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Costs of reproduction in a long-lived bird: large clutch size is associated with low survival in the presence of a highly virulent disease

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Fitness costs of reproduction are expected to be more pronounced when the environmental conditions deteriorate. We took advantage of a natural experiment to investigate the costs of reproduction among common eiders (*Somateria mollissima*) nesting at a site in the Arctic, where an avian cholera epizootic appeared at different magnitudes. We tested the predictions that larger reproductive effort (clutch size) is associated with lower survival or breeding probability the following year, and that this relationship was more pronounced under heightened exposure to the disease. Our results indicate that large clutch sizes were associated with lower survival of female eider ducks, but only when there was heightened exposure to avian cholera, as indexed by eider mortality on site. No cost was observed when cholera was absent or when lesser exposure was evident. This supports the hypothesis that fitness costs of high reproductive effort are higher under unfavourable conditions such as a disease epizootic, and further indicates that being a conservative breeder can increase survival probability, given the presence of a highly virulent disease.

Keywords: avian cholera; clutch size; common eider; reproductive effort; survival

1. INTRODUCTION

The existence of trade-offs between life-history traits, and in particular of fitness costs of reproduction, is at the core of life-history theory (Roff 2002). As costs of reproduction generate covariation between demographic rates, a comprehensive understanding of population dynamic processes requires examination of the costs of reproduction (Proaktor *et al.* 2008).

Fitness costs of reproduction have proven difficult to study in the wild because variation in individual quality often overrides the costs of reproduction, and leads to apparent positive associations between demographic components (Reznick 1985). Given the difficulty of studying the costs of reproduction, it is particularly challenging to understand how they vary with environmental conditions. It has been suggested that under unfavourable conditions, fitness costs of reproduction should be more pronounced (Reznick 1985), but empirical evidence is extremely rare. Unfavourable conditions often originate from high population density (Festa-Bianchet *et al.* 1998), starvation (Penn & Smith 2007) and harsh weather (Tavecchia *et al.* 2005). Infectious disease can have dramatic effects on individuals' life histories, but its influence on reproductive costs has rarely been investigated (but see Festa-Bianchet 1989).

We took advantage of the appearance of an avian cholera epizootic in a nesting colony of common eiders (*Somateria mollissima*) in the Canadian Arctic (hereafter called the East Bay colony) to study variation in fitness costs of conservative versus higher investment in reproduction in relation to the magnitude of a disease epidemic. Common eiders are long-lived, iteroparous sea ducks, whose females exhibit a strong philopatry to breeding areas (Goudie *et al.* 2000). Female eiders incubate alone, do not feed during the entire incubation period and can lose more than 40 per cent of their body mass during laying and incubation (e.g. Parker & Holm 1990). It has been shown in common eiders that an increase in reproductive effort decreases their immune function, with potential cascading effects on future fitness prospects (Hanssen *et al.* 2004, 2005).

Female common eiders nesting at the East Bay colony offer a rare opportunity to investigate variation in fitness costs of reproduction as a function of environmental conditions (i.e. degree of exposure to a disease), and to test the hypothesis that costs of reproduction increase under conditions of heightened exposure.

2. MATERIAL AND METHODS

Our study was done at East Bay, Southampton Island, Nunavut, Canada, where between 4000 and 8000 eider pairs breed depending on the year. This site is the largest known common eider colony in the Canadian Arctic. An avian cholera (*Pasteurella multocida*) epidemic first appeared in 2005, but its impact at first was very limited (5% of the breeding female eiders died during this breeding season); in comparison, the cholera epidemic had a very large to moderate impact on eider survival during the 2006 and 2007 breeding seasons (2006: approx. 32% of the breeding females died versus approx. 14% in 2007; I. Buttler & H. G. Gilchrist 2008, unpublished data).

In precocial birds, maternal energetic allocation to reproduction, or reproductive effort (*sensu* Evans 1990), mainly corresponds to egg production and incubation. Energetic costs of egg production and incubation are influenced by clutch size and both can have fitness costs (Erikstad & Tveraa 1995; Thomson *et al.* 1998; Williams 2005). As a consequence, we used the clutch size of female eiders as a proxy of their reproductive effort.

To study whether costs of reproduction varied with respect to lesser or heightened exposure to the disease, we used the modelling of capture–mark–recapture (CMR) data (Lebreton *et al.* 1992) of 158 females of known clutch size banded between 2004 and 2007 (70 were banded in 2004, 29 in 2005, 28 in 2006 and 31 in 2007) and model selection based on AICc (Akaike Information Criterion corrected for small sizes; Burnham & Anderson 2002). Our procedure is detailed in appendix 1 of the electronic supplementary material.

