ORIGINAL ARTICLE

FLUCTUATING SELECTION AND THE MAINTENANCE OF INDIVIDUAL AND SEX-SPECIFIC DIET SPECIALIZATION IN FREE-LIVING OYSTERCATCHERS

Martijn van de Pol,[1,2,3] Lyanne Brouwer,[1] Bruno J. Ens,[4] Kees Oosterbeek,[4] and Joost M. Tinbergen[5]

[1]Department of Ecology, Evolution and Genetics, Research School of Biology, Australia National University, Canberra, ACT 0200, Australia

[2]Centre for Conservation Biology, Norwegian University of Science and Technology, Trondheim, Norway

   [3]E-mail m.van.de.pol@myscience.eu

[4]SOVON Dutch Centre for Field Ornithology, Beek-Ubbergen, The Netherlands

[5]Animal Ecology Group, University of Groningen, Haren, The Netherlands

Fluctuating and disruptive selection are important mechanisms for maintaining intrapopulation trait variation. Nonetheless, few field studies quantify selection pressures over long periods and identify what causes them to fluctuate. Diet specialists in oyster-catchers differ in short-term payoffs (intake), but their long-term payoffs are hypothesized to be condition dependent. We test whether phenotypic selection on diet specialization fluctuates between years due to the frequency of specialists, competitor density, prey abundance, and environmental conditions. Short-term payoffs proved to be poor predictors of long-term fitness payoffs of specialization. Sex-differences in diet specialization were maintained by opposing directional fecundity and viability selection between the sexes. Contrasting other studies, selection on individual diet specialization was neither negative frequency- or density-dependent nor dependent on prey abundance. Notwithstanding, viability selection fluctuated strongly (stabilizing↔disruptive) over the 26-year study period: slightly favoring generalists in most years, but strongly disfavoring generalists in rare harsh winters, suggesting generalists cannot cope with extreme conditions. Although selection fluctuated, mean selection on specialists was weak, which can explain how individual specialization can persist over long periods. Because rare events can dramatically affect long-term selective landscapes, more care should be taken to match the timescale of evolutionary studies to the temporal variability of critical environmental conditions.

KEY WORDS: **Annual fitness, cultural evolution, environmental variability, nonlinear selection gradient, response to selection, trophic polymorphism.**

Variation between individuals has important consequences for both evolutionary and ecological processes (Łomnicki 1978; Bolnick et al. 2003). An extreme—but potentially common—case of individual variation is individual specialization, in which some individuals consistently use only a subset of the resources or

This paper is dedicated to the memory of Rudi H. Drent.

behavioral strategies available to the whole population (Skulason and Smith 1995; Bolnick et al. 2003). For example, in a population with a niche width of two types of prey, some individuals might feed exclusively on prey type A, whereas other individuals feed exclusively on prey type B (i.e., a trophic polymorphism).

Generally, it is assumed that individual specialization is maintained in a population by disruptive selection against

nonspecialists (i.e., generalists) and/or by fluctuating selection in time or space on specialists (Partridge and Green 1985; Skulason and Smith 1995; Bolnick et al. 2003). Selection on specialization can fluctuate due to intrinsic factors, such as variation in the frequency or density of competitors (e.g., Fitzpatrick et al. 2007; Svanbäck and Persson 2009), or due to extrinsic factors such as variability in prey abundance or other environmental factors (e.g., Meyer 1989; Pfennig 1992). Many studies have shown that the short-term payoffs such as intake rate or body condition differ between diet specialists (e.g., Sutherland et al. 1996; Svanbäck and Persson 2009) and that these payoffs are condition dependent (e.g., depend on the frequency/density of competitors or on prey availability; Hori 1993; Schindler et al. 1997; Svanbäck and Persson 2009). Nevertheless, surprisingly few studies have used actual fitness measures (i.e., fecundity and/or survival) to quantify annual selection pressures on different types of specialists over appropriate ecological timescales in the wild. Even less is known about what causes fecundity or viability selection on specialists to fluctuate between years (but see e.g., Sinervo et al. 2000).

DIET SPECIALIZATION IN OYSTERCATCHERS

Eurasian oystercatchers (*Haematopus ostralegus ostralegus*) are a classical example of individual and sex-specific feeding and diet specialization (Hulscher 1996; Sutherland et al. 1996). Although the name of this long-lived shorebird suggests otherwise, oystercatchers specialize on eating either worm or shellfish species (which typically do not include oysters). Worm and shellfish specialists differ in bill morphology. Females are most likely to be worm specialists and males most likely to be shellfish specialists, although both types of specialists occur among both sexes (Hulscher and Ens 1992; Durell et al. 1993). Adult oystercatchers are quite consistent in their specialization within as well as between years, nevertheless some phenotypic plasticity occurs (Goss-Custard and Sutherland 1983; Hulscher 1985). Switching specialization requires morphological remoulding of the bill shape, which is time consuming and reduces intake rate (Swennen et al. 1983; Hulscher 1985).

Although the ecological, developmental, morphological, and behavioral aspects of oystercatchers' diet specialization have been studied in great detail (see reviews by Sutherland et al. 1996; Hulscher 1996 and references therein), the mechanisms maintaining this trophic polymorphism are not well understood. In contrast to some fish species with trophic polymorphisms (Skulason and Smith 1995), different oystercatcher specialists often use the same feeding grounds, suggesting that spatial heterogeneity does not play a crucial role in maintaining intrapopulation variation. Moreover, as an oystercatcher's feeding specialization is most likely culturally and not genetically inherited (learned from the parents; Norton-Griffiths 1967a), heterozygote advantage is also not a likely mechanism for maintaining this polymorphism. Fi-

nally, different specialists on the same feeding grounds differ consistently in their short-term payoffs. Shellfish specialists typically attain the highest intake rates (Goss-Custard and Durell 1988; Stillman et al. 1996; Wanink and Zwarts 1996), need the least feeding-time to reach their daily energy requirements (Caldow et al. 1999; Durell et al. 2001), have the highest body condition (Durell et al. 2001) and are least likely to have damaged bills (van de Pol et al. 2009a).

To explain the paradoxical coexistence of various specialists with different short-term payoffs, two hypotheses have been put forward explaining why short-term payoffs might not necessarily reflect long-term fitness differences in oystercatchers (Sutherland et al. 1996). The first hypothesis suggest that the fitness of specialists is not solely determined by the profitability (mean intake rate), but also by the risks associated with different diet specializations (Sutherland et al. 1996; Durell 2007). The spatiotemporal variability in intake rate (Sutherland and Anderson 1987) and in prey availability (Beukema et al. 1993) is predicted to differ between specialists, which may affect their mortality risk during the energetically demanding winter period. Furthermore, handling risk (Rutten et al. 2006; van de Pol et al. 2009a) and disease risk (Goss-Custard et al. 1993; Norris 1999) are different for worm and shellfish- specialists, for example oystercatchers can die from handling (too) large shellfish (Hulscher 1988). The second hypothesis to explain the paradox suggests that the intake rates of different specialists are condition-dependent and thus vary between years. The payoff of specializing on shellfish is expected to be high when shellfish are abundant and/or when few other individuals specialize on shellfish (Sutherland et al. 1996). Furthermore, different types of specialist differ in their susceptibility to interference competition (Caldow et al. 1999). Short-term payoffs measured under one set of conditions consequently may not reflect long-term payoffs over a wide range of environmental conditions.

Understanding how a (culturally or genetically) heritable trophic polymorphism is maintained in nature—and particularly in oystercatchers—requires (1) that we use payoff measures that integrate both the short-term profitability and risks of specific strategies over the conditions during the entire year (i.e., annual fitness) and (2) that we quantify how these selection pressures vary over a wide range of conditions (i.e., across many years). So far, only two studies have compared survival differences among diet specialists in oystercatchers over time, resulting in mixed results from the same overwintering population (Durell et al. 2001; Durell 2007). Both male and female shellfish specialists had highest survival averaged over the years 1988–1991 (Durell et al. 2001) whereas survival of shellfish and worm specialists did not differ over the period 2002–2006 (Durell 2007). These two studies suggest that selection fluctuates between years, although sample sizes were insufficient to estimate annual viability selection gradients.

OBJECTIVES

We will investigate how phenotypic selection on bill shape varied over a period of 26 years in a breeding population of oystercatchers. Experiments and detailed observations have shown that diet specialization causes distinct variation in bill shape (Swennen et al. 1983; Hulscher 1985), implying that bill shape is a proxy for diet specialization in oystercatchers (Verhulst et al. 2004; van de Pol et al. 2009a). For each sex, we will estimate the fecundity and viability selection gradients on bill shape. Subsequently, we will quantify how fecundity and viability selection contribute to the overall annual selection gradient, using a measure of annual relative fitness suitable for age-structured populations living in stochastic environments. We specifically test the hypotheses whether variation between years in the linear (directional) and nonlinear (disruptive) component of the selection gradients on bill shape/diet specialization covaries with: (1) the frequency of specialist-types, (2) the density of conspecific competitors, (3) prey abundance and (4) general environmental conditions (which may affect the opportunity for selection; Wilson et al. 2009). Subsequently, we quantify the expected response to selection to evaluate whether the observed selection pressures can maintain the individual and sex-specific variation in bill shape and diet specialization in this population.

