

**LIFE HISTORY AND POPULATION DYNAMICS
OF SABLE ISLAND HORSES**

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ABSTRACT

Individual-level life-history strategies are the rails that guide population dynamics. Due to the difficulty of conducting long-term, individual-based studies, current management practices often focus on estimating and controlling demographic rates with little consideration for the individual-level responses that guide them. This approach cannot account for important factors such as age-specific responses to changes in population density or long-term impacts of conspecific density and resource limitation. As such, population-level approaches may fail to predict age structure or the rate of population growth. Recent studies of mammals and birds have shown that short-term changes in factors such as population density can have lasting impacts on vital rates of individuals. These results highlight the importance of long-term individual-based analyses in understanding population dynamics. However, very few researchers have thus far been able to isolate and study interacting effects of density and resources on life histories apart from processes such as predation, interspecific competition, and management of anthropogenic disturbance.

The feral horses (*Equus ferus caballus*) of Sable Island, Nova Scotia, Canada, exist in a natural though simplified system without predation, human interference, or interspecific competition (they are the island's only terrestrial mammal, numbering approximately 500 individuals). Here I determined the roles of local conspecific density and an interacting resource gradient in guiding the reproduction and survival of adult female Sable Island horses (2008–2012). I used body condition (estimates of subcutaneous fat) as an indication of resource allocation towards the often conflicting purposes of reproduction and maintenance. Reproduction was best predicted by body condition (reproducing females were in relatively poorer condition)

but there was also evidence of density-dependence in reproductive success. Survival was predicted by and positively related to body condition. Survival was also predicted by an interaction between conspecific density and location on the island consistent with expectations of a known east-west resource gradient that occurs on Sable Island (in available water and forage). Greater variability in fitness estimates in resource-poor, eastern Sable Island suggests that regions of low density and resources may be high risk/high reward habitats. Such habitats may be disproportionately avoided by young animals and exploited by senescent animals.

All feral horses are descended from domesticated animals and recent work has found evidence of artificially selected life-history traits in unmanaged populations of domestic mammals like cattle, sheep, and horses (e.g., reproducing even at high densities and earlier in life than expected). I therefore attempted to determine if effects of artificial selection existed in the Sable Island population by examining age-based contributions to population growth and the relationship between reproduction (foaling) and female mortality. Perhaps due to the population's long history of low management (>250 years), I failed to find any strong evidence of artificially selected life-history traits in Sable Island horses. That is, life history trade-offs in survival and reproduction in Sable Island horses were more similar to wild species of large herbivores inhabiting natural environments, than other populations of feral ungulates. My research suggests a rarely documented but fascinating instance of reversal of artificial selection by natural selection for a domesticated species like the horse.

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LIST OF ABBREVIATIONS AND NOTATIONS

λ	Intrinsic rate of increase
IFD	Ideal free distribution
r	Intrinsic rate of increase = $\ln(\lambda)$
R_0	Per-capita rate of increase
LRS	Lifetime reproductive success
SWS	Simple weighted sum
$p_{t(i)}$	Individual contribution to population growth <i>sensu</i> Coulson <i>et al.</i> (2006)

1.0 INTRODUCTION

1.1 ESTIMATING FITNESS

1.1.1 History, Semantics, and Application of Fitness Estimates

The term “survival of the fittest” was coined in 1864 by Herbert Spencer to describe Charles Darwin’s theory of evolution by the process of natural selection. Following Darwin’s adoption of the phrase in later editions of *On the Origin of Species*, the concept of fitness became an integral part of biology. Stearns (1976) more recently defined fitness as: “something everyone understands but no one can define precisely.” Today, fitness remains a key component of ecological and evolutionary studies; however, Stearns’ definition is still appropriate and no single estimate of fitness can be agreed upon by biologists. In introducing my thesis, I thought to here first discuss the different methods of estimating fitness, concluding with a newly developed, shorter-than-generational estimate of fitness (Coulson *et al.* 2006). I adopt the latter as my estimate of fitness in this thesis.

Even prior to the recognition of Gregor Mendel’s 1866 discovery of inheritance and diploid genetics, the definition of fitness in the literature of biology was necessarily different from the traditional definition. Darwin (1873), upon adopting the term “survival of the fittest,” used fitness to describe the ability of an organism to survive and reproduce rather than the physical or cardiovascular condition of the organism. Darwin understood phenotypic change in populations could be effected by the actions of differential survival and fecundity upon the prevalence of heritable traits (Christiansen & Prout 2000). This understanding of evolution facilitates the assessment of fitness through a simple count of an individual’s progeny or grand-progeny. Though simple counts of progeny are less popular measures of fitness than they once were, Darwin’s idea of fitness as a character upon which natural selection acts (Christiansen & Prout 2000) remains the basis for many models of natural selection in use today.

Because evolutionary fitness is defined simply as the character of an organism upon which natural selection acts, estimating fitness requires us to identify the quantifiable characters on which natural selection

can act. Estimating fitness then requires us decide upon a suitable method of measuring those characters and interpreting the results. Stearns (1992) identifies such characters as size at birth, growth pattern, age at maturity, size at maturity, number and sex ratio of progeny, age- and size-specific reproductive investment or mortality changes, and length of life. As with any experiment in ecology, data can be simple to gather and difficult to interpret (McElreath and Boyd 2007).

First, we must determine whether each quantified character truly is acted upon by natural selection for the organism in question (Fisher 1958). Next, we must determine whether the quantified characters account for enough variability in fitness to provide a useful model (Christiansen & Prout 2000). Even when the character is acted upon by natural selection, the effect of the character on the fitness of the organism will vary depending upon one's view of evolution. Some researchers may assess an organism's fitness over its entire life while others may examine fitness as it changes over shorter time periods; some researchers concern themselves with only the direct descendants of an individual while others concern themselves with an organism's genetic contribution to following generations in both descendants and kin (i.e., inclusive fitness). Others are interested in the absolute contribution of an individual to subsequent generations while some are interested in the proportion of their descendants or genes within subsequent generations. Combinations of these approaches we choose to use in defining fitness should depend on the organism we study, the data available, and the questions we wish to answer.

Thomas Hunt Morgan synthesized Gregor Mendel's laws of inheritance and Hugo De Vries's mutation theory, into the chromosomal theory of inheritance in the early twentieth century (Bowler 1977; Moore 1983); this allowed scientists, for the first time, to consider the gene rather than the individual as the unit of selection (Williams 1966). Work by mathematicians such as R. A. Fisher, William Hamilton, and George Price showed that it is possible for genes to evolve that diminish fitness of the individual so long as they provide a proportional benefit to close kin (summarized by Fisher 1958); this is called kin selection.

In inclusive fitness models, organisms are expected to use kin selection to maximize the total number of replica genes rather than simply maximizing their number of progeny (Hamilton 1964). Evidence of kin

selection has been observed in prokaryotes (Olivieri & Frank 1994; Simms & Bever 1998), plants (Kelly 1996; Shimizu & Okada 2000; Westoby & Rice 1982), invertebrates (Peters *et al.* 1999; Queller & Strassmann 1998), and most vertebrate classes (see: Halverson *et al.* 2006 for amphibians; Russell & Hatchwell 2001 for birds; and Mappes *et al.* 1995 for mammals); however, most of these studies have measured traditional individual fitness rather than inclusive fitness. The reluctance of researchers to estimate inclusive-fitness characters in their experiments may, in part, stem from the difficulty and expense of determining genetic relatedness in organisms. It is therefore unsurprising that much assessment of inclusive fitness characters in recent research has taken place in the field of microbiology.

Studies of bacterial fitness are among the simplest because populations composed of genetically identical individuals can easily be created and maintained (Elena & Lenski 2003). This method allows inclusive fitness to be assessed through the differential success of entire populations and eliminating the need for complicated models of relatedness. Moreover, relatedness within bacterial populations can be easily manipulated by controlling the number of bacterial clones from which a population is propagated from (Griffin *et al.* 2004). In their influential 1991 paper, Lenski *et al.* conducted an assessment of relative fitness in different lineages of *Escheria coli* bacteria by placing two strains in direct competition for resources and comparing the rate of population growth of each strain; their observations of fitness and genetic variance were statistically indistinguishable from theoretical estimates based on R. A. Fisher's fundamental theorem of natural selection which states that mean fitness of any organism will increase proportionately to the genetic variance in fitness at that time (Edwards 1994). Subsequent studies have successfully estimated inclusive fitness of bacteria in the same manner (Andersson & Levin 1999; Elena & Lenski 1997). Although inclusive-fitness effects have been hypothesized in multicellular, clonal organisms such as plants (Semchenko *et al.* 2007) and insects (Mondor & Roitberg 2004), no attempt to quantify inclusive fitness in such organisms has been published.

Even in eusocial animals where the relatedness of all group members is known and only one group member is reproducing, measuring inclusive fitness becomes complicated and abstract. Attempts to estimate inclusive fitness of organisms with varying relatedness have been controversial. One of the most common

measures of inclusive fitness is the simple weighted sum (SWS). The simple weighted sum is defined as the sum of an organism's reproductive success and the reproductive success of each of its kin devalued proportionately to the genetic difference. The SWS is used—some say erroneously—by field ecologists as a measure of inclusive fitness. The results of Bygott *et al.*'s (1979) field study that used SWS to show inclusive fitness benefits of multi-male groups in lions (*Panthera leo*) were contested by Packer and Pusey's (1982) analysis of a different set of data. Bygott *et al.*'s statistical approach was criticized in Grafen's 1982 letter to *Nature* entitled "How not to measure inclusive fitness." Grafen argued that SWS fails to 1) strip individual fitness of the components due to the social environment, 2) strip the contributions of relatives of components not attributable to the actor, and 3) account for the harmful effects of an organism on its kin. Grafen also asserted that it is impossible to know of all of an animal's kin and therefore all measurements of relatedness in field studies must be rough estimates. Even where modern genetic technology enables us to determine the relatedness of each member in a population, is it impossible to accurately determine the number of offspring that each member would have produced without the intervention of all other organisms. Grafen accused McGregor *et al.* (1981) of overlooking this point and, despite his warnings, the mistake continues to be repeated in peer-reviewed literature (e.g., Creel & Waser 1994; Oli 2003). Grafen concluded his discussion with the idea that inclusive fitness is best suited to modeling whereas individual fitness is best suited to field studies.

Dobson *et al.* (2012) estimated inclusive fitness in ground squirrels with a novel approach: first by estimating and subtracting the fitness benefit provided by kin from their direct fitness measurements, then by estimating and including only the benefit provided to kin in the indirect fitness measurement. This approach mitigates one shortcoming of SWS because the indirect fitness measurement generated includes only genes attributable to the action of the individual; moreover the direct fitness measurement excludes genes in the individual's own offspring attributable to the actions of kin. The direct fitness estimates in this study were very similar to the unaltered fitness measurements of animals that lacked opportunities for cooperation, supporting the accuracy of the estimation. To date, this is the only published estimate of inclusive fitness that attempts to address all of Grafen's (1982) concerns.

Perhaps owing to the difficulty of estimating inclusive fitness (Grafen 1982) and the confusing semantics surrounding it (Griffin & West 2002; Oli 2003; Ricklefs & Miller 2001), the great majority of field studies rely on measures of individual fitness. Assessments of individual fitness are still valuable in and suitable to field studies despite the superiority of inclusive fitness theory in modeling. As asserted by Grafen (1982) and supported empirically by Dobson *et al.* (2012), traditional measures of individual fitness do include a kin-selection component as a portion of each individual's offspring may be attributable to benefits provided to them by kin. Grafen's prediction that individual fitness measures from field studies would be similar enough to predictions of inclusive fitness models to produce meaningful results was also supported by Viblanc *et al.* (2010) and Dobson *et al.* (2012). Though simpler to apply than inclusive fitness, individual fitness is also a complex topic and the past century has seen considerable progress in its estimation.

Simple measures of individual fitness such as survival of offspring to reproductive age are often used but they fail to account for the simultaneous action of natural selection on survival as well as reproduction. Darwin recognized both survival and reproduction as the key components of fitness yet there was no standard measure of individual fitness until well into the 20th century (Lewontin 1974). Richard Howard (1979) summarized the existing estimates of reproductive success and established the idea of lifetime reproductive success (LRS) as a standard measure of individual fitness that accounts for both survival and reproduction. LRS is calculated by estimating reproductive success of an organism over successive time steps throughout its life and summing them. Howard recommends using estimates of reproductive success that include as many generations of progeny as possible. Use of LRS began almost immediately (McGregor *et al.* 1981) and continues to the present (e.g., *Kruuk et al.* 1999; Warner & Shine 2008). Despite its utility both in testing theoretical predictions and in generating new hypotheses (Merila & Sheldon 2000; Konig 1994; Simmons 1988; Fleming *et al.* 2000), LRS does not accurately estimate fitness under certain conditions. Lifetime reproductive success may represent both reproduction and, to a lesser degree, survival, but it fails to capture reproductive rate. Genes that allow bearers to produce the same number of progeny as the rest of the population but within a shorter time frame would

allow them to achieve greater proportional genetic representation in subsequent generations than the rest of the population while having identical LRS.

The Malthusian parameter, r_{max} , and net reproductive rate, R_0 , are widely used measures of fitness in life-history studies that quantify the rate of growth within a population; however, both are limited in use to specific regimes of population growth and are found mainly within literature concerning theoretical models (e.g., Budilova & Teriokhin 2010; Kozlowski 1993). Another approach to incorporating reproductive rate in measures of fitness is to define fitness in terms of the efficiency of acquiring and applying energy to reproduction (Brown *et al.* 1993). This approach requires a radical divergence from any traditional definition of fitness because efficiency in reproduction may be much less important to the propagation of genes than factors such as net resource acquisition and reproductive timing (Bonnet *et al.* 1998). The limitations of these approaches may explain the continuing popularity of LRS in estimating fitness in ecology; however, they shouldn't prevent us from developing and using new and more suitable approaches.

1.1.2 Selecting a Method: Shorter-Than-Generation Estimates

Setting aside issues surrounding the semantics of the word “fitness,” selecting the proper fitness estimate is challenging. Historically, investigations of fitness have been grounded in game theory (Roughgarden 1973): conclusions are drawn from theoretical mathematics, which predict evolutionarily stable populations, i.e., populations in which novel, invading phenotypes would be unsuccessful (Maynard Smith 1972). In the mid-to-late twentieth century, evolutionarily stable strategies were defined using population-level estimates of fitness such as intrinsic rate of increase (r_{max}) or per-capita rate of increase (r). These methods are adequate to studies that examine large-scale trends in populations in which density-dependence is respectively dependent or independent of the environment (Mylius & Diekmann 1995); however, insight into the differential success of

phenotypes within a population is better attained by long-term tracking of individuals and individual-based fitness estimates (Lande 1982; McGraw & Caswell 1996).

Individual-based fitness estimates grew from the population-level theory of previous generations; they include individual fitness (λ_{ind}) as an analogue for intrinsic rate of increase (McGraw & Caswell 1996), and LRS as an analogue for per-capita rate of increase (Clutton-Brock 1988). McGraw and Caswell (1996) developed λ_{ind} to account for the timing of reproductive events, which is an important consideration because age-specific vital rates often have dramatic fitness consequences (Stearns 1992). Individual fitness (λ_{ind}) is a good measure of fitness in growing populations with little spatio-temporal variation; however, it often places far too much importance on offspring created early in life and gives inaccurate estimates of fitness for populations in highly variable environments (Brommer 2000). Because reproductive timing is not expected to affect fitness in populations at equilibrium, LRS is the most suitable single-generation estimate of fitness in stable populations (Brommer 2000). In the case of both estimates, fitness is determined by lifetime performance; this complicates any analysis of short-term changes in the pressure of selection on various phenotypes (Coulson *et al.* 2006) such as those presented by variable weather or conspecific density. Questions of short-term evolutionary change have prompted ecologists to develop shorter-than-generation estimates of individual fitness.