As non-breeders are less likely to be spotted on the island when compared with breeders (see details in appendix 1 of the electronic supplementary material), a lower recapture probability in a given year can be interpreted in terms of a lower breeding probability. Using our CMR modelling, we tested for a relationship between

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Table 1. Effects of clutch size on survival and recapture probabilities of female common eiders, East Bay colony, Southampton Island, Nunavut, Canada. (np indicates the number of estimated parameters for each model, AICc is the Akaike information criterion corrected for small sample sizes and ΔAICc is the difference in AICc between the model with the lowest AICc and the model considered. w_i indicates the AICc weight of a given model among the whole set of models fitted.)

model	np	deviance	AICc	ΔAICc	w_i
(*a*) clutch size effect on recapture probabilities (survival and recapture probabilities were modelled as: $\phi_{04-06,06-07,07-08}\ p$; see appendix 2 in the electronic supplementary material for details).					
no effect of clutch size	4	505.566	513.695	0.000	0.431
linear effect of clutch size on recapture probabilities in 2004 and 2005	5	504.812	515.007	1.312	0.224
linear effect of clutch size on recapture probabilities in 2007	5	505.272	515.467	1.772	0.178
linear effect of clutch size on recapture probabilities in 2006	5	505.391	515.586	1.891	0.167
(*b*) clutch size effect on survival probabilities (survival and recapture probabilities were modelled as: $\phi_{04-06,06-07,07-08}\ p$; see appendix 2 in the electronic supplementary material for details)					
linear effect of clutch size on survival between 2006 and 2007	5	497.601	507.796	0.000	0.915
no effect of clutch size	4	505.566	513.695	5.899	0.048
linear effect of clutch size on survival between 2007 and 2008	5	505.301	515.496	7.700	0.019
linear effect of clutch size on survival between 2004 and 2006	5	505.528	515.723	7.927	0.017

clutch size and either survival or breeding probability at three different periods: 2004–2006, where there was no (or extremely limited) effect of avian cholera on mortality; 2006–2007, which was the year following the largest cholera outbreak; and 2007–2008, where cholera had a limited effect on eider mortality. Any difference in survival estimates could correspond to an actual difference in survival and/or permanent emigration, and CMR survival analyses do not allow disentangling these two alternatives. Thus, we also used the data on female eiders recovered dead during the breeding season of the year of the largest cholera outbreak ($n=28$) to determine, using a logistic regression, whether mortality on the island in 2006 was linked to clutch size (no female of known clutch size was found dead during the 2007 breeding season).

Additional details on methods are presented in appendix 1 of the electronic supplementary material.

3. RESULTS

Recapture probabilities were relatively constant throughout the period of our study and equal to 0.63 ± 0.05 s.e. (appendix 2 in the electronic supplementary material). Recapture probabilities were not related to the clutch size of females, whether they bred before or during a cholera outbreak (table 1*a*; figure 1*a*; appendix 3 in the electronic supplementary material). Annual survival of female eider ducks varied with the period considered (2004–2006: 0.89 ± 0.03 s.e.; 2006–2007: 0.44 ± 0.06 s.e.; 2007–2008: 0.68 ± 0.08 s.e.; appendix 2 in the electronic supplementary material). Annual survival was not related to clutch size before the severe cholera epidemic or during the period of moderate cholera effect, but was strongly and negatively associated with clutch size during the period of intense cholera effect (table 1*b*; figure 1*b*; appendix 3 in the electronic supplementary material). An increase of one egg in the clutch was associated with an estimated average decrease of 15 per cent in survival.

The probability of mortality on the island in 2006 increased significantly with clutch size (slope of 0.85 on a logit scale; effect of clutch size: score-test statistic = 3.93, $p=0.048$; figure 2).

4. DISCUSSION

In the years prior to cholera outbreak, the survival of female eiders was independent of clutch size. Similar results have been found for females breeding in 2007, a year with apparently lessened exposure of eiders to avian cholera. This suggests that, when the environment was not unfavourable (no avian cholera epizootic or limited exposure to avian cholera), no cost was detectable. This probably reflects that the costs of reproduction, if any, were limited and masked by individual heterogeneity (van Noordwijk & de Jong 1986). In favourable environmental conditions, females could adjust their reproductive effort in relation to their pre-breeding body condition so that females in good condition could deal with the higher energetic demands required by laying and incubating a larger clutch without paying extra cost of reproduction. This led to no association, or a positive association, between clutch size and return rates (Yoccoz *et al.* 2002).

In the year of the greatest exposure of eiders to avian cholera, as indexed by on-site estimates of eider mortality, survival of females was strongly and negatively related to their clutch size. Other environmental

