in other regions. In addition, the west contained permanent water ponds and associated emergent plants that were less common in the center of the island and absent in the east, where horses were forced to excavate wells to obtain water in summer (Lucas et al. 2009, Contasti et al. 2012). Contasti et al. (2012) divided the island into 3 zones (west, central, east) based on hierarchical cluster analysis of points of water availability and an indicator species analysis of vegetation; these divisions respectively contained the summer movements of 3 population clusters of horses (females only). We adopted the clusters of Contasti et al. (2012) here as subunits (1–3) in a west–east gradient to analyze population source-sink dynamics (Fig. 1).

Originally introduced to Sable Island in the mid-1700s, the feral horses have always been free-ranging with minimal interference by humans (Christie 1995), and are most closely related to the Nordic breeds of horses and ponies (Prystupa et al. 2012). Though introduced, they are treated by Parks Canada Agency as a naturalized species constituting an important part of the ecosystem. Feral horses exhibit a mating system characterized by female-defense polygyny with persistent, non-territorial breeding groups (bands) and transitory mixed adolescent or bachelor groups (Linklater et al. 2000). Bands consist of adult and adolescent females, their pre-dispersing offspring, and 1–3 stallions (where ≥2-year-old stallions are multi-stallion bands). Males that are not members of bands live in unstable bachelor groups or as solitary individuals. Number of bands, band sizes, and counts of bachelors decreased from west to
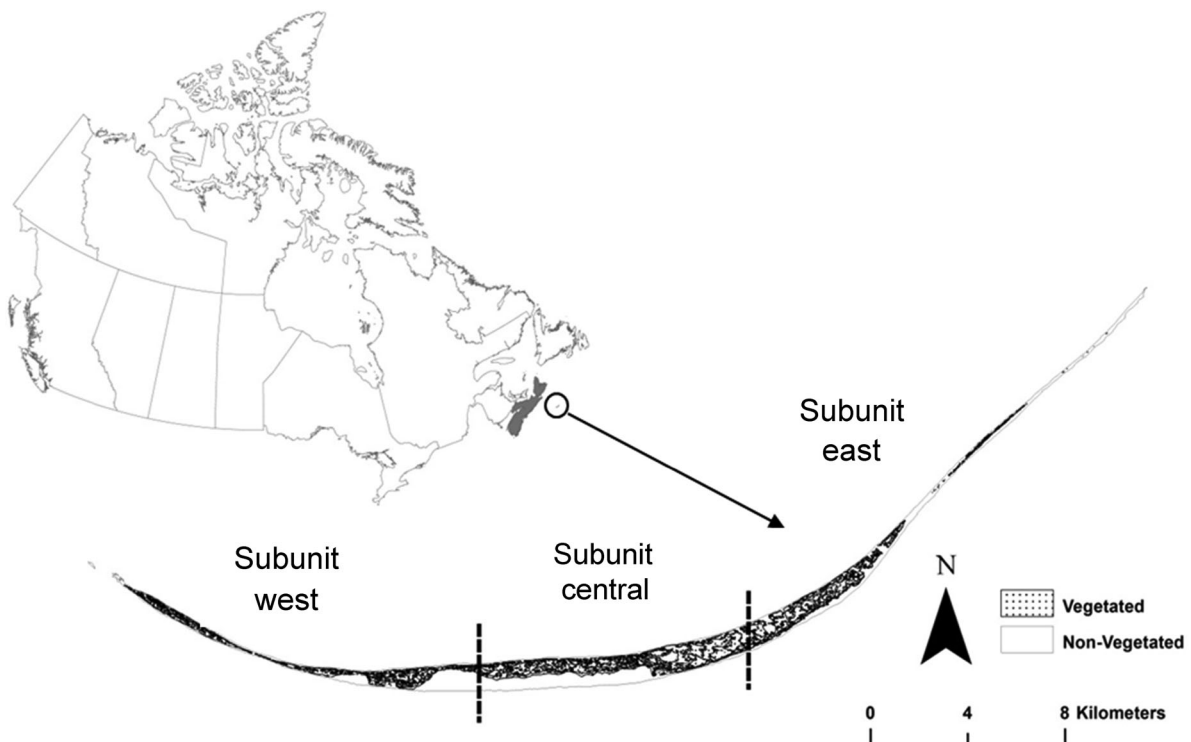

Figure 1. Map of Sable Island and its geographic position (dotted circle) relative to Nova Scotia, Canada, with vertical black lines delineating 3 subunits (1 = west, 2 = central, and 3 = east) of horses (females) according to a west–east gradient in water and forage availability.