While life-history traits such as annual survival and fecundity were used for many years as shorter-than-generational estimates of fitness, more recent measures include components of both survival and reproduction. The simplest of these, annual fitness (Qvarnstrom *et al.* 2006), is the sum of an organism's own survival (1 or 0) and the number of offspring produced during the focal period where offspring are weighted by a factor of their relatedness to parents (e.g., a factor of $\frac{1}{2}$ for diploid organisms). This method provides an estimate of the absolute proportion of an organism's genes contributed to the population. Annual fitness is useful for population-level analyses examining extrinsic effects such as climate. Annual fitness provides insight into population-level trends but extrinsic factors are likely to mask phenotypic responses to changes in the

environment. Therefore annual fitness may fall short when the goal is to examine differential phenotypic responses

Coulson *et al.* (2006) developed individual contributions to population growth ($p_{t(i)}$) as a relative estimate of shorter-than-generational fitness. There are other possible applications of their “de-lifing” method; however, the primary intended use is to measure $p_{t(i)}$ over time-steps shorter than the generation in order to identify short-term changes in evolutionary pressures. This method expresses fitness as the quotient of the individual’s difference from mean performance over the population size. Because it includes a term for mean performance of the population, de-lifing accounts for population-level trends and allows examination of differential performance of different phenotypes. Because the calculation also includes a term for population size, individual contributions to population growth can be thought of as the change in an individual’s proportional genetic representation within the population. These same traits introduce difficulties in analysis: first, the use of population means necessitates a high level of knowledge of the study population which can be difficult and expensive to collect in field studies; second, the inclusion of population size complicates comparison of data from years with very different population sizes. Estimates of fitness based on the de-lifing approach have been used successfully in studies of feral sheep (Pelletier *et al.* 2007), cervids (Stopher *et al.* 2008), equids (Grange *et al.* 2009) and passerine birds (Cockburn *et al.* 2008). Individual contributions to population growth can be calculated yearly and they account for changes in the relative importance of survival and reproduction; consequently, they are good fitness estimates where lifetime-scale data are unavailable or where shorter than lifetime variation in the environment is of interest because they.

As has been the case for decades, there is still no universally applicable estimate of fitness. Fitness estimates in each study must be carefully selected based on the data available, the dynamics of the population, and the hypotheses being tested. Brommer *et al.* (2004) provided a table of the most common fitness estimates in practical ecology, I expanded it to include considerations for shorter-than-generational fitness estimates (Table 1.1). Inclusive fitness adjustments can be made to any individual-level fitness estimate; however, as theorized by Grafen (1986), they are rarely necessary and, as demonstrated by Dobson *et al.* (2012), the data

required to properly carry out such corrections are difficult to gather in the field and require a painstakingly designed and implemented study.

Table 1.1: Estimates of fitness and their ideal application adapted from Brommer *et al.* (2004).

Sensitivity indicates whether long-term estimates are sensitive to reproductive timing and whether individual short-term estimates are more sensitive to differential phenotypic or population-level changes.

Name	Description	Symbol	Level	Sensitivity	Application
Net reproductive ratio	Expected number of same-sex offspring	R_o	Population Short Term	No	sparse data, density-dependence interacts with environment
Lifetime reproductive success	Total number of offspring produced	LRS	Individual Long Term	No	long-term individual-based data, stable or declining population
Intrinsic rate of increase	Part time-unit increase in number	$\ln(\lambda_{\text{pop}}) = r$	Population Short Term	Yes	sparse data, density-dependence unaffected by environment
Age-discounted LRS	Propensity of rate of increase	λ_{ind}	Individual Long Term	Yes	long-term individual-based data, growing population
Absolute annual fitness	Genes present in the population at the end of study period	varies	Individual Short Term	Population	sparse data, short-term responses to extrinsic factors of interest
Individual contribution to population growth	Genes contributed to the population relative to mean performance	$p_{r(i)}$	Individual Short Term	Phenotype	accurate estimates of demographic rates available, short-term responses of variable phenotypes of interest

1.2 UNGULATE LIFE-HISTORY STRATEGIES AND POPULATION DYNAMICS

Life-history strategies of animals are shaped by both intrinsic and extrinsic forces. Among the extrinsic forces are weather, resource availability, inter- and intra-specific competition, predation, parasitism, and the rate of change of each of these (Gaillard *et al.* 2000; Sæther 1997). Among the intrinsic forces are the size of the animal, its rate of development, and the energy necessary to bring offspring to term (Stearns 1976; Stearns 1992). As relatively large animals which require a large energy investment to reproduce (Gaillard *et al.* 2000), ungulates tend live long lives and reproduce slowly, and fall on the *K*-selected side of the *r-K* continuum (Stearns 1972).

One important contrast among ungulate life-histories is that of the “capital” vs. “income” breeding strategy (Drent & Daan 1980). Income breeding, which relies on increased energy intake to fuel reproduction, is most beneficial in warmer environments and in habitats where forage is most available when resource demands are greatest (Jönsson 1997). Because income breeding does not rely on a slow accumulation of energy, it lends itself to extreme population cycling when conditions are variable (Stearns, 1972). In years of plentiful resources, income-breeding populations are able to respond with immediate growth. In years of meagre resources, a lack of stored energy may lead to population crashes among income breeders as survival and reproduction decrease dramatically (Coulson *et al.* 2000). The ability to produce multiple offspring is a benefit in such variable populations because it allows survivors to rapidly proliferate their genes in a population following a crash (Stearns, 1972). Many income-breeding species are able to produce multiple offspring in each reproductive event; i.e., they are polytocous (e.g., Coulson *et al.* 2000 for saiga antelope, *Saiga tatarica*; Tavecchia *et al.* 2005 for Soay sheep, *Ovis aries*; Hamel *et al.* 2009 for roe deer, *Capreolus capreolus*).

In contrast to income breeding is the capital breeding strategy in which animals accumulate stored energy (i.e., capital) over long periods and then expend it to fuel reproduction (Jönsson 1997). Capital breeding species include red deer (*Cervus elaphus*: Clutton-Brock *et al.* 1983), mountain goats (*Oreamnos americanus*: Hamel *et al.* 2009), bighorn sheep (*Ovis canadensis*: Hamel *et al.* 2009), and horses (Boyd & Keiper 2005).

Though storing energy for later use is metabolically less efficient than immediately allocating it to growth, reproduction, or maintenance, it confers a number of indirect benefits: it provides stored energy as a buffer against environmental stochasticity, it provides fat as insulation in cold weather, and it allows reproduction to take place at a time most beneficial to the offspring in habitats where that does not coincide with a time of abundant forage (Bonnet *et al.* 1998; Drent & Daan 1980; Jönsson 1997). Because capital breeding relies on energy accumulated over longer periods, capital-breeding animals tend to be long-lived and exhibit large changes in body condition corresponding to reproductive investment. At the population level, capital breeders express more subdued responses to changes in their environments (Clutton-Brock *et al.* 1997).

It is clear that, not only are life-history strategies guided by the characteristics of the individual and environment, but population dynamics are largely influenced by the resulting life-history strategies. A firm understanding of life-history strategies is therefore vital in understanding and managing a species at the population level. The absence of human management, predators, and guild members in the Sable Island horse population (Nova Scotia, Canada; see Section 2.1)—the subject of research in this thesis—makes it an ideal system for understanding the effects of environmental stochasticity and conspecific interaction on life-history strategies.

One basic area of interest in the study of life-history is the variation of different demographic rates in response to changes. Matrix analyses performed by Richard *et al.* (2014) found that the population of horses on Sable Island is typical of other large ungulates in that its growth rate is most sensitive changes in adult female survival; hence, my studies in this thesis will focus on the responses of demographic rates in female Sable Island horses to changes in resource availability and conspecific density.

1.3 LIFE-HISTORY TRADE-OFFS IN FERAL HORSES

Fecundity and the timing of reproductive events can have strong effects on population dynamics but age-based variability in these life-history traits varies by population. When facing high conspecific density and/or resource

limitation, populations of long-lived animals are expected to reduce reproductive rate. In polytocous species, changes in the number of offspring produced by prime-aged females can be an important component of population dynamics; however, in monotocous species, reproduction of prime-aged females is often among the most consistent life-history traits (Gaillard *et al.* 2000). Horses, as a long-lived and monotocous species, should be expected to respond to high density and resource limitation at the population level through increased age of primiparity and reduced fecundity in young females (Sæther 1997). However, a recent analysis of reproduction in Camargue horses (Grange *et al.* 2008) failed to find any evidence of this phenomenon.

Grange *et al.* (2008) speculated that artificial selection for rapid and early reproduction in horses created a suboptimal life-history trade-off of survival for reproduction in two-year-old mares. This is an adequate explanation of poor performance of that age-class in the Camargue population which had been released from heavy management immediately prior to the study; however, the negligible level of management of the Sable Island population since its introduction in the mid-18th century (Christie 1995; Plante *et al.* 2007) raises suspicion that artificially selected life-history is less prominent in this population of feral horses than it might be in others. This suspicion is strengthened by recent evidence that the sensitivity of the Sable Island population to changes in various demographic rates is typical of wild ungulates (Richard *et al.* 2014) but diminished by evidence of early senescence typical of feral populations (Richard *et al.* 2014).

Life history traits are traits —such as number of offspring or length of life— that “figure directly in reproduction and survival” (Stearns 1992). As life-history traits are strongly linked to evolutionary fitness, it can be assumed that they are under high selective pressure. Selective pressure is an important factor in rate of evolution and high selective pressure can result in rapid evolutionary change; however, rate of evolution depends not only on selective pressure but also on opportunity for selection (Stearns 1992). Opportunity for selection, i.e., the genetic variability in a trait, is necessary for rapid evolutionary change and it is typically inversely proportional to pressure of selection (Stearns 1992). All of this makes it difficult to predict the interactions between artificial and natural selection.

1.4 NATURAL HISTORY OF FERAL HORSES

1.4.1 Social Structure, Home Range Size, Habitat Selection, and Dispersal

Feral horses adopt a polygynous, female-defense mating system in which social groups called bands are formed by a group of mature females (a harem) and their recent offspring, a dominant male (a band stallion), and occasionally one or more subordinate males (Boyd & Keiper 2005; Welsh 1975). Stallions with no band affiliation form loose, ephemeral associations with other such “bachelors” known as bachelor groups. Band stallions attempt to monopolize mating opportunities with the unrelated females in their bands by coercing the harem into a cohesive group, forcing subordinate stallions to the periphery, and repelling extraband stallions through ritualized contests (Rubenstein 1981). Bands maintain home ranges which often overlap heavily but they rarely interact with one another, remaining far apart except near important resource patches such as shelter during poor weather or water holes during dry seasons (Welsh 1975). Band position and movement appears to be led by different individuals depending on the situation. Movement to resources is most often initiated by lactating females (Rubenstein 1994) but stallions often herd and drive their bands when extraband stallions are encountered (Welsh 1975).

Home range size among feral horses is variable and depends on resource availability. Estimates range from as low as 0.6 km² in Kaimanawa, New Zealand (Linklater *et al.* 2000), to as high as 78 km² in Sone Cabin Valley, USA (Green & Green 1977). Boyd and Keiper’s (2005) review of home range sizes in feral horses reveals trends of smaller home ranges in island and mesic habitats. Moreover, horses in xeric habitats may regularly travel up to 25 km beyond their home ranges to reach water (Stoffel-Willame & Stoffel-Willame 1999).

The social organization and habitat selection of feral horses are subject to strong seasonal variation. In Misaki feral horses (Toi Cape, Japan), bands often break into small, sometimes all-female, units during the winter and reunite during the summer (Kaseda *et al.* 1995). Home range size may vary seasonally and the season of largest home range size is not consistent among populations (Linklater *et al.* 2000; Zervanos & Keiper 1979). Lastly, the period between excursions beyond the home range may also vary. Stoffel-Willame & Stoffel-Willame (1999) observed an increase from 30 hours in the summer to 72 hours in the winter. In nearly all cases, temporal variation in the habitat selection of feral horses appears to be most strongly driven by demand for, and availability of, water (summarized by Boyd & Keiper 2005).

Fidelity among intraband mares coupled with the herding and defense from stallions creates fairly stable harems; however, there are occasional changes in band membership, particularly among juveniles. Female horses reach sexual maturity around one year of age; unless the dominant stallion of a band has been replaced by an extraband stallion, they will begin to disperse from their natal bands at this time (Contasti 2011; Welsh 1975). Male offspring typically disperse to join bachelor groups between one and four years of age (Contasti 2011; Welsh 1975).

Dispersal of adult females from breeding groups is positively correlated with both band size and local conspecific density (Marjamäki *et al.* 2013); however, they may be reluctant to disperse from bands for a variety of reasons. Band hierarchy may be based on residence time (Monard & Duncan 1996). Dominant females spend more time foraging and produce more successful offspring (Duncan 1992; Feh 1999) than subordinate females. Dispersing females can also experience severe harassment as stallions attempt to herd them. In the worst cases, dispersing females are herded alternately towards the band by the stallion and away from the band by dominant mares (personal observation). Mares that suffer such harassment can receive serious bites and their young offspring may be forced to run frequently. Perhaps as a consequence of such behaviour, mares that experience less band stability have may have less reproductive success than mares that remain in stable bands (Khalil *et al.* 2010).

As with habitat selection, life-history of feral horses is also unique. As large, long-lived animals, horses are monotocous breeders that rely on stored energy capital (rather than increased intake) to fuel reproduction (i.e., capital breeders: Stephens *et al.* 2009). This capital breeding strategy lends itself to slow, cautious reproduction; however, domestication may have selected for more rapid reproduction in horses, perhaps with consequences for survival (Grange *et al.* 2009). A trade-off in survival for reproduction may still be present in feral herds where horses are heavily managed through removal, sterilization, and/or veterinary care (Boyd & Keiper 2005).

1.4.2 Natural History of Sable Island horses

Because populations of feral horses differ so widely in habitat selection and life-history traits, it is helpful to review the characteristics of Sable Island horses, the population of interest in this thesis. The behaviour and population dynamics of the Sable Island horse population have been described in great detail by Welsh (1975), Contasti (2011), and Richard *et al.* (2014); their findings are briefly summarized here. Horses were introduced to the island in the mid-eighteenth century, and they have been largely unmanaged since that time and strictly unmanaged since 1940 (Christie 1995; Plante *et al.* 2007). Welsh (1975) reports that the population fluctuated between 80 and 400 animals in the years between 1753 and 1952 but counts from this period are unreliable. Accurate counts in the 1960s showed population sizes between 130 and 230. During the period of my study, the population ranged from 458 to 538 and grew at a λ of 1.053 (Richard *et al.* 2014).

Contasti (2011) reported adult, survival between 0.86 and 1.00 during the first three years of my study and a slightly female-skewed adult sex ratio (0.88 males per female). Welsh (1975) provided some evidence of extreme population cycling in the first two centuries following the establishment of the population, but the only population decrease during my study saw only a 9% decline in population size (Richard *et al.* 2014).

Primiparity (i.e., a female's first reproductive event) on Sable Island begins to occur at three years of age but is most common at four (Richard *et al.* 2014; Welsh 1975). Mares will typically nurse their offspring for up

to two years or until their next foal is born (Welsh 1975); however, I have observed some mares simultaneously nursing offspring of two different years.

Current reports on social dynamics of Sable Island horses (e.g., Marjamäki *et al.* 2013) are limited and Welsh's (1975) study took place at lower population densities than are present today. Welsh (1975) reports that dispersal between social groups occurs most often between March and June. During the first three years of my study, natal dispersal in both sexes was most common among yearlings (Contasti, 2011) but, during Welsh's (1975) study, natal dispersal of males took place most often at three years of age.