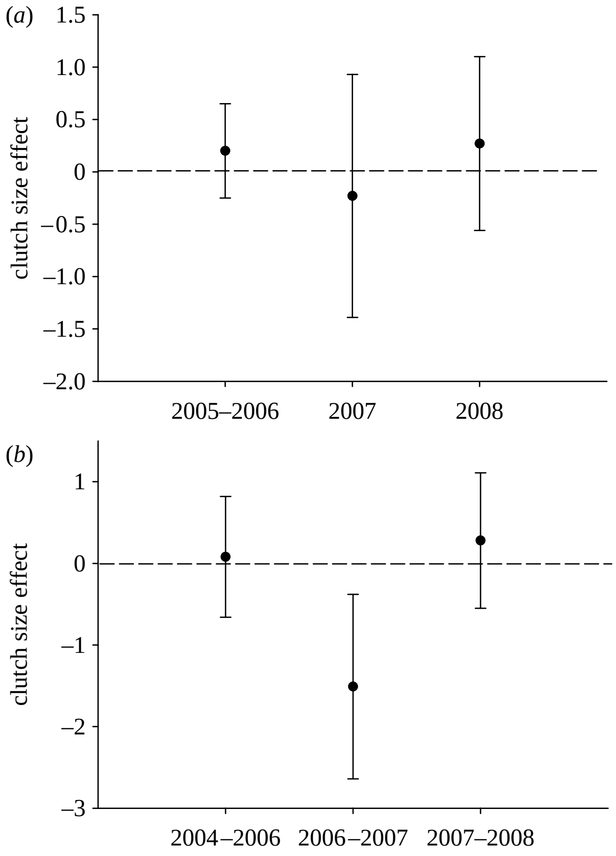

Figure 1. Slopes (±CI 95%) of the estimated relationships (on a logit scale) between clutch size and (*a*) recapture probabilities or (*b*) apparent survival for female common eiders breeding at East Bay, Southampton Island, Nunavut, Canada.

parameters (e.g. temperature and precipitation) were not worse during the 2006 breeding seasons when compared with other years, and density was lower in 2006 than in 2005. Therefore, an increase in the costs of reproduction because of the presence of a highly virulent pathogen remains the most likely explanation.

We found no effect of clutch size on recapture probabilities, either before or during the cholera epizootic, which suggests that the probability of breeding was not a function of the size of the clutch laid in the previous year. Consequently, it seems that the clutch size affected only the survival ability of females but for those who survived, there was no long-lasting effect of previous reproduction on the current breeding propensity.

Our study thus supports the hypothesis of higher costs of reproduction under very unfavourable breeding conditions (Reznick 1985). In the presence of a highly virulent infectious disease, whatever the condition or quality of female eiders, a higher energetic allocation to reproduction required by laying and incubating a larger clutch led to higher survival costs of reproduction. Three non-exclusive mechanisms can be proposed for this observed relationship. First, laying and incubating a large clutch may be energetically demanding (Thomson *et al.* 1998; Williams 2005) and affect immune function of individuals (Gustafsson *et al.* 1994; Hanssen *et al.* 2004, 2005). Such effects could have few, if any, consequences when environmental conditions are good but could be exacerbated under unfavourable conditions such as the presence of a disease, leading thus to increased mortality. Second, clutch size is correlated with arrival date and breeding success, so that females laying a large clutch tend to arrive earlier on the colony (H. G. Gilchrist & J. Bêty 2004, unpublished data) and are more likely to complete the incubation (Bourgeon *et al.* 2006). Consequently, female eiders laying a small clutch may have spent a shorter time on the island. Such females could have been less exposed to the disease either because they arrived and laid later or because they left the island earlier after nesting failure. A third possibility is that females laying larger clutches require more recesses to replenish water reserves; freshwater on the island can be the source of *P. multocida*, so that a greater fresh water consumption could be associated to a greater exposure to the disease.

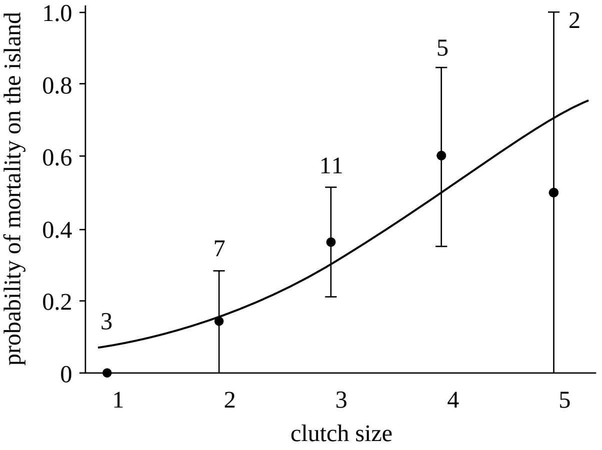

Figure 2. Relationship between clutch size and the probability of mortality on the island for female common eiders breeding during a severe avian cholera outbreak at East Bay, Southampton Island, Nunavut, Canada. The line represents the estimated relationship from a logistic regression. Numbers correspond to sample sizes for each clutch size category.

Whatever the underlying mechanism behind the relationship between survival and clutch size, our main results and conclusions remain the same: an increase in reproductive effort led to a decrease in survival in the year when avian cholera outbreak had the greatest magnitude. This relationship might be due to the physiological and/or ecological costs of reproduction (e.g. decrease in immune function and thus, higher susceptibility to the disease once infected versus longer or greater exposure to the disease and thus, higher risk of infection).

Our study supports previous theoretical findings, which suggest that ‘during poor breeding conditions, maximum fitness is achieved either by not breeding at all or by abandoning the brood’ (Erikstad *et al.* 1998, p. 1781). Erikstad *et al.* (1998) proposed that breeding conditions are determined by variables such as territory quality, weather conditions, food supply and/or predator density. Our study indicates that the presence of a disease might be another important determinant of breeding conditions, which can affect the survival of breeding individuals and trade-offs between reproduction and survival.

The study has been approved by the Canadian Council on Animal Care.

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