Methods

BILL SHAPE AND DIET SPECIALIZATION

Prey specialization in Eurasian oystercatchers is associated with distinct searching behaviors and handling techniques (Hulscher 1996). Specializing on worms requires frequent probing in the mudflats in search for these deep-buried animals. When a worm is found it can be eaten without much handling. Probing for worms results in a pointed bill shape as a result of a high rate of lateral and dorsal abrasion of the horny sheath covering the bill-tip (Fig. 1A; see also Swennen et al. 1983). Shellfish specialist search for surface-living or shallowly buried bivalves by sight and touch (Hulscher 1996). Shellfish have to be opened before the meat can be consumed, either by stabbing between the two shells to cut the posterior adductor muscle that keeps the shells closed or by hammering the shells of the bivalves until they fracture. Stabbing shellfish mainly causes lateral abrasion of the bill-tip and consequently results in a chisel-shaped bill-tip, whereas hammering shellfish causes frontal abrasion of the bill-tip and therefore results in a hammer-shaped bill-tip (Fig. 1A; see also Swennen et al. 1983).

Bill shapes are categorized by eye in the field, using both a lateral, dorsal, and frontal view of the bill-tip (Fig. 1A). Besides the three main types of bill shapes (pointed, chisel, and hammer), three mixture-types (pointed-chisel, pointed-hammer, and chisel-hammer) can be distinguished (Swennen et al. 1983). The classification of bill shapes is repeatable and bill shapes also differ in quantitative measures of the bill-tip width and depth (Fig. 1B; see van de Pol et al. 2009a for more details). Because we are primarily interested in diet specialization, we followed the approach of earlier studies (e.g., Hulscher 1985; Verhulst et al. 2004; Rutten et al. 2006) to combine chisel, hammer, and chisel-hammer bill shapes into one group called "blunt" bills (Fig. 1B), because hammering and stabbing are different techniques for handling the same prey species (Sutherland et al. 1996). Similarly, pointed-chisel and pointed-hammer bill shapes also exhibit large overlap in diet (Hulscher and Ens 1991) and were combined in one functional group called "intermediate" bills (Fig. 1B).

Birds with a pointed (P), intermediate (I), or blunt (B) bill systematically differ in their diet choice in our study population (Fig. 1C; Hulscher and Ens 1991). Birds with a P-bill mainly specialized on ragworms (*Nereis diversicolor*), whereas birds with a B-bill specialized on the bivalve Baltic tellin (*Macoma Balthica*). In addition, birds with a P-bill also fed more on deep-buried soft-shell clams (*Mya arenaria*), of which generally only the siphon can be retrieved and eaten, whereas birds with a B-bill fed more on blue mussels (*Mytilus edule*). The diet of birds with I-bills consisted of similar amounts of ragworm and Baltic tellin and was intermediate to the diets of birds with P- and B-bills. For practical reasons, we will henceforth refer to birds with P-bills as worm specialist, to birds with B-bills as shellfish specialists, and to birds with I-bills as generalists. Nevertheless, it is important to keep in mind that worm specialists sometimes also eat shellfish and shellfish specialists sometimes also eat worms, and thus the degree of individual diet specialization is gradual (Fig. 1C). As in other studies (Hulscher and Ens 1992; Durell et al. 1993), females are more likely to be worm specialist, whereas males are more likely to be shellfish specialists in our study population (Fig. 1D; van de Pol et al. 2009b).

DATA COLLECTION

From 1983 to 2008, we followed a breeding population on the Dutch Wadden Sea barrier island of Schiermonnikoog, for details on the standardized protocol see Ens et al. (1992). In short, each year we caught a substantial number of male and female breeders on the nest (on average 84 birds per year; total 2117 catches) and classified their bill shape (Swennen et al. 1983; Hulscher 1985). In addition, we followed the fecundity of these breeders (the number of fledglings produced) and recorded whether a bird was seen each year or not. Mortality mainly occurred in winter (Camphuysen et al. 1996).

POPULATION MODEL, ANNUAL FITNESS, AND SELECTION GRADIENTS

Oystercatchers are long-lived birds in which survival improves until sexual maturity (age 3) and delayed reproduction is typical (van de Pol et al. 2007). Pairs are highly territorial and socially
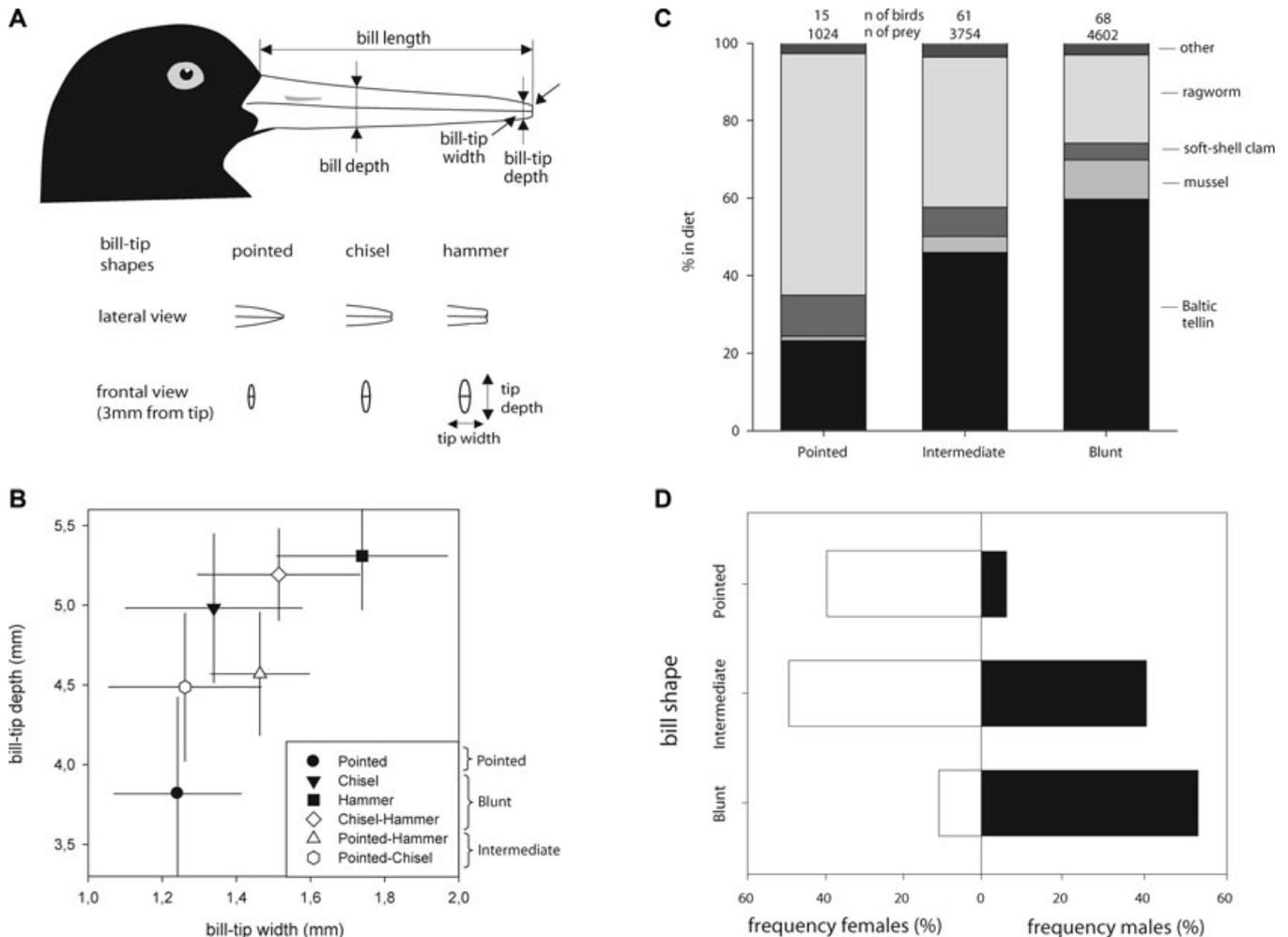
Figure 1. Types of bill shapes occurring among Eurasian oystercatchers and their relationship to diet choice. (A) Three main types of bill shape can be visually distinguished by taking a lateral, dorsal, and frontal view of the bill-tip. (B) The three types of bill shape (black symbols) and three mixture types of bill shapes (white symbols) differ in the quantitative dimensions of the bill-tip (error bars represent one SD around the mean; $n = 1429$). (C) The six types of bill shapes can be pooled into three functional groups that differ in diet (adapted from Hulscher and Ens, 1991). (D) Distribution of bill shapes for both sexes in our study.

and genetically monogamous (Heg et al. 1993). The main sources of age and stage-structure in vital rates of oystercatchers are described in the life-cycle graph of Figure 2A. For notation, we use capitals for stages (F = fledgling, O = one-year-old juvenile, T = two-year-old juvenile, N = adult nonbreeder, R = breeder), use lower case for survival s, fecundity f, stage-transition m, fledgling sex ratio g, number of individuals in a stage class n, annual fitness w, reproductive value v, year t, and use capital theta for bill shape states ($\Theta = $ P, I, and B). Stage transitions are conditional on survival; fledgling sex ratio was assumed at unity in this population ($g = {}^1/_2$; Heg et al. 2000).

