Costs of social dispersal in a polygynous mammal

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INTRODUCTION

Dispersal is a fundamental life history trait that occurs in most species with important consequences for ecology and evolution (Johnson and Gaines 1990; Clutton-Brock et al. 1991; Bowler and Benton 2005; Ronse 2007). Social dispersal refers to the permanent movement of an individual from one social group to another and involves a change in reproductive partners (Clutton-Brock 1989; Isbell and VanVuren 1996; Clutton-Brock and Luks 2012). Social dispersal may include both natal and secondary dispersal events but can be dissociated from other forms of dispersal. Indeed, in nonterritorial species where social groups are overlapping, social dispersal is not necessarily associated with a change in physical location (Isbell and VanVuren 1996). Regardless of type of dispersal, moving individuals may seek to alter their ecological context (e.g., levels of resource competition or predation risk) and/or their social environment, notably in terms of mating opportunities.

Dispersal may provide potential benefits from decreasing competition (Matthysen 2005), increasing mate choice (Daniels and Walters 2000) allowing for the targeting of good genes (Hamilton 1990) or compatible genes (Zeh and Zeh 1996), and reducing inbreeding (Pusey and Wolf 1996). However, dispersal is usually assumed to be a risky behavior that entails costs (Ronse 2007; Bonte et al. 2012). These can be classified into four categories (Bonte et al. 2012): 1) energetic costs, usually spent during the dispersal movement itself but also including costs linked to the development of specific organs, tissues, or reserves involved in dispersal; 2) time costs, as the time invested in dispersal to search for a new habitat or new partner is not allocated to other activities such as feeding or resting; 3) risk costs, related to increased mortality during dispersal or attrition; and 4) opportunity costs, due to the loss of familiarity or social rank within the new environment or as incurred by selecting a suboptimal habitat in which to settle. How costs and benefits of dispersal balance is the subject of great debate. For example, approximately half of the studies reviewed by Belichon et al. (1996) and Doligez and Part (2008) failed to find differences in reproductive outcomes between philopatric and dispersing individuals.

A better understanding of the demographic consequences of social dispersal is critical to evaluating theories on its evolution (Johnson and Gaines 1990; Belichon et al. 1996; Doligez and Part 2008). Although much has been learned from theoretical models of distance-based dispersal and associated empirical tests, much less is known with respect to social dispersal. We should, however, expect differences in how the latter evolves due to different underlying

Key words: feral horse, reproductive success, Sable Island, social dispersal.
costs and benefits. For example, social dispersal may occur without a change in familiar area; hence, costs linked to loss of habitat familiarity after dispersing (Mabry and Stamps 2008; Bonte et al. 2012) may not be incurred (Ishell and VanVuren 1996). However, other costs may arise: for social species, it is not uncommon to observe greater agonistic encounters being directed toward newly arrived individuals to a group, relative to existing members (Ydenberg et al. 1988; Ishell and VanVuren 1996). Moreover, social dispersal is not necessarily voluntary as in some cases males will use force or the threat of force to gain mates (“sexual coercion”; reviewed in Smuts and Smuts 1993). Male aggression and sexual coercion during changes in social groups have been linked to female costs to current reproduction, including infanticide (Smuts and Smuts 1993; Gray et al. 2012) and induced abortions (Bartoš et al. 2011).

The feral horse (Equus ferus caballus) is a model species for conducting cost–benefit analyses of social dispersal. Feral horses are a social species that live in breeding groups (bands) that overlap in space and persist year round; their social system thus differs from most other polygynous ungulates and is more similar to that of some primates (Linklater and Cameron 1999, 2000). Both sexes disperse and will move among bands (Berger 1986; Marjamäki et al. 2013). Marjamäki et al. (2013) recently showed that social dispersal is positively density dependent in feral horses, for all sex and age categories, and that band size also affects social dispersal. However, net movement of individuals after dispersal can be very low (Linklater and Cameron 2009; Marjamäki et al. 2013). Distinguishing effects of dispersal on individuals separate from an “area effect” (lack of familiarity with habitat) can be challenging (Belichon et al. 1996; Linklater and Cameron 2009); however, in the case of feral horses because social dispersal may not be accompanied by a major change in area used, assessing costs of dispersal may be divorced from area effects. There has been only limited research on the costs and benefits of social dispersal in feral horses although some behavioral data is available to develop hypotheses and predictions. For example, mares fertilized by other males than the band stallion can have higher rates of induced abortion (Bartoš et al. 2011) and their foal survival may be lower, potentially due to infanticide (Gray et al. 2012), as observed in plains zebra (Equus burchellii; Pluháček and Bartoš 2000). Few researchers in general, however, have investigated effects of philopatry and social dispersal on the relative reproductive outcomes of females according to their dispersal status (Clutton-Brock and Lukas 2012).