Table 1. Annual distribution of bachelors and bands (and average size of bands) of feral horses within subunits 1, 2, and 3 on Sable Island, Nova Scotia (2008–2010). Average band size includes males and females.

Year	n	Total bachelors			Total bands			Average ($\pm$SE) band size		
		Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3
2008	390	14	17	4	22	15	15	6.95 (0.69)	6.6 (0.71)	5.4 (0.62)
2009	442	19	16	6	25	15	18	7.00 (0.59)	7.57 (0.75)	5.72 (0.62)
2010	484	18	11	13	29	24	18	6.59 (0.52)	6.33 (0.63)	5.89 (0.51)

east according to the density gradient identified in Contasti et al. (2012), though band sizes did not significantly differ among subunits (Table 1).

METHODS

Population Census

From 2008 to 2010, we obtained direct observations ($n = 2,991$) from 239 unique females via systematic censuses of the entire population in summer (weekly observations from Jul to Sep). We kept detailed and up-to-date appearance notes and photographs (to document unique face and body markings, coat phenotype) for every horse on the island, which is a reliable method for individual-based monitoring of feral horses (e.g., Saltz and Rubenstein 1995, Heitor et al. 2006). We could identify almost all females from repeated contact (98.7%) and only used these females for analysis. We also evaluated whether the annual census was adequate (i.e., if we sampled all horses present on the island) by comparing, for 2010 data, our summer counts of non-foals (yearlings and older) with that obtained from high-resolution aerial photography in April 2010 prior to foaling. This confirmed that our summer census in 2010 accounted for >99% of the horses present in April. Horses were largely undisturbed by our presence, which allowed us to approach all individuals (both males and females) to within a few meters during censuses. We recorded each horse's location using a hand-held global positioning system (GPS) with location error to within 5 m, identity, sex, reproductive status, and group membership. Mortality was assumed by the absence of a horse from the island between years. We were interested in the ramifications of density-dependent migration during a phase of population growth on source-sink dynamics and so only include data to 2010. We restricted our analysis only to females as subunit clusters in Contasti et al. (2012) were identified based on females. We sampled following University of Saskatchewan Animal Care Protocol (20090032) and under guidance of the Canadian Council on Animal Care.

Analysis

We identified annual survival, fecundity, immigration, and emigration events from 1 summer to the next (t to $t + 1$). We calculated age class-specific (foal, yearling, 2-year-old, 3-year-old, and adult [age ≥ 4]) survival rates as the proportion of subunit residents from surveys at time t that were observed alive in the same subunit at $t + 1$ for each year, and defined fecundity (i.e., recruitment) as the number of foals produced by females of age classes 3 and 4+ that survived to post-birth pulse censuses ($t + 1$). Two-year-olds

did not reproduce during our study, although females of this age reproduce in other feral horse populations (Berger 1986). We determined the foals that belonged to residents and those that belonged to immigrants in each year, which allowed us to calculate recruitment values for residents without considering births from immigrants (Fig. 2). Contasti et al. (2012) performed a detailed comparison of these rates from 2008 to 2010; in this study, we only use annual values in our projection matrices. Calculated demographic rates were not based on a sample of the island population, but rather were actual rates as observed from census data (i.e., our sample was our population of inference). Hence, year-to-year variation was a function of process variation only, including environmental and demographic stochasticity.

