J. Avian Biol. 000: 000–000, 0000
doi: 10.1111/j.1600-048X.2010.05196.x

Received 19 March 2010, accepted 28 August 2010

Avian cholera, post-hatching survival and selection on hatch characteristics in a long-lived bird, the common eider *Somateria mollisima*

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Infectious diseases can have dramatic impacts on animal population dynamics, but how they influence vital rates remains understudied. We took advantage of the appearance of an avian cholera epizootic in an arctic colony of common eiders *Somateria mollissima* to study variation in juvenile survival and selection on hatch characteristics in relation to this highly infectious disease. Avian cholera is one of the most important infectious diseases affecting wild birds and is thought to primarily affect adult survival. Here, we show that avian cholera was associated with a 90% decline in duckling survival, leading to almost zero recruitment. Before the cholera outbreak, there was significant stabilizing selection on hatching date and significant positive directional selection on hatching mass. During cholera outbreaks, selection on hatch characteristics was no longer significant. These results were based on a low sample of surviving ducklings in cholera years, but suggested that date and mass at hatching did no longer affect duckling survival in the presence of cholera. These effects of avian cholera on post-hatching survival were likely not only the consequence of the disease *per se*, but also a consequence of an increase in predation rates that followed the emergence of avian cholera. Our results emphasize the dramatic direct and indirect impacts that infectious disease can have on vital rates, and thus population dynamics.

Variation in juvenile survival can be a major factor influencing population dynamics in short- but also long-lived species (e.g. Gaillard et al. 1998, Cooch et al. 2001, Altwegg et al. 2005). Population growth rate of long-lived species is generally more sensitive to changes in adult survival than changes in juvenile survival (Gaillard et al. 1998, Saether and Bakke 2000). However, juvenile survival often exhibits large temporal variation (Stearns and Kawecki 1994, Gaillard and Yoccoz 2003), which has the potential to greatly affect population growth rate (Saether and Bakke 2000). Consequently, determining factors affecting juvenile survival is crucial for understanding population dynamics even in long-lived species.

In birds, as in other vertebrate species, juvenile survival often exhibits large inter-annual fluctuation due to variation in factors such as harvest pressure (e.g., Anderson et al. 2001 on canvasbacks *Aythya valisineria*), population density (e.g., Armstrong et al. 2005 on saddlebacks *Philesturnus rufusater*), climatic conditions (e.g. Nicoll et al. 2003 on Mauritius kestrels *Falco punctatus*) and/or food availability (e.g. Wiens et al. 2006 on northern goshawks *Accipiter gentilis*). Infectious diseases are a relatively frequent phenomenon in wild bird populations (Friend et al. 2001), and what is known suggests that disease can have dramatic impacts on bird population dynamics, and accelerate population extinctions (see Warner 1968, van Riper et al. 1986 for examples on Hawaiian birds, Weimerskirch 2004 for an example on southern ocean albatrosses). Despite the dramatic effects that disease can have on bird population dynamics, quantitative assessments of the impacts of diseases on vital rates are very rare. Moreover, effects of diseases on the strength and direction of selection are virtually unknown in free-living populations.

To understand mechanisms of adaptation and evolution requires obtaining accurate measures of the strengths and modes of selection acting on life-history traits. The response of traits across multiple generations will be very difficult to predict if selection varies in space and/or time (Merilä et al. 2001). For example, if the shape and/or strength of selection fluctuates widely from year to year, this may slow any expected evolution (Merilä et al. 2001). In such situations, it seems very unlikely that a single estimate of selection in natural populations will adequately reflect the response, and thus evolution, of life-history traits (McAdam and Boutin 2003). Relatively few studies have investigated such temporal variation in the strength and/or direction of selection, and to our knowledge, none have investigated this variation in relation to the presence of an infectious disease.

Here, we took advantage of the appearance of an avian cholera *Pasteurella multocida* epizootic in an Arctic colony of a long-lived sea duck, the common eider *Somateria mollissima* to study variation in selection on hatch characteristics (hatching date and mass) through post-hatching survival in relation to the presence of this highly infectious disease. Avian cholera is one of the most important infectious diseases affecting wild waterfowl, especially in North America (Friend 1999). Avian cholera currently stands out as a major problem because of: *1*) the magnitude of mortality it causes, *2*) the broad spectrum of species affected, *3*) the annual frequency of epizootics, and *4*) the disease's continuing geographic expansion (Friend 1999, Friend et al. 2001). Unfortunately, very little is known regarding the effects of avian cholera on demographic parameters.

At our study site, hundreds of common eider ducklings have been banded soon after hatching each year since 2003, which offers a rare opportunity to investigate the effects of avian cholera, which appeared in 2005, on juvenile survival and on the strength and form of selection on hatch characteristics. Appearance of avian cholera epidemics were associated with a clear increase in the number of herring gulls *Larus argentatus* (see details in the Methods section), a predator of eider ducklings (Swennen 1989). Avian cholera thus had the potential to affect duckling survival through direct or indirect (i.e. predator-mediated) effects.