The population of feral horses on Sable Island, Nova Scotia, Canada, is the subject of an individual-based monitoring program of movements, behavior, group membership, and life history, where all members of the population \( n = 552 \) horses in 2014) are identified and followed (374 life histories from 2008 to 2014). Using the Sable Island horse dataset, we compared differences in reproductive success (RS; current and future reproduction and annual survival of foals) between philopatric females and those that had engaged in social dispersal. Specifically, we used path analysis to investigate the causal effect of social dispersal on reproduction (probability of producing a foal that survived through the summer of observation) and RS (producing a foal that survived to age 2) at successive years.

Social dispersal can be costly; therefore, we predicted that 1) dispersal would negatively impact the current reproduction of dispersing relative to philopatric females. In part, we expected this because induced abortion rates can be higher when mares are forced to copulate with a new stallion (Berger 1986; Pluháček and Bartoš 2000). However, because dispersal might then lead to better mating opportunities, we predicted 2) a positive effect of social dispersal for long-term reproduction (i.e., probability of reproducing \( x \) years after settlement). Dispersal costs and benefits are known to be balanced by environmental properties and individual condition (Bonte et al. 2012). Hence, we also included in our analyses a suite of ecological variables thought to influence reproduction and survival in Sable Island horses (e.g., Welsh 1975; Contasti et al. 2012; Richard et al. 2014), such as local abundance, band size, body condition, and distance to freshwater. We also expected 3) that if social dispersal leads to improved opportunities for fitness (through good genes, compatible genes, or inbreeding avoidance), the survival of foals produced postdispersal would be better than those produced by a female prior to dispersing. For those foals conceived before dispersal, depending on when a mare disperses (i.e., pregnant or followed by their young foal during the first winter of life), the consequences of social dispersal on foal survival might be different. Hence, we predicted 4) a stronger, negative effect when the mare disperses while pregnant because direct costs of social dispersal might be the highest just after the dispersal event (e.g., group transfer positively predicts levels of fecal cortisol 2 weeks postbehavior in feral horses [Noviéz et al. 2014]). Infanticide directed toward foals not sired by the band's stallion may also be a risk factor (Gray et al. 2012), so like foals born to dispersing females that are pregnant, we expected 5) survival of foals accompanying dispersing mothers to be lower than those conceived and born after dispersal.

**MATERIALS AND METHODS**

**Study area**

Sable Island National Park Reserve (43°55′N; 60°00′W) is a vegetated sandbar located 275 km southeast of Halifax, Nova Scotia. It is 49 km long and 1.3 km wide at its broadest point. The climate of the island is temperate oceanic with warm summers and cool, wet winters. The island is treeless and characterized by wide beaches, sand dunes of up to 30-m height, and grassy plains. The vegetation is dominated by American beach grass or marram (Ammophila brevigulata), and human presence is low. Several permanent freshwater ponds, located in the western and central areas and covering approximately 20 ha in total, are used by horses. Since their introduction in the mid-1700s, a free-ranging population of horses has roamed the island (Christie 1995). During the study period (2008–2014), the horse population ranged from 380 individuals in 2008 to as high as 559 individuals in 2013. The feral horses of Sable Island are known to compete for space and forage resources (van Beest et al. 2014) yet live in a natural though simplified environment without predation, human interference, or interspecific competition (they are the island's only terrestrial mammal).

**Data collection**

Population and life history information was collected through systematic ground census performed during the mid-late breeding season (July to September) starting in 2008. Each daily sampling effort occurred in one of 7 sections of the island, stratified to allow complete canvassing of a section in 1 day and complete coverage of the island in 1 week. We approached horses on foot, which largely ignored our presence, and determined the location of an individual using a handheld GPS with error to within 5 m. At every sampling event, we recorded each horse's coloration, facial features and other distinguishing marks, sex, field age, reproductive status, and group membership. Identifications were verified using digital photographs. Sampling was performed under University of
Saskatchewan Animal Care Protocol 20090032 and under guidance of the Canadian Council on Animal Care.