Many feral horse populations are less than 100 years old and subject to heavy management. Because the Sable Island population has a history of no predation, little competition from guild members, and relaxed management spanning over 250 years, I expected to find several differences with other feral horse populations. Examination of the survival and reproduction of every member of the population will provide insight into population dynamics and allow investigation into differential "fitness" performance of phenotypes in the population. Lastly, the lack of predators and competing guild members for Sable Island horses will allow me to isolate and examine the effects of conspecific interactions among horses on their individual fitness.

1.5 RESEARCH OBJECTIVES, HYPOTHESES, AND PREDICTIONS

1.5.1 Documenting Individual Contributions to Population Growth in Sable Island Horses

Study of ungulate life-history is confounded by complex and varied responses of different species to changes in their environments and by evidence of artificially selected life-history strategies in other feral ungulate populations. Adult female survival may be variable in some species but relatively constant in others (Clutton-Brock *et al.* 1997). Some species respond to resource limitation with reduced fecundity among adult females whereas others—typically capital breeders—respond to the same stimulus with delayed primiparity and increased interbirth interval among young females (Sæther 1997). Moreover, the recruitment and reproductive success of offspring is often heavily influenced by weather, resource availability, and conspecific density during

their development (Taborsky 2006; Tavecchia *et al*2005) leading to strong cohort effects within the population (Brommer *et al*1998; Gaillard *et al*1996). One of my main goals for this thesis was to provide broad insight into the population dynamics of the horse population on Sable Island by explaining variation among individual contributions to population growth (fitness).

To this end, examined candidate models predicting recruitment, survival, and $p_{t(i)}$ in adult female Sable Island horses. Recruitment contains components of fecundity (i.e., whether or not the mare produces a foal) and survival (i.e., survival of foals to one year of age). Both recruitment components are expected to strongly impact body condition scores because bringing a foal to term then nursing it are both extremely energetically costly and should rely heavily on energy stored as subcutaneous fat. As a result, the abundance of fat in female horses should vary cyclically with reproduction. Female horses should therefore exhibit a general trend of decreasing body condition during pregnancy and lactation but increasing body condition otherwise. Where data are insufficient to assess change in body condition, these trends should bear out high body condition in years without parturition and low body condition in the years of parturition and lactation. As such condition in a given year may be used to model a horse's reproductive state in that year.

Foal survival may also be influenced by local density and band size, following Welsh's (1975) hypotheses of winter resource limitation and shelter through huddling. Survival of Sable Island mares is among the most variable demographic rates (Richard *et al.* 2014). Variables other than body condition may be more apparent in models of survival than recruitment because much variation in body condition is expected to stem from cyclic resource storage and allocation to reproduction; still, poor condition is sometimes a sign starvation which I expect to be driven by local conspecific density in relation to resource availability. I expect higher mortality in poor-condition mares. Local density, in driving resource limitation, may play a role in predicting survival; if it does, the strength of density dependence may vary along Sable Island's resource gradient. My fitness estimate, $p_{t(i)}$, was designed to identify differential performance of phenotypes within a population. As such, I expect its analysis to reveal stronger evidence of the effects of habitat selection than the other analyses: i.e., effects of density and location should be more pronounced in models of $p_{t(i)}$. I tested the following predictions:

1. Recruitment is weakly density-dependent;
2. Body condition in the year of parturition will be lower among reproducing females;
3. Location and local density interact in predicting survival;
4. Animals in poor condition are more likely to die;
5. Body condition of dying horses covaries positively with density; and,
6. Models of $p_{t(i)}$ will show stronger responses to small-scale spatial heterogeneity.

1.5.2 Understanding Trade-Offs Between Survival and Reproduction in Sable Island Horses

Human management may have altered the life-history strategies of feral horses as farmers and breeders selected for rapid reproduction and reduced selection against early reproduction by providing ample food and veterinary care. While the population dynamics of other feral horse populations are widely published, most of these studies focus on either newly established or heavily managed populations. One interesting finding of Grange *et al.*'s (2008) study of the Camargue population was evidence of a life-history trade-off of survival for reproduction in young horses. The authors speculated that this trade-off—which is not seen in long-lived wild ungulates—was a result of artificial selection. Clutton-Brock *et al.* (1997) argue that artificially selected life-history can have strong effects on population dynamics and lead to over-compensatory population cycling, a trait that has been observed in many feral ungulate populations (Boussès *et al.* 1992; Clutton-Brock *et al.* 1997; Fowler 1981; Pople & McLeod 2010). It is also suggested that population cycling is exaggerated in predator-free island populations (Clutton-Brock *et al.* 1997).

The extent to which the Sable Island horse population exhibits artificially selected traits such as premature reproductive investment and extreme population cycling is yet to be determined. As a feral population on a predator-free island, these traits could be expected; however, I expect Sable Island's weather to exert strong selective force against them. For a horse population, Sable Island winters are cold, wet, and

resource-poor. Stored body fat is a buffer against cold weather and periods of resource limitation; moreover, it allows energy gathered during the summer and fall to fuel reproduction in the spring.

In wild, long-lived ungulates, the prospect of future reproduction heavily outweighs the benefit of reproduction that risks mortality in young and prime-age animals (Stearns 1992). Only in senescent animals are the prospects of future reproduction expected to be low enough that parents engage in risky reproduction. The artificially selected life-history trade-off suspected in the Camargue population is a trade of survival for reproduction in young mares. This trade-off would be maladaptive because young mares have high prospects of future reproduction. My first analysis on this topic compares individual contributions to population growth ($p_{r(i)}$) among different-aged Sable Island mares and relates them to that of their counterparts in the Camargue population. My second analysis searches for a relationship between foaling and mortality in Sable Island mares. If young Sable Island mares have contributions to population growth similar to young Camargue mares, there may be a similar life-history trade-off; a direct relationship between foaling and reproduction at young ages will be even stronger evidence of this. Because the Sable Island horse population is older and has a history of little to no management reaching back many generations, I do not expect to find evidence of artificially-selected life history. I tested the following predictions:

1. The youngest age-group of reproductive Sable Island mares contributes negatively to population growth;
and,
2. Reproduction predicts mortality in young Sable Island mares more strongly than it does in prime-aged mares.

2.0 GENERAL METHODS

2.1 STUDY SITE

Sable Island, Nova Scotia ($43^{\circ} 56' N$, $60^{\circ} 00' W$) rests on a large bank of sand and gravel atop the continental shelf. It is 290 km east of Halifax and 135 km from the nearest point on the mainland. The island is a thin crescent of sand only 50 km in length and 1.25 km in width at its widest and its dunes reach no higher than 25 m (James and Stanley 1968). The topography of Sable Island changes rapidly over short time scales. Wind-driven dune succession gives rise to cycles of dune formation, drift, and blow-out (Tissier 2011) while the spits at either end of the island change in size and shape from year to year.

Sable Island's climate is moderated by the cold, south-flowing Labrador Current and the warm, north-flowing Gulf Stream Current which flow to either side of it. During summer months Sable Island is colder than the mainland, reaching a maximum monthly mean temperature of $17.8^{\circ} C$ in August (Environment Canada 2014); whereas the mean minimum temperature in February—the coldest month—is $-1.4^{\circ} C$, approximately $5^{\circ} C$ warmer than nearby Halifax, NS. (Environment Canada 2014). In contrast to temperature, the amount of precipitation is similar to that of the mainland. Southwesterly winds averaging $17.5\text{--}31.5$ km/h carry 146 cm of precipitation to Sable Island each year (Environment Canada 2014).

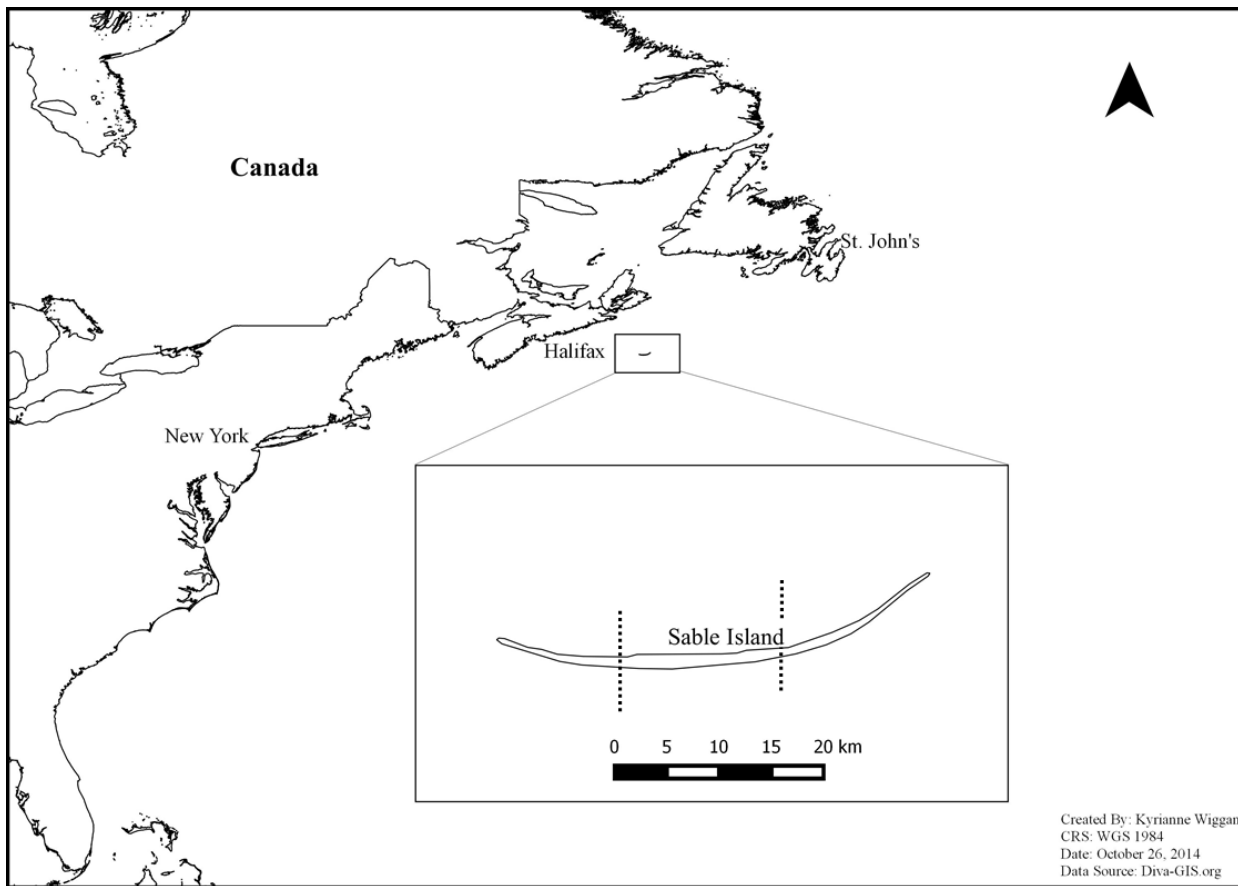


Figure 2.1: Location of Sable Island, NS, Canada. Dotted lines on the inset represent the boundaries of three regions defined by Contasti (2011) based on the horses’ use of, and fidelity to, water sources.

Both animal and plant communities of Sable Island are unique. Marram (*Ammophila breviligulata*) occurs throughout all of the vegetated area, dominating plant associations. Although 40% of the island is vegetated (de Villiers & Hirtle 2004), repeated attempts to introduce a wide variety of trees to the island (as detailed by Patterson, 1894) have failed, leaving Sable Island host to a single Scots pine (*Pinus sylvestris*) but no other trees (Catling *et al.* 1984). Harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are the only mammals native to Sable Island and horses —believed to have been introduced in 1738 (Welsh 1975)— are its only terrestrial mammals.

Topography includes ridges of vegetated and bare sand dunes running parallel to the shores and bounding the inland bog, heath, and grassland communities. In the west, Sable Island is spotted with several small, permanent, freshwater ponds covering 21.8 ha (Catling *et al.* 1984). Ponds in the east of Sable Island dry

up during the summer months, forcing horses to dig in the sand to reach freshwater (Contasti 2011; de Villiers & Hirtle 2004; Lucas *et al.* 2009). In addition to emergent pond vegetation used by horses, the west contains important foods such as sandwort (*Honckenya peploides*) and beach pea (*Lathyrus japonicus* var. *maritimus*) that are less common in other areas of Sable Island (Lucas *et al.* 2009; Tissier 2011).



Figure 2.2: Resource gradient on Sable Island. Permanent ponds (top) are common in the western region of Sable Island but they become ephemeral in the central region and are absent in the east. Water digs (bottom) are found mainly in the central and eastern regions. Prime forage near water digs is often heavily browsed.

2.2 DATA COLLECTION

2.2.1 Census Methods

Data were collected by field crews between late July and early September each year between 2008 and 2013 except 2010, when the field season ran from May until July. Sable Island was divided into seven census zones, each (or a portion of each), being sampled in a single day by a crew of 1 to 3 members. Census methods were designed to locate each horse on the island as many times as possible without encountering the same horses on subsequent days. If a horse was observed more than once within 24 hours, only the first observation was included in my data. To census one zone, workers traveled by vehicle along the beaches to the boundaries of that day's zone and move on foot to meet in the center. Each horse encountered during a census was photographed while workers recorded its location and the members of its social group if applicable. Each horse on the island can be identified using unique natural markings and is given a unique identification number. Annual re-sighting probability of female Sable Island horses was 99.4% over the period of this study.

All spatial analyses are based on the median of all observed locations ($\bar{N} = 5$) of each horse in a given year. Contasti (2011) divided the island into three distinct zones (Figure 2.1) based on water availability and on horses' fidelity to water sources. Water is most available in the westernmost zone and least available in the easternmost zone (Figure 2.2). I assigned locations to horses in each year based on which zone their median location fell within. I calculated each horse's summer exposure to local conspecific density by summing the number of horses with median locations less than 8000 m from its own median location and dividing that number by the number of km² of vegetated area with the same radius. Because horses interact differently with band members as they do others, horses within one's own social group were excluded from the local density calculation. I calculated band (i.e., social group) size as the number of horses within the focal individual's band excluding its offspring of the current year to ensure that band size is independent of reproduction.

2.2.3 Vital Rates

I recorded recruitment and survival as binary variables. Because horses cannot emigrate from Sable Island, horses observed in year t but not in year $t + 1$ are assumed to have died and assigned a “0” for their survival in year t . Horses observed in the field season subsequent to year t have survived and are assigned a “1” for their survival year t . I defined recruitment as the production of a foal in year t that survives until year $t + 1$. Sable Island horses rarely nurse foals which are not their own (Contasti 2011; Welsh 1975) so maternal parentage is easily determined by observation of nursing/suckling behaviour. When a mare produces offspring in year t that is observed in year $t + 1$, she is assigned a recruitment value of “1” in year t ; otherwise, she is assigned a value of “0”. I determined the age of each horse using known year of birth when possible or by comparing its size, proportions, and pelage to known-aged horses.

I estimated fitness in year t using the de-lifing method (Coulson *et al.* 2006) which calculates each individual’s contribution to population growth ($p_{t(i)}$) through both survival and recruitment in year t and expresses it relative to the mean performance of the population in that year. Individual contributions to population growth can be calculated for each member of a population in each year. As a result, individual contributions to population growth can be used to examine fitness impacts of variables which vary significantly over periods shorter than the generation time of a population because a value. Individual contributions to population growth are also well suited to populations with highly variable demographic rates because the components of $p_{t(i)}$ are calculated relative to the mean performance of the population. Both of these traits make $p_{t(i)}$ the best fitness estimate for studying the effects of local conspecific density in Sable Island horses where both density and demographic rates vary significantly from year to year (Richard *et al.* 2014).