We sampled the bill shape of breeders and consequently we can only investigate the effect of bill shape on fecundity and breeder survival. Potentially, diet choice also affects juvenile or nonbreeder survival, or recruitment into the breeding population

(Fig. 2A). Nonetheless, in oystercatchers, fecundity and breeder survival are the vital rates to which mean fitness is most sensitive (van de Pol et al. 2006) and these two vital rates are thus most likely to exert the strongest selective pressures (assuming that differences among specialists in other vital rates are not much larger in magnitude). To study evolutionary and ecological dynamics on the same (annual) timescale, we quantified annual fitness for (st)age-structured populations living in stochastic environments (Caswell 2001; Lande et al. 2003). This method specifically accounts for the fact that the annual contributions of fecundity ($^1/_2f$) and parental survival (s_R) to the annual fitness of breeders (w_t) have to be weighed, as the reproductive value of a fledgling (v_F) does not equal the reproductive value of a surviving parent (v_R^*):

$$w(\Theta)_t = \frac{1}{2} \times f(\Theta)_t \times v_F + s_R(\Theta)_t \times v_R^*. \qquad (1)$$
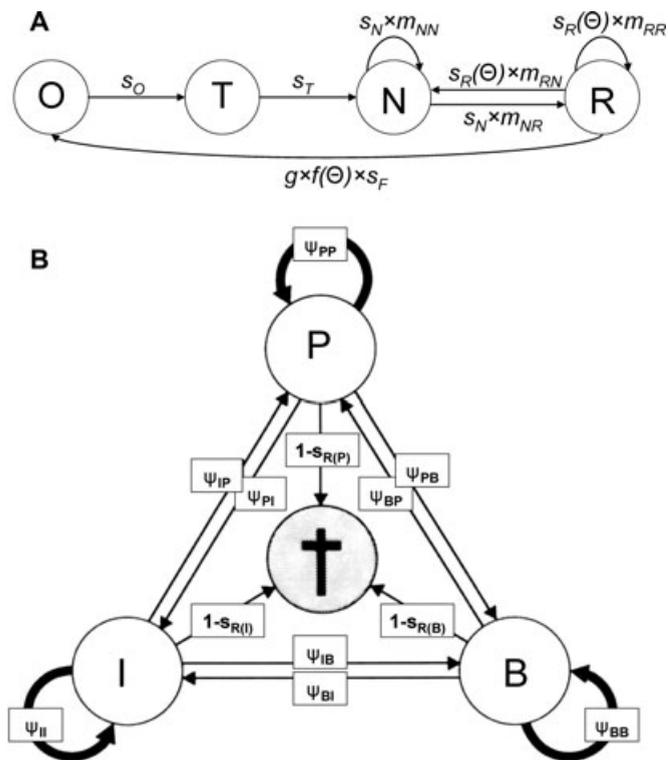
Figure 2. (A) The age and stage-structured life-cycle of oyster-catchers used to model the population dynamics (see eq. 2). Four stages are modeled explicitly (O = one-year-old juvenile, T = two-year old juvenile, N = adult nonbreeder, R = breeder), whereas fledglings (F) are not modeled explicitly in our prebreeding census model. Stage-dependent survival (*s*), reproduction (*f*), and movement between stage-classes (*m*) describe the flows between states (*g* = fledgling sex ratio). Only *f* and *s*$_R$ are assumed to depend on bill shape (Θ), see text. (B) A schematic depiction of the statistical model used to estimate state-dependent breeder survival ($s_R(\Theta)_t$) and plasticity (ψ) between bill shapes states (P = pointed, I = intermediate and B = blunt).

The life-cycle graph in Figure 2A can be written as a prebreeding census stage-structured population matrix model (Caswell 2001):

$$
\begin{pmatrix} n_O \\ n_T \\ n_N \\ n_R \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & \frac{1}{2} \times f \times s_F \\ s_O & 0 & 0 & 0 \\ 0 & s_T & s_N \times m_{NN} & s_R \times m_{RN} \\ 0 & 0 & s_N \times m_{NR} & s_R \times m_{RR} \end{pmatrix} \begin{pmatrix} n_O \\ n_T \\ n_N \\ n_R \end{pmatrix}_t .
\tag{2}
$$

From which it follows that $v_F = s_F \times v_O$ and $v_R^* = m_{RR} \times v_R + m_{RN} \times v_N$. Using parameter estimates of vital rates averaged over the study period (reflecting the average environment), stage-dependent reproductive values v_O and v_R can be calculated using standard methods (Caswell 2001). We assumed a closed population model, but rare dispersal does occur (van de Pol 2006). Because we have no reason to assume that dispersal is dependent on bill shape, we did not model dispersal explicitly and

focus on the local dynamics (i.e., we assumed emigration equaled immigration).

Selection gradients are typically expressed in terms of relative fitness (Lande and Arnold 1983) and equation (1) can be rewritten as

$$
\frac{w(\Theta)_t}{\bar{w}} = \frac{\frac{1}{2} \times f(\Theta)_t \times s_F \times v_O}{\bar{w}} + \frac{s_R(\Theta)_t \times (m_{RR} \times v_R + m_{RN} \times v_N)}{\bar{w}}
\tag{3}
$$

or more shortly as

$$
\tilde{w}(\Theta)_t = \tilde{w}_f(\Theta)_t + \tilde{w}_{s_R}(\Theta)_t.
\tag{4}
$$

Equation (4) shows how annual relative fitness of birds with a specific bill shape ($\tilde{w}(\Theta)_t$) is composed of additive contributions due to fecundity ($\tilde{w}_f(\Theta)_t$) and parental survival ($\tilde{w}_{s_R}(\Theta)_t$). We calculated annual relative fitness estimates for males and females separately, but with the exception of $f(\Theta)_t$ and $s_R(\Theta)_t$ all other parameter estimates used in the calculation of $\tilde{w}(\Theta)_t$ were assumed to be identical for both sexes, as earlier studies found little evidence for sex-differences in these vital rates (van de Pol et al. 2006).

We used quadratic regression on annual relative fitness to estimate the linear ($\beta_t^{(\tilde{w})}$; directional) and nonlinear ($\gamma_t^{(\tilde{w})}$; disruptive) component of the selection gradient on bill shape (Lande and Arnold 1983). By coding P-bills as $+\frac{1}{2}$, I-bills as 0 and B-bills as $-\frac{1}{2}$, it follows that the linear regression coefficient is given by $\beta_t^{(\tilde{w})} = \tilde{w}(P)_t - \tilde{w}(B)_t$ (representing directional selection toward P-bills) and that the quadratic regression coefficient is given by $\gamma_t^{(\tilde{w})} = 2(\tilde{w}(P)_t - \tilde{w}(I)_t + \tilde{w}(B)_t - \tilde{w}(I)_t)$ (representing disruptive selection when positive and stabilizing selection when negative). As all fitness components are additive on the same scale we can use equation (4) to derive separate expressions for fecundity ($\beta_t^{(\tilde{w}_f)}, \gamma_t^{(\tilde{w}_f)}$) and viability ($\beta_t^{(\tilde{w}_{s_R})}, \gamma_t^{(\tilde{w}_{s_R})}$) selection components, such that $\beta_t^{(\tilde{w})} = \beta_t^{(\tilde{w}_f)} + \beta_t^{(\tilde{w}_{s_R})}$ and $\gamma_t^{(\tilde{w})} = \gamma_t^{(\tilde{w}_f)} + \gamma_t^{(\tilde{w}_{s_R})}$. Note that the choice of bill shape coding does not affect our results as long as coding(P)-coding(B) = coding(I) = 0.

PARAMETER ESTIMATION

We estimated annual survival of breeders with different bill shapes ($s_R(\Theta)_t$) using a multistate mark–recapture–recovery model described in Figure 2B. Our approach involved the following steps: as previous studies (van de Pol et al. 2006, 2007, 2009c) have shown that annual resighting rate is virtually one for breeders in this intensively monitored population (breeders are resighted on average >30 times per breeding season), this means we are effectively dealing with known fate (year of death) data. However, the state of an individual (bill shape) is not known in all years. By using a multistate model, we specifically allowed for the possibility of between-year within-individual plasticity in bill shape to occur (ψ_{BI}, ψ_{IP}, etc.; Fig. 2B). In addition, we included males

and females as separate groups in the analyses to allow breeder survival and state-transitions to be sex dependent. We constructed a random effects variance components model in program MARK (White and Burnham 1999) to estimate the temporal variation in survival for male and female birds with P-, I-, and B-bills, using Markov Chain Monte Carlo methods in a Bayesian framework with uninformative priors (Cooch and White 2008). From this model, we retrieved the best linear unbiased predictors (Lynch and Walsh 1998) of $s_R(\Theta)_t$ for both males and females, which were used for further calculations of annual fitness and selection gradients.