Females immigrated to new bands between subunits almost exclusively outside census months (we observed 1 band move from subunit 1 to 3 in 2010), though we observed band interchange within each subunit during this time (27 occurrences). We excluded this interchange from analyses because we were interested in the effect of immigration on local population growth. We did not monitor horse distribution during the winter or early breeding season and cannot comment on the factors that led to these movements. However, for the purpose of calculating immigration and emigration rates, we assumed that movement between subunits occurred after the census of year t, but before the summer breeding season of $t + 1$. We estimated immigration as

$$\frac{I}{(R_{t+1} + I)}$$

where I is the number of immigrants in a subunit at $t + 1$ and R_{t+1} is the number of residents alive in the subunit at $t + 1$. We estimated emigration as

$$\frac{E}{R_t + E}$$

where E is the number of emigrants from a subunit that left prior to censuses at $t + 1$ and R_t is the number of residents alive in the subunit at t.

We determined annual population size for each subunit (1 = west, 2 = central, 3 = east) from the census (Fig. 3). We calculated the realized finite rate of annual population increase (λ_C) for each subunit directly using the formula N_{t+1}/N_t for the first ($t = 2008$) and second ($t = 2009$) intervals. Because λ_C is calculated from total counts, it collectively includes recruitment, survival, emigration, and immigration for each subunit (Peery et al. 2006). Thus, we
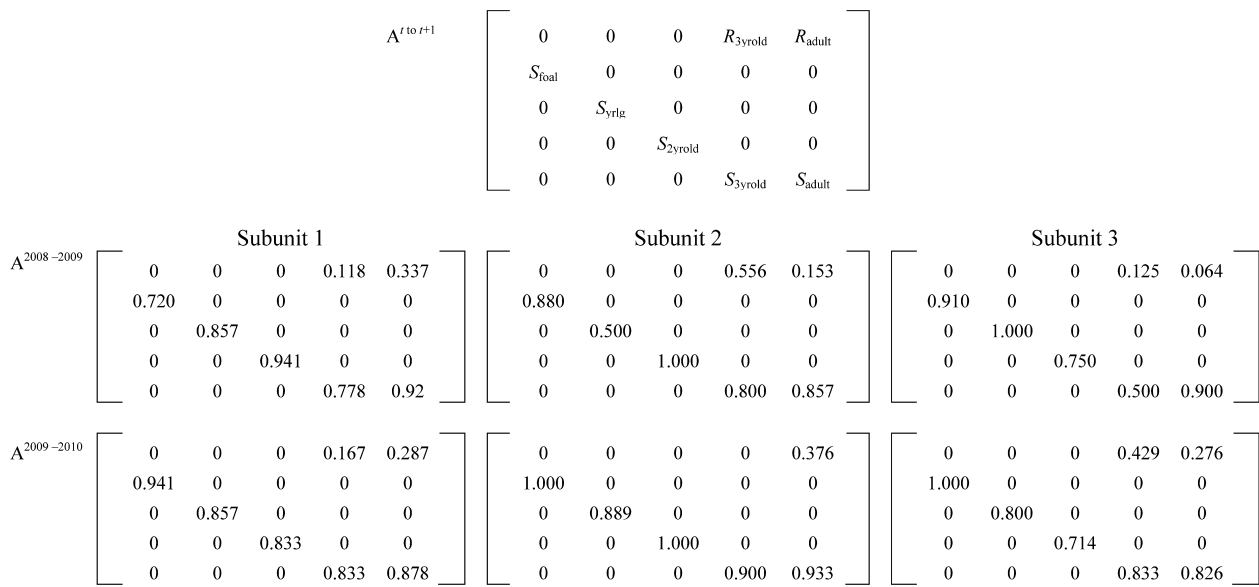
$$A^{t \text{ to } t+1} \quad \begin{bmatrix} 0 & 0 & 0 & R_{3\text{yrold}} & R_{\text{adult}} \\ S_{\text{foal}} & 0 & 0 & 0 & 0 \\ 0 & S_{\text{yrlg}} & 0 & 0 & 0 \\ 0 & 0 & S_{2\text{yrold}} & 0 & 0 \\ 0 & 0 & 0 & S_{3\text{yrold}} & S_{\text{adult}} \end{bmatrix}$$