2.2.3 Body Condition Scores

I assigned a body condition score to adult female horses using a method adapted from Carroll and Huntington (1988). Scores were assigned on an eight point scale based on the appearance of subcutaneous fat covering the hips, ribs, and spine of the animal in photographs of each sighting and then averaged overall observations in each field season (as outlined in section 2.2.1 *Census Methods*). Carroll and Huntington’s (1988) method was

not designed with pregnant mares in mind; however, parturition most often occurred prior to the field season.

Carroll and Huntington (1988) reported an effect of sex but no effect of age on the mass of horses with the same size and condition score.

In the 11 known cases in which parturition occurred during a field season, there was no evidence that the mass/volume of the gravid uterus affected body condition assessments. In eight cases there was no change in body condition score following parturition. In the remaining three cases, ribs became progressively more prominent following parturition but no other changes were apparent; this change likely reflects the high cost of lactation. Although body condition is certain to vary throughout the year, Julian date is not a useful predictor of body condition in my data ($\Delta\text{BIC} = 16$ versus null model). I concluded that body condition scores did not vary significantly during the field season and I used z-scores of body condition to account for annual differences in observers and the timing of the field season.



Figure 2.3: Examples of adult female horses across the range of observed body condition scores. Scores were based on the appearance of subcutaneous fat covering the pelvis as well as the ribs and spine. I used several photos from different angles to make each assessment.

2.3 STATISTICS

2.3.1 Fitness Data

I limited the data in my initial analyses of recruitment, survival, and contributions to population growth to those describing female horses four years of age or older for a number of reasons: the growth rate of the Sable Island population is most sensitive to changes in the demographic rates of mares greater than three years old (Richard *et al.* 2014) and fitness of prime-aged (i.e., mature but not senescent) mares in a another feral horse population did not differ by age (Grange *et al.* 2008). Sable Island mares reach maturity at four years of age (Contasti 2011) and there is no significant difference in fitness among known-aged mares of ages four and up ($F_{2,75} = 0.522, P = 0.596$). While it would be helpful to exclude the small number of senescent mares from this sample, I lacked any non-invasive method of distinguishing between prime-aged and senescent mares of unknown birth year. Analyses of adult female recruitment, survival, and contributions to population growth included only individuals which were alive and greater than three years old at the beginning of the field season of year t .

Fixed effects in the maximal models of recruitment and survival were selected to represent both the endogenous and exogenous energy available to each animal. Body condition represents endogenous energy as an estimate of subcutaneous fat available for metabolism. Exogenous energy is determined equally by resource abundance and competition for resources. The categorical location variable is intended to represent the predicted gradient in resource availability whereas both band size and local conspecific density are intended to represent competition for resources. Because habitat and resource selection of the Sable Island population is density-dependent (Van Beest *et al.*, 2013), there is no *a priori* reason to expect strong correlation between location and body condition; moreover; regression of standardized body condition scores by location was less parsimonious than the null model ($\Delta\text{BIC} = -1.434$). Though condition in the year prior to parturition ($t-1$) may be a more straightforward way to model recruitment, I examined condition in the year of parturition (t). By examining the same pool of energy over the same time period in each set of models, I was able to directly compare energy availability and its impacts on various vital rates.

I used Akaike's information criterion (AIC) to apply information theoretic model selection (Burnham & Andersson 2002) to models predicting recruitment, survival, and contributions to population growth of 166 horses between 2008 and 2012 ($n = 509$). I selected the model among candidate models with the lowest AIC. When more than one model produced ΔAIC of less than two, the model with the fewest parameters was considered the best approximating model (Burnham & Andersson 2002). Other models were discussed as competing models if they did not include all of the fixed effects of the best model (Devries *et al.* 2008). In order to account for repeated measures, all candidate models included year of the observation (as an integer between 1 and 5) and the unique identification number of each horse as random effects. I used the best approximating models of recruitment and survival to inform the selection and interpretation of the more complicated fitness models because binomial family models are robust and make no assumptions about the distribution of residuals.

I modeled recruitment attributable to adult females in year t (as described in section 2.2.3 *Vital Rates*) using a binomial family generalized linear mixed effects model (GLMM) with the logit link function. I constructed a set of 83 candidate models that included body condition in year t , local density in year t , and band size in year t , as continuous explanatory variables alongside a categorical variable for location in year t . I also included all plausible two- and three-way interactions in the maximal model. The complimentary log-log link function was most appropriate for analyses of survival because the response variable is heavily skewed. The set of 83 candidate models of survival in year t (as described in section 2.2.3 *Vital Rates*) was therefore identical to that of recruitment with the exceptions of the response variable and the link function.

Fitness data ($p_{t(i)}$) would be best modeled using generalized additive mixed effects models (GAMMs) because they are bimodal and heavily left-skewed; however, current GAMM methods deal poorly with interactions involving categorical variables. Because the best model of survival included an interaction between density and the categorical variable for location, contributions to population growth in year t were transformed using Equation 1 and fit to GLMMs. This transformation converted the data to values between zero and one to allow the square transformation to behave similarly on all values (Osborne 2002). Though no transformation

can completely normalize bimodal data, the residuals of models fit using the transformed data were much closer to normal than those generated using untransformed data.

$$[1] \quad y_i = \left(\frac{p_{t(i)} - \text{minimum } p_t}{\text{maximum } p_t - \text{minimum } p_t} \right)^2$$

The set of 16 candidate models predicting fitness was created using the explanatory variables from the best models of recruitment and survival; it included terms for body condition, local density, location and all possible interactions. I performed all analyses using R, version 3.0.2 (R Development Core Team 2013).

2.3.2 Trade-Offs Between Survival and Reproduction

Using data describing 600 observations of 234 individual known-aged mares of ages 0 to 6, I calculated the $p_{t(i)}$ by age across all years of the study. I used ANOVA followed by Tukey HSD *post hoc* tests to identify differences in $p_{t(i)}$ among ages.

To examine survival costs of reproduction, I created a set of 17 candidate models predicting survival in year t in relation to body condition, age, and production of a foal in year t . Age is a categorical variable in which 2 and 3 year-old mares belong to one category and mares greater than 3 years old belong to the second. The division was made between 3 and 4 years of age for two reasons. Four years old is the most common age of primiparity in Sable Island mares (Contasti 2011) and there is a significant difference in reproductive success between three- and four-year-old mares (Richard *et al.* 2014). These models use data from 610 observations of 228 mares. In all candidate models, I included random effects for year and horse identification number in order to account for repeated measures. Among the candidate models, I selected the one with the lowest AIC. When more than one model produced ΔAIC of less than two, the model with the fewest parameters was considered the best approximating model (Burnham & Andersson 2002). Other models are discussed as competing models if they did not include all of the fixed effects of the best model (Devries *et al.* 2008).

3.0 RESULTS

3.1 FITNESS IN SABLE ISLAND HORSES

The model of recruitment which best fit the data included body condition as the only fixed effect (Table 3.1.1). Models including band size, density, and an interaction between the two had $\Delta\text{AIC} < 2$ but were eliminated from consideration as competing models because they contained all of the fixed effects in the best approximating model. Effects of local conspecific density and location were both insignificant ($P > 0.05$) and detrimental to model fit ($\Delta\text{AIC} > 0.46$). In the best model, recruitment attributable to adult females declined steeply as body condition increased (Figure 3.1.1); that is, females in poor condition during year t were more likely to produce a foal that survived until year $t + 1$. The model correctly classified 70% of the observations used to generate it. The random effects of individual and study year accounted for a large portion of the variance in predicted recruitment.

Survival in year t was best modeled using body condition, local conspecific density, and location in year t (Table 3.1.2). The best approximating model also included a two-way interaction between location and local density. Two models with $\Delta\text{AIC} < 2$ were eliminated from consideration as competing models because they contained all of the terms of the best model. One of these models included a fixed effect for band size and the other included an interaction between density and body condition—The two easternmost location categories were combined in the best model because the resulting decrease in model fit was minimal ($\Delta\text{AIC} = -0.70$). Horses with high body condition scores in year t were likely to survive until year $t + 1$ regardless of density in year t . As density increased, predicted survival decreased for horses with lower body condition scores. The effect of body condition on survival did not vary by location but the effect of local density was greater in the eastern region than in western Sable Island (Figure 3.1.2). The best model of survival accurately classified 90% of observations used to generate it.

The best model of fitness included body condition, density, location, and all possible interactions (Table 3.1.3). At low densities, fitness was high in horses with low body condition scores and moderate in horses with high body condition scores. At high densities, fitness was greatest in horses with good body condition but lowest in horses with poor body condition. The range of predicted fitness approached both the upper and lower extreme values in the eastern region but, in the west, it covered only a small range of values just above mean performance for the population. The interaction between density and body condition was greatest in the easternmost region (Figure 3.1.3). As in survival, the random variables included in my models accounted for a smaller portion of variance in fitness than they did in reproduction (Table 3.1.3).

Table 3.1.1: The best model of reproduction shows that body condition was a strong predictor of reproduction but a relatively high degree of variation resulted from unmeasured individual characteristics and from unmeasured environmental changes.

Fixed Effect	Coeff.	SE	<i>z</i>	<i>p</i>
(Intercept)	0.14605	0.09510	1.536	0.12462
Body Condition	-0.28607	0.09203	-3.108	0.00188
Random Effect	SD			
Individual	0.6256			
Study Year	0.3070			

Table 3.1.2: The best model of survival shows that body condition, local density, and location were strong predictors of survival. Density-dependent effects varied by location and random effects accounted for relatively little variance.

Fixed Effect	Coeff.	SE	<i>z</i>	<i>p</i>
(Intercept)	-3.24532	0.69558	-4.666	<0.0001
Body Condition	-0.28607	0.09203	-3.108	<0.0001
Local Density	-0.66863	0.10755	-6.217	0.0769
Location	-2.62681	1.33335	-1.970	0.0488
Local Density* Location	0.12644	0.05070	2.494	0.0126
Random Effect	SD			
Individual	4.275e-05			
Study Year	5.087e-06			

Table 3.1.3: The best model of $p_{t(i)}$ shows that the interaction of body condition, local density, and location were strong predictors of fitness. The interaction between body condition and density was stronger in the eastern region of the island.

Fixed Effect	Coeff.	SE	t	p
(Intercept)	0.6462935	0.05776275	11.188760	< 0.0001
Body Condition	-0.0269781	0.06561305	-0.411170	0.6812
Density	-0.0005084	0.00143691	-0.353848	0.7237
Location	0.0294220	0.10268894	0.286516	0.7747
Condition*Density	0.0009011	0.00157319	0.572758	0.5672
Condition*Area	-0.2384539	0.09626704	-2.477004	0.0137
Density*Area	-0.0019730	0.00418149	-0.471831	0.6374
Condition*Density*Area	0.0123413	0.00356388	3.462885	0.0006
Random Effect	SD			
Individual	2.855e-05			
Study Year	1.774e-06			

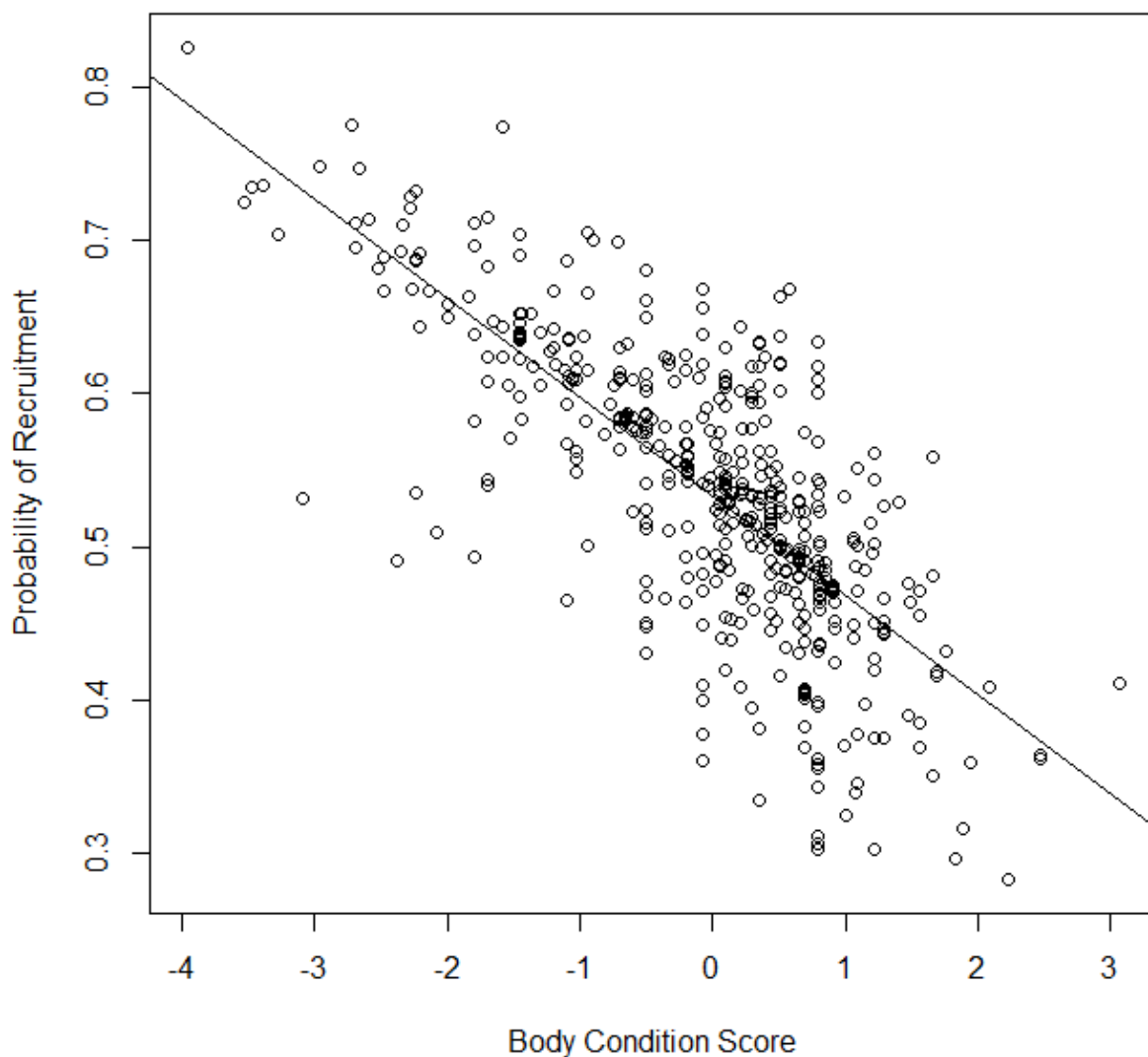


Figure 3.1.1: Recruitment in year t was correlated with lower average body condition during late summer of year t ($p = 0.002$), reflecting reproductive investment. Deviation from the regression line is a result of random inter-annual and individual differences. This model accurately classified 72% of the data used to generate it.