To estimates how annual fecundity of birds with different bill shape $(f(\Theta)_t)$ varied over time for both sexes, we used a generalized linear mixed model (GLMM) in program MLwiN 2.0 (Rasbash et al. 2004). We assumed fecundity could be approximated by a Poisson distribution and modeled it as a function of sex, bill shape, and time (using random year intercepts for each type of bill shape). We assumed that the random between-year variation in fecundity followed a normal distribution on the scale of the link function used (i.e., $\log_e$). From this model we retrieved the best linear unbiased predictors of $f(\Theta)_t$ for both males and females, which were used for further calculations of annual fitness and selection gradients. All other parameter estimates used in equations (1) and and (2) were taken from van de Pol et al. (2009c).

STATISTICAL MODELS OF FLUCTUATING SELECTION HYPOTHESES

We identified a number of a priori hypotheses from the literature on Eurasian oystercatchers that predicted that the directional component of viability selection $(\beta_t^{(\tilde{w}_{s_R})})$ would depend on the sex of birds, the frequency and density of competitors, worm and shellfish abundances and on winter temperatures (including various two-way interactions). The biological hypotheses and expected directions are explained in Table 1, and were tested by jointly modeling the annual linear viability selection gradients of males and females as:

$$\begin{aligned} \beta_t^{(\tilde{w}_{s_R})} \sim\ & intercept + sex + frequency + density + worms \\ & + shellfish + temperature \\ & + frequency^*density \\ & + sex^*(frequency + density + worms + shellfish) \\ & + temperature^*(sex + frequency + density \\ & + worms + shellfish) \\ & + year_{random\ intercept} + error. \end{aligned} \tag{5}$$

We also identified a number of a priori hypotheses in the literature that predicted that the directional component of fecundity selection $(\beta_t^{(\tilde{w}_f)})$ would depend on the sex of birds, prey abundances, and on flooding events (including various two-way

interactions). The biological hypotheses and expected directions are explained in Table 1, and were tested by jointly modeling the annual linear fecundity selection gradients of males and females as:

$$\begin{aligned} \beta_t^{(\tilde{w}_f)} \sim\ & intercept + sex + worms + shellfish + flooding \\ & + sex^*(worms + shellfish) \\ & + flooding^*(worms + shellfish) \\ & + year_{random\ intercept} + error. \end{aligned} \tag{6}$$

There is no a priori reason to expect fecundity selection to be frequency or density-dependent among breeders, as we have no evidence that reproductive success is affected by intraspecific competition in our study population.

Most of the hypotheses described in Table 1 can be adapted to the case of nonlinear selection, and therefore we modeled $\gamma_t^{(\tilde{w}_{s_R})}$ and $\gamma_t^{(\tilde{w}_f)}$ similar to equations (5) and (6), respectively. In these GLMMs, year was added as a random intercept to account for the fact that selection gradients of males and females in the same year might be correlated. We assumed that both the random year effect and random residual error term were normally distributed. Model selection was performed by backward deletion of nonsignificant terms. As stepwise multiple testing can lead to bias and spurious results (Whittingham et al. 2006), we first compared the statistical significance of the full models in equations (5) and (6) against null models including an intercept, sex, and random year effect.

The annual frequency of competitors was defined as the proportion of birds with P-bills minus the proportion of birds with B-bills, which results in positive values when P-bills are most abundant, in negative values when B-bills are most common, and in values close to zero when I-bills are omnipresent. Annual population density was determined by counts of breeding territories and counts of nonbreeders at high-tide roosts (van de Pol 2006). The abundance of ragworm and Baltic tellin, the main food source of oystercatchers during the breeding season (Fig. 1C), were sampled each year at 13 sites on the local mudflats in the first week of July (van de Pol 2006). We included only prey items that are accessible to (i.e., in the top-layer of the mudflats) and selected by oystercatchers (i.e., bivalves <1 cm were excluded). As an alternative to absolute prey abundance, we also considered relative (per capita) prey abundance. Data on mean winter temperatures (December–March) were obtained from the island's weather station. Each year it was recorded whether or not a major flooding event occurred during the breeding season. All continuous temporal covariates were standardized to z-scores; missing values for prey abundances in 1983–1984 were set to zero (excluding these two years gave similar results). Flooding years were coded as $-1/2$ and years without flooding as $+1/2$; the variable sex was coded as $-1/2$ for females and $+1/2$ for males.

Table 1. Explanation of how different factors are predicted to affect the annual viability and fecundity selection gradients and in what direction, as described by the models of equations (5) and (6) in the main text.

Predictors	Expected direction	Response variable	Suggested mechanism	Hypothesized by
Sex	Negative	Viability and fecundity	♀♀ have long and slender bills that may predispose them to specialize on deep-buried worms, whereas ♂♂ have short and sturdy bills that may predispose specialization on hard-shelled shellfish	Hulscher and Ens (1992)
Frequency	Negative	Viability	Competition among same type specialists	Sutherland et al. (1996)
Density	Positive	Viability	Competition is strongest at high densities and shellfish specialists are most prone to interference competition	Goss-Custard and Durell 1988; Stillman et al. 1996
Worms	Positive	Viability and fecundity	Worm specialist do better when ragworms are abundant	Sutherland et al. (1996)
Shellfish	Negative	Viability and fecundity	Shellfish specialist do better when Baltic tellins are abundant	Sutherland et al. (1996)
Temperature	Positive	Viability	Ragworm activity is strongly reduced at freezing temperatures, whereas Baltic tellins are more cold resistant, which may favor shellfish specialist in cold winters	Goss-Custard et al. 1996; Durell 2007
Frequency × density	Negative interaction	Viability	Competition among same type specialists is strongest at high population densities	Goss-Custard and Durell (1988)
Sex × (frequency + density + worms + shellfish)	Negative interactions	Viability and fecundity	♂♂ are thought to have higher dominance than ♀♀ and thus might be less strongly affected by above-mentioned effects	Durell (2007)
Temperature × (sex + frequency + density + worms + shellfish)	Negative interactions	Viability	In warm winters, there is little opportunity for viability selection as almost all birds survive whereas in harsh winters the above-mentioned mechanisms might be more important and/or easily detected	van de Pol et al. (2009c)
Flooding × (worms + shellfish)	Negative interactions	Fecundity	In years when nesting grounds flood there is little opportunity for fecundity selection as almost no offspring fledge and effects of prey abundance might be less important and/or more difficult to detect	van de Pol et al. (2009c)

Results

FECUNDITY, SURVIVAL, AND FITNESS LANDSCAPES

The fitness landscape for males and females with different bill shapes varied substantially among years. In most years, the fecundity landscape was quite flat. However, in rare years with high fecundity, variation in fecundity among bill shapes was substantial (Fig. 3A,B). Similarly, fitness differences among bill shapes due to differences in breeder survival were strongest in years with lowest survival (Fig. 3C,D). However, the survival landscape was typically not flat in years with high survival, but exhibited a fitness peak for I-bills. In sharp contrast, in rare years with mass mortality, $\tilde{w}_{s_R}(\Theta)_t$ showed a clear fitness valley for I-bills (Fig. 3C,D). The above-described patterns were remarkably similar for females and males. Nonetheless, averaged over all years B-bills

had lowest fitness among females, whereas in males P-bills had lowest fitness (Fig. 3E,F), both in terms of fecundity and survival (Fig. 3A–D).

