THE DEMOGRAPHIC CONSEQUENCES OF THE COST OF REPRODUCTION IN UNGULATES

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Abstract. The cost of reproduction can generate covariation between demographic rates that can potentially influence demography and population dynamics in long-lived iteroparous species. However, there has been relatively little work linking the survival cost of reproduction and population dynamics. The apparent scarcity of information on this important link is potentially due to covariation between vital rates, which can substantially influence fluctuations in population size. In this paper we examine the opportunity for survival costs of reproduction to leave a dynamic signature using a simulation model based broadly on an ungulate life history. We find that an increase in the cost delays the onset of reproduction and reduces reproductive rates of young, but not of prime-age, females. Accordingly, the number of offspring produced declines and the interval between reproductive events increases among young females experiencing high cost. These effects are translated to an age structure skewed toward young ages and reduced population density. These results suggest that, by delaying reproduction when conditions deteriorate, females protect their survival during the critical first three years of life, after which the negative effect of reproduction on survival declines. Unless conditions for reproduction are severe, it is not profitable to delay reproduction beyond age 3 years due to the high risk of death before having a chance to reproduce. We also demonstrate that lack of adjustment of reproductive strategies to elevated levels of the cost of reproduction, for example due to rapid changes in environmental conditions, results in lower average density and longevity compared to females that have sufficient time to adjust to changes in the cost. This suggests that even moderate costs of reproduction may have a major negative effect on population dynamics of ungulates.

Key words: Cervus elaphus; cost of reproduction; individual-based models; population dynamics; reproductive strategies; Scottish red deer; stochastic density-dependent model; trade-off; ungulates.

INTRODUCTION

The dynamics and structural characteristics of populations depend on processes affecting the rates of dispersal, survival, and fecundity, and on the amount of variation in each of these processes (Krebs 1994, Benton and Grant 1999, Coulson et al. 2000). A major constraint on the mean and variation in survival and fecundity rates is embodied in the concept of costs of reproduction. This concept represents trade-offs between current reproduction and survival, and future fertility (Williams 1966, Bell 1980, Reznick 1985). Although past work has greatly contributed toward our understanding of the cost function and its influence on the evolution of life-history tactics under various environmental conditions (Rose and Charlesworth 1981, Caswell 1982, Linden and Moller 1989, Erikstad et al. 1998), little attention has been given to the link between costs of reproduction and the dynamics of the population (Benton et al. 1995, Silvertown and Dodd 1999). Given that survival and fecundity rates are determined by the intensity of the age- or size-specific survival and reproductive costs, it is implicit that variation in the age-specific costs influences the demography and, hence, the dynamics of the population. But how this influence is mediated and to what extent it shapes the population dynamics is yet to be resolved.

Assessing the relationship between the age-specific cost of reproduction and population dynamics in empirical studies is difficult due to the large number of confounding variables that interact with the effect of the costs (Partridge and Harvey 1988, Reznick 1992). Additionally, translating age-specific effects of the cost observed in a single individual or a group to the population level requires complex manipulative experiments on many individuals. An alternative approach is to use computer-based models because the modeler can easily change the level of the age-specific cost and assess the consequences for the entire population. Furthermore, by changing the survival cost of reproduction independent of the density, the modeler is able to differentiate confounding effects of the cost and density dependence. This paper considers the link between the cost of reproduction and demography and reproduction. Within that context, individual-based models (IBM) are particularly useful because interindividual variation in reproductive strategies and reproductive history affects
the interactions between individuals and thereby their demography and dynamics (Grimm et al. 1999).

This paper presents an IBM of population dynamics that explicitly incorporates the survival cost of reproduction for females. The model is used to investigate the impact of the cost of reproduction on the reproductive characteristics and population dynamics of a stochastic, density-dependent female red deer (Cervus elaphus) population. Specifically, this paper explores the effects of variation in the age-specific survival cost of reproduction on the distribution of the age at first reproduction, reproductive rates, and on density. Additionally, the paper assesses demographic consequences of a scenario in which a sudden increase in the cost implies that the population does not have time to adjust its reproductive strategies. An important strength of our modeling approach is that it enables us to disentangle confounding effects such as density-dependent and environmental conditions that may interact with the observed cost of reproduction in empirical studies.