	Subunit 1						Subunit 2						Subunit 3				
$A^{2008-2009}$	0	0	0	0.118	0.337		0	0	0	0.556	0.153		0	0	0	0.125	0.064
	0.720	0	0	0	0		0.880	0	0	0	0		0.910	0	0	0	0
	0	0.857	0	0	0		0	0.500	0	0	0		0	1.000	0	0	0
	0	0	0.941	0	0		0	0	1.000	0	0		0	0	0.750	0	0
	0	0	0	0.778	0.92		0	0	0	0.800	0.857		0	0	0	0.500	0.900
$A^{2009-2010}$	0	0	0	0.167	0.287		0	0	0	0	0.376		0	0	0	0.429	0.276
	0.941	0	0	0	0		1.000	0	0	0	0		1.000	0	0	0	0
	0	0.857	0	0	0		0	0.889	0	0	0		0	0.800	0	0	0
	0	0	0.833	0	0		0	0	1.000	0	0		0	0	0.714	0	0
	0	0	0	0.833	0.878		0	0	0	0.900	0.933		0	0	0	0.833	0.826

Figure 2. General structure of matrix models (A) for calculating annual subunit-specific population growth rate (λ_M) and annual matrices for subunits 1 (west), 2 (central), and 3 (east). Models are parameterized with age-class survival and fecundity calculated from all females on Sable Island, Canada from 2008 to 2010. Survival notations are foal (S_{foal}), yearling (S_{yrlg}), 2-year-old ($S_{2\text{yrold}}$), 3-year-old ($S_{3\text{yrold}}$), and adult (S_{adult}). Fecundity rates (production of females only) are noted as 3-year-old ($R_{3\text{yrold}}$) and adult (R_{adult}).

used λ_C to represent the actual growth trend for each subunit in the presence of immigration and emigration.

To determine the time-specific influence of immigration on subunit population growth, we followed Peery et al. (2006) and calculated the annual subunit-specific population growth rate (λ_M) using 6 age-structured projection matrices (1 for each subunit in each year; Caswell 2001) parameterized with apparent survival (where emigration was considered

Figure 3. Changes in local density (no. horses/vegetated km^2) of females (all age categories) for subunits 1 (west), 2 (central), and 3 (east) on Sable Island, Canada from 2008 to 2010 with emigration (no. emigrants/no. of surviving residents) and immigration (no. immigrants/no. residents + no. immigrants) rates of reproductive females (ages 2+). Numbers of individuals in each subunit per year are indicated above bars. We do not report errors as we derived densities and rates from total population census.

death) and recruitment of residents at time t (Fig. 2) for each age class (females only; Appendix 1). Thus, λ_M assumed neither immigrants nor their newborn offspring influenced local population growth for each year (i.e., we closed the subunit to all effects of immigration). Matrix models are used to project the future state of a population from structured conditions (age and vital rates) present at the beginning of a projection interval (van Groenendael et al. 1988, Caswell 2001), and so our models predict the asymptotic growth rate of each subunit if immigration never occurred. We did not calculate λ in the absence of immigration by simply excluding immigrants from total counts and using N_{t+1}/N_t because the matrix-based approach allowed us to also explore how variation in resident age structure and vital rates translated into growth patterns. This information would be ignored if we only used total counts. We constructed annual matrices because a different number of immigrants interrupted the projection interval each year, and thus immigration had a different influence on projected growth from year to year. These matrices also captured the influence that changes in age structure resulting from immigration had on projected growth for the following year (i.e., once immigrants become residents). Conversely, we did not use a matrix model to describe realized growth (λ_C) because immigrants were not present in a given subunit at the beginning of the year. Thus, we cannot say with certainty where each immigrant survived, which prevented us from calculating age-specific survival rates for matrix parameterization.