On average, each horse was observed 5 ± 2 times (± standard deviation [SD]), with a maximum of 17 times a summer. The population counts derived since the start of the monitoring program in 2008 are \( n = 380, 437, 503, 448, 534, 559, \) and 552 individuals known to be alive at 1 September for years 2008 through 2014, respectively. The data include 874 life histories with 484 foals born since 2007. Since 2008, more than 20 000 locations of horses were collected, and our resighting probability was very high: 0.994 for females and 0.992 for males (2008–2013). Hence, if a horse was not observed during an entire field season, it was considered dead.

Based on digital photographs, we also assessed body condition score for each adult female horse from 2008 to 2013. This score reflects the amount of subcutaneous fat deposition on the hips, ribs, and spine of the animal and was averaged over the study season (following Henneke et al. 1983). Body condition scores range from 0 (very poor condition) to 5 (obese) with half point gradations when different regions of the body varied in score (Carroll and Huntington 1988). Body condition scores were standardized within each year to account for differing observers and for 1 year in which the early field season (2009) resulted in significantly lower average body condition scores. The local abundance of conspecifics to which an individual was exposed was estimated as the total number of adults in bands within an 8000-m buffer around the centroid of the individual’s summer locations (see Marjamäki et al. 2013, for more details). Local abundance was highly correlated to habitat quality, with the best quality habitat supporting the highest densities (van Beest et al. 2014). We also recorded distance to freshwater as it is known to affect reproduction and survival of foals in feral horses (Berger 1986).

We recorded long-term movements of individuals between bands by comparing band membership of individual horses between successive observations. All movements between bands were hence recorded. The majority (79%) of band changes occurred during the winter and outside our census period, that is, between field seasons (Marjamäki et al. 2013). For each philopatric and dispersing adult female in a given year, we assessed subsequent reproductive status and annual survival of foals for 3 consecutive years. We retained in our analysis only adult females (>4 years old) that were known to have reproduced at least once previously (\( n = 131 \) horses), allowing us to focus exclusively on questions of secondary dispersal and that were monitored during 3 consecutive years between 2008 and 2013.

**Data analysis**

We used path analysis (package “Lavaan” in R [Rosseel 2012]) with a maximum-likelihood estimator to investigate the effect of social dispersal, which was a binomial variable (1 = dispersed, 0 = remained philopatric to a band), on probability to reproduce (produce a foal observed during the summer of observation that survived to the end of the field season [census period]) and RS of adult females (defined here as the probability to produce a foal that survived at least 2 years). The latter excluded in utero losses and losses immediately postparturition for births undetected by our sampling (prior to our arrival for summer field work). Path analysis is a powerful multivariate technique that provides a method for structuring cause and effect relationships among variables in a multiple regression framework (Mitchell 1992). Path analysis aims to infer causes from observational data and describe directed dependencies among a set of variables included as models (as linear models) and not solely correlation between variables (Shipley 2004). The method also allows for measuring the relative statistical importance of different aspects of an a priori hypothesis described in a path diagram (Sih et al. 2002). Path analysis permits evaluating the relative importance of each relationship in a path diagram and dissociation of the direct and indirect effects of a variable (Mitchell 1992; Shipley 2004). The recommended sample size for path analysis is at least 5 times the number of paths (Petraitis et al. 1996). With 131 individuals in total (120 without any missing values), and 13 paths for our most complex model, we were above this threshold for analysis.

We constructed an initial model representing a priori hypotheses about the relationships among variables of interest, with the exogenous variable being dispersal status at year \( t \); and the endogenous variables of dispersal status at \( t+1 \) and \( t+2 \); reproductive status or success at \( t \) reproductive status or success at \( t+1 \); and reproductive status or success at \( t+2 \). The corresponding path diagram (Figure 1) reflects our hypotheses concerning how social dispersal might affect reproductive probability or RS.

Starting from the full model inclusive of all biologically meaningful variables and possible relationships, we tested and progressively simplified the model by subsequently removing the least significant path to create a nested model, and we compared the fit of these 2 nested models. We performed deletion testing until no further improvement of the model fit to the observed data could be achieved and this last, simplest model derived from the full model was considered as our best model. We also generated the independent model (i.e.,

![Figure 1](https://academic.oup.com/beheco/article-lookup/doi/26/6/1476/204975)