Ungulates are particularly suitable for demographic studies of the cost of reproduction (Clutton-Brock et al. 1982, Clutton-Brock 1984, Tavecchia et al. 2005), because females have a relatively long life span, which enables an examination of the cost across several different age classes. Furthermore, many populations of ungulates have important economic and cultural values and have attracted considerable scientific research that has provided detailed demographic and ecological information needed to parameterize an IBM. Here we show that the survival cost of reproduction influences the dynamics and reproductive characteristics of the population, suggesting that a comprehensive understanding of population dynamic processes may require explicit examination of the effects of the cost of reproduction on demographic rates.

METHODS

Model overview

The model developed here is a stochastic, density-dependent IBM, broadly based on a Scottish red deer Cervus elaphus population, that explores the dynamics and reproductive characteristics of red deer females subject to varying levels of the survival cost of reproduction (this is a modified version of the model developed in Proaktor et al. [2007], which is based on data from different temperate ungulate populations). The model simulates the life cycles of individually distinct females that are born, reproduce at certain ages according to their lifetime reproductive strategy, and eventually die. Each offspring inherits her reproductive strategy from her mother with a certain chance of mutation (Appendix A). Mutations increase the range of reproductive strategies that are explored by the model, hence facilitating the model’s chance of finding the set of reproductive strategies that is most suitable to the simulated conditions. In order to shorten convergence time, nonviable strategies that reproduce either once or never are not permitted to emerge. Mortality rates depend on age, density of adult females, and reproductive status (cost of reproduction) (Appendix B), according to a broad, common pattern observed in different ungulate populations: high mortality at young and old ages, and low mortality at prime age (Gaillard et al. 1998).

The distribution of reproductive strategies evolves when suboptimal females are outcompeted by females that are more suitable to the simulated conditions and, consequently, produce, on average, more viable copies of their particular strategy. Only females are modeled because males have little effect on female reproductive schedules (Clutton-Brock et al. 1983, Holand et al. 2003). Moreover, interactions between the sexes are largely restricted to the rut and therefore males have little effect on the calf’s survival during its first year (Clutton-Brock et al. 1982). Because body mass and condition affect reproductive decisions and success, an alternative approach could model strategies specific to body mass. However, the focus here is on age-specific responses in reproduction to variation in the cost of reproduction. This approach enables a more wide comparison with empirical studies, the majority of which report age-specific rather than body-mass-specific observations. Additionally, modeling age-specific rather than body-mass-specific strategies is simpler and requires fewer assumptions (Proaktor et al. 2007).

Model implementation

We assess the effects of variation in the cost levels on population demography and dynamics by modeling a total of eight cost levels, such that each level elevates the cost-related mortality from the previous level by 10%. Under the model’s lowest cost level (baseline condition), a reproductive female is subjected to 23% additional mortality if she is reproducing at age 2 relative to a nonreproductive age-2 female (Appendix B). This cost function declines rapidly to almost zero between ages 4 and 6 years, and subsequently it gradually increases, up to ~33% at age 14 years. We also model cases in which a rapid change in the reproductive cost, for example due to altered environmental conditions, does not permit females to adjust their reproductive strategies. This non-adjusting population consists of a fixed set of reproductive strategies that originally evolved under cost level 1 (lowest cost). We compare the dynamics of the adjusting, “normal,” population to the dynamics of the non-adjusting population.

Each simulation is run for 500 years and is repeated 1000 times. Model output values (frequencies of age-specific reproductive strategies, reproductive rates, longevity, and density [total number of live animals age 1 or older per square kilometer]) are the means of the values taken in the last year of each simulation. Model convergence is assessed according to the variance in the number of strategies within the population. Convergence is assumed when the variance remains
constant for 50 years or more. The average time required for the model to converge is 300 years.