We projected our matrices using the R package popbio (R Development Core Team 2012). Models were linear, time-invariant calculations (McPeek and Kalisz 1993), which described dynamics of the female portion of the population only. Projections described the relationship
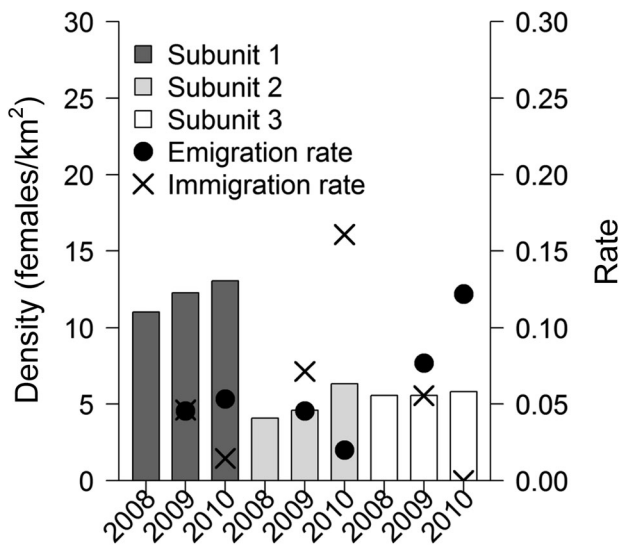
Table 2. Finite rate of population increase (λ) contrasted with and without effects of immigration for post-birth pulse censuses across population subunits 1, 2, and 3 of feral horses on Sable Island, Nova Scotia, Canada (2008–2010). Calculations are based on females only. We do not report errors as we derived rates from whole-island counts.

Subunit	λ_C[a]			λ_M[b]		
	1	2	3	1	2	3
2008–2009	1.115	1.130	1.000	1.050	0.951	0.932
2009–2010	1.072	1.377	1.041	1.034	1.123	0.999

[a] λ_C is the observed (realized) rate of population increase calculated from post-birth pulse counts of individuals; λ_C considers all demographic parameters: birth, death, emigration, and immigration.

[b] λ_M is the estimated rate of population increase calculated from a projection matrix model parameterized with resident survival and fecundity rates; λ_M considers emigration as death but does not consider immigration nor births of immigrants.

between N_{t+1} and N_t for each year (2008–2009 and 2009–2010) as

$$N_{t+1} = A^{t \text{ to } t+1} \cdot N_t$$

where N_{t+1} is the age-structure vector at the end of each interval, N_t is the age-structure vector at the beginning of each interval, and $A^{t \text{ to } t+1}$ is the matrix model for each year. We treated each successive study period as an independent replicate; that is, we did not compound the potential lasting effects of lost immigration in 2008–2009 again in 2009–2010.

We used the difference between λ_C and λ_M to assess the influence of immigration on subunit growth and to predict how growth trends would have responded without immigration following Peery et al. (2006). Because λ_M is based on recruitment, survival, and emigration only, λ_C will always be $\geq \lambda_M$. We also compared local density and emigration and immigration rates of reproductive-aged females (2-year olds, 3-year-olds, and adults) for each year.

RESULTS

Island-wide population size increased from 190 to 237 females across the 3 demographic clusters (subunits) from

2008 to 2010 (24.7% increase in density); however, population growth was heterogeneous (Fig. 3). All subunits experienced an increase in abundance of females from 2008 to 2010, with the fastest rate of growth occurring in subunit 2 (Fig. 3, Table 2).

We observed 22 movements by individual females between subunits to affect apparent population growth rates (Appendix 2). Foals exclusively moved with their mothers, whereas yearlings moved alone. Seven of 22 movements were associated with the immigration of an entire band between subunits. Subunit 2 had a significantly greater ratio of immigrants to residents compared to subunits 1 and 3, whereas emigration rates were consistently greatest for subunits 1 and 3 (Table 3).

Predicted trends of population growth for each subunit in the absence of immigration were less than those calculated from counts of individuals (λ_M vs. λ_C; Table 2). Immigration affected population growth for all subunits in all years ($\lambda_C - \lambda_M \neq 0$), although population increase occurred without immigration for subunit 1 (Table 2). Population decline was predicted for subunits 2 and 3 for 2008–2009 in the absence of immigration (Table 2). In 2009–2010, subunit 2 had positive growth in the absence of immigration and subunit 3 had a slight decline (Table 2). Increased local density was associated with increased emigration of reproductive-aged females from subunits 1 and 3, but the opposite was true for subunit 2 (Fig. 3).