**Figure 1**

Path diagram showing the hypothesized causal relationships of social dispersal \((D)\) on reproductive probability \((R)\); probability of producing a foal that survived to end of census in the summer of observation) and RS (probability of producing a foal that survived at least 2 years) in adult female Sable Island horses, Nova Scotia, Canada (2008–2014), from the focal year \((0)\) up until 1 \((1)\) and 2 \((2)\) years later. The number beside variables \((D, R, R_S)\) and RS refers to the year considered (starting from the focal year labeled 0; i.e., dispersing at \( t = 2 \) is depicted as \( D_2 \)). Pathways corresponding to the effect of social dispersal on reproduction or RS are represented by solid lines.
the null model which assumed uncorrelated variables) to ensure that the selected model had a better fit than the independent model. We evaluated the best model based on complementary goodness-of-fit measures: the $\chi^2$ statistic, the root mean square error of approximation (RMSEA), and the Tucker–Lewis index (TLI). A nonsignificant $\chi^2$ ($P$ value) indicated that the model was coherent and provided an adequate description of the data. In other words, if the predicted and observed covariance matrices were identical then the maximum-likelihood $\chi^2$ statistic would be 0; note that this value was sensitive to sample size (Mitchell 1992; Shipley 2000). The RMSEA is an index insensitive to sample size that tested the null hypothesis of a poor fit with values close to 0 indicating good model fit (Steiger 1990). Finally, TLI measured the fit improvement compared with a null model and was relatively independent of sample size with values close to 1.0 indicating good model fit (Mitchell 1992). Path analysis models are sensitive to nonhomogenous scales between variables, but note that in our case, all dependent variables were binomial.

We generated path coefficients (i.e., the standardized partial regression coefficients of a dependent variable on a predictor) for each causal relationship (between each pair of variables) included in the best model, and the significance of each regression coefficient. Path coefficients represent the relative strength of the effect (in SDs) that a given explanatory variable has on a dependent variable, while holding statistically constant all other explanatory variables, and enabling the identification of more influential variables in the path diagram (Mitchell 1992; Shipley 2000). Path analysis therefore allowed us to compare the direct and indirect effects (obtained by multiplying the coefficients of the successive links) of dispersal probability on the probability to reproduce and RS (Shipley 2000, 2004). To investigate the potential indirect effects of ecological variables (body condition, distance to freshwater, band size, local abundance) on how dispersal relates to reproduction and RS, we constructed a path diagram including these indirect effects derived for each significant path of the first path analysis (see Supplementary Figures A1 and A2 for the path diagram).

In addition to our path analyses, we investigated the effect of social dispersal on the next reproductive attempt using a log-rank test. Log-rank tests are usually used for survival analysis from censored data but can be used for any transition probability between nonreversible states (Fieberg and Del Giudice 2008). For female reproduction, possible states were “no reproduction” (coded 0) versus “reproduction” (coded 1). Cumulative probability curves for the status “no reproduction” were generated using the Kaplan–Meier estimate, and we tested for differences between probability curves using the $G$-rho family of tests implemented in the R “survival” package (Harrington and Fleming 1982; Therneau and Lumley 2010). We used the same approach to investigate the effect of a mother’s social dispersal on foal survival from 1 up to 3 years after the focal year for the foals born between 2009 and 2013 ($n = 390$). We considered in separated analyses the effect of mare social dispersal just before conception, while pregnant (the winter before the birth of the foal), and with the foal during its first winter. We performed all data analyses in R version 3.1.1 (R Development Core Team 2010).

RESULTS

From the 131 adult females we followed (all of which had reproduced at least once previously and had already dispersed from their natal band), 30.5% dispersed during the first year they were subsequently followed, 24.4% during the second, and 34.2% during the third year (the maximum number of intervals considered). Adult females were never observed outside of a band setting. A total of 22.5% of females in the sample switched bands more than once in 3 years while 33.3% were always philopatric; the remaining females moved only once. Of 2- and 3-year-old females, 27.3% ($n = 11$) dispersed; of females aged 4+, 30.8% ($n = 120$) dispersed. When horses dispersed, the distance between the barycentre of the pre- and post-dispersal bands of the female was very small (41.2 ± 50.9 m [$\pm$ standard error], min = 1.3 m, max = 263.0 m, $n = 218$).