Validation of the model

The model’s predictions are validated against the data used to parameterize it by running it with cost level 5, which approximates the average age-specific differences in mortality between reproductive and nonreproductive hinds on Rum during the 1990s, when population density has reached carrying capacity (Milner-Gulland et al. 2004, Proaktor et al. 2007). Cost level 5 provides the best fit between the predicted and observed average age-specific numbers of hinds (Fig. 1). Despite the considerable variation, the model’s predictions for young and prime-age females fit well to the data. However, for older females (age 12–15 years), the model underpredicts, but because the proportion of animals in this age group is small it has little qualitative effect on the model’s output. These similarities between model predictions and the data suggest that the model adequately represents the dynamics and demography of the Rum population.

RESULTS

Reproductive strategies

The survival cost of reproduction has a strong negative effect on the onset of reproduction, which is delayed as the cost level increases (Fig. 2). Under the lowest cost level, ~90% of the females start reproduction at age 2 years. As the cost approaches the level experienced by females on Rum (cost level 5), there is a rapid shift in the age at first reproduction from age 2 to age 3 years, with a few females that delay reproduction to age 4. Age 3 remains the main age at first reproduction under intermediate and high cost levels. At extreme conditions (above cost level 6), age 4 becomes the main age at first reproduction. However, only a few females delay their onset of reproduction beyond age 4, indicating a limit to the effect of the cost on the onset of reproduction.

The mean proportion of reproductive females in the population declines linearly as the cost intensifies, but there are marked differences in age-specific responses to variation in the cost (Fig. 3). The average reproductive rate of age-2 females drops sharply as the cost level increases beyond very low rates, indicating that even a small decline in the mother’s survival at this age is sufficient to shift the balance between the relative contribution to fitness of survival and of reproduction, in favor of survival. At age 3, however, reproductive rates remain high among females experiencing low-to-intermediate cost levels, but drop rapidly as the cost
further increases. In contrast, the vast majority of young adults and prime age females (ages 4–9 years) continue to reproduce even under severe reproductive costs, indicating that fitness benefits from reproduction at these ages are substantially higher than from a further investment in survival. At older ages, reproductive rates decline as the cost increases. This is attributed to a weaker selection on suboptimal reproductive strategies at old ages resulting from senescence-induced decline in survival and the relatively small contribution that reproduction at old ages makes to fitness.

These responses to the cost of reproduction are manifested as effects on productivity. Overall, the average number of offspring per hind up to age 9 years, which approximates the population average lifetime reproductive success (LRS), declines as the cost increases: from an average of 7.39 offspring under low cost down to 3.64 offspring under high cost (Table 1). Decomposing these effects to young (3–5) and prime-age (6–8 years) groups shows that under low cost, >80% of both age groups reproduce every year. The rest skip reproduction once, i.e., reproduce two times in three years, and of these, about 5% in either age group avoid reproduction in consecutive years. In contrast, under high cost only, 13% of the young and 23% of the prime-age group reproduce every year. Additionally, the occurrence of consecutive reproduction declines to 0.53 and 0.58 among the young and prime-age groups, respectively.

**Demographic effects**

The cost of reproduction has a negative linear effect on density, which declines from 23 females/km² under low cost to approximately half that density under extreme cost. Additionally, the age structure shifts toward young ages (Fig. 4). Under low cost, approximately one-fourth of the females are young (<3 years), and the age-specific proportions of older hinds very gradually decline with age. In contrast, under high cost, the proportion of young females increases above one-third of the population, and subsequent female numbers decline very rapidly with age, so only very few

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**Table 1.** Proportion of females that reproduce 0–3 times and that reproduce in two or more consecutive years, for young (3–5 years) and prime-age (6–8 years) hinds, under low and high survival cost of reproduction.