More specifically, our main goal was to quantify the effect of avian cholera on duckling survival in this long-lived Arctic-breeding bird. Avian cholera is generally assumed to affect adult survival (but see Weimerskirch 2004) so that its effect on juveniles remains largely unknown. We then tested the following predictions regarding duckling mass and hatching date. First, as mass is correlated with condition and ability to escape predators in common eiders (Swennen 1989, Christensen 1999), heavier ducklings should have higher survival after hatching compared with lighter ducklings. We thus expected directional selection on hatching mass. Second, two complementary predictions can be proposed for selection on hatching date. Eiders that hatch early in the season should have a longer time to feed and grow before leaving their summer ground and migrate to Greenland or Atlantic Canada (Mosbech et al. 2006). Therefore, hatching date should be negatively correlated with post-hatching survival, and selection on hatching date should be directional. Alternatively, ducklings that hatch too early in the season may: (1) be targeted by predators such as herring gulls (Swennen 1989) and not benefit from a predator-swamping effect (Ims 1990), or (2) face harsh environmental conditions at hatching if sea ice has not yet fully left the bay around the colony (Love et al. 2010). Consequently, hatching too early may be detrimental, so that early and late hatching date should both be associated with lower survival, albeit for different reasons. Stated another way, survival would be highest for ducklings that hatched during peak times, and selection on hatching date should be stabilizing.

Furthermore, we tested the prediction that disease affects selection on hatch characteristics but that the effect of avian cholera on the strength and form of selection was a function of the trait considered. Body mass is likely positively correlated with immune function (Møller et al. 1998, Hanssen et al. 2003) so that large mass should confer a better resistance to infectious disease. Moreover, mass is related to the ability to escape predation in common eiders (Swennen 1989). As the appearance of avian cholera epidemics was associated with a clear increase in the number of duckling predators at the colony, an improved ability to escape predation might confer greater advantages in years of intense predation. Consequently, because of such direct and/or indirect effects of avian cholera, we predicted that selection on hatching mass should be strongest during cholera epidemics, yet retain a similar form.

Finally, avian cholera is a highly infectious disease (Friend 1999). At the peak of hatching, eider ducklings, who often form crèches (Bustnes and Erikstad 1991), are more likely to be close to other ducklings and/or mothers, and thus to contract the disease. The probability of being infected should thus be a function of hatching date, with the greatest risk being around hatching peak. Consequently, if duckling mortality is caused primarily by direct effects of cholera, there should be a disruptive selection on hatching date in cholera years, and being born before or after hatching peak should be associated with higher survival. Alternatively, if duckling mortality is mainly caused by predator-mediated effects of cholera, the form of selection on hatching date should not change during cholera epidemics (i.e., highest survival around hatching peak), but the strength of selection should be higher.

Material and methods

Study population

The study was conducted in the Canadian Arctic on Mitivik Island (64° 02′N, 81° 47′W) in the East Bay Migratory Bird Sanctuary, Nunavut between 2003 and 2009. The small (800 m × 400 m), low-lying (< 8 m elevation) island consists of granite rock interspersed with small patches of tundra, and several small ponds. This island supports the largest known nesting colony of common eiders in the Canadian Arctic (up to 8500 pairs annually, Buttler 2009). Common eiders are iteroparous sea ducks that can live > 20 years (U.S. Geological Survey, http://www.pwrc.usgs.gov/BBL/homepage/long1290.cfm#Ducks); females exhibit strong philopatry to breeding areas and first-time female breeders are faithful to their natal colony (Wakeley and Mendall 1976, Swennen 1990, Tiedemann et al. 1999).

Banding and re-sighting of ducklings

Hatching generally occurred during the last two weeks of July and the first week of August (Table 1). Immediately following hatching ducklings leave the colony making their way to the sea with their mother, and eventually feed there with attending hens (Bustnes and Erikstad 1991, McKinnon et al. 2006). Hens and ducklings on their way to the sea were funnelled into wire traps set up on beaches of the nesting island. Ducklings were then banded, weighed to the nearest 0.5 g with a Pesola scale, and released at the water's edge. Because ducklings leave their nest just after hatching, date and mass at capture are good proxies of their hatching date and mass. Ducklings were banded with both a metal band and a unique color band (total weight of the

Table 1. Descriptive statistics for hatching date and mass of common eiders banded at the East Bay colony, Southampton Island, Nunavut, Canada. Results are from cohorts 2003 to 2007 (cohorts 2005 to 2007 experienced avian cholera epidemics in their year of birth).

	Hatching date		Hatching mass (g)	
	2003–2004	2005–2007	2003–2004	2005–2007
Average	July, 27	July, 24	59.5	58.9
Standard deviation	3.7	3.3	5.7	5.4
Minimum	July, 18	July, 14	32	38
Maximum	August, 2	July, 31	75	73

bands ~2 grams and thus <4% of duckling average body mass; see Supplementary material) so that individuals could later be re-sighted at a distance using observation blinds situated around the colony and accessed through above-ground canvas tunnels. These observational methods were followed to minimize disturbance to common eider ducks on the island.

From 2003 to 2007, 943 ducklings of unknown sex were banded and weighed (n = 235, 200, 181, 58 and 269 in 2003, 2004, 2005, 2006 and 2007, respectively). From 2004 to 2009, 89 ducklings (9.4% of all banded ducklings) have been re-sighted at the colony (Table 2). Among these 89 re-sighted birds, sex has been recorded for 80 individuals and 77 (96%) were females and 3 were males (4%). As a consequence of low male but high female philopatry and high natal return rate for first year breeding females (Goudie et al. 2000), our duckling survival estimate represented an underestimate of overall duckling survival (i.e. sex was not determined at banding and surviving males likely dispersed to other nesting colonies). However, our goal was not to provide the best estimates of duckling survival in common eiders, but rather to determine how avian cholera and individual characteristics (mass and date at hatching) affect survival. As date of and mass at hatching do not differ between the sexes (see Supplementary material) our results and conclusions should not be affected by sex being unknown at banding.