Path analysis on probability to reproduce and RS

The full model integrating all relationships represented in Figure 1 provided a good fit to the observed data on probability to reproduce: $n = 120$, $\chi^2 = 2.30$, degrees of freedom [df] = 2, $P = 0.32$, RMSEA = 0.03, TLI = 0.62; see Supplementary Table A1; on RS: $n = 120$, $\chi^2 = 0.73$, df = 2, $P = 0.69$, RMSEA = 0, TLI = 3.66; see Supplementary Table A1). However, the fit was improved by deleting 3 less-significant paths for probability to reproduce, with a final model containing 5 paths from the 13 included in the full model ($n = 120$, $\chi^2 = 2.79$, df = 7, $P = 0.90$, RMSEA = 0, TLI = 2.50; Supplementary Table A1; Figure 2a), and 5 for RS with a final model including 8 paths from the 13 included in the full model performed better than the independent model ($n = 120$, $\chi^2 = 1.03$, df = 5, $P = 0.96$, RMSEA = 0, TLI = 3.43; Supplementary Table A1; Figure 2b). For probability to reproduce, the fit provided by the full model and that of the final model were both better than the fit provided by the independent model ($n = 120$, $\chi^2 = 11.66$, df = 10, $P = 0.31$, RMSEA = 0.04, TLI = 0; Supplementary Table A1). However, for RS, the independent model provided a better fit than the full model ($n = 120$, $\chi^2 = 5.93$, df = 10, $P = 0.82$, RMSEA = 0, TLI = 1; Supplementary Table A1). Path analysis indicated that the probability to reproduce on the focal year $t$ (path coefficient $= -0.23 \pm 0.09$) and on year $t + 1$ (path coefficient $= -0.21 \pm 0.09$) depended on the dispersal status of that year (Table 1; Figure 2a), and second that RS at year $t + 1$ (path coefficient $= -0.21 \pm 0.05$) and $t + 2$ (path coefficient $= -0.17 \pm 0.05$) depended on the dispersal status of the year $t$ (Table 1; Figure 2b). The indirect effects of dispersal on future reproductive probability and on future RS via its effects on moving the year after or on reproduction in the same year were weak (path coefficient $\leq -0.02$; Table 2). Moreover, using a separate path analysis, the indirect effect of dispersal on reproductive probability and on future RS mediated by effects of local abundance, body condition, band size, and distance to freshwater were also weak (Table 3; see Supplementary Figure A1).

Time elapsed before reproduction

Time before next reproduction after the focal year was significantly longer for adult females that dispersed compared with philopatric females (log-rank test stratified to take into account the reproductive status the year before: $n = 131$, $\chi^2 = 4.5$, df = 1, $P = 0.03$; Figure 3). Indeed, females that dispersed had a median latency of at least 1.5 years before next reproduction while nonmoving (philopatric) females had a median latency of 0.5 years (Wilcoxon rank-sum test: $n = 120$, $W = 2307.5$, $P = 0.004$); the latter conservatively assumed that females that did not reproduce after dispersing in any year did so at 3.5 years. The difference was still visible 3 years after the focal year, and fewer females that had dispersed during the focal year had reproduced compared with females that remained in their social group, even if the highest differences between dispersal and philopatric females occurred the year following the focal year (Figure 3).
Foal survival

Probability of foal survival (excluding in utero mortality or mortality prior to our field season starting) for mothers that had dispersed just before conception or while pregnant did not significantly differ from the probability of survival of foals from philopatric mothers (log-rank test for dispersal before conception: $n = 388$, $\chi^2 = 0$, $df = 1$, $P = 0.85$; log-rank test for dispersal while pregnant: $n = 390$, $\chi^2 = 0$, $df = 1$, $P = 0.87$; Figure 4a,b). However, foals that had dispersed by accompanying their mother into another band had higher survival at 3 years (~10%), though this difference was not quite statistically significant using the log-rank test ($n = 231$, $\chi^2 = 2.4$, $df = 1$, $P = 0.12$; Figure 4c).

DISCUSSION

Our results suggest that, in adult female feral horses, social dispersal may have costs on subsequent reproductive attempts relative to philopatric females. Both probability to produce a surviving foal during the summer and RS for females that had previously changed bands was lower than for philopatric individuals, and these dispersing females had a longer latency period before producing their next foal. Alternatively, nonrandom dispersal, with for instance females of lower phenotypic quality dispersing more, may lead to similar pattern. Foal survival until 3 years of age did not appear to be affected by either the dispersal of its mother before conception and while pregnant, whereas foals dispersing with their mother had a 10% higher survival rate (although this tendency was not quite statistically significant). Regardless, our data and observations do not suggest that infanticide is a common behavior in this population: survival of foals from philopatric mares sired by the previous band’s stallion certainly did not show reduced survival. Finally, the effects of social dispersal on reproductive probability and success were mostly direct, as the indirect effects of dispersal mediated via environmental (i.e., distance to freshwater, local abundance), social (i.e., band size), or phenotypic variables (i.e., body condition) were weak.