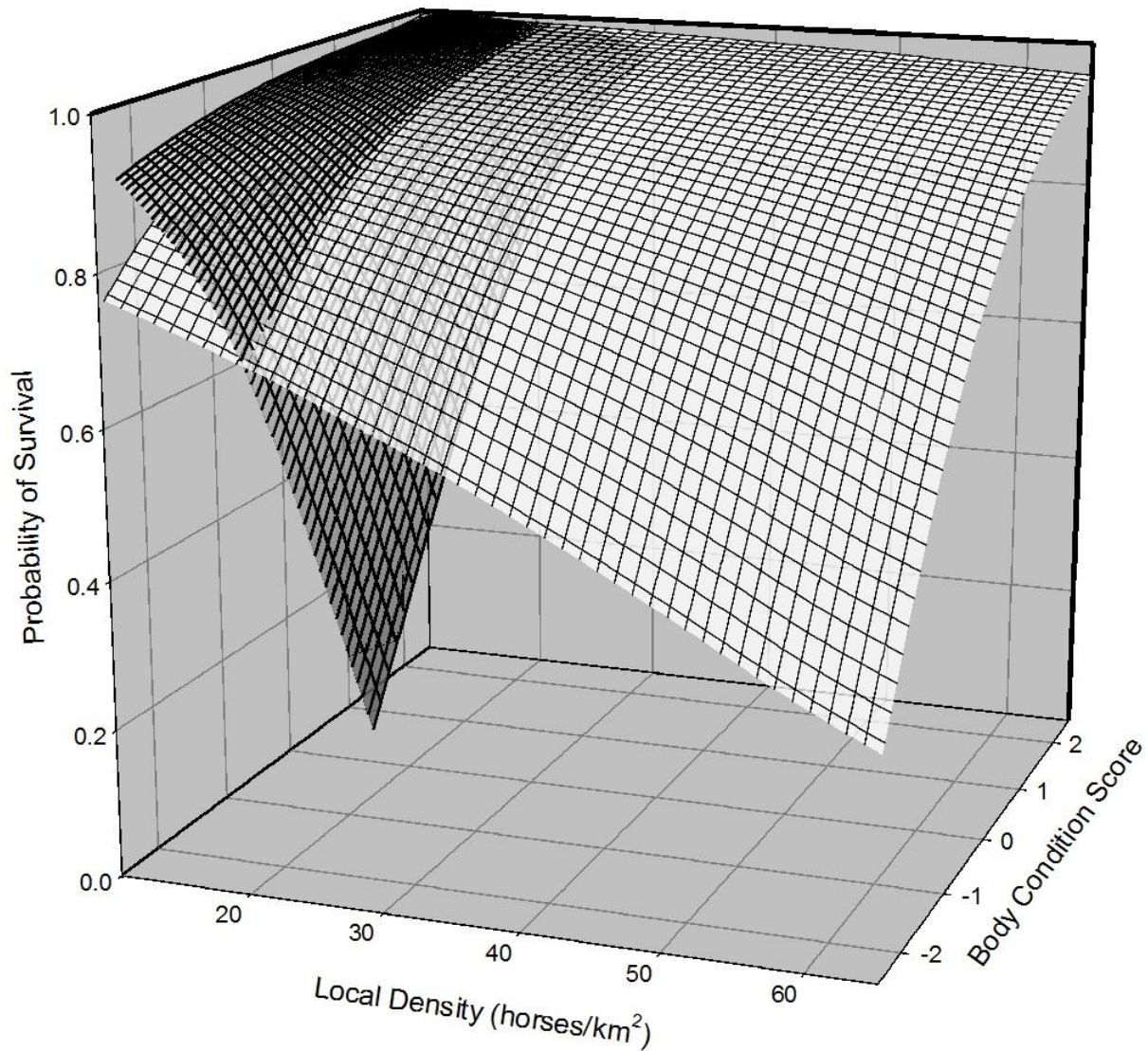


Figure 3.1.2: Predicted survival in year t of horses in (white) the resource-rich western region and (grey) the resource-poor eastern region. Survival declined rapidly with poor body condition and moderately with increased local density but density-dependence was stronger in the east than in the west. In both cases, there is minimal deviation from the model surface due to random effects. This model accurately classifies 89% of the data used to generate it.

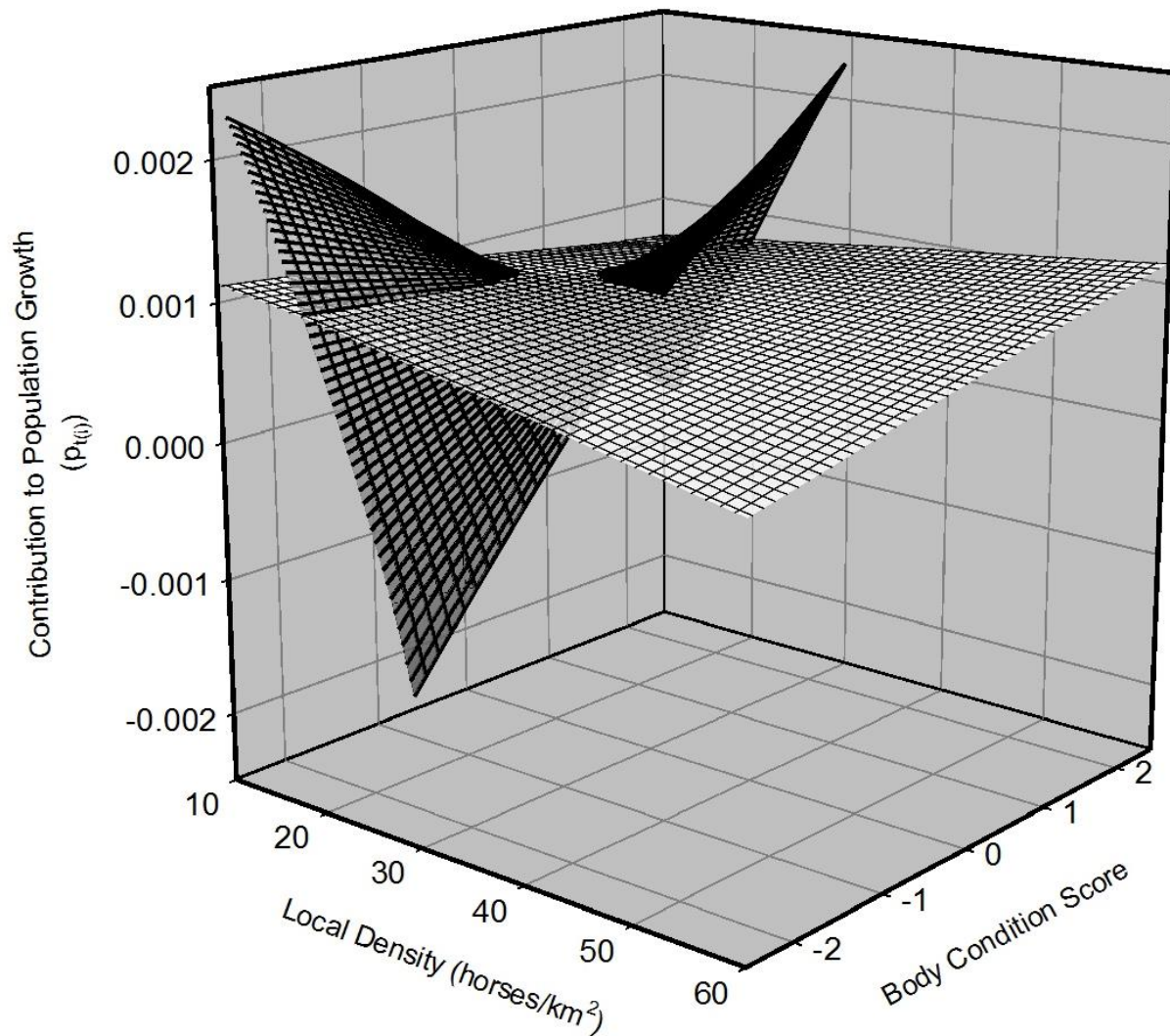


Figure 3.1.3: Predicted individual contributions to population growth ($p_{(i)}$) of Sable Island horses in (white) the resource-rich western region and (grey) the resource-poor eastern region. Body condition was negatively correlated with fitness at low densities and positively correlated with fitness at high densities. Predicted fitness remained near the mean for horses under all conditions in the west but covered the entire range of observed values for horses in the east. In both cases, there was little deviation from the model surface due to random effects.

3.2 TRADE-OFFS BETWEEN SURVIVAL AND REPRODUCTION IN SABLE ISLAND HORSES

Mares between 0 and 2 years of age all had below-average fitness (Figure 3.2.1) and there was no significant difference among them (Table 3.2.1). Mares greater than 2 years of age had greater fitness than the younger group and no significant difference among them. Body condition was the only fixed effect in the best approximating model of survival. The model showed a positive correlation between survival and body condition. Age and foaling were not important predictors of survival in these models, nor were there any interactions between age and reproduction (Table 3.2.2). Although three models were given consideration as competing models, each of them contained all of the fixed effects in the best model. None of the models in consideration included the interaction between age and production of a foal which would indicate a life-history trade-off of survival for reproduction.

Table 3.2.1: Results of Tukey HSD tests comparing $p_{t(i)}$ by age. Sable Island mares can be grouped by age into two subsets with a significant difference in fitness between but not within groups.

Ages	P
1-0	1.000
2-0	1.000
3-0	< 0.001
4-0	< 0.001
5-0	0.001
6-0	0.037
2-1	1.000
3-1	< 0.000
4-1	< 0.000
5-1	0.001
6-1	0.050
3-2	< 0.000
4-2	< 0.000
5-2	0.003
6-2	0.064
4-3	1.000
5-3	1.000
6-3	0.999
5-4	1.000
6-4	0.999
6-5	1.000

Table 3.2.2: The best model shows that body condition is an important predictor of survival but age and production of a foal are not. This model correctly classifies 88% of the data used to generate it.

Fixed Effect	Coeff.	SE	<i>z</i>	<i>P</i>
(Intercept)	-3.24532	0.69558	-4.666	<0.0001
Body Condition	-0.28607	0.09203	-3.108	<0.0001
Random Effect	SD			
Individual	4.275e-05			
Study Year	5.087e-06			

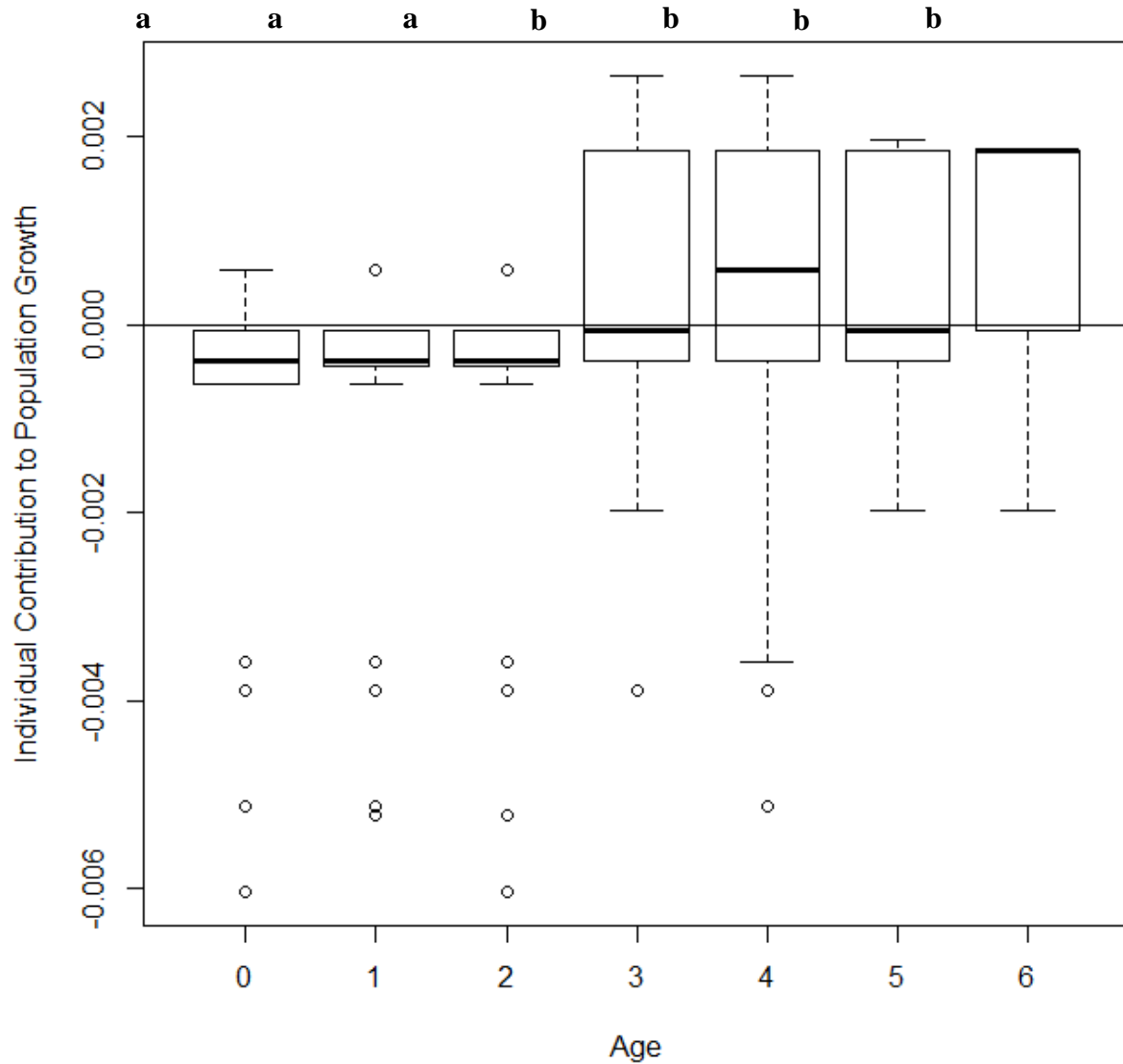


Figure 3.2.1: Contributions to population growth ($p_{t(i)}$) of Sable Island mares by age. Values below zero represent horses that contributed less to population growth than the average mare in that year. Boxes enclose the 25th to 75th percentile. Whiskers enclose the 5th to 95th percentile and dark lines represent the median value.

4.0 DISCUSSION

4.1 FITNESS COMPONENTS

4.1.1 Recruitment

It may be surprising that I did not find an important effect of local density in my models of recruitment.

Density-dependent effects on population-level reproductive rate are expected in large ungulates (Clutton-Brock 1983; Festa-Bianchet *et al*1998; Tavecchia *et al*2005); however, depending on the species, these effects may be mediated by different life-history traits at the individual level (Coulson *et al*2000). While life-history strategies such as litter-bearing and income-breeding may result in mature females that produce fewer offspring in years when resources are limited (Hewison & Gaillard 1996; Koivula 2003). Such strategies are rare in large and long-lived mammals; particularly among sedentary populations in temperate climates where resource availability can be unpredictable (Festa-Bianchet *et al*1998; Skogland 1986).

Among feral horse populations, Sable Island horses are perhaps the most strongly affected by restricted movement and changes in resource availability. Not only is the Sable Island population restricted to a small island in the North Atlantic but it also exhibits consistent growth (Contasti 2011) in the complete absence of management; this suggests the presence of the overcompensatory population cycles typical of predator-free island populations of feral ungulates (Clutton-Brock *et al.* 1997). Delayed reproduction, and capital breeding provide protection against the environmental stochasticity that causes population crashes in *r*-selected ungulates (Coulson *et al.* 2000; Grenfell *et al.* 1992) and should be selected for in the Sable Island population.

Density-dependent effects of reproduction are apparent in other long-lived ungulates such as red deer; however, they operate through the reproductive rate of young, rather than prime-aged, adults (Coulson *et al.* 2000). Moreover, horses often require several years of foraging to store enough energy to produce and wean a single foal. Therefore, density-dependent effects of reproduction in prime-aged Sable Island horses may be small and only detectable over periods of spanning several years. Red deer share similar body size, reproductive

rates, and climates with Sable Island horses. Clutton-Brock *et al.* (1983) report the same negative correlation between reproduction and body condition in red deer that I found in Sable Island horses and, in other studies, Clutton-Brock *et al.* report a density-dependent effect on reduced fecundity in the year following successful reproduction (2000) and density dependence of population-level fecundity caused by late maturation at high densities (1997). While my analyses failed to provide strong evidence of density-dependent reproduction over single-year periods, I expect density-dependent effects on reproductive rate and interbirth interval to become evident at longer time scales and in younger animals.