Avian cholera epidemics

Avian cholera is a naturally occurring disease caused by a highly contagious bacterium, *Pasteurella multocida*, infectious to many different avian and mammalian hosts (Botzler 1991). Previous avian cholera outbreaks have been observed in common eiders (Friend et al. 2001), but are extremely rare (and only recently documented) in Arctic eider populations. Avian cholera at the East Bay common eider colony was first confirmed in 2005, when about 5% of all breeding females died (Buttler 2009, Descamps et al. 2009). From 2006 to 2008, avian cholera was still present on the island and its effect on eider mortality varied annually (>30% of breeding females died on the island in 2006 and 2008 and approximately 15% in 2007, Buttler 2009).

Table 2. Age at first re-sighting for common eider ducklings banded at the East Bay colony, Southampton Island, Nunavut, Canada. Results are from cohorts 2003 to 2007 monitored during the period 2003–2009.

		Age (in years)						
	Year (total ducklings banded)	1	2	3	4	5	6	Total
Cohort	2003 (235)	6	31	8	2	1	1	49
	2004 (200)	6	18	5	1	2	0	32
	2005 (181)	2	0	1	0	0	0	3
	2006 (58)	1	1	0	0	0	0	2
	2007 (269)	0	3	0	0	0	0	3
	Total	15	53	14	3	3	1	89

The impact of avian cholera on adult survival was relatively low in 2005. However, the situation was very different for ducklings. Indeed, following the appearance of about 200 adult eider carcasses on the island in 2005, the number of gulls (mainly herring gulls), increased from 60 to about 160 individuals in 2005, and remained very high in subsequent years (up to 420 gulls in 2006). This large increase in the number of gulls (mostly non breeders), one of the main predators of eider ducklings (Swennen 1989), led to a clear increase in predation pressure on hatchlings either on their way to the ocean or when they were released after banding (I. Buttler and R. Kelly pers. comm.).

Survival analyses

Survival analyses were carried out using Capture-Mark-Recapture (CMR) methods (Lebreton et al. 1992), implemented in the software MARK (White and Burnham 1999). This allowed estimates of local duckling survival while taking into account a re-sighting rate <1 (Lebreton et al. 1992). Goodness-of-fit test of the Cormack-Jolly-Seber (CJS) model (i.e., the full time dependent model $\phi_t p_t$) was performed with the software U-CARE (Choquet et al. 2003). This test indicated a clear lack of fit between female eider data and the CJS model ($p < 0.01$). Therefore, the "iii" assumption (i.e., independence of fates and identity of rates among individuals), required for CMR analyses, was not met. This problem was likely due to heterogeneity in re-sighting and survival among individuals of different ages. Indeed, common eider ducklings rarely come back to the colony before 2 or 3 years of age (Baillie and Milne 1982, this study) so that their re-sighting probability is clearly age-dependent. Moreover, it seems obvious that survival of newly-hatched ducklings will be different than survival of one- or two-year old birds for example, so that survival is likely age-structured. A boot-strap goodness-of-fit test (program MARK, White and Burnham 1999) of a model including an age effect (with 2 modalities: hatching - 1 year old, and >1 year old) in both re-sighting and survival rates model $\phi_t^{a(1,>1)} p_t^{a(1,>1)}$ indicated a good fit between our model and data ($p = 0.60$; 1 000 simulations). Consequently, we are confident that, by including the age effect in our CMR analyses, our results were not biased by heterogeneity among individuals.

Model selection was based on the Akaike Information Criterion (corrected for small sample size, AICc), as recommended when several non-nested models are fitted (Burnham and Anderson 2002). We based our model selection on ΔAICc (difference in AICc between a given model and the model with lowest AICc) and models' weight (w_i); w_i measures the relative likelihood that a given model is the best among a set of fitted models (Burnham and Anderson 2002). A $\triangle \mathrm{AICc} < 2$ between two competing models suggests that they cannot be distinguished in their ability to model the data (Burnham and Anderson 2002). As survival rates were the parameters of interest in our study, we first modelled re-sighting rates to have more statistical power when modelling survival (Lebreton et al. 1992). We considered time and age effects when modelling re-sighting and survival probabilities. Age was defined as a two-modality variable (survival from hatching to 1 year old, and then from 1 year old onwards). The time variable was either a full year effect (one modality per year) or a "cholera effect" (two modality variable: period 2003–2005 with no cholera, period 2005–2009 with cholera outbreaks). The proportion of temporal variance in survival explained by this cholera effect was calculated as $\frac{Dev_{03-05,\,05-09} - Dev_i}{Dev_t - Dev_i}$ (Schemper 1990), where $Dev_{03\text{–}05,05\text{–}09}$ represents the deviance of the model where survival varied with the presence/absence of cholera (model $\phi^a_{03-05,\,05-09}\,p^a$, see Table 2), Dev_i represents the deviance of the model where survival was constant (model $\phi^a p^a$, see Table 2) and Dev_t represents the deviance of the model where survival was time-dependent (model $\phi^a_t\,p^a$, Table 2).