On average, the contribution of breeder survival to total annual relative fitness was much higher than the contribution of fecundity to total annual relative fitness $(\overline{\tilde{w}_{s_R}(\Theta)_t} > \overline{\tilde{w}_f(\Theta)_t};$ Fig. 3). This difference results from the fact that in long-lived oystercatchers breeder survival $(\overline{s_{R_t}} = 0.94)$ is typically much higher than fecundity $(\frac{1}{2}\overline{f_t} = 0.10)$ and from the fact that the reproductive value of a surviving parent is much higher than that of a fledgling $(v_R^*/v_F = 3.0)$, see equation (1). Nonetheless, this result does not necessarily imply that viability selection on bill shape is much more important than fecundity selection, as selection works on fitness differentials. In fact, variation in fecundity among bill shapes was quite large in some years (Fig. 3A,B) and
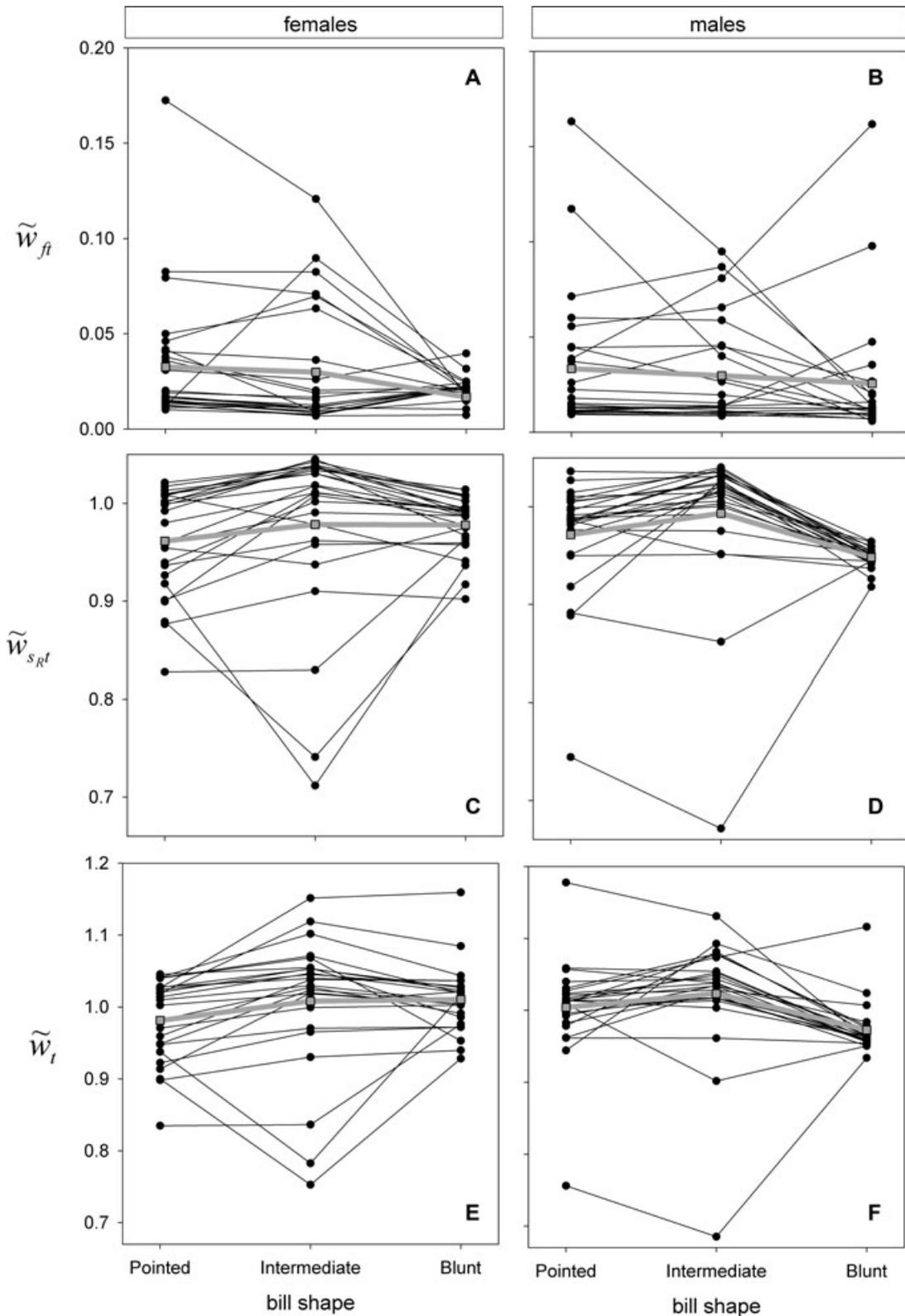
Figure 3. Annual fitness landscape for females (left panels) and males (right panels) with different bill shapes. Presented are differences among bill shapes in the contributions by fecundity ($\tilde{w}_{ft}$; panels A,B) and by survival of breeders ($\tilde{w}_{s_R t}$; panels C,D) to total annual relative fitness ($\tilde{w}_T$; panels E,F). Note that $\tilde{w}_t = \tilde{w}_{ft} + \tilde{w}_{s_R t}$ and that y-axes differ in scale. Means over the 26-year study period are depicted by gray symbols and gray lines.
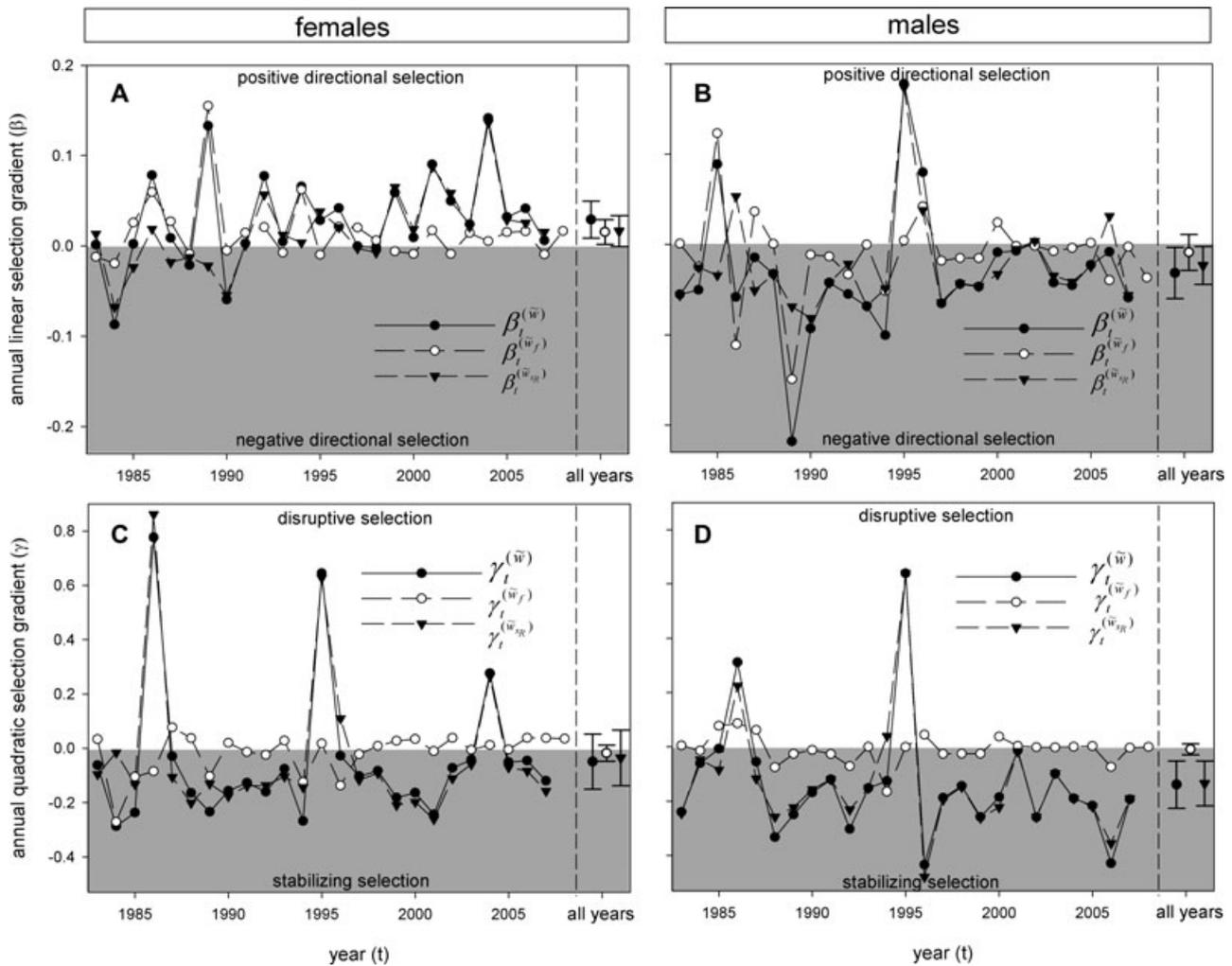
Figure 4. Annual linear (A,B) and quadratic (C,D) selection gradients over time for females (left panels) and males (right panels). When β changes sign, directional selection changes from positive (favoring pointed bills) to negative (favoring blunt bills); when γ changes sign, selection changes from stabilizing (favoring intermediate bills) to disruptive selection (favoring pointed and blunt bills). Separate estimates are plotted for selection due to differences in fecundity ($\beta_t^{(\bar{w}_f)}$ and $\gamma_t^{(\bar{w}_f)}$), differences in survival ($\beta_t^{(\bar{w}_{s_R})}$ and $\gamma_t^{(\bar{w}_{s_R})}$) and due to their combined effects on relative fitness ($\beta_t^{(\bar{w})} = \beta_t^{(\bar{w}_f)} + \beta_t^{(\bar{w}_{s_R})}$ and $\gamma_t^{(\bar{w})} = \gamma_t^{(\bar{w}_f)} + \gamma_t^{(\bar{w}_{s_R})}$). Mean selection gradients over all years are plotted in the rightmost part of each panel, with error bars representing 95% confidence intervals around the mean. Viability selection in 1983 concerns the period from the start of the breeding season in 1983 to 1984, etc.

consequently the mean linear component of fecundity selection on bill shape was of similar magnitude as the mean linear component of viability selection on bill shape over all years in females ($\left|\overline{\beta_t^{(\bar{w}_f)}}\right| \approx \left|\overline{\beta_t^{(\bar{w}_{s_R})}}\right|$; Fig. 4A), but not in males ($\left|\overline{\beta_t^{(\bar{w}_f)}}\right| < \left|\overline{\beta_t^{(\bar{w}_{s_R})}}\right|$; Fig. 4B).

Although viability selection on bill shape appears to have a distinct nonlinear component, the nonlinear component of fecundity selection contributed little to the overall nonlinear selection pressure on bill shapes (Fig 4C,D). The GLMM used to estimate how fecundity varied as a function of bill shape among years, estimated that there was little systematic variation between years in the quadratic component of the regression of bill shape on fecundity. This low variance of the nonlinear component, suggests that

fecundity selection on bill shape is mostly directional (see also Fig. 3A,B) and we therefore did not further explore interannual variation in $\gamma_t^{(\bar{w}_f)}$ henceforth.