<table>
<thead>
<tr>
<th>Breeding pattern</th>
<th>Low cost</th>
<th>High cost</th>
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<tbody>
<tr>
<td>Proportion of females in population that reproduce</td>
<td></td>
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<tr>
<td></td>
<td>Young</td>
<td>Prime</td>
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<tr>
<td>No. times female reproduces</td>
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<tr>
<td>0</td>
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<tr>
<td>1</td>
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<td>0</td>
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<tr>
<td>2</td>
<td>0.16</td>
<td>0.18</td>
</tr>
<tr>
<td>3</td>
<td>0.84</td>
<td>0.82</td>
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<tr>
<td>Consecutive reproduction</td>
<td>0.95</td>
<td>0.94</td>
</tr>
</tbody>
</table>

*Note:* The average number of offspring produced from birth up to age 9 years is 7.39 for low-reproductive-cost females (level 1, young and prime age pooled) and 3.64 for high-cost females (level 8, young and prime age pooled).
individuals survive to senescent ages. This indicates that longevity declines because the accumulated negative effects of reproduction on survival exceed the benefits for survival resulting from density-dependent-release, expected in populations below carrying capacity.

Effects of a sudden increase in the cost

The effects of the cost of reproduction become more severe when a rapid change in the cost, for example following a sudden shortage in food supply, or different environmental conditions experienced by translocated individuals, does not leave sufficient time for adjustments in reproductive strategies (Fig. 5). Under favorite conditions (low cost), the density and average longevity of the non-adjusting population are slightly smaller compared to the adjusting population, largely due to stochastic variation that requires modest adjustments in reproduction. However, as the cost rises further, the density and average longevity of the non-adjusting population rapidly decline relative to the adjusting population. Under extreme cost conditions, the non-adjusting population collapses. The relative decline in longevity is less steep than that of density because there is a minimum age at which females can successfully reproduce and maintain the population.

DISCUSSION

Previous research on the survival cost of reproduction indicates that the cost exists in a range of populations of different species (Nur 1984, Finke et al. 1987, Festa-Bianchet et al. 1995, Sinervo and DeNardo 1996, Orell and Belda 2002), and that it can have fitness conse-
quences for the mother (Oli et al. 2002). In ungulates, the cost of reproduction is more pronounced in young than in prime-age females (Clutton-Brock et al. 1983, Tavecchia et al. 2005), but it is unclear to what extent this variation in the cost affects females’ reproductive characteristics and demographic rates. Our results show that an early onset of reproduction, at age 2 years, is extremely sensitive to the cost of reproduction, even under cost levels well below those experienced by females on Rum. This is because survival of females at this age is considerably lower than that of older females and therefore the fitness benefits from delayed reproduction, enhanced survival, and thus higher potential for future reproduction, may outweigh the benefits from current reproduction (Clutton-Brock et al. 1987). An increase in the cost shifts the balance between the fitness benefits of current and future reproduction in favor of future reproduction and, consequently, reproduction is delayed. Delaying reproduction to age 3 remains the dominant strategy under most cost levels because the rate of decline in survival peaks between age 3 and 4, so a further delay in reproduction increases the risk of death before having a chance to reproduce.

Consistent with these results, theoretical explorations have suggested that iteroparous females that experience adverse conditions may delay the onset of reproduction due to the low fitness value of current reproduction, which results from an increase in the expected mortality of the mother and her offspring (Stearns 1989, Charnov 1990). Additionally, empirical studies suggest that females experiencing a deterioration in the conditions for reproduction, for example due to shortage of food or adverse climatic conditions, may delay the onset of reproduction or avoid current reproduction if they are experienced breeders (Clutton-Brock 1984, Schwarzkopf 1993). The cost of reproduction forms the link between such environmental changes and the resulting adjustments made to the reproductive characteristics of females, and the intensity of the cost shapes the extent of the age-specific changes in the reproductive strategy of each individual female. Whether delaying reproduction when conditions deteriorate has a clear fitness benefit is still under debate (Viallefont et al. 1995, McGraw and Caswell 1996, Pyle et al. 1997). For long-lived species like red deer, reduction in the number of females producing offspring under adverse environmental conditions has been suggested as a strategy that enhances the female’s fitness, because fitness is assumed to be primarily driven by survival rather than fecundity (Nelson and Peek 1982, Gaillard et al. 1998).