We then tested for hatching date and mass effects (used as individual covariates) on survival between hatching and one year of age. Hatching date and mass were normalized (*z*-transformed) before analyses, and were not correlated with each other (Pearson's correlation coefficient $= 0.044$). We tested for both linear and quadratic effects of hatching date and mass. Preliminary analyses indicated that survival was independent of the interaction between hatching date and duckling mass, so we present results from models with no interaction between these two variables. We tested for hatching date and mass effects on juvenile survival for the periods before and during the cholera epidemics (2003–2005 and 2005–2009, respectively).

Selection gradients

Selection on hatch characteristics was determined with the logistic regression approach of Janzen and Stern (1998). The regression coefficients we used to determine selection gradients came from our survival models including individual covariates. This methodology is similar to logistic regression (see chapter 12 in Cooch and White 2005) and regression coefficients from our CMR modelling could be used in the same way.

First, we only considered survival models with linear variables (hatching date and mass) to estimate directional selection (β), and then considered models that also included quadratic variables to estimate disruptive or stabilizing (γ) selection (see Lande and Arnold 1983, Stinchcombe et al. 2008). This quadratic selection gradient estimates the curvature of the relative fitness surface as a function of the trait considered; stabilizing selection implies negative curvature, and disruptive selection positive curvature. Selection gradients were then multiplied by constant $\frac{1}{\bar{W}}$, where $\bar{W}$ represents the average predicted fitness (or more specifically, average predicted duckling survival), and were thus placed on a relative fitness scale (which allows comparisons among studies).

Results

Re-sighting rates

Re-sighting rates after hatching were dependent on age (Table 3a). Models with two age-classes were better than models with a larger number of age classes (Table 3a; average recapture rate at 1 year of age: 0.034 ± 0.015; from 2 years of age onwards: 0.540 ± 0.037). Once age-variations were accounted for, yearly variation in re-sighting rates were limited (model $\phi^a_t\,p^a$ preferred over model $\phi^a_t\,p^a_t$ or $\phi^a_t\,p^{a+}_t$; Table 3a).

Age- and time-specific variation in survival

Survival of common eiders after hatching was age-dependent and exhibited strong yearly variation (Table 3b) that appeared related to a cholera effect (e.g., simplifying by $\phi_{03-05,\,05-09}$ led to better models; Table 3b). This two-modality cholera effect explained 95% of the temporal variation in survival (Table 3b). Apparent survival of juvenile eiders declined during the period 2005–2009 and was higher after one year of age (survival from hatching to one year of age before and after cholera epidemics, respectively: 0.33 ± 0.06 SE and 0.04 ± 0.01 SE; survival from one year of age onwards before and after cholera epidemics, respectively: 0.82 ± 0.15 SE and 0.60 ± 0.04 SE).

Effects of hatching date and mass on duckling survival

During the period 2003–2005 (before the cholera epidemics), survival of common eider ducklings from hatching to one year of age was a function of their hatching date and mass (Table 4a; Fig. 1). The best model was a model where survival from hatching to one year of age (for cohorts 2003 and 2004) was a quadratic function of hatching date (95% confidence intervals for the slope of the effects of hatching date and hatching date^2, respectively, on a logit scale: $[-0.50, 0.11]$ and $[-0.71, -0.02]$), and a linear function of hatching mass (95% confidence interval for the slope of the effects of hatching mass on a logit scale: [0.03, 0.60]; Fig. 1; Table 4a). This model indicated that, for cohorts 2003 and 2004, ducklings that hatched very early or very late in the season had lower rates of survival, and that survival increased with duckling mass (Fig. 1). From 2005 onwards, survival of common eider ducklings from hatching to one year of age was independent of their date of hatching, but was slightly higher for the heaviest and lightest mass ducklings (95% confidence intervals for the slope of the effects of hatching mass and hatching mass^2, respectively, on a logit scale: $[-0.31, 0.89]$ and [0.06, 0.99]; Table 4b; Fig. 1).

Table 3. Age and time effects on re-sighting (*p*) and survival (ϕ) rates of common eider ducklings, East Bay colony, Southampton Island, Nunavut, Canada. Results are from cohorts 2003 to 2007 monitored during the period 2003–2009. Superscript "*a*" refers to an age effect with two modalities (from hatching to one year of age; from 1 year of age onwards). Sign "+" indicates an additive age effect. Subscript "*t*" refers to time effect (with one modality per year) and subscript "*03–05, 05–09*" refers to a time effect with two modalities (before and during cholera epidemics; see Methods for details). *np* indicates the number of estimated parameters for each model, *AICc* is the Akaike Information Criterion corrected for small sample sizes and *ΔAICc* the difference in AICc between the model with lowest AICc and the model considered. w_i indicates the AICc weight of a given model among the whole set of models fitted.

(a) Re-sighting rate modelling

Model	np	Dev	AICc	△ AICc	w_i
$\phi_t^a\, p^a$	12	934.419	958.715	0.000	0.96
$\phi_t^a\, p_t^{a+}$	16	932.651	965.168	6.453	0.04
$\phi_t^a\, p_t^a$	20	927.848	968.650	9.935	0.01
$\phi_t^a\, p_t$	16	958.282	990.800	32.085	0.00
$\phi_t^a\, p$	11	985.268	1007.518	48.803	0.00

(b)Survival rate modelling

Model	np	Dev	AICc	△ AICc	w_i
$\phi_{03-05,\,05-09}^{a+}\, p^a$	5	938.872	948.929	0.000	0.64
$\phi_{03-05,\,05-09}^{a}\, p^a$	6	938.262	950.341	1.412	0.32
$\phi_t^{a+}\, p^a$	9	936.259	954.429	5.500	0.04
$\phi_t^a\, p^a$	12	934.419	958.715	9.786	0.00
$\phi^a\, a$	4	1015.048	1023.085	74.156	0.00
$\phi_t\, p^a$	8	1007.332	1023.468	74.539	0.00
$\phi\, p^a$	3	1041.687	1047.709	98.780	0.00

Selection analyses

The strength and form of selection varied among the traits considered and between periods (Fig. 1 and 2). Before the cholera epidemics, hatching date was subject to significant stabilizing selection and there was selection against hatching too early and too late (Fig. 1c and 2). During the same period, hatching mass was subject to significant directional selection and heavy ducklings were favoured (Fig. 1a and 2).