Although it was not part of the best model, my analysis of recruitment did show a moderate positive correlation between band size and reproductive success. This result may support Welsh's (1975) hypothesis that winter huddling allows larger bands to provide shelter to vulnerable foals during winter. Alternately, this result may be a result of large bands having greater access to water or prime foraging habitat as was seen in the Grand Canyon (Berger 1977) and Red Desert (Miller & Denniston 1979) horse populations. The fact that neither density nor band size is part of the best approximating model of recruitment also explains the absence of an effect of area in the best model. The area variable in my models was included to account for variation in resource availability which I expected to determine the strength of density-dependent relationships. I did not expect to find an effect of area in the absence of effects of band size or density. The limited strength and the direction of the band-size effect run counter to the hypothesis that intraband harassment retards breeding in feral horses (Rho *et al.* 2009) but an effect of intraband harassment would be better examined by analysis of social rank than group size. This result may also be explained by the age of my sample group. Band size may be a stronger predictor of recruitment in young mares which tend to have lower social ranks (Rho *et al.* 2009) but, in older mares, this effect is probably overshadowed by the benefits of large bands.

The strong effect of body condition is consistent with the prediction that Sable Island horses rely heavily on capital for reproduction and indicates that reproductive horses are unable to recover spent energy by late summer. As horses continue to nurse into the winter, mares with foals at heel are most likely to enter winter in poor condition. Because fall body condition is often an important predictor of winter survival in ungulates

(Bardsen *et al.* 2008; Parker *et al.* 2009; Taillon *et al.* 2006), reproductive investment may play a role in survival of Sable Island mares.

Both individual and year were necessarily part of my best model of recruitment because they were included in all candidate models; however, the strengths of these effects are greater in models of recruitment than they are in any other set of models. The large effects of individual and year may be explained by individual quality and environmental variation respectively. In other capital breeding animals, individual quality and environmental variation interact to play important roles in reproductive success. The fat doormouse (*Myoxus glis*) attains a survival rate similar to large herbivores by reproducing only in years of abundant forage (Pilastro *et al.* 2003) and long-lived birds achieve maximum fitness by avoiding reproduction or abandoning their broods during poor breeding conditions (Erikstad *et al.* 1998). Among ungulates, researchers have observed correlation between environment and reproductive effort in white tailed deer (*Odocoileus virginianus*: Therrien *et al.* 2007), reindeer (*Rangifer tarrandus*: Aanes *et al.* 2000), mountain goats (Hamel *et al.* 2010), and red deer (*Cervus elaphus*: Clutton-Brock *et al.* 1997).

Environmental stochasticity plays a role in resource availability and resource use. While harsh winters can restrict resource availability year round (Mysterud *et al.* 2001), spring conditions can affect the length of the prime foraging season (Pettorelli *et al.* 2007), and dry summers limit water availability and may restrict foraging to suboptimal areas (Rozen-Rechels 2014). If the effect of climate was mediated by resource availability, I would expect to see density dependence in my best models of reproduction. Density-dependence of reproductive success is weak or absent not only in my results but also studies of other large ungulates (Sæther 1997), particularly in mature females (Clutton-Brock *et al.* 1997). The more likely explanation is one of weather-related resource demands and cold stress. Richard *et al.* (2014) linked winter severity to population dynamics of Sable Island horses. I believe increased metabolic demands during harsh winters (Clutton-Brock 1997) and potential fitness consequences to reproduction in poor years (Bardsen *et al.* 2008; Brommer *et al.* 1998; Therrien *et al.* 2007) encourage prime-aged mares to reproduce more often in years of good weather even when resource limitation is not imposed.

Environmental stochasticity also carries long-term consequences that may explain the strong effect of individual in my models of reproduction. In other animals, conditions during development result in large variations in the reproductive success of adults. In a lab study of mouth-brooding cichlids (*Simochromis pleurospilus*), size of offspring and number of offspring produced by adults was predicted by the diet provided to them as juveniles but not by the diet provided as adults (Taborsky 2006). Regarding ungulates: Soay sheep born after wet and windy winters produce fewer twins as adults than sheep born in dry winters (Forchhammer *et al.* 2001) and Hamel *et al.* (2009) showed that early life conditions accounted for between 35% and 55% of variation in individual quality of roe deer, mountain goats, and bighorn sheep.

Though individual quality appears to account for a large proportion of variation in reproductive success among large herbivores, the random effect of individual may also account for some variation due to band structure and reproductive history. In Grevy's zebra (*Equus grevyi*) lactating females suffer less harassment when they spend more time with a single male (Sundaesan *et al.* 2007) and foals of feral horses suffer increased harassment when born to mares with lower positions in the dominance hierarchy (Rho *et al.* 2009). Both the structure of a mare's band and her position within its dominance hierarchy are therefore likely to influence her reproductive success. A mare's reproductive history is also likely to influence her reproductive success in a given year. On the short term, the energy expended on reproduction cannot always be replaced before the subsequent breeding season. Large, capital-breeding herbivores often show reduced fecundity in the year following reproduction (Clutton-Brock *et al.* 1983; Hamel *et al.* 2010). On a longer term, age and reproductive experience affect resource allocation strategies during reproduction, allowing a greater reproductive rate in older, more experienced mares (Clutton-Brock *et al.* 1983).

One discrepancy between my analysis of reproduction and the literature is with Sæther's (1997) assertion that survival will be density dependent. My reproduction term contains a survival component (i.e., the survival of foals to one year of age); however, density was absent from the best approximating model. I see three possible explanations for the weak evidence of density dependence in recruitment. First, density dependence of survival may be weak or absent in foals because they rely on stored energy provided by a parent;

this explanation is consistent with previous findings that pre-weaning survival is not density dependent in monotonous species (Gaillard *et al.* 2000). Second, variation in reproductive success due to survival of foals may be minor in comparison to variation in parturition. Lastly, some variation due to survival of foals may appear as variation in the parturition among our data in cases where foals died before they could be observed. None of these explanations are mutually exclusive and each of them likely played a role in this result.

In general, my analyses of recruitment attributable to adult female horses agree with work in wild ungulates. These results show that, because female horses often take multiple years to store enough energy for reproduction, their body condition reflects resource allocation towards reproduction; moreover, their reproductive success is governed mainly by individual quality and weather but not short-term resource availability. The only unexpected finding of my analyses was the low importance of band size but investigations of young horses. Long-term effects should reveal more complicated relationships between environment and population dynamics than were provided by my analyses.

4.1.2 Survival

As was the case in models of recruitment, the importance of body condition in models of survival was not surprising: autumn body condition has been linked to survival in several other ungulate species (Clutton-Brock *et al.* 1983; Parker *et al.* 2009; Taillon *et al.* 2006). While body condition appears in the best models of both survival and reproduction, the relationship between body condition and survival is far more complicated. The relationship between body condition and reproductive success of adult females—both among Sable Island horses and in other capital breeders— appears to be driven by mainly resource allocation; however, body condition is not driven solely by reproductive investment and it can be difficult to determine the direction of causality between body condition and its other correlates.

I can only speculate on which factors play the largest role in survival of Sable Island horses because most mortality occurs during the winter and nearly always goes unobserved. Although predation can be ruled out, disease and starvation are each likely to play a large role in the population dynamics of Sable Island horses

and these factors cannot be distinguished from one another. Diseases may cause starvation and the reduced immune function of a starving animal can make it more susceptible to fatal infection (Nelson & Demas 1996). On Sable Island, I observed horses suffering from laminitis which grew emaciated throughout the field season and subsequently failed to survive the winter. Welsh (1975) reported extremely high endoparasite loads in some horses which died of starvation. By the same token, it's possible for an otherwise healthy animal to starve if resources are limited or energy demands are high. My results show that lower-than-average body condition is an important predictor of mortality but it cannot be assumed that all of these deaths result from resource limitation.

Populations where resource limitation was a major driver of mortality are often characterized by extreme fluctuations in population size where population crashes are triggered by high population density coinciding with extreme weather (Clutton-Brock *et al.* 1997). Ungulate populations which undergo this sort of population cycling tend to be polytocous income breeders. Clutton-Brock *et al.* (1997) suggest that such population cycling can be exacerbated in populations of feral animals and in populations free of predators. Conversely, Gaillard *et al.* (2000) held that growth of slowly reproducing wild populations is limited by juvenile survival and reduced reproductive rate. This prediction finds support in studies of, moose (*Alces*: Testa 2004), mule deer (*Odocoileus hemionus*: Bartmann *et al.* 1992), and asses (*Equus asinus*: Choquenot 1991). The Sable Island population—as a monotocous, feral population living free of predators—could be expected to exhibit intermediate population cycling in which adult mortality is weakly affected by resource limitation under severe conditions. A population crash has not been observed on Sable Island for many decades (Welsh 1975; Contasti 2011); however, there is some evidence that they may occur.

First, the population on Sable Island has grown three-fold since the last accurate census was undertaken by Welsh (1975) in the 1970s. Welsh's study covered three years from 1970 to 1972: the population reached its peak at 165 horses in 1971 and declined to 121 in 1972 when many horses died during a wet winter. Welsh attributed most horse deaths on Sable Island during his study to weather. Sable Island's population was at its greatest ever observed level in the last year of this study when 538 horses were counted in the census. While part of this growth may be a result of changes resource abundance, the near constant growth of the Sable Island

population in the absence of significant changes to the island, coupled with recent evidence of overexploitation of forage near water sources (Rozen-Rechels 2014) suggest a population reaching or exceeding its carrying capacity.

Second, my results show strong evidence of density-dependent survival in adult females along with weak evidence that this density dependence is related to body condition. In a long-lived ungulate population, adult females are expected to have the most uniform rates of survival (Gaillard & Yoccoz 2003). Decreasing survival is predicted at high densities as resources become limited but, in other long-lived ungulates, this effect is strongest in young animals. The appearance of a strong relationship between density and survival, as well as the evidence that it may be tied to body condition, is an indication that resource limitation is beginning to take effect on Sable Island. This hypothesis is also supported by the interaction of Sable Island's resource gradient with the strength of density dependence in survival.

My best model shows that density dependence is far stronger in the resource-poor region of the island than in the resource-rich area. While parasite incidence is often density-dependent (Body *et al.* 2011) and parasites can be a major cause of death in Sable Island horses (Welsh 1975), I do not expect parasite incidence to be strongly correlated with resource availability. Therefore, I do not believe that parasites are the primary cause of density-dependent survival in Sable Island horses. Similarly, I would expect density-dependent costs resulting from social conflict to be tied more strongly to density at larger spatial scales. If social costs are arising from conflicts over resources, this is further evidence of resource limitation. The region interaction in my best approximating model of survival is strong evidence of resource limitation resulting in reduced winter survival.

In all, these findings lead me to predict moderate population cycling. Cycling is expected because the population is unregulated by predators or management and density-dependent survival of adult females is evidence of a population approaching or surpassing carrying capacity. Cycling should be moderate because population crashes in ungulates tend to occur when high densities coincide with extreme weather (Coulson *et al.* 2000); however, horses, as capital breeders, use body fat as a buffer against environmental stochasticity.

An unexpected finding of this analysis was the weak strength of the random effect for year. Island-level population and weather varied significantly within this study period. Richard *et al.* (2014) found relationships between demographic rates in this population and both winter climate and island-level population. I believe large-scale effects of population and weather were overshadowed by in my analyses by effects of resource limitation on smaller spatial scales. Because both weather and population-level density are most influential during population crashes, the random effects in my model may have been stronger if one or more population crashes occurred within the study period.

Another unexpected finding was the absence of an effect of band size from the best model. Welsh (1975) found significant effects of band size on survival. Welsh speculated that larger bands aided the survival of horses by providing shelter through huddling during the winter storms to which he attributed much of the mortality he observed. During the more extreme winters of my study period, Richard *et al.* (2014) report a positive relationship between island-level population and survival. Under the winter huddling hypothesis, I expected larger bands to provide greater winter survival to their members. I found that adult female horses survived just as well regardless of band size. This finding does not exclude the possibility of band size playing a role in the survival of young and senescent horses which are more vulnerable to hostile conditions. It is also possible that band size plays a role in adult females only under the most severe conditions. Based on the lack of population crashes during my study period, severe conditions did not occur during my study.

4.1.4 Contributions to Population Growth

My analysis of fitness was meant to gauge changes in the relative importance of survival and reproduction in driving population dynamics; it revealed complex relationships between resource availability, survival, and reproduction. Whereas my first two analyses predict absolute values of survival and reproduction, my analysis of fitness predicts the performance of horses relative to the population mean: survival yields a greater $p_{t(i)}$ value in years of low survival than years of high survival and recruitment yields a greater $p_{t(i)}$ in years of low recruitment than years of high recruitment. My best model of fitness is consistent with the trends identified in

my analyses of survival and reproductions; however, the application of a less robust method to more abstract data resulted in unrealistically muted or exaggerated relationships. The analysis of fitness also identified one relationship which was not strongly supported by previous analyses. I draw my conclusions from this analysis based on the trends it presents, with the understanding that the strength of relationships may not be accurate. I exercised caution with conclusions which aren't supported by the more robust analyses discussed above.

The most distinctive result of my best approximating model of fitness is the extreme difference in the strength of the two-way interaction between the two regions. Predictions for horses in the resource-limited eastern region of the island cover nearly the entire range of observed fitness values. By contrast, predictions for the western region cover only a narrow band of observed values; all of which are slightly above zero. One explanation is that local density and body condition are poor predictors of fitness in the west. I find this explanation unlikely because it conflicts with the results of my survival analysis which used the same variables to accurately predict survival in both regions. The more likely explanation is that fitness in the west is more uniform than it is in the east and this relationship is exaggerated in my best model. Because they appear to experience greater absolute abundance of resources, horses in the west may be less susceptible to environmental stochasticity than horses in the east; this is consistent with my model of survival which showed significantly stronger density-dependence in the east.

Though the interaction between density and location reflects a difference in the magnitudes of relationships, the directions of relationships are the same in each region. The moderate fitness of mares in good condition at high density appears because horses in good condition are always predicted to survive but horses that have invested little energy in reproduction are unlikely to produce a foal that survives through the winter. Horses in poor condition have low fitness at high densities because they are more likely to die. Conversely, horses in poor condition have high fitness at low densities because they are unlikely to die but more likely to have invested enough in reproduction to raise a foal through the winter. These results are generally consistent with the results of survival and reproduction analyses in which reproductive horses exhibited poor body condition and horses in poor condition were unlikely to survive when facing high local densities.

The result that horses in good condition had higher fitness at high densities than at low densities is less in keeping with my previous results and demands critical inspection. In the eastern region, the difference in fitness is too great to be explained by survival alone and density-dependent reproduction was not strongly supported by earlier analyses. To begin with, declining reproduction under resource limitation is expected but, in other long-lived ungulate populations, such declines resulted from later age of primiparity and increased interbirth interval among young females. Density-dependent reproduction in prime-aged mares is not predicted by studies of other ungulate populations; however, the extremely high mortality of mares with low body condition at high densities would provide strong selective pressure against resource allocation to reproduction at high density. Richard *et al.* (2014) found preliminary evidence of rapid change in life-history traits of this population so the observed effect is somewhat supported by both my analysis of survival and by previous study of this population. The model of fitness suggests that only mares in the best condition are able to reliably reproduce at the highest densities. While this result is supported by both theory and previous work, there remains the question of why it was not apparent in the more robust analysis of recruitment performed earlier. I offer three explanations: the first, that the relationship may be more apparent in this model because it shows performance relative to the yearly mean as opposed to an absolute value; the second, that collinear trends in survival and reproduction caused exaggerated prediction at the extreme observed values of body condition and density; the third, that body condition at high densities is correlated with some unmeasured variable such as social rank. More rigorous analysis of a larger data set should reveal which, if any, of these explanations is correct.