The relatively small effect that reproduction has on adult survival is the key reason for the observed diminishing effect that the cost has on the overall reproductive rates of hinds older than age 3, even when the cost is high. This result implies that the observed decline in the average reproductive rate of the entire population when the cost increases is largely attributed to responses in the onset of reproduction at young ages rather than responses across the entire life span. This negative effect of the cost is translated to the observed decline in the LRS resulting from the spread of reproductive events over longer time intervals. This strategy enables a period of recovery after reproduction during which females can accumulate body mass and consequently improve their survival and prospect for future reproduction (Clutton-Brock 1984, Festa-Bianchet et al. 1998). However, whether the expected increase in body mass is proportional to the increase in the investment in the offspring is still debated (Reznick and Yang 1993, Loison and Strand 2005); i.e., do females that avoid reproduction and thereby accumulate more body mass invest the additional resources in their own or in their offspring’s survival?

Variation in vital rates of ungulates, particularly in adult survival and fecundity, has been previously linked to changes in age structure and population density (Nelson and Peek 1982, Albon et al. 2000, Festa-Bianchet et al. 2003). Other factors, such as deterioration in environmental conditions, can also drive similar changes in reproductive strategies (Tavecchia et al. 2005, Basilone et al. 2006, Ergon 2007). When the cost of reproduction is not explicitly considered, a delay in the onset of reproduction and reduction in reproductive rates are broadly linked to increased population density (Eberhardt 2002). However, this link is based on short-term empirical studies and, consequently, describes a short to intermediate timescale tendency. Our model describes the demographic consequences of variation in the cost of reproduction over a much longer (evolutionary) timescale. Furthermore, the explicit consideration of the cost of reproduction as done here highlights its potential role as a selection mechanism of demographic rates. The effects of an increased cost of reproduction on reproductive rates are linked to long-term demographic changes: an age structure skewed to young animals and a decline in density. This reflects a decline in average life expectancy under high cost despite the reproductive adjustments made by females in order to minimize the negative effect that reproduction has on their survival. Hence, for females experiencing intermediate to strong levels of the cost of reproduction, the cost can be an important determinant not only of reproductive strategies but also of population dynamics.

Although there is a lack of empirical studies that directly link reproductive cost to population dynamics, our findings are implicitly supported by studies showing that the cost of reproduction affects reproductive rates (Gustafsson and Sutherland 1988, Linden and Möller 1989), and by other studies that link changes in reproductive rates to demographic processes. For example, Oli and Armitage (2004) found that delayed onset of reproduction and lower reproductive rates are major negative determinants of the population dynamics of the yellow-bellied marmot *Marmota flaviventris* L. Here, the effect of the cost of reproduction is mediated
through delay in reproductive schedules and reduced survival of young hinds.

Finally, we show that density and mean longevity decline faster when females cannot adjust their reproductive strategies. The strategies followed by the non-adjusting females become increasingly suboptimal as the cost level further deviates from the level under which these strategies originally evolved. It is also likely that adjustment is more important as the conditions for reproduction are more severe, due to the greater penalty females pay in terms of survival and, consequently, future reproduction.

The insights arising from this model are broadly applicable to other species and ecosystems, particularly the link between the survival cost of reproduction and demographic changes through the adjustment of reproductive strategies. The model can be applied and tested on other intensively studied species, such as long-lived iteroparous bird (Linden and Moller 1989) and fish (Hutchings 1994) species, for which there are sufficiently detailed information on demographic rates and on the cost of reproduction. The model’s applicability could be further broadened to other species under different environmental and density-dependent conditions, depending on future studies of demographic rates and the key factors affecting them in case study species. This will enable use of the model for an in-depth exploration of the role of the cost of reproduction in shaping reproductive strategies and population dynamics as demonstrated here.

ACKNOWLEDGMENTS

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LITERATURE CITED


APPENDIX A
Reproductive strategies (Ecological Archives E089-146-A1).

APPENDIX B
Mortality rates (Ecological Archives E089-146-A2).