DISCUSSION

We show that the exchange of individuals between population subunits has important consequences for area-specific population growth on Sable Island. We identified subunit 1 (west Sable Island) as a source following predictions of source-sink theory (Pulliam 1988). Habitat quality was greatest in subunit 1, based on forage resource availability (Contasti et al. 2012), and density was relatively high and would have increased in all years in the absence of immigration. In subunit 1, emigration also increased with increasing density (Fig. 3). Identifying subunits 2 (center) and 3 (east) as sink habitats was more complicated despite having lower densities because of poorer habitat (Contasti

Table 3. Annual age-class-specific immigration and emigration rates[a] for female horses among population subunits 1, 2, and 3 observed at post-birth censuses, Sable Island, Nova Scotia, Canada (2008–2010). Numbers in parentheses are the total number of individuals moved (immigrated or emigrated).

Year	Age class	Immigration[b]			Emigration[c]		
		Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3
2008–2009	Yearling	0.071 (1)	0.222 (2)	0	0.111 (2)	0	0.091 (1)
	2-year-old	0	0	0.143 (1)	0	0.250 (1)	0
	3-year-old	0.111 (2)	0.100 (1)	0	0.059 (1)	0	0.250 (2)
	Adults	0.024 (1)	0.067 (2)	0.044 (1)	0.044 (2)	0.030 (1)	0.036 (1)
2009–2010	Yearling	0	0.083 (1)	0	0.059 (1)	0	0
	2-year-old	0	0.200 (2)	0	0.077 (1)	0	0.100 (1)
	3-year-old	0	0.500 (2)	0	0	0	0.286 (2)
	Adults	0.019 (1)	0.119 (5)	0	0.051 (3)	0.025 (1)	0.069 (2)

[a] Immigration and emigration events are assumed to have occurred pre-birth pulse for each year. We do not report errors as we derived rates from a whole-island census.

[b] Immigration is calculated as the proportion of immigrants to the number of residents that survived the current year.

[c] Emigration is calculated as the proportion of emigrants to the number of residents that were known to be alive at the end of the previous year.

et al. 2012). Our data suggest that subunits 2 and 3 showed properties of hidden sinks: horse counts increased year to year in these subunits, but these increases were primarily because of density-dependent immigration. In the absence of immigration, subunit 2 would have declined in year 1 and had the lowest rates of emigration of all subunits. Similarly, in the absence of immigration, subunit 3 would have declined during the course of our study (particularly from 2008 to 2009).

A striking trend of our analysis of survival on Sable Island is that females appear to be relatively late to reproduce for the first time compared to other feral horse populations, and female survival is also quite high even in the face of marked increases in density (Appendix 1). Grange et al. (2009) presented a brief survey of fecundity and annual survival for feral horses, and documented 2–3 years as age at first reproduction and annual adult female survival in the range of 0.79–1.0; female survival was lower, but fecundity was still relatively high for horses, at high density when food was limiting. They concluded that feral ungulates including horses, cattle, and sheep respond differently from wild ungulates to increases in density by trading adult survival for reproduction. Our data do not agree with this, as no 2-year-olds ever produced foals, and we observed adult foaling rates (note that ours are for female production only, multiply by 2 if assuming a 50:50 sex ratio) at the low end of the range identified by Grange et al. (2009). Unlike many populations of feral horses, we think that the Sable Island horse has experienced a remarkably long period of feralization (e.g., 250 years), which may have allowed for more time (approx. 50 generations) for natural selection to reverse some of the effects of artificial selection and domestication highlighted by Grange et al. (2009). The reversibility of artificial selection by natural selection on horse life history traits is an intriguing area of research that we are now pursuing with respect to this population.