The weak influence of random effects in the best model of fitness is another peculiar result given the importance of random effects in predicting reproduction. This may be explained by idiosyncrasies of the de-lifing method. Since the de-lifing method calculates performance in comparison to the mean performance in that year, it should already account for the differences due to inter-annual variation in weather or density. Individual quality may be less detectable using this estimate of fitness because it is primarily evident in reproduction and is overshadowed by variation in survival.

There are several general conclusions that can be drawn from the fitness analysis. Resources are more limited in the eastern region than the western region. Body condition predicts recruitment at low densities and mortality at high densities. These relationships are tied to resource availability because they are strongest where resources are limited. Fitness is more variable in the resource-poor region: presenting greater opportunity for reproduction and greater risk of mortality. These results are all supported by studies of other populations and by my own and others' work on the Sable Island population. While there is some evidence of density-dependent recruitment in prime-aged females, results are too confounded to be certain. Further analysis of reproduction would provide insight into a life-history strategy that might be unique among capital-breeding ungulates.

My results provide a novel description of the life-history of an unmanaged feral animal and they highlight areas where future research is needed. Recruitment may or may not be density dependent. Only the analysis designed to highlight differential phenotypic performance showed strong evidence of density dependence in recruitment but this analysis was less robust than the analysis of absolute recruitment; moreover, band size appears to play a weak role if any in recruitment attributable to adult females. Survival is clearly density dependent and appears to be driven by resource limitation as animals in poor condition are at greater risk of mortality.

Beyond these conclusions, the implications of these results to models of population distribution should not be overlooked. Ideal free distribution predicts that populations will distribute themselves proportional to resource availability so that their expected fitness is equal across all habitat patches (Fretwell & Lucas 1970). When populations fail to meet IFD, researchers examine their adherence to the various assumptions of the theory as a framework for further understanding of their ecology. In their defining publication, Fretwell & Lucas (1970) outlined five assumptions of IFD which have been well-studied in many populations (Krivan *et al.* 2008). In recent years, new assumptions have emerged dealing with avoidance of inbreeding (Leturque & Rousset 2002) and avoidance of kin competition (Morris 2001). One assumption which has yet to be discussed is spatial variability in the impact of environmental stochasticity.

In both my models of survival and fitness, density has far stronger effects in the resource-poor area than in the resource-rich area. We already know that long-lived animals manage risks relating to environmental stochasticity and I believe they may account for susceptibility to environmental stochasticity in their evaluations of habitat suitability. Horses in the resource-poor area of Sable Island appear to be more vulnerable to stochastic changes. A common trend among long-lived animals is that they will avoid trading survival for reproduction until senescence. During senescence, an animal's expectation of future reproduction is low enough that the risk of mortality is outweighed by reproduction in the current year. Loss of body condition is a greater risk in the east of the island than in the west. Small changes in density have a greater impact on fitness on horses in the east than in the west. Resource-rich habitats provide resilience against environmental stochasticity that is not provided by resource-poor areas; as a result, I expect pre-senescent Sable Island horses to value them disproportionately to resource availability.. In such a case, we might see young horses moving west on Sable Island and senescent horses moving east, exaggerating the differences in population dynamics between the two regions. This effect should be considered in addition to cost of dispersal (van Beest *et al.* 2013) in driving the Sable Island population away from IFD.

4.2 TRADE-OFFS IN SURVIVAL AND REPRODUCTION

Although some feral horse populations appear to exhibit artificially selected life-history strategies (Grange *et al.* 2008), most studies of feral horses are conducted on managed populations (Boyd & Keiper 2005) rather than unmanaged populations like that of Sable Island. Reproduction of Sable Island horses seems to be more similar to wild ungulates than feral ungulates. Parallels may be found in studies of wild ungulates for each aspect in my model of the recruitment of Sable Island horses; this applies to the importance—or lack thereof—of each fixed and random effect that I examined.

Other capital-breeding animals maximize fitness by avoiding reproduction under dangerous circumstances (Erikstad *et al.* 1998; Pilastro *et al.* 2003); however, Grange *et al.* (2008) found that this wasn't a strategy employed by the Camargue feral horse population. My previous analyses hinted at life-history strategies among Sable Island horses which are more similar to those of wild ungulates than those of the Camargue horse population. The results in this chapter provide a better understanding of resource allocation in female Sable Island horses. These results have implications on subjects of density-dependent reproduction and the effects of artificial selection. The inclusion of age in these analyses allows comparison with the Camargue population but introduces some complications that were absent from earlier chapters.

The only reliable way of determining age in this study is by observing horses in their birth-year or the following year. Because the study only began in 2008, the oldest horses in my age-based analysis are only six years old. Additionally, though young horses were recorded in every year, known-aged horses greater than three years old were only recorded in the later years of the study. Another complication was introduced by examining foaling rather than successful reproduction: foals that are born and die prior to the census would not be observed and their dams would be incorrectly recorded as not having foaled. Lastly, Sable Island horses are known to die during parturition (personal observation) but, because each Sable Island horse is only under intermittent

observation and only during the short study season, most of these deaths go unobserved. In this study, deaths resulting directly from reproduction have not been recorded as such.

In comparing age-based fitness of Sable Island horses to that of Camargue horses, the patterns are similar. Horses below three years of age contribute negatively to population growth while older horses contribute positively. A difference in the magnitude of contributions to population growth is a result of the difference in size of the populations, with the Sable Island population being an order of magnitude larger than the Camargue population. The greatest difference between the populations is the magnitude of the difference between adult and juvenile horses. In the Camargue, the median $p_{t(i)}$ of prime-aged horses was very positive, indicating high reproductive success among this group. The median $p_{t(i)}$ of prime-aged Sable Island horses, while positive, were closer to zero. This difference can be explained by history of management. The Camargue study began immediately following release of the population from heavy management and occurred during unnaturally rapid population growth. I believe that lower relative reproductive success of prime-aged Sable Island mares is primarily a result of the Sable Island population remaining close to carrying capacity in the absence of management.

The similarity in age-based performance is intriguing given the differences in life histories between the two populations. In both cases, two-year-old horses contributed negatively to population growth; however, only in the Camargue population do two-year-old horses reproduce. Grange *et al.* (2008) attribute the negative contribution of a reproductive demographic to an artificially selected life-history trade-off of survival for reproduction. Relative to the rest of the population, Sable Island horses provide a similarly negative contribution to population growth at two years old despite an apparent absence of reproductive effort. Both the age group in which reproduction begins (i.e., three years old) and the age group in which primiparity is most common (i.e., four years old) contribute positively to population growth at a level similar to other prime-aged mares. In this context, the fitness of horses aged two to four years old is evidence that the artificially selected life-history observed in Camargue horses is absent in the Sable Island population.

Lastly, survival was not linked to foaling, age, or an interaction of the two in known-aged mares. Again, this is evidence that Sable Island horses do not trade survival for reproduction. It provides further support to the hypothesis generated by my previous chapter that, while body condition predicts both survival and reproduction, pre-senescent Sable Island horses avoid life-history trade-offs of survival for reproduction. Whether or not Sable Island horses were ever selected for the same unnaturally rapid reproduction that Camargue horses were may never be known but evidence of early senescence reported by Richard *et al.* (2014) does suggest that life-history of Sable Island horses has been subject to artificial selection. I believe that the difference in life history between these two populations was caused by the reversal of artificial selection by 250 years of natural selection acting on the Sable Island population. I failed to find evidence of a life-history trade-off of survival for reproduction in young Sable Island mares. I am unable to examine the presence of the expected life-history trade-off in older horses because I lack data describing known-aged senescent horses. The strength of natural selection on life-history traits of a feral population is an unexplored field of study which promises to be illuminated as the long-term study of Sable Island proceeds and data describing the age and relatedness of population members become more abundant.

5.0 CONCLUSIONS

I used long-term individual-based data describing life-histories of female Sable Island horses and the conditions they experienced from 2008 to 2012. I used measures of body condition to gain insight into resource allocation within the population and I used estimates of local conspecific density to examine density dependence of vital rates within the population. I confirmed that body condition is strongly indicative of reproductive investment in female horses on Sable Island. I also found spatial heterogeneity in the strength of density-dependent survival which supports the existence of the resource gradient proposed by Contasti (2011).

The objectives of my analysis of fitness components were to characterize the relationship between body condition and life-history, to search for evidence of density dependence in survival and recruitment, and to examine the effect of the resource gradient on the roles of body condition and local density. I determined that female horses relied heavily on stored body fat to fuel reproduction. I also found that horses in poor condition were in greater danger of mortality but I found no evidence that reproductive investment was related to mortality. I found weak evidence of density-dependent reproduction and strong evidence of density-dependent survival. The resource gradient had a large effect on the strength of density-dependent relationships.

The objective of my analysis of life-history trade-offs was to search for evidence of artificially-selected life-history in the Sable Island population. Although evidence of early senescence (Richard *et al.* 2014) and population cycling suggest effects of artificial selection, I was unable to identify the life-history trade-off of survival for reproduction in young horses as was suspected in another feral horse population (Grange *et al.* 2008). Age based estimates of fitness do not appear to differ between the Sable Island population and the Camargue population despite the difference in life-history.

Though vital rates (Contasti 2011) and habitat selection (van Beest *et al.* 2014) have already been examined within this population, my analysis of body condition and local density provided a stronger understanding of life-history and the conditions on the island. Most importantly: my focus on small spatial scales allowed me to discover an effect of the island's resource gradient on the vital rates of its inhabitants

which would have otherwise been difficult to observe. Inclusion of body condition as an explanatory variable illuminated the cautious reproductive investment exercised by Sable Island mares and allowed me to show that life-history of Sable Island horses is typical of large-bodied and long-lived wild ungulates. The de-lifing method for calculating individual contributions to population growth as an estimate of fitness proved unwieldy but it did appear to identify differential phenotypic performance based on the selection of low- versus high-density habitats and resource-rich versus resource poor-habitats.

My analyses of reproduction and recruitment provided new, if unsurprising, results; however, they were limited to relatively small temporal scales and often ignored the reproduction of young females. Because these rates are more variable (Gaillard *et al.* 2000), they might have strong effects on population dynamics. As this study progresses, better data describing weather and age of primiparity should allow analyses of long-term effects on reproduction and the influence of variable reproduction among young mares on population dynamics. More complete age data would also have strengthened my analyses, allowing me to account for the changes in vital rates which are expected among senescent animals.

My work also has interesting theoretical implications. First: the greater variability in fitness in resource-poor areas may impact habitat selection in unexpected ways. Since resource-poor areas appear to represent high risk/high reward habitats, and since young animals should avoid risk, young horses may value resource-rich areas disproportionately to resource availability while senescent horses may value underexploited but risky resource-poor areas. Again, investigations into this question will not be possible in the Sable Island population until data describing the senescent animals become available. Second: the apparent difference between life-history strategies of Sable Island and Camargue horses may be a result of natural selection driving the population towards wild-type behaviour. The Sable Island herd—as a very old, very isolated, and unmanaged population of feral animals—presents a unique opportunity to explore potential changes in the life-history of a feral population after many generations of natural selection. This work should be aided not only by increasing age-based data but also by future work in the genetics of the horses.

6.0 LITERATURE CITED

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7.0 APPENDICES

Appendix A. Candidate models of recruitment based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m buffer), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	delta AIC	weight
Cond	5.00	-345.73	701.47	0.00	0.09
Band + Cond	6.00	-344.88	701.77	0.30	0.08
Dens + Cond	6.00	-344.94	701.87	0.40	0.08
Dens + Cond + Dens:Cond	7.00	-344.04	702.08	0.61	0.07
Band + Dens + Cond	7.00	-344.21	702.42	0.95	0.06
Band + Dens + Cond + Dens:Cond	8.00	-343.21	702.43	0.96	0.06
Band + Cond + Band:Cond	7.00	-344.76	703.53	2.06	0.03
Band + Dens + Cond + Band:Dens	8.00	-343.82	703.64	2.17	0.03
Band + Dens + Cond + Band:Dens + Dens:Cond	9.00	-342.95	703.90	2.43	0.03
Band + Dens + Cond + Band:Cond + Dens:Cond	9.00	-343.09	704.17	2.70	0.02
Band + Dens + Cond + Band:Cond	8.00	-344.10	704.20	2.73	0.02
Band + Cond + Area	8.00	-344.32	704.64	3.18	0.02
Dens + Cond + Area	8.00	-344.72	705.44	3.98	0.01
Dens + Cond + Area + Dens:Cond	9.00	-343.79	705.57	4.10	0.01
Band + Dens + Cond + Band:Dens + Band:Cond	9.00	-343.79	705.58	4.12	0.01
Band + Dens + Cond + Band:Dens + Band:Cond + Dens:Cond	10.00	-342.90	705.79	4.33	0.01
Band + Dens + Cond + Area + Dens:Cond	10.00	-343.07	706.14	4.67	0.01
Band + Dens + Cond + Area	9.00	-344.10	706.20	4.73	0.01
Band + Cond + Area + Band:Cond	9.00	-344.17	706.34	4.87	0.01
Band + Cond + Area + Band:Area	10.00	-343.67	707.35	5.88	0.00
Band + Dens + Cond + Area + Band:Dens	10.00	-343.74	707.49	6.02	0.00
Band + Dens + Cond + Area + Band:Dens + Dens:Cond	11.00	-342.83	707.67	6.20	0.00
Band + Dens + Cond + Area + Band:Cond + Dens:Cond	11.00	-342.92	707.83	6.37	0.00
Band + Dens + Cond + Area + Band:Cond	10.00	-343.97	707.94	6.47	0.00
Dens + Cond + Area + Dens:Area	10.00	-344.17	708.33	6.87	0.00
Band	5.00	-349.33	708.66	7.20	0.00
Dens + Cond + Area + Dens:Cond + Dens:Area	11.00	-343.36	708.72	7.25	0.00
Band + Dens + Cond + Area + Dens:Area	11.00	-343.42	708.85	7.38	0.00
	4.00	-350.47	708.94	7.47	0.00
Band + Dens + Cond + Area + Band:Area	11.00	-343.48	708.95	7.49	0.00
Band + Dens + Cond + Area + Dens:Cond + Dens:Area	12.00	-342.54	709.07	7.60	0.00
Band + Dens + Cond + Area + Band:Area + Dens:Cond	12.00	-342.55	709.09	7.63	0.00
Band + Cond + Area + Band:Cond + Band:Area	11.00	-343.63	709.27	7.80	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond	11.00	-343.70	709.40	7.94	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond	12.00	-342.76	709.53	8.06	0.00