Selection gradients on hatching date and mass were not significantly different during cholera epidemics than before (all 95% confidence intervals overlapped; see Fig. 2). However, there was no significant selection on hatching date during the epidemics (Fig. 1d and 2). Selection on hatching mass appeared to be slightly disruptive (Fig. 1b and 2), but this effect was driven by a single individual who survived despite a surprisingly small mass at hatching (38 grams). When removing this individual from our sample (considering that such a small mass may have been the result of a measurement error as only 0.1% of banded ducklings weighed less than 40 grams), selection gradients on hatching mass were no longer significant (Supplementary Materials).

Discussion

Avian cholera and juvenile survival

Avian cholera is one of the most important infectious diseases affecting wild waterfowl (Friend 1999) and it is now widespread throughout North America (Samuel et al. 2007). Despite potentially dramatic effects of such infectious diseases, evaluations of their effects on wild populations have essentially been at gross scale and are at best only associated with changes in population numbers (Friend et al. 2001). Therefore, very little is known regarding the demographic consequences of infectious diseases in free-living populations. Our study clearly indicates that avian cholera not only affects population dynamics through its effect on adult survival (i.e., the main reported effect of avian cholera; Friend 1999), but can also dramatically decrease duckling survival. Indeed, survival of common eiders from hatching to one year of age decreased by almost 90% in years of cholera outbreak (Fig. 1), and a single factor presence/absence of cholera explained 95% of the temporal variation in survival. Of course, as our study was not experimental, the observed pattern of variation in duckling survival may have been caused by some unknown confounding factor(s). However, considering the obvious and dramatic changes in duckling predation pressure from 2005 onwards (most likely linked to the presence of eider carcasses, and thus to avian cholera epidemics), as well as in breeding female mortality (Buttler 2009, Descamps et al. 2009), we are confident that the changes in duckling survival were essentially caused, directly or not, by avian cholera.

Avian cholera effects on post-hatching survival might have occurred in different ways. First, ducklings may have died directly from avian cholera infection after hatching. Second, their mothers may have died from avian cholera, and thus left ducklings unattended. Third, the number of herring gulls, one of the main predators of eider ducklings (Swennen 1989), dramatically increased at the colony since 2005 (the first cholera outbreak), following the appearance of eider carcasses. This increase has led to a very steep increase in predation pressure on ducklings (I. Buttler and R. Kelly pers. comm.). In these two latter cases, the decrease in duckling survival in the presence of avian cholera would have been an indirect consequence of avian cholera through the death of attending hens and/or increased predation by gulls.

Table 4. Effects of duckling hatch date and mass on survival (ϕ) between hatching and 1 year of age in common eiders, East Bay colony, Southampton Island, Nunavut, Canada. Superscript a_1 refers to survival between hatching and 1 year of age and superscript a_2 to survival after 1 year of age. Superscript *date* and *mass* refer to the date and mass at capture, respectively, used as proxies for the date and mass at hatching. *np* indicates the number of estimated parameters for each model, *AICc* is the Akaike information criterion corrected for small sample sizes and Δ *AICc* the difference in AICc between the model with lowest AICc and the model considered. w_i indicates the AICc weight of a given model among the whole set of models fitted. Resighting rates are modelled as p^{a2} in all models (see Table 3a for details on re-sighting rates modelling). $\phi^{a_1}_{03-05}$corresponds to survival between hatching and age 1 before cholera outbreaks (i.e., for cohorts 2003 and 2004), and $\phi^{a_1}_{05-09}$ to survival between hatching and age 1 during cholera outbreaks (i.e., for cohorts 2005, 2006 and 2007). $\phi^{a_2}_{03-05,\,05-09}$ represents survival after age 1 for the two periods considered (before and during cholera outbreaks). Note that model noted $\phi^{a_1}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$ here corresponds to model noted $\phi^{a2+}_{03-05,\,05-09}$ in Table 3b.