SEX DIFFERENCES IN SELECTION

For females, there was overall directional selection for P-bills, as the linear component of both fecundity and viability selection was positive for females averaged over all years ($\overline{\beta_t^{(\bar{w}_f)}} = 0.015$, $\overline{\beta_t^{(\bar{w}_{s_R})}} = 0.016$; 95% confidence intervals (CI) did not overlap with zero; Fig. 4A). In contrast, for males there was overall directional selection for B-bills, because the linear component of both fecundity and viability selection was negative for males averaged over all years ($\overline{\beta_t^{(\bar{w}_f)}} = -0.012$, $\overline{\beta_t^{(\bar{w}_{s_R})}} = -0.023$; but 95% CI included zero for $\beta_t^{(\bar{w}_f)}$; Fig. 4B).

In both sexes, selection typically favored generalists (I-bills), as the nonlinear component of viability selection was negative (stabilizing) in 21 of 25 years. However, sometimes worm and shellfish specialist were strongly favored, because $\gamma_t^{(\bar{w}_{s_R})}$ was highly positive (disruptive) in two to three other years (Fig. 4C, D). On average, selection favored generalist more strongly in males than in females. The nonlinear selection component of viability selection was more negative for males ($\overline{\gamma_t^{(\bar{w}_{s_R})}} = -0.134$; 95% CI did not overlap with zero) than for females ($\overline{\gamma_t^{(\bar{w}_{s_R})}} = -0.035$; 95% CI included zero; Fig. 4C,D), and this sex-difference was statistically significant (paired t-test: $t = 2.5$, $P = 0.022$, $n = 25$ yearly intervals).

PREDICTORS OF ANNUAL SELECTION COMPONENTS

We found little evidence in either sex that the directional component of annual fecundity selection on bill shape was dependent on prey abundances (absolute or per capita) or flooding events (as was a priori hypothesized; see Methods). In fact, the model of equation (6) did not explain the observed interannual variation in $\beta_t^{(\bar{w}_f)}$ better than a null model with only sex-differences (Table 2A).

The model described in equation (5) explained the observed interannual variation in the directional component of viability selection significantly better than a null model with only sex-differences included (Table 2B). Nonetheless, we found little evidence in support of any of the nine a priori hypotheses (see Table 1) that tried to explain how and why $\beta_t^{(\bar{w}_{s_R})}$ varies between years (Table 2B). In contrast to the prediction that directional viability selection on bill shape is negative frequency-dependent, we found that in females (but not in males) directional viability selection for P-bills increased with the frequency of P-bills (Fig. 5A; Table 2B). Moreover, in contrast to expectation cold winters seemed to have been associated with viability selection for males with P-bills, whereas warm winters have been associated with viability selection for males with B-bills; further investigation suggested this dependency on winter temperatures was nonlinear around freezing temperatures (Fig. 5B; Table 2B).

The model described in equation (5) also explained the observed interannual variation in the nonlinear component of viability selection significantly better than a null model with only sex-differences incorporated (Table 2C). Nonetheless, the only predictor that explained any substantial amount of the interannual variation in $\gamma_t^{(\bar{w}_{s_R})}$ was winter temperature (Table 2C). In cold winters, viability selection was strongly disruptive, whereas in warm winters it was stabilizing in both sexes; and further investigation suggested this dependency on winter temperatures was also nonlinear around freezing temperatures (Fig. 5C).

RESPONSE TO SELECTION

To assess for each sex the expected response of the trait bill shape to selection, we performed a simulation experiment. We were specifically interested whether the above-reported sex-specific and fluctuating temperature-dependent selection pressures could sustain the observed intrapopulation variation in bill shapes for a substantial period of time. We modeled the response to selection by assuming a starting trait distribution as in Figure 1D, demographics as in Figure 2A, sex-differences in selection as in Figure 4, temperature-dependent viability selection as in Figure 5 and cultural inheritance of bill shape due to learning ($h^2 = 1$; Norton-Griffiths 1967a). Cultural inheritance was assumed to be sex-specific, as suggested by father–son and mother–daughter regressions of bill shape (M. van de Pol, unpubl. data). We used 100 years of historical winter temperatures to generate fluctuating selection pressures. Finally, we ignored the association found between the frequency of competitors and $\beta_t^{(\bar{w}_{s_R})}$ in females (Fig. 5A), as this is unlikely to reflect causal positive frequency-dependent selection (see Discussion).

Simulation results suggested that the observed sexual dimorphism in bill shape is quite stable over time (Fig. 6A,B), likely due to the opposite sign of directional selection pressures in males and females (Fig. 4A,B). Moreover, simulations suggested that the distribution of bill shapes within sexes is also quite stable over a period of 100 "years", especially in males (Fig. 6A,B). In females, years with extreme cold winters nonetheless are expected to cause substantial trait shifts toward P-bills (see arrows in Fig. 6A), probably due to the fact that selection is more strongly disruptive in females than in males in such years (Fig. 5C). Overall, the two coldest years were responsible for most of the systematic change in frequency of P- and I-bills over the entire century in females (Fig. 6A; 52% and 80%, respectively).

Subsequently, we considered a hypothetical scenario that assumes winter temperatures would be 1.5°C higher than observed over the last 100 years, as is (minimally) predicted by climate models (+1.5°C to +4.5°C in the year 2100; van de Hurk et al. 2006). Under this scenario, the observed intrapopulation variation in bill shapes is much less likely to persist for long, and both worm- and shellfish-specialists are predicted to gradually disappear (Fig. 6C,D).

Discussion

Variation in bill morphology among Eurasian oystercatchers is so distinct that it was once thought the various bill shapes reflected different subspecies (Salomonsen 1930). Later it was realized that bill shape variation is caused by diet specialization and co-occurs on the same feeding grounds (White and Gittins 1964; Swennen et al. 1983; Hulscher 1985). The evolution and maintenance of specialization in oystercatchers has fascinated researchers ever since, and the mystery only increased by studies showing that shellfish specialists typically have higher short-term payoffs (Goss-Custard and Durell 1988; Stillman et al. 1996;

Table 2. GLMMs of annual linear (β) and quadratic (γ) components of (A) fecundity and (B,C) viability selection gradients, see equations (5) and (6) in the Methods. Each datapoint is based on one year, with data for males and females pooled in the analyses.

Predictor	Estimate±SE	df	χ^2	P
(A) Dependent variable: $\beta_t^{(\bar{w}_f)}$ $(n=52)$[1]				
Intercept	0.003±0.007	1	0.2	0.68
Sex	−0.030±0.013	1	5.1	0.024
Worms	0.003±0.007	1	0.2	0.69
Shellfish	0.002±0.007	1	0.1	0.78
Flooding	−0.006±0.014	1	0.2	0.69
Sex × worms	−0.006±0.014	1	0.2	0.68
Sex × shellfish	−0.008±0.014	1	0.3	0.58
Flooding × worms	−0.004±0.016	1	0.1	0.82
Flooding × shellfish	−0.009±0.015	1	0.4	0.54
(B) Dependent variable: $\beta_t^{(\bar{w}_{s_R})}$ $(n=50)$[2]				
Intercept	−0.003±0.007	1	0.2	0.65
Sex	−0.040±0.009	1	17.9	<0.001
Frequency	0.018±0.007	1	6.5	0.011
Density	−0.011±0.010	1	1.3	0.26
Worms	−0.001±0.009	1	0.1	0.86
Shellfish	0.007±0.008	1	0.7	0.40
Temperature	−0.018±0.007	1	6.5	0.011
Frequency × density	0.014±0.011	1	1.7	0.19
Sex × frequency	0.018±0.009	1	3.9	0.048
Sex × density	−0.001±0.015	1	0.0	0.94
Sex × worms	0.005±0.013	1	0.2	0.70
Sex × shellfish	−0.005±0.012	1	0.2	0.66
Temperature × sex	0.027±0.010	1	7.2	0.007
Temperature × frequency	−0.001±0.010	1	0.0	0.92
Temperature × density	0.008±0.009	1	0.8	0.37
Temperature × worms	−0.016±0.011	1	2.1	0.15
Temperature × shellfish	0.008±0.007	1	1.2	0.27
(C) Dependent variable: $\gamma_t^{(\bar{w}_{s_R})}*$ $(n=50)$[3]				
Intercept	−0.081±0.036	1	5.0	0.025
Sex	−0.098±0.045	1	4.8	0.028
Frequency	0.025±0.060	1	0.2	0.68
Density	0.006±0.051	1	0.0	0.90
Worms	0.005±0.044	1	0.0	0.91
Shellfish	0.023±0.042	1	0.3	0.58
Temperature	−0.145±0.043	1	11.3	<0.001
Frequency × density	−0.011±0.050	1	0.1	0.82
Sex × frequency	−0.075±0.073	1	1.0	0.31
Sex × density	−0.013±0.062	1	0.1	0.83
Sex × worms	−0.052±0.055	1	0.9	0.34
Sex × shellfish	−0.047±0.051	1	0.8	0.36
Temperature × sex	0.022±0.053	1	0.2	0.67
Temperature × frequency	0.043±0.044	1	0.7	0.40
Temperature × density	−0.060±0.041	1	2.2	0.14
Temperature × worms	−0.073±0.056	1	1.7	0.19
Temperature × shellfish	−0.023±0.035	1	0.4	0.53

[1]Full versus null model test: χ^2=3.5, df=7, P=0.89. Intraclass correlation coefficient for the random effect year: 0.03.