Appendix A. Candidate models of recruitment based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m buffer), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	delta AIC	weight
Band + Dens + Cond + Area + Band:Dens + Dens:Area	12.00	-343.01	710.01	8.55	0.00
Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	15.00	-340.08	710.15	8.69	0.00
Band + Dens	6.00	-349.17	710.33	8.87	0.00
Band + Dens + Cond + Area + Band:Dens + Dens:Cond + Dens:Area	13.00	-342.24	710.48	9.01	0.00
Dens	5.00	-350.24	710.49	9.02	0.00
Band + Dens + Cond + Area + Band:Cond + Dens:Area	12.00	-343.32	710.64	9.18	0.00
Band + Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	16.00	-339.35	710.69	9.22	0.00
Band + Dens + Cond + Area + Band:Cond + Dens:Cond + Dens:Area	13.00	-342.41	710.83	9.36	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area	12.00	-343.45	710.89	9.42	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area	12.00	-343.46	710.93	9.46	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond	13.00	-342.50	711.00	9.53	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond	13.00	-342.54	711.09	9.62	0.00
Band + Dens + Cond + Area + Band:Area + Dens:Area	13.00	-342.74	711.47	10.01	0.00
Band + Dens + Band:Dens	7.00	-348.80	711.60	10.13	0.00
Band + Area	7.00	-348.84	711.69	10.22	0.00
Band + Dens + Cond + Area + Band:Area + Dens:Cond + Dens:Area	14.00	-341.96	711.92	10.45	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Area	13.00	-342.99	711.98	10.51	0.00
Band + Dens + Cond + Area + Band:Dens + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	17.00	-339.02	712.04	10.57	0.00
Band + Dens + Cond + Area + Band:Cond + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	17.00	-339.05	712.10	10.63	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond + Dens:Area	14.00	-342.20	712.39	10.93	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area	13.00	-343.44	712.88	11.41	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond	14.00	-342.50	713.00	11.53	0.00
Dens + Area	7.00	-349.61	713.22	11.75	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Area	14.00	-342.72	713.44	11.97	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Area	14.00	-342.72	713.44	11.97	0.00
Band + Dens + Area	8.00	-348.75	713.49	12.02	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	18.00	-338.86	713.73	12.26	0.00
Band + Dens + Cond + Area + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	18.00	-338.91	713.81	12.35	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond + Dens:Area	15.00	-341.93	713.86	12.39	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond + Dens:Area	15.00	-341.95	713.91	12.44	0.00
Band + Area + Band:Area	9.00	-348.26	714.51	13.04	0.00
Band + Dens + Area + Band:Dens	9.00	-348.44	714.88	13.42	0.00

Appendix A. Candidate models of recruitment based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m buffer), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	delta AIC	weight
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Area	15.00	-342.71	715.42	13.95	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	19.00	-338.76	715.53	14.06	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	19.00	-338.86	715.73	14.26	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond + Dens:Area	16.00	-341.93	715.86	14.39	0.00
Band + Dens + Area + Band:Area	10.00	-348.18	716.36	14.89	0.00
Dens + Area + Dens:Area	9.00	-349.22	716.44	14.98	0.00
Band + Dens + Area + Dens:Area	10.00	-348.23	716.46	15.00	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	20.00	-338.75	717.49	16.02	0.00
Band + Dens + Area + Band:Dens + Dens:Area	11.00	-347.88	717.76	16.29	0.00
Band + Dens + Area + Band:Dens + Band:Area	11.00	-348.18	718.36	16.89	0.00
Band + Dens + Area + Band:Area + Dens:Area	12.00	-347.59	719.18	17.72	0.00
Band + Dens + Area + Band:Dens + Band:Area + Dens:Area	13.00	-347.59	721.18	19.71	0.00

Appendix B: Candidate models of survival based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m radius), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	Delta AIC	weight
Dens + Cond + Area + Dens:Area	10	-159.80	339.60	0.00	0.20
Band + Dens + Cond + Area + Dens:Area	11	-159.36	340.71	1.12	0.12
Dens + Cond + Area + Dens:Cond + Dens:Area	11	-159.69	341.39	1.79	0.08
Band + Dens + Cond + Area + Band:Cond + Dens:Area	12	-158.88	341.76	2.17	0.07
Band + Dens + Cond + Area + Dens:Cond + Dens:Area	12	-159.26	342.52	2.92	0.05
Band + Dens + Cond + Area + Band:Dens + Dens:Area	12	-159.33	342.65	3.06	0.04
Band + Dens + Cond + Area + Band:Cond + Dens:Cond + Dens:Area	13	-158.77	343.55	3.95	0.03
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Area	13	-158.88	343.75	4.16	0.03
Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	15	-157.16	344.32	4.72	0.02
Band + Dens + Cond + Area + Band:Cond + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	17	-155.17	344.34	4.74	0.02
Band + Dens + Cond + Area + Band:Dens + Dens:Cond + Dens:Area	13	-159.21	344.42	4.83	0.02
Band + Dens + Cond + Area + Band:Area + Dens:Area	13	-159.22	344.44	4.84	0.02
Dens + Cond	6	-166.24	344.49	4.89	0.02
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Area	14	-158.58	345.17	5.57	0.01
Band + Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	16	-156.61	345.23	5.63	0.01
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond + Dens:Area	14	-158.77	345.54	5.95	0.01
Band + Dens + Cond	7	-166.07	346.14	6.55	0.01
Band + Dens + Cond + Area + Band:Area + Dens:Cond + Dens:Area	14	-159.08	346.17	6.57	0.01
Dens + Cond + Area	8	-165.11	346.22	6.62	0.01
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	18	-155.14	346.28	6.68	0.01
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Area	14	-159.22	346.43	6.84	0.01
Dens + Cond + Dens:Cond	7	-166.22	346.45	6.85	0.01
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond + Dens:Area	15	-158.46	346.92	7.33	0.01
Band + Dens + Cond + Area + Band:Dens + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	17	-156.54	347.07	7.48	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Area	15	-158.56	347.13	7.53	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	19	-154.85	347.69	8.10	0.00
Band + Dens + Cond + Band:Cond	8	-165.90	347.80	8.20	0.00
Band + Dens + Cond + Area	9	-164.98	347.95	8.36	0.00
Dens + Cond + Area + Dens:Cond	9	-165.04	348.07	8.48	0.00
Band + Dens + Cond + Dens:Cond	8	-166.04	348.09	8.49	0.00
Band + Dens + Cond + Band:Dens	8	-166.07	348.14	8.54	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond + Dens:Area	15	-159.08	348.16	8.57	0.00

Appendix B: Candidate models of survival based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m radius), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	Delta AIC	weight
Band + Dens + Cond + Area + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	18	-156.42	348.83	9.24	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond + Dens:Area	16	-158.43	348.87	9.27	0.00
Band + Dens + Cond + Area + Band:Cond	10	-164.70	349.40	9.80	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	20	-154.77	349.55	9.95	0.00
Band + Dens + Cond + Band:Cond + Dens:Cond	9	-165.87	349.73	10.13	0.00
Band + Dens + Cond + Band:Dens + Band:Cond	9	-165.89	349.78	10.18	0.00
Band + Dens + Cond + Area + Dens:Cond	10	-164.90	349.79	10.20	0.00
Band + Dens + Cond + Area + Band:Dens	10	-164.97	349.95	10.35	0.00
Cond	5	-170.02	350.04	10.44	0.00
Band + Dens + Cond + Band:Dens + Dens:Cond	9	-166.04	350.08	10.49	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	19	-156.42	350.83	11.24	0.00
Band + Dens + Cond + Area + Band:Cond + Dens:Cond	11	-164.60	351.21	11.61	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond	11	-164.68	351.36	11.76	0.00
Band + Dens + Cond + Area + Band:Area	11	-164.71	351.43	11.83	0.00
Band + Dens + Cond + Band:Dens + Band:Cond + Dens:Cond	10	-165.85	351.70	12.10	0.00
Band + Dens + Cond + Area + Band:Dens + Dens:Cond	11	-164.90	351.79	12.20	0.00
Band + Cond	6	-169.97	351.94	12.35	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area	12	-164.18	352.36	12.76	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Dens:Cond	12	-164.58	353.16	13.56	0.00
Band + Dens + Cond + Area + Band:Area + Dens:Cond	12	-164.66	353.31	13.72	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area	12	-164.70	353.40	13.80	0.00
Band + Cond + Band:Cond	7	-169.79	353.58	13.98	0.00
Band + Dens + Cond + Area + Band:Cond + Band:Area + Dens:Cond	13	-164.10	354.21	14.61	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area	13	-164.18	354.36	14.76	0.00
Band + Cond + Area	8	-169.29	354.58	14.99	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Area + Dens:Cond	13	-164.64	355.28	15.69	0.00
Band + Dens + Cond + Area + Band:Dens + Band:Cond + Band:Area + Dens:Cond	14	-164.10	356.20	16.61	0.00
Band + Cond + Area + Band:Cond	9	-169.11	356.21	16.61	0.00
Band + Cond + Area + Band:Area	10	-169.02	358.04	18.45	0.00
Band + Cond + Area + Band:Cond + Band:Area	11	-168.68	359.36	19.76	0.00
Dens + Area + Dens:Area	9	-179.24	376.48	36.89	0.00
Band + Dens + Area + Dens:Area	10	-179.18	378.36	38.77	0.00
Dens	5	-185.03	380.05	40.46	0.00
Band + Dens + Area + Band:Dens + Dens:Area	11	-179.13	380.26	40.66	0.00
	4	-186.19	380.38	40.78	0.00
Dens + Area	7	-183.30	380.61	41.01	0.00

Appendix B: Candidate models of survival based on band size (“Band”: number of horses in the focal individual’s band), local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m radius), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	Delta AIC	weight
Band + Dens	6	-185.02	382.05	42.45	0.00
Band + Dens + Area + Band:Area + Dens:Area	12	-179.17	382.34	42.75	0.00
Band	5	-186.18	382.37	42.77	0.00
Band + Dens + Area	8	-183.30	382.61	43.01	0.00
Band + Dens + Band:Dens	7	-185.02	384.04	44.44	0.00
Band + Dens + Area + Band:Dens + Band:Area + Dens:Area	13	-179.11	384.23	44.63	0.00
Band + Dens + Area + Band:Dens	9	-183.30	384.60	45.00	0.00
Band + Area	7	-186.05	386.10	46.50	0.00
Band + Dens + Area + Band:Area	10	-183.29	386.58	46.98	0.00
Band + Dens + Area + Band:Dens + Band:Area	11	-183.22	388.44	48.84	0.00
Band + Area + Band:Area	9	-186.00	390.01	50.41	0.00

Appendix C: Candidate models of body condition based on reproduction (“Rep”: successful reproduction), Density (“Dens”: horses/km² of vegetated area within an 8000 m radius), and Survival (“Surv”).

Parameters	df	logLik	AIC	delta AIC	weight
Rep + Dens + Surv + Rep*Dens + Dens*Surv	10	-659.99916	1339.9983	0	0.3227132
Rep + Dens + Surv + Rep*Den	9	-661.77264	1341.5453	1.5469599	0.1489013
Rep + Dens + Surv + Rep*Dens + Rep*Surv + Dens*Surv	11	-659.99857	1341.9971	1.998829	0.1187891
Rep + Dens + Surv	8	-663.17072	1342.3414	2.3431241	0.1000032
Rep + Dens + Surv + Dens*Surv	9	-662.17558	1342.3512	2.3528419	0.0995184
Rep + Dens + Surv + Rep*Dens + Rep*Surv + Dens*Surv + Rep*Dens*Surv	12	-659.39319	1342.7864	2.7880644	0.0800564
Rep + Dens + Surv + Rep*Dens + Rep*Surv	10	-661.74875	1343.4975	3.4991765	0.0561022
Rep + Dens + Surv + Rep*Surv	9	-663.16108	1344.3222	4.3238477	0.0371454
Rep + Dens + Surv + Rep*Surv + Dens*Surv	10	-662.17367	1344.3473	4.3490198	0.0366808
Rep + Surv	7	-671.60425	1357.2085	17.210173	5.91E-05
Rep + Surv + Rep*Surv	8	-671.51499	1359.03	19.031669	2.38E-05
Dens + Surv + Dens*Surv	8	-673.22132	1362.4426	22.444313	4.32E-06
Dens + Surv	7	-674.68746	1363.3749	23.3766	2.71E-06
Surv	6	-681.03951	1374.079	34.080712	1.28E-08
Rep + Dens + Rep*Den	8	-680.41131	1376.8226	36.824309	3.25E-09
Rep + Dens	7	-682.785	1379.57	39.571687	8.24E-10
Rep	6	-688.22052	1388.441	48.442727	9.76E-12
Dens	6	-690.69436	1393.3887	53.390404	8.23E-13
	5	-694.92542	1399.8508	59.85253	3.25E-14

Appendix D: Candidate models of fitness ($P_{t(i)}$) based on local conspecific density (“Dens”: horses/km² of vegetated area within an 8000 m radius), body condition (“Cond”: unitless), and area (“Area”: west, center, or east).

Parameters	df	logLik	AIC	delta AIC	weight
Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area + Dens:Cond:Area	12	-49.32	122.64	0.00	0.88
Cond	6	-58.98	129.97	7.33	0.02
	5	-60.27	130.54	7.90	0.02
Dens + Cond + Area + Dens:Cond + Cond:Area	10	-55.58	131.15	8.51	0.01
Cond + Area	7	-58.95	131.89	9.25	0.01
Dens + Cond	7	-58.95	131.90	9.26	0.01
Dens + Cond + Dens:Cond	8	-58.04	132.09	9.45	0.01
Area	6	-60.08	132.16	9.52	0.01
Dens	6	-60.27	132.54	9.90	0.01
Dens + Cond + Area + Dens:Cond + Dens:Area + Cond:Area	11	-55.34	132.68	10.04	0.01
Dens + Cond + Area + Dens:Cond	9	-57.76	133.51	10.87	0.00
Dens + Cond + Area	8	-58.77	133.54	10.90	0.00
Cond + Area + Cond:Area	8	-58.80	133.61	10.97	0.00
Dens + Area	7	-59.94	133.89	11.25	0.00
Dens + Cond + Area + Dens:Area	9	-58.16	134.31	11.67	0.00
Dens + Area + Dens:Area	8	-59.20	134.40	11.76	0.00
Dens + Cond + Area + Dens:Cond + Dens:Area	10	-57.31	134.62	11.98	0.00
Dens + Cond + Area + Cond:Area	9	-58.66	135.32	12.68	0.00
Dens + Cond + Area + Dens:Area + Cond:Area	10	-58.05	136.09	13.45	0.00

Appendix E: Candidate models of survival based on age, production of a foal (“Foal”), and body condition

(Cond).

Parameters	df	logLik	AIC	delta AIC	weight
Cond	5	-208.43	426.9592	0	0.242758
Foal + Cond	6	-207.933	428.0048	1.045597	0.143921
Foal + Cond + Foal*Cond	7	-207.28	428.7461	1.786907	0.099346
Age + Cond	6	-208.342	428.8238	1.864577	0.095562
Age + Cond + Age*Cond	7	-207.48	429.145	2.185868	0.08138
Age + Foal + Cond	7	-207.649	429.4842	2.525027	0.068686
Age + Foal + Cond + Age*Foal	8	-206.884	430.0079	3.048705	0.052863
Age + Foal + Cond + Foal*Cond	8	-206.907	430.0526	3.093429	0.051694
Age + Foal + Cond + Age*Cond	8	-206.931	430.1019	3.142693	0.050437
Age + Foal + Cond + Age*Foal + Foal*Cond	9	-206.211	430.7226	3.763399	0.03698
Age + Foal + Cond + Age*Cond + Foal*Cond	9	-206.479	431.2587	4.299477	0.028285
Age + Foal + Cond + Age*Foal + Age*Cond	9	-206.564	431.4289	4.469672	0.025977
Age + Foal + Cond + Age*Foal + Age*Cond + Foal*Cond	10	-206.106	432.5793	5.620073	0.014615
Age + Foal + Cond + Age*Foal + Age*Cond + Foal*Cond + Age*Foal*Cond	11	-205.737	433.9145	6.955345	0.007496
	4	-227.386	462.8374	35.87823	3.93E-09
Foal	5	-226.434	462.9671	36.00794	3.68E-09
Age	5	-226.818	463.7344	36.77522	2.51E-09
Age + Foal	6	-226.785	465.7092	38.75006	9.35E-10
Age + Foal + Age*Foal	7	-226.432	467.051	40.09179	4.78E-10