(a) Effects of date and mass at hatching before cholera outbreak (2003–2005)

Model	np	Dev	AICc	ΔAICc	w_I
$\phi^{a_1/date+date^2+mass}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	8	927.278	943.414	0.000	0.358
$\phi^{a_1/date+date^2+mass+mass^2}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	9	926.523	944.693	1.279	0.189
$\phi^{a_1/date+mass}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	931.309	945.415	2.001	0.132
$\phi^{a_1/date+date^2}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	931.708	945.813	2.399	0.108
$\phi^{a_1/date+mass+mass^2}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	8	930.363	946.498	3.084	0.077
$\phi^{a_1/date}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	6	935.424	947.503	4.089	0.046
$\phi^{a_1/mass}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	6	935.430	947.509	4.095	0.046
$\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	5	938.872	948.929	5.515	0.023
$\phi^{a_1/mass+mass^2}_{03-05}\,\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	934.914	949.020	5.606	0.022

(b) Effects of date and mass at hatching during cholera outbreak (2005–2009)

Model	np	Dev	AICc	ΔAICc	w_i
$\phi^{a_1/mass+mass^2}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	934.686	948.792	0.000	0.246
$\phi^{a_1}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	5	938.872	948.929	0.137	0.229
$\phi^{a_1/date}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	6	938.096	950.175	1.383	0.123
$\phi^{a_1/date+date^2+mass+mass^2}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	9	933.481	951.651	2.859	0.059
$\phi^{a_1/date+mass+mass^2}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	8	933.593	949.729	0.937	0.154
$\phi^{a_1/mass}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	6	938.868	950.947	2.155	0.084
$\phi^{a_1/date+date^2}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	938.072	952.178	3.386	0.045
$\phi^{a_1/date+mass}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	7	938.096	952.202	3.410	0.045
$\phi^{a_1/date+date^2+mass}_{05-09}\,\phi^{a_2}_{03-05,\,05-09}$	8	938.072	954.208	5.416	0.016

Hatch characteristics and juvenile survival before cholera epidemics

Before the appearance of avian cholera, post-hatching survival of ducklings was a function of hatching date, and was lower for very early- and very late-hatching (Fig. 1c). As hatching date is strongly correlated with laying date (i.e. little flexibility in incubation duration, Love et al. 2010), our results suggest that commencing incubation too early or too late was detrimental to breeding females as their juveniles had lower survival prospects. This supports the hypothesis that timing of reproduction can be a critical component of fitness in seasonal environments (Rowe et al. 1994, Bêty et al. 2003), and that laying date is subject to stabilizing selection through duckling survival. The stabilizing selection we observed ($\gamma = -0.11 \pm 0.06$ SE) was relatively strong as compared to other selection studies (see Kingsolver et al. 2001 for a review). Indeed, the magnitude of quadratic selection according to Kingsolver et al. (2001) was typically small with a median $|\gamma|$ of 0.02 for selection via survival. As outlined earlier, a potential mechanism explaining this selection pattern could be that late hatched eiders had a shorter time to feed and grow before migrating from their summer grounds, which could then affect their survival. Likewise, ducklings that hatched too early in the season might have faced severe foraging conditions (i.e., hatched before ice-free conditions in the bay, Love et al. 2010). Moreover, they may have been relatively isolated and thus targeted by gulls as compared to ducklings that hatched during the peak of hatching which could have benefited from a predator-swamping effect (Ims 1990).

Before cholera epidemics, post-hatching survival of ducklings was positively related to their mass (Fig. 1a), as often observed in birds (Lindén et al. 1992, Gaston 1997, Christensen 1999, Anderson et al. 2001, Monros et al. 2002). This supports our prediction of directional selection on hatching mass. The strength of this selection was relatively weak ($\beta = 0.046 \pm 0.024$ SE) in agreement with Kingsolver et al. (2001), who observed a median magnitude of directional selection (median $|\beta|$) via survival of 0.09. A potential mechanism explaining this selection pattern could be that heavy ducklings suffered lower predation rate (i.e., more able to escape from predator attack), and thus higher survival before fledging, as observed in another common eider population (Swennen 1989). Alternatively, ducklings in good condition might have a better ability to forage and grow, and thus survive.