Dispersal costs have been found in several species of birds, the probability of forgoing reproduction was higher in dispersing individuals (e.g., kittiwake *Rissa tridactyla*, Danchin and Cam 2002; spotted owls *Strix occidentalis*, Gutierrez et al. 2011; Mauritius kestrel *Falco punctatus*, Nevoux et al. 2013). Our result highlighting a delay on timing of next foaling in dispersing females agrees with these findings. Moreover, fitness-associated dispersal, which assumes that the location of settling depends on individual competitive ability leading to individuals in better condition settling closer to their natal area and dispersal of the poorer individuals, has been reported in many groups of organisms including birds or mammals (Hardany et al. 2004). For instance, using stochastic simulations, Guççijnman et al. (2013) showed that low-quality individuals have higher probability to disperse than fitter ones, an association also reported in an empirical study on a mountain goat (*Oreamnos americanus*) population (Shafer et al. 2011).
## Table 1
Standardized partial regression coefficients and residual variances estimated with their associated SE for the full model derived from the path diagram presented in Figure 1

<table>
<thead>
<tr>
<th>Path</th>
<th>Standard coefficient</th>
<th>SE</th>
<th>( z )</th>
<th>( P ) value</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_s - D_s )</td>
<td>-0.23</td>
<td>0.09</td>
<td>-2.62</td>
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<tr>
<td>( R_s - D_s )</td>
<td>-0.21</td>
<td>0.09</td>
<td>-2.31</td>
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<tr>
<td>( D_s - R_s )</td>
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<td>0.08</td>
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<tr>
<td>( R_s - D_s )</td>
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<td>0.09</td>
<td>-1.19</td>
<td>0.24</td>
</tr>
<tr>
<td>( R_s - D_s )</td>
<td>0.07</td>
<td>0.09</td>
<td>-0.80</td>
<td>0.43</td>
</tr>
<tr>
<td>( R_s - D_s )</td>
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<td>0.09</td>
<td>-0.72</td>
<td>0.47</td>
</tr>
<tr>
<td>( R_s - R_s )</td>
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<td>0.10</td>
<td>-0.67</td>
<td>0.50</td>
</tr>
<tr>
<td>( D_s - D_s )</td>
<td>-0.05</td>
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<td>0.59</td>
</tr>
<tr>
<td>( D_s - B_s )</td>
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</tr>
<tr>
<td>( D_s - J_s )</td>
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<td>0.09</td>
<td>0.22</td>
<td>0.83</td>
</tr>
<tr>
<td>( R_s - R_s )</td>
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<td>0.97</td>
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</table>

<table>
<thead>
<tr>
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<tr>
<td>( R_s )</td>
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<td>0.03</td>
<td>0.24</td>
<td>0.03</td>
</tr>
<tr>
<td>( R_s )</td>
<td>0.22</td>
<td>0.03</td>
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<tr>
<td>( R_s )</td>
<td>0.22</td>
<td>0.03</td>
<td>0.24</td>
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<tr>
<td>( D_s )</td>
<td>0.22</td>
<td>0.03</td>
<td>0.22</td>
<td>0.03</td>
</tr>
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</table>

The values represent the relationships between social dispersal of adult female Sable Island horses (2008–2014) at different times (\( D_s, D_s, \) and \( D_s \)) and reproductive probability (\( R_s, R_s, \) and \( R_s \)) or RS (\( R_s, R_s, \) and \( R_s \)). A \( z \) value and a \( P \) value based on a Wald test are provided. Paths included in the final model are in bold. The number beside a variable’s letter (\( D_s, R_s, \) and RS) refers to the year considered (starting from the focal year 1 labeled 0, i.e., dispersing at \( t = 2 \) is depicted as \( D_s \)). SE, standard error.

## Table 2
Total effect, direct, and indirect effects of dispersal (\( D \)) on reproductive probability (\( R \)) and RS in adult female Sable Island (2008–2014) based on the selected models standardized estimates (see text)