[2]Full versus null model test: χ^2=34.3, df=15, P=0.003. Intraclass correlation coefficient for the random effect year: 0.30.

[3]Full versus null model test: χ^2=25.2, df=15, P=0.047. Intraclass correlation coefficient for the random effect year: 0.45.

Wanink and Zwarts 1996; Caldow et al. 1999; Durell et al. 2001; van de Pol et al. 2009a).

We showed that in contrast to the observation that shellfish specialists have highest short-term profitability, they did not have the highest mean annual fitness in either sex (Fig. 3). A high short-term profitability of shellfish specialization may have been associated with higher long-term risks (Sutherland et al. 1996), causing short-term payoffs to be a poor predictor of annual fitness. Using fecundity and survival measures to determine selection pressures is thus not only important because they represent the two major annual fitness components, but also because they are likely to be good integrators of profitability and risks of various specializations over the entire year. Our study suggests that the common approach of using short-term payoffs—such as intake rate—to make inferences about selection pressures among specialist can be very misleading.

SEX-SPECIFIC DIET SPECIALIZATION

For the first time, we have shown that selection pressures on oystercatchers' bill shapes differ between the sexes (Figs. 3 and 4), which helps us understand why females specialize most often on worms and males most often on shellfish in the wild (Fig. 1D; Hulscher and Ens 1992; Durell et al. 1993). But what causes female worm specialist to do better than male worm specialists, and not the reverse? Sex-specific diet specialization is generally associated with sex-differences in behavior, dietary requirements, or body size (Partridge and Green 1985). In oystercatchers, most behavior is strikingly similar between the sexes (roughly equal parental care and territory defense) and there is an overlap in diet composition (Fig. 1). However, other bill characteristic might predispose females to specialize on worms and males on shellfish (Hulscher and Ens 1992). Bills of females are on average 12% longer than bills of males with the same bill shape (Hulscher 1985), which might be especially useful when feeding on deep-buried prey such as ragworms and soft-shell clams (Hulscher 1996). Contrastingly, bills of males have a 4% higher bill depth than bills of females with the same bill shape; short and sturdy bills are thought to be better tools for opening hard-shelled shellfish (Hulscher and Ens 1992). Whether sex-specific diet specialization is ultimately caused by sexual selection or ecological processes (niche partitioning; Shine 1989) remains unclear, not in the least because bill size and body size positively covary (females are also 4% heavier than males).

INDIVIDUAL DIET SPECIALIZATION

In addition to opposing directional selection between the sexes (which cannot explain why individuals of the same sex differ in their diet), we showed that both the directional and disruptive component of especially viability selection was strongly fluctuating between years (Fig. 4). At first sight this result supported
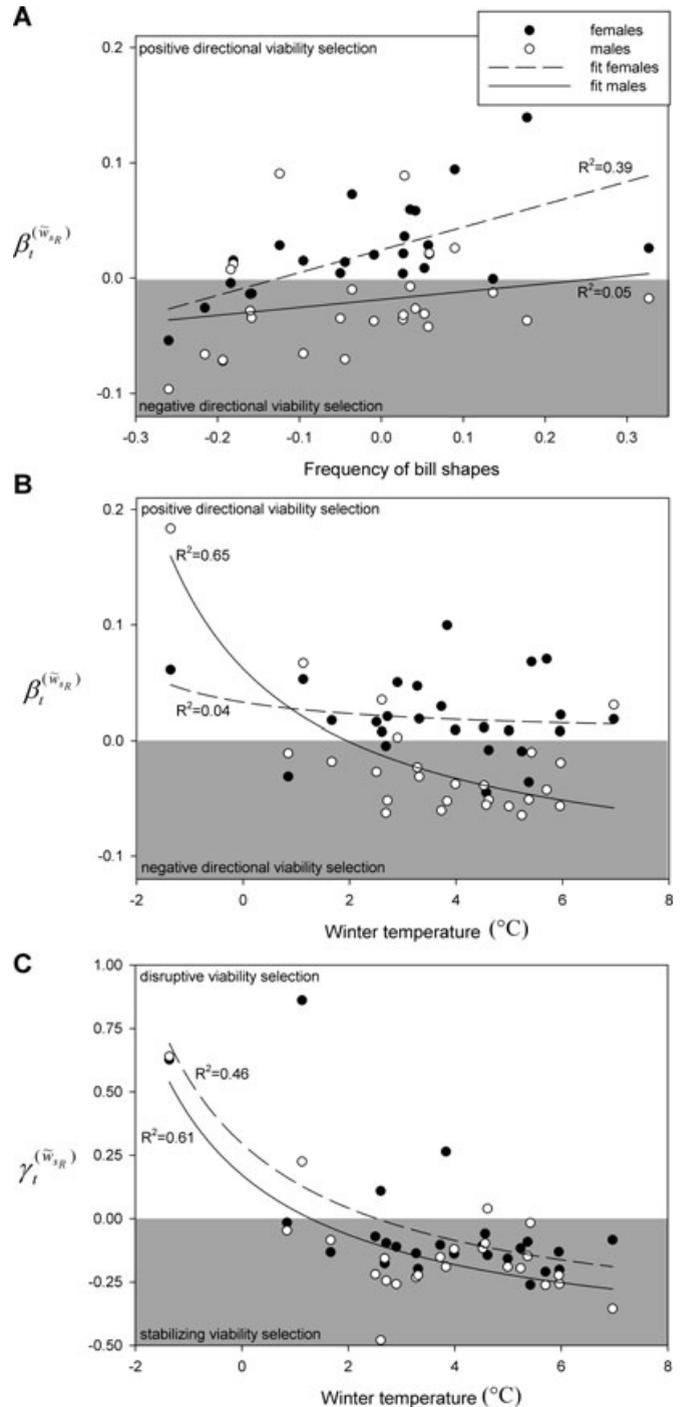

Figure 5. (A) The relationship between the annual frequency of bill shapes in the population (i.e., proportion pointed minus blunt bills) and the linear viability selection gradients. (B) The relationship between winter temperature and the annual linear viability selection gradients. (C) The relationship between winter temperature and the annual quadratic viability selection gradients. In (A) values of $\beta_t^{(\bar{w}_{s_R})}$ were corrected for effects due to winter temperature; in (B) values of $\beta_t^{(\bar{w}_{s_R})}$ were corrected for effects due to the frequency of bill shapes (see Table 2B). Fitted regression lines in (B,C) are first-order inverse functions ($y = a + b/[\text{temperature} + 4]$).
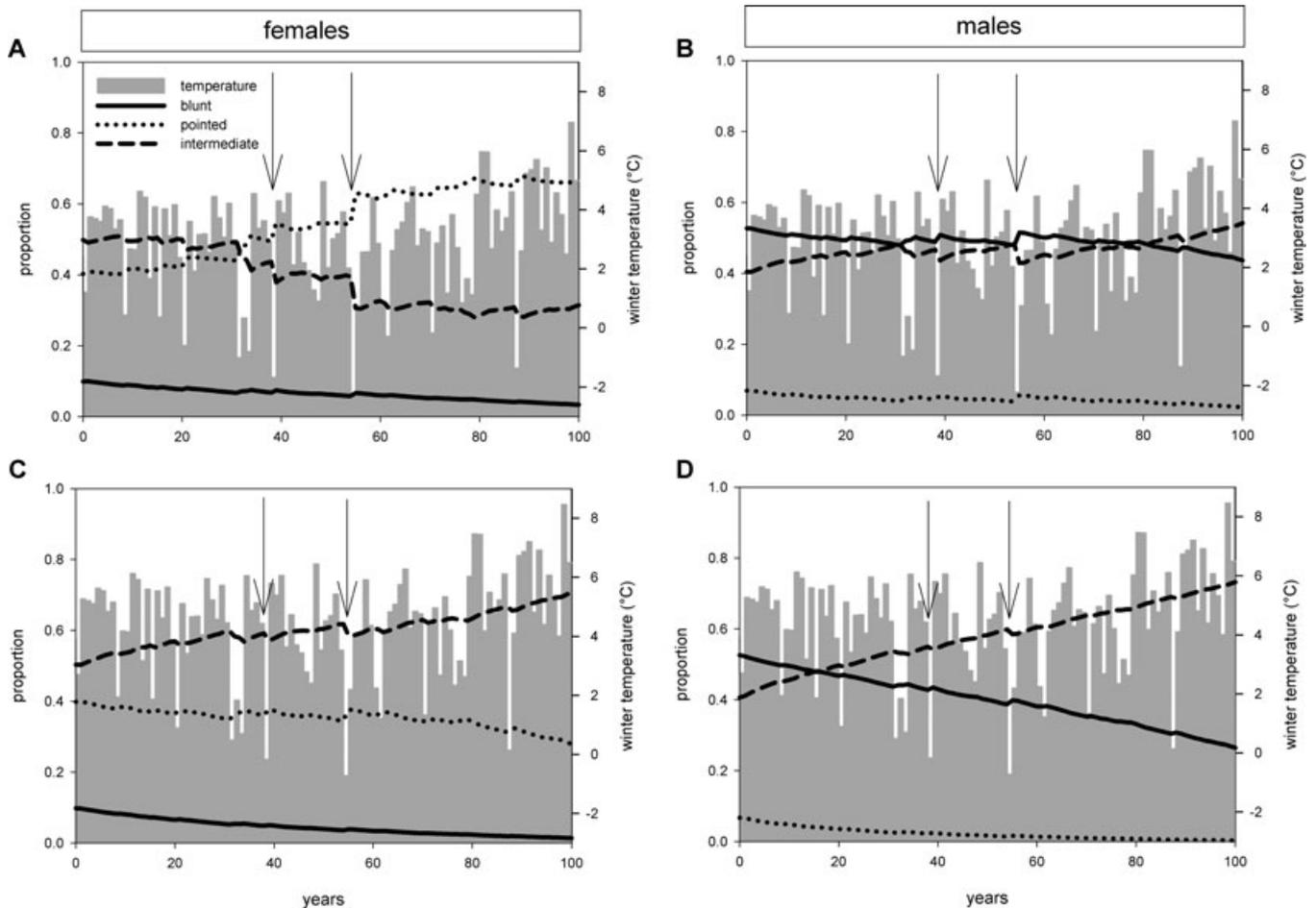
Figure 6. The predicted response of female (left panels) and male (right panels) bill shapes to sex- and temperature-dependent selection for two climate scenarios. In (A,B) the response to selection is presented for a scenario in which winter temperatures of the previous century would repeat itself in the coming century. In (C,D) a scenario is presented in which winter temperatures over the previous century would repeat itself in the next century, but the mean temperature has increased with 1.5°C, as minimally predicted by climate models for the year 2100 (van de Hurk et al. 2006). Two arrows point toward the impact of two years with extremely cold winters.