Our data are from a 3-year period and should be considered preliminary, and we acknowledge that stochastic events could have influenced our results (especially for the smallest subunit 3 and age categories for subunits with few individuals [e.g., yearlings in subunit 2]). Nonetheless, individual immigration (and emigration) events will have a different effect from year to year, and we are able to show the time-sensitive influence of immigration on subunit population growth for each year of our study. We consider that the rapid growth observed in subunit 2 was clearly the result of immigration and not high survival and productivity of resident females (although immigrating females in year 1 enhanced productivity in year 2), which underlines the importance of considering individual fates and movements when identifying sources from sinks.

Our ability to identify a subunit's status is based on what Thomas and Kunin (1999) characterized as a compensation axis, where the shifting position of each subunit is determined by localized survival, recruitment, immigration, and emigration in each year. As our study shows, a sink habitat can appear as an area of productivity (presenting very fast rates of population growth) when localized losses (mortality and emigration) are over-compensated for by immigration from adjacent areas. Similarly, Robinson et al. (2008) showed that in areas experiencing population decline ($\lambda < 1.0$), immigration of individual cougars (*Puma concolor*) from surrounding areas can lead to little or no reduction in local density, thus masking the effect of losses in what was otherwise considered a sink area. In a field experiment, Turgeon and Kramer (2012) showed that short-term reductions in population size of 2 species of damselfish (*Stegastes diencaeus* and *S. adustus*) were recovered by compensatory immigration from adjacent areas. In the latter study, habitat quality of the sink area and density of potential migrants were identified as the primary drivers of immigration. We found that most immigrants on Sable Island entered an area of poorer habitat quality relative to their area of origin, which may reflect movements to minimize competition (for limiting resources, including food and mates) and thus increase fitness as predicted by density-dependent habitat selection (Fretwell and Lucas 1969). Indeed, high local density was associated with increased emigration of reproductive-aged females from subunits 1 and 3 and only immigrants moving into subunit 2 (compared to other immigrants) reproduced after taking residency. Overall, our data support the notion that density-habitat quality relationships alone are insufficient to accurately describe population dynamics (Van Horne 1983) and that supporting demographic and movement data are essential to differentiate between sources and sinks.

Managers must identify and evaluate the factors that influence long-term population viability, especially for threatened species. For example, recent observations of greater than expected numbers of polar bears (*Ursus maritimus*) in Western Hudson Bay, Canada (Atkinson et al. 2011), despite clear indications of reduced survival rates in connection with loss of sea ice due to climate change (Regehr et al. 2007), raises concerns about the prospects of a hidden sink in this local subpopulation. Incorporating, or at least considering, source-sink dynamics in this process is imperative as relatively small sources may sustain a population that resides predominantly in sink habitat (Pulliam 1988). Management efforts directed at source habitats are thus considered more effective in terms of species conservation and population management, which places much value on accurately delineating source from sink habitat (McCoy et al. 1999, Schwartz et al. 2010, Kerbiriou et al. 2012). We demonstrate that identification of true sources and sinks can be achieved by considering individual-specific fates (survival and recruitment) corrected for immigration and emigration events.

MANAGEMENT IMPLICATIONS

Reliance on apparent estimates of survival and recruitment to quantify population growth or decline may present the risk of not identifying sink habitat where it exists. This may be especially problematic during periods of landscape-scale population growth, where the characteristics that distinguish sources from sinks may be hidden by migration events. Managers of wide-ranging species with long population

cycles (e.g., large mammals), which are often enumerated with assumptions of apparent survival and recruitment (e.g., from mark-recapture analysis or surveys), may be at particular risk of mistaking source from sink habitat. In light of our findings, a more reliable approach to monitoring the status and population dynamics of large mammals is to track movements and fates of individuals as opposed to relying on localized abundance surveys. Doing so will assist in the development of more effective and directed conservation and management plans, which is especially critical for preserving or promoting viability of endangered species that live in connected subpopulations.

ACKNOWLEDGMENTS

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Appendix 1. Age-class vital rates for resident and immigrant feral horse females of subunits 1, 2, and 3 on Sable Island, Nova Scotia, calculated in the presence of immigration from post-birth census data (Jun–Sep 2008–2010). Survival rates consider emigration events as mortality.