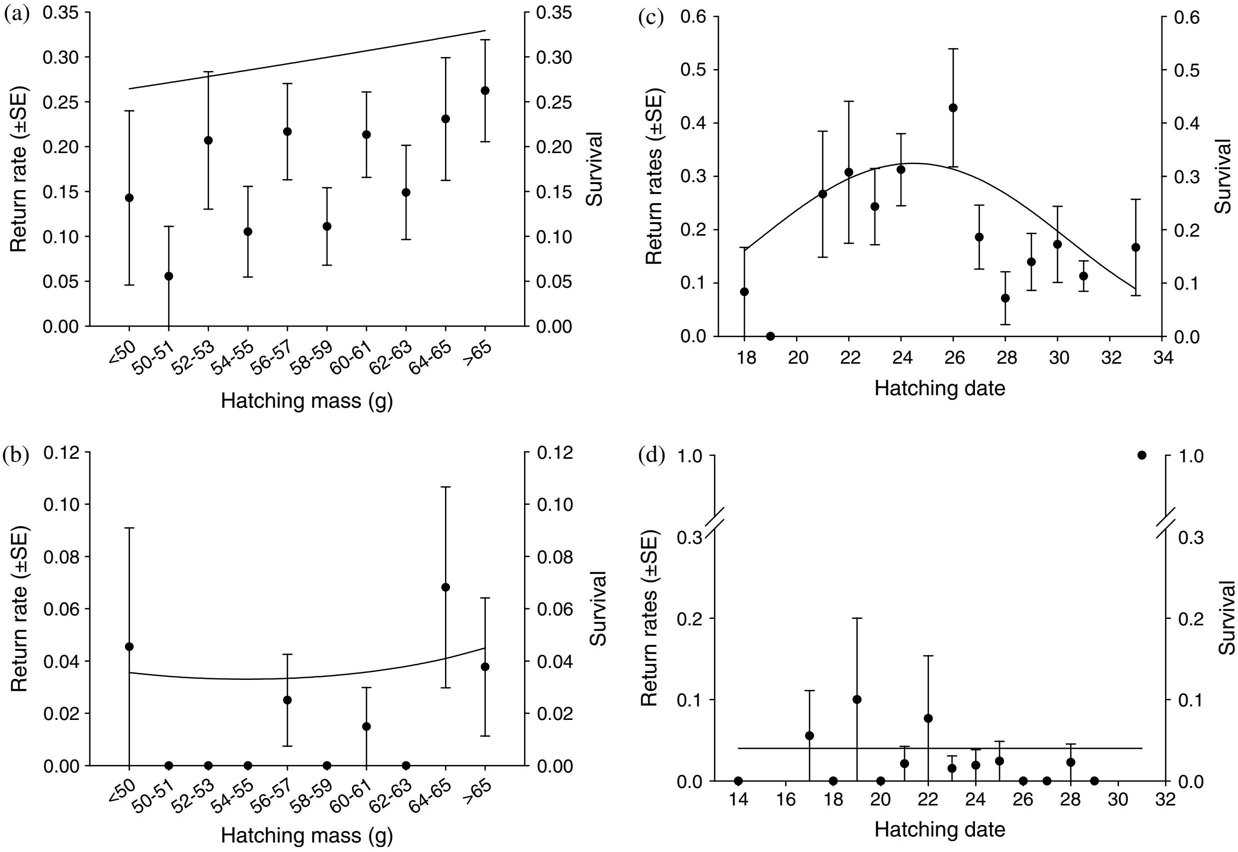

Figure 1. Observed return rates (± SE) and estimated post-hatching survival (from hatching to 1 year of age) of female common eiders in relation to their hatching mass (a, b) and hatch date (c, d), East Bay colony, Southampton Island, Nunavut, Canada. Graph (a) and (c) represent post-hatching survival before cholera epidemics (based on 81 re-sighted ducklings), and graphs (b) and (d) during cholera epidemics (based on 8 re-sighted ducklings). Hatching date corresponds to the number of days from July 1st; masses were measured to the nearest 0.5 g, but were pooled into 2g-intervals for graphic readability. Lines represent estimated survival from hatching to 1 year of age based on capture-mark-recapture modelling (see Table 4 for details).

Avian cholera and selection on hatch characteristics

Few studies have dealt with temporal variation in the strength and/or form of selection, and even fewer studies have identified the causes of temporal variation in selection (Siepielski et al. 2009). Our study suggests that selection on hatch characteristics through post-hatching survival may have varied with the presence of avian cholera (but no significant differences in selection coefficients were detected). Before the epidemic, a clear stabilizing selection was found on hatching date, whereas no significant selection was found on this trait during cholera epidemics (Fig. 1d, 2) despite a similar range and variation in hatching date (Table 1): in cholera years, hatching in mid- or late-July was associated with very similar survival rates (Fig. 1d). This could be explained by the increase in predation pressure during the period of cholera. Indeed, since the first outbreak in 2005, the number of non-breeding gulls has dramatically increased at the colony (see *Methods*). This increase was concomitant with a steep decline in the number of female common eiders that bred successfully and thus a steep decline in the number of ducklings. Consequently, even those ducklings that were born during the peak of hatching might have suffered very high predation pressure. Alternatively, ducklings that hatched around the peak may have suffered a higher rate of infection due to a higher probability of contact with an infected duckling or mother. Such higher risk of infection could also explain why ducklings born around the peak of hatching had similar survival in the presence of cholera.

Results were very similar for hatching mass. Before the epidemics, we observed significant positive directional selection on this trait, whereas during the epidemics, there was potentially no selection on hatching mass (see Supplementary Materials) despite a similar range and variation in hatching mass before and during the cholera years. Thus, it appears that during the period of cholera (and therefore of severe predation), heavy ducklings were not more prone to survive up to and after fledging. Again, two potential mechanisms that are not mutually exclusive could explain this result. First, predation might have been so intense on ducklings that a small difference in their ability to escape predators would not have been apparent in such conditions. Second, differences in body mass may not be related to avian cholera resistance and all ducklings might have had the same probability of dying from cholera.

Because of the strong decrease in survival during the cholera outbreak, the number of surviving ducklings was

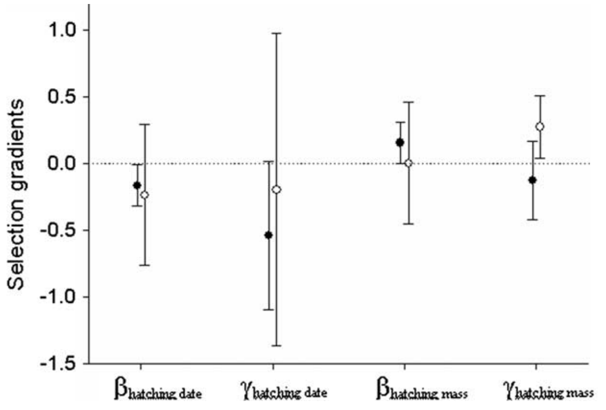

Figure 2. Selection gradients on hatch characteristics through post-hatching survival in the East Bay common eider colony (Southampton Island, Nunavut, Canada) before (black symbols) and during (white symbols) the avian cholera epidemics. Results are from cohorts 2003 to 2007 monitored during the period 2003–2009. Standardized selection gradients (β and γ) and their associated 95%-confidence intervals (CI) have been calculated following Janzen and Stern (1998). coefficients describe directional selection and β coefficients stabilizing (if <0), or disruptive (if >0) selection.