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Independent variable</th>
<th>Direct effect</th>
<th>Independent variable</th>
<th>Indirect effect</th>
<th>Independent variable</th>
<th>Total effect</th>
</tr>
</thead>
<tbody>
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<td>( R_s )</td>
<td>( D_s )</td>
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<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.23</td>
</tr>
<tr>
<td>( R_s )</td>
<td>( D_s )</td>
<td>-0.11</td>
<td>( D_s ) via ( D_s )</td>
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<td>( D_s )</td>
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<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.21</td>
</tr>
<tr>
<td>( R_s )</td>
<td>( D_s )</td>
<td>-0.13</td>
<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.13</td>
</tr>
<tr>
<td>( R_s )</td>
<td>( D_s )</td>
<td>-0.21</td>
<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.21</td>
</tr>
<tr>
<td>( R_s )</td>
<td>( D_s )</td>
<td>-0.17</td>
<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.21</td>
</tr>
<tr>
<td>( R_s )</td>
<td>( D_s )</td>
<td>-0.07</td>
<td>( D_s ) via ( R_s )</td>
<td>( D_s ) via ( D_s )</td>
<td>( D_s ) via ( R_s )</td>
<td>-0.07</td>
</tr>
</tbody>
</table>

O indicates that the path was not present in the selected model. The number beside a variable’s letter (\( D_s, R_s \), and RS) refers to the year considered (starting from the focal year 1 labeled 0; i.e., dispersing at \( t = 2 \) is depicted as \( D_s \)).

Despite potential costs suffered by dispersing individuals, a high proportion (66.7%) of females socially dispersed at least once during the 3 years of monitoring, they may be less than the costs linked to philopatry, and social dispersal could enhance individual fitness (Van Vuren and Armitage 1994). For instance, in yellow-bellied marmots (Marmota flaviventris), despite a higher mortality for dispersers during the summer when the dispersal occurred, dispersing individuals reproduced earlier and suffered less aggression from conspecifics (Van Vuren and Armitage 1994). In western lowland gorillas (Gorilla gorilla gorilla), females changed groups to reduce the risk of infanticide (Stokes et al. 2003). In feral horses on Sable Island, which adopt a similar social structure to that of gorillas, we found that foals changing bands with their mother during their first winter tended to have better survival. This is consistent with the lower survival experienced by foals born in a female’s natal band in a herd of Camargue horses (Monard and Duncan 1996) and the higher probability of social dispersal observed for mares with foals in a population of feral ponies (Rutberg 1990). In the latter case, because subordinate mares with foals suffered more aggression than subordinate mares without foals (Rutberg and Greenberg 1990), they may gain benefits by dispersing...
Dispersal is not necessarily linked to a change of home range (i.e., philopatry in space), the dispersal costs can be minimized by keeping the spatial philopatric advantage (Bonte et al. 2012) linked to the benefit of site familiarity (e.g., Mabry and Stamps 2008; Linklater and Cameron 2009; Péron et al. 2010).

In Sable Island horses, social dispersal had short-term negative effects on probability of reproduction, and hence no effect of dispersal in year $t$ was found on reproduction at year $t + 1$ and year $t + 2$. High rates of induced abortions after dispersal may contribute to this pattern. Indeed, domestic mares that have not been fertilized by the home “herd” stallion experienced a high level of induced abortion, with a fetal loss rate of 40% (Bartoš et al. 2011), as well as zebra mares from herds with introduced males (Pulháček and Bartol 2000). Concerning this direct, short-term effect of social dispersal, dispersal for year $t$ and $t + 2$ negatively influenced reproductive probability for year $t$ and $t + 2$, respectively, but unexpectedly dispersal in year $t + 1$ did not influence reproductive probability for year $t + 1$ (Figure 1). To ensure that females were minimum of 4 years old, the analysis used more data from the latter half of our study; for example, the year 2011 accounted for 63% of the females entering the analysis. Hence, a year effect might have led to this pattern. In contrast, the effect of dispersal on RS acts over the longer term, with only an influence detected 1 and 2 years after dispersal.

Long-term consequences of dispersal on fitness have been reported in Mauritius kestrels (*Falco punctatus*; Nevoux et al. 2013) and in green-rumped parrotlets (*Forpus passerinorum*; Tarwater and Beissinger 2012). In order to investigate long-term effects of social dispersal on reproductive outcomes with potential benefits on foal survival, however, we will require more years of data than are presently available. It would be especially interesting to compare the long-term survival and RS of foals produced after dispersal. Under the hypothesis of long-term benefits of a better mate (e.g., due to outbreeding or good genes), better fitness of foals from postdispersal matings would be expected. RS combines both the probability to reproduce and foal survival to 2 years old, hence opposing effects of dispersal on reproductive probability and foal survival could lead to an absence of consequences on RS. Indeed, a potential, positive effect of
Dispersal is a multicausal process, driven by individual characteristics and environmental factors (Clobert et al. 2001; Bowler and Benton 2005; Clobert et al. 2009), so understanding its long-term consequences is challenging. However, a better knowledge of the consequences of dispersal on individual fitness is important to comprehending how dispersal is maintained in populations and how it evolves. Our results suggest a potential cost of social dispersal on the future reproduction of female feral horses; however, our data also suggest that there may be potential benefits for the survival of accompanying offspring of dispersing females which may balance some of these costs. Quantifying the net benefit of this to dispersion and band contests (76 h of sampling) for feral horses drinking at excavated holes similar to what is found on eastern Sable Island (at Rachel Carson Estuarine Sanctuary, NC, USA). Not all stallions were equal in being able to defend harem access to water, and on Sable Island, it seems feasible that females with accompanying offspring may disperse to those stallions that are noted winners at defending access to water.