			Survival[a,b]			Fecundity[c]		
			Subunit 1	Subunit 2	Subunit 3	Subunit 1	Subunit 2	Subunit 3
2008–2009	Resident	Foal	0.720 (18)	0.880 (8)	0.910 (11)			
		Yearling	0.857 (7)	0.500 (4)	1.000 (6)			
		2-year-old	0.941 (17)	1.000 (9)	0.750 (8)			
		3-year-old	0.778 (9)	0.800 (5)	0.500 (4)	0.118 (16)	0.556 (9)	0.125 (6)
		Adult	0.917 (36)	0.857 (28)	0.900 (20)	0.337 (40)	0.153 (28)	0.064 (22)
	Immigrant	3-year-old				0.500 (2)	0 (1)	0 (0)
		Adult				0 (1)	0 (2)	0 (1)
2009–2010	Resident	Foal	0.940 (17)	1.000 (11)	1.000 (3)	—	—	—
		Yearling	0.857 (14)	0.889 (9)	0.800 (10)	—	—	—
		2-year-old	0.833 (6)	1.000 (2)	0.714 (7)	—	—	—
		3-year-old	0.833 (18)	0.900 (10)	0.833 (6)	0.167 (5)	0 (4)	0.429 (5)
		Adult	0.878 (41)	0.933 (30)	0.826 (23)	0.287 (22)	0.376 (37)	0.276 (24)
	Immigrant	3-year-old				0 (0)	0.500 (2)	0 (0)
		Adult				0 (1)	0 (5)	0 (0)

[a] Survival rates consider emigration from a subunit at $t+1$ as death. Survival rates are calculated for females only; foal survival rate is the survival of foals at the end of each summer that lives to the next year's census.
[b] Numbers in parentheses are the number of individuals alive in each subunit at t.
[c] Numbers in parentheses are the number of reproductive-aged females alive in each subunit at $t+1$. Fecundity refers to production of female foals only.

Appendix 2. Annual movements ($n = 22$) of feral horse females between subunits 1, 2, and 3 on Sable Island, Nova Scotia (2008–2010) showing emigration (pre-movement) and immigration (post-movement) location and band information.

			Emigration				Immigration			
Year observed (t to $t+1$)	ID	Age class (t)	Subunit	Band size	No. stallions	Age class ($t+1$)	Subunit	Band size	No. stallions	Notes
2008–2009	36	0	1	9	1	1	2	5	1	Moved with mother (37)
	37	4	1	9	1	4	2	5	1	Moved with foal (36)
	69	2	1	8	1	3	2	7	1	
	103	0	1	11	1	1	2	3	1	Recruited with mother (108) by bachelor
	108	4	1	11	1	4	2	3	1	Recruited with foal (103) by bachelor
	180	1	2	8	1	2	3	4	1	
	233	4	2	3	1	4	3	4	1	Entire band moved[a]
	276	2	3	9	1	3	1	7	1	Entire band moved[b]
	278	0	3	9	1	1	1	7	1	Entire band moved[b]
	280	2	3	9	1	3	1	7	1	Entire band moved[b]
	304	3	3	9	1	4	1	7	1	Entire band moved[b]
2009–2010	16	4	1	10	1	4	2	9	1	
	121	4	2	13	1	4	1	11	1	
	157	3	1	7	Multi	4	2	9	1	Moved with foal (440)
	180	2	3	4	1	3	2	4	1	Entire band moved[a]
	271	1	3	7	1	2	2	5	1	
	307	2	3	2	1	3	2	3	1	Entire band moved
	342	2	3	9	1	3	2	13	Multi	
	370	1	1	7	Multi	2	2	8	1	
	379	2	1	7	Multi	3	2	11	1	
	440	0	1	7	Multi	1	2	9	1	Moved with mother (157)
	547	4	3	11	1	4	2	5	1	

[a] Females are members of same band; horse identified dead in 2010.
[b] Females are members of same band.