the hypotheses of previous studies that the payoffs of specialization are condition dependent. However, the specific hypotheses put forward in previous studies could not explain why selection varied between years in our study.

First, we found little evidence in favor of negative frequency-dependent selection among specialists. Instead, we showed that among females viability selection favored worm specialist in years when worm specialists were the most frequent. We have no good explanation why this positive association exists, but we do not think it reflects a causal relationship. Positive frequency-dependent selection would result in a quick fixation of one type of specialist and is thus not easily reconcilable with the trophic polymorphism observed.

Second, we found no evidence that selection was density-dependent, even though earlier studies showed that specialists differ in their susceptibility to interference competition (Goss-Custard and Durell 1988; Stillman et al. 1996). Potentially, the

breeding densities we used do not accurately reflect the competitor densities on the feeding grounds in winter, when competition for food is most fierce and mortality is highest. Nonetheless, local breeding densities were highly correlated with overwintering numbers in the entire Dutch Wadden Sea ($r_{\text{pearson}} = 0.94$, $n = 23$ years). A more likely explanation for the null result of a density effect is that densities in our population were typically too low for interference competition to be detected. Intake rates have been shown to be density dependent at our study site in the late 1970s (Zwarts and Drent 1981), but since then oystercatcher numbers have more than halved (van de Pol et al. 2009c) and interference competition has likely weakened.

Third, we found no evidence that absolute or relative (per capita) worm and shellfish abundance in summer affected the strength and direction of fecundity and viability selection among specialists. Possibly, heterogeneity in food abundance among territories obscured any effect between-year variation in food

abundance has on selection. However, we annually sampled 13 sites and 40–50% of the variation in food abundances between samples could be attributed to between-year differences (M. van de Pol, unpubl. data), making it unlikely that spatial heterogeneity completely obscured any association between annual prey abundance and selection. Potentially, viability selection is dependent on abundance of typical winter prey species (mussels and cockles *Cerastoderma edule*), for which data were lacking in this study (see also next subsection).

Fourth, we found mixed evidence for the hypothesis that the opportunity for selection is largest in years when environmental conditions are worst (e.g., Wilson et al. 2009). Although winters with mean temperatures below freezing point resulted in mass mortality, cold winters did not only affect the strength of selection, but also the direction of selection (Fig. 5A,B). Furthermore, in contrast to the hypothesis of Durell (2007) that viability selection should favor shellfish specialists most in cold winters (as shellfish are more cold resistant than worms), we found that the opposite was true for males (Fig. 5B). Finally, none of the a priori hypotheses in Table 1 predicted that viability selection would change from disruptive to stabilizing with increasing winter temperatures (Fig. 5C). It seems generalists have more difficulty reaching their daily energy requirements when conditions are most demanding. A similar conclusion was reached for sea otters *Enhydra lutris*, in which diet specialists had a higher handling efficiency than generalists under poor food conditions, but specialists nonetheless switched to a generalist diet when food was abundant (Tinker et al. 2008).

Even though the mechanism behind the temperature-dependent fluctuating selection pressures on diet specialization requires further investigation, we were able to show that such temporally varying selection pressures (stabilizing↔disruptive) can sustain the observed intrapopulation variation in bill shapes for ecologically long periods (Fig. 6A,B). The response to selection of the categorical trait bill shape was rather weak, although a direct comparison with the strength and response of selection of continuous traits in other studies is problematic due to standardization issues (Kingsolver et al. 2001). Interestingly, our study suggests that a trophic polymorphism can persist for long periods even in the absence of negative frequency- and density-dependence and dependency on resource abundance, a possibility that is typically not considered (Partridge and Green 1985; Durell 2000; Bolnick et al. 2003).

REALIZED AND FUNDAMENTAL NICHE

The realized niche and diet specialization observed in this study is smaller than the fundamental niche and types of specializations observed over the entire range of conditions that oystercatchers as a species experience. In other breeding populations various other types of shellfish-specialist (on mussels, cockles or limpets *Patella* spp.; Norton-Griffiths 1967b; Safriel 1985; Ens et al. 1996) and worm-specialists (on earthworms *Lumbricus* spp.; Hulscher 1985; Safriel 1985) occur. Mussel- and cockle-specialists were previously common in the Dutch Wadden Sea area (Swennen et al. 1983; Ens et al. 1996), but commercial over-harvesting of mussels and cockles during much of the study period (Ens 2006) is likely to have stimulated specialization on ragworms or Baltic tellin in our and other breeding populations. The low mussel and cockle stocks probably also have prohibited many individuals from switching completely to these preferred preys in winter (Hulscher 1996). This idea is supported by the observation that the distribution of bill shapes in the Dutch Wadden Sea area does not differ between summer and winter catches in recent years (van de Pol et al. 2009a), while this was the case before (Swennen et al. 1983). Thus, the current realized variation in diet specializations is quite restricted probably due to selection pressures that are at least partly anthropogenic.

RARE EVENTS AND APPROPRIATE TIMESCALES

The mean selection landscape on diet specialization was strongly influenced by a few years with extremely cold winters (Fig. 4). When studying selection pressures it thus seems crucial to measure selection over an appropriate ecological timescale during which a wide range of environmental conditions have occurred. But what timescale is appropriate? It is interesting to note that if we divide our 26-year study period in two periods of 13 years, then mean selection in males was directional in the first 13 years of study when the coldest winters occurred ($\overline{\beta_t^{(\tilde{w})}} = -0.06 \pm 0.02$), but was nondirectional in the last 13 years of study when winters were mild ($\overline{\beta_t^{(\tilde{w})}} = -0.01 \pm 0.02$). Also, mean selection in males was only slightly stabilizing in the first 13 years of study ($\overline{\gamma_t^{(\tilde{w})}} = -0.07 \pm 0.08$), but was strongly stabilizing in the last 13 years of study when winters were mild ($\overline{\gamma_t^{(\tilde{w})}} = -0.22 \pm 0.03$). Consequently, if we would have studied the selective landscape for 13 years—a period still much longer than most studies achieve—our conclusions would not only have been very different, but would also depend on the specific years in which the study was performed. Our study itself is in fact relatively short, as the mean selective landscape would still change moderately if one additional cold winter would have occurred in the 26 years under study.

An appropriate ecological timescale that includes rare, but extreme, events may also be important for understanding the mechanism by which environmental change affects the (cultural) evolution and maintenance of diet specialization. The predicted long-term response to selection in oystercatchers was primarily driven by rare years with strong disruptive selection, with the two coldest years causing over 50% of the total shift in trait values observed over a century (Fig. 6A,B). Moreover, the result that future climate change will make coexistence of diet specialists less likely

(Fig. 6C,D), is also mediated by these rare years: global warming is expected to make extremely cold winters become even rarer, resulting in less years with disruptive selection on the long-term.

Similar to our study, several others have recently shown that a reliable impression of temporal variability in fitness components requires several decades of data for perennial species (Altwegg et al. 2006; Frederiksen et al. 2008). Yet, in a meta-analysis of selection gradients Kingsolver et al. (2001) reported that all studies that published annual selection gradients had (much) less then 10 replicates. Although since then some impressive exceptions have been published on free-living animals (e.g., Nussey et al. 2005; Charmantier et al. 2008), it seems that many studies quantify selective landscapes over relatively short and potentially inappropriate ecological timescales. We suggest more care should