low and we had little power to detect the effects of hatching date and mass on survival. Consequently, even if significant selection on hatching date and mass was found in the absence of avian cholera and no significant selection was found in the presence of cholera, differences in selection coefficients between both periods (before and during the epidemics) were not significant (Fig. 2). Therefore, it is possible that selection on hatch characteristics did not change during cholera epidemics, but rather that our small sample size did not allow us to detect any selection. One argument against this alternative hypothesis is that, even with the small number of surviving ducklings during the cholera outbreak, our results did not indicate any tendency in the variation of post-hatching survival with hatch characteristics, despite the fact that hatching date and mass were well scattered in those years (the mass of surviving ducklings ranged from 38 to 67 grams, and their hatching date from July 17th to July 31st). Therefore, the conclusion that selection on hatch characteristics was no longer present in the presence of avian cholera remains plausible, but clearly would need further investigation based on a larger sample size of surviving ducklings.

Conclusion

Our study showed a dramatic impact of avian cholera on post-hatching survival in eiders. Further analyses are required to determine the relative contribution of this decline in juvenile survival to variation in population growth rate. However, this will clearly affect recruitment into the breeding population and thus its dynamics through direct numerical cohort effects (Albon et al. 1987, Gaillard et al. 2003). Our study emphasizes the importance of disease on the dynamics and even the extinction risk of wild populations (Harvell et al. 2002, de Castro and Bolker 2005, LaDeau et al. 2007), a relatively neglected area of research in conservation biology. Our study supports the idea that infectious disease can represent a substantial threat to the conservation of global biodiversity (Daszak et al. 2000), an important topic considering the predicted increase in frequency and severity of diseases associated with global climate warming (Harvell et al. 2002, Møller 2010).

Acknowledgements – This study was supported by grants from the Canadian Wildlife Service of Environment Canada, Nunavut Wildlife Management Board, Greenland Institute of Nature, Polar Continental Shelf Project, Canadian Network of Centres of Excellence ArcticNet, Fonds Québécois de la Recherche sur la Nature et les Technologies, Natural Sciences and Engineering Research Council of Canada, and the Northern Studies Trust Program of the Department of Indian Affairs and Northern Development. We wish to thank all of the summer research assistants that worked so hard to collect the data, Marie Fast for proofreading the manuscript, Maureen Kay, Myra Robertson, Rob Kelly and Isabel Buttler for their help at different stages of the study, and Joe Williams and two anonymous referees for very helpful comments on an earlier draft.

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Supplementary material

(a) Metal and plastic bands used on eider ducklings at hatching (photo: S. Descamps). The metal band was filled with plasticine to fit duckling legs while leaving room for growth to be completed. The plastic bands were similar to the ones used on adult legs; as they were put above the metal band, they could not get out of the leg. Observations of banded ducklings running and/or swimming/diving suggest that these bands had no marked adverse effect on duckling behaviour.

(b) Between-sex variation in hatching date and hatching mass in summer 2009 (n = 68 ducklings of known sex, determined by cloacal inspection). Results were based on linear models performed with software SAS (SAS Institute 2004).

	F	p	R^2
Hatching date[‡]	$F_{1,\ 33} = 0.04$	0.84	< 0.001
Hatching mass[$]	$F_{1,\ 33} = 0.77$	0.38	0.01

[‡]: same result if we tested for a hatching date effect on the average sex ratio of the brood (Kruskal-Wallis test, p = 0.25).

[$]: same result if we include the hatching date as a covariate and/or a random factor "Brood".

(c) Relationship between post-hatching survival (survival from hatching to 1 year of age) and hatching date and hatching mass in common eiders during avian cholera epidemics (2005–2009) from the East Bay common eider colony, Southampton Island, Nunavut, Canada . Notation and analyses are the same as in Table 3. One individual (born in 2007 with a mass of 38 g and that returned to the colony in 2009) has been removed from the sample to determine whether or not the observed quadratic effect of mass at hatching on survival was driven by this individual. Without this individual, no effect of hatching mass and (hatching mass)^2 on survival was apparent.

Model	np	Dev	AICc	ΔAICc
$\phi^{a_1}_{03-05}\ \phi^{a_1}_{05-09}\ \phi^{a_2}_{03-05,\ 05-09}$	5	929.645	939.701	0.000
$\phi^{a_1}_{03-05}\ \phi^{a_1/mass}_{05-09}\ \phi^{a_2}_{03-05,\ 05-09}$	6	928.969	941.049	1.348
$\phi^{a_1}_{03-05}\ \phi^{a_1/mass+mass^2}_{05-09}\ \phi^{a_2}_{03-05,\ 05-09}$	7	928.814	942.920	3.219

(d) Selection analyses on hatch characteristics through post-hatching survival in the East Bay common eider colony, Southampton Island, Nunavut, Canada during the period of cholera epidemics (2005–2009). One individual weighing 38 grams at hatching and that survived to ≥ 2 years of age was excluded from our sample. β coefficients describe directional selection and γ coefficients stabilizing (if < 0), or disruptive (if > 0) selection. Without this individual, no significant selection seemed to occur on hatching mass during the cholera years.

	β	CI lower bound	CI upper bound	γ	CI lower bound	CI upper bound
Hatching mass	0.81	−0.28	1.90	0.96	−0.75	2.67