Whether female social dispersal is voluntary rather than forced might influence the link between these movements across bands and their consequences on reproductive outcomes. Indeed if dispersal is voluntary, we can expect that it may occur only if beneficial. However, in feral horses, some evidence suggests that dispersal is not always voluntary. Nonreproductive females might be forced to leave their band (Berger 1986; Nuñez et al. 2009), some mares can suffer from high levels of aggression by other mares (Runberg and Greenberg 1990; Cameron et al. 2009), and males might be able to steal a female from another band in order to directly increase their own RS (Berger 1986). It is likely that both voluntary and forced dispersal, which might have contrasting consequences on reproduction, coexist in the same population. Unfortunately, like in most studies, we were unable to differentiate these 2 motivations for dispersal.

An additional source of bias in our results may be caused by phenotype-dependent dispersal (Clobert et al. 2001; Bowler and Benton 2005), where dispersers are not a random subset of the population. Indeed, if individuals of a particular phenotype have a higher probability to socially disperse, the consequences of dispersal on reproductive outcomes would be confounded with the consequences due to differences in reproductive performance between phenotypes (Doligez and Part 2008; Bonte et al. 2012; Nevoux et al. 2013). Even if condition-dependent social dispersal is unlikely to occur in our study population, as suggested by the absence of direct and indirect effect of body condition in the path diagram and the absence of a link found between dispersal probability and body condition in adult females (logistic regression: \( n = 126, F = 0.03, df = 124, P = 0.86 \)), such nonrandom dispersal may still contribute to the observed pattern.

Finally, results on the effect of dispersal on reproductive outcomes may be confounded by variation in phenotype and environmental conditions, especially in the case of interactions between dispersal and phenotypic and environmental factors (Doligez and Part 2008; Tarwater and Beissinger 2012). For example, Tarwater and Beissinger (2012) showed that in a tropical parrot species where both lifetime RS and dispersal behavior were condition dependent, dispersal increased or decreased lifetime RS depending on an individual’s natal environment (i.e., natal population, rainfall) and phenotype (i.e., body condition, time hatched, clutch size). Contrary to what was expected, on Sable Island, the effect of dispersal on both reproductive probability and RS were direct, and all tested indirect effects (from local abundance, body condition, band size, or distance to freshwater) were weak, suggesting a small impact of environmental conditions on dispersal.

Dispersal is a multicausal process, driven by individual characteristics and environmental factors (Clobert et al. 2001; Bowler and Benton 2005; Clobert et al. 2009), so understanding its long-term consequences is challenging. However, a better knowledge of the consequences of dispersal on individual fitness is important to comprehending how dispersal is maintained in populations and how it evolves. Our results suggest a potential cost of social dispersal on the future reproduction of female feral horses; however, our data also suggest that there may be potential benefits for the survival of accompanying offspring of dispersing females which may balance some of these costs. Quantifying the net benefit of this to

![Figure 4](https://example.com/figure4.png)

**Figure 4**
Estimated cumulative foal survival (a) from adult female Sable Island horses (2008–2014) that socially disperse just before conception (i.e., at year \( t - 1, n = 121 \)) and from philopatric mares \( (n = 267) \); (b) from adult females that socially disperse while pregnant (i.e., at year \( t, n = 116 \)) and from philopatric mares \( (n = 274) \); (c) from adult females that socially disperse with an accompanying foal during its first winter (i.e., at year \( t + 1, n = 86 \)) and from philopatric mares \( (n = 145) \). The Kaplan–Meier estimator was used; philopatric adult females are in gray and dispersers are in black. Dashed lines represent associated 95% confidential intervals.
a female’s overall fitness and potential for an evolutionary stable strategy of social dispersal is beyond the scope of this study, but it does present a testable hypothesis for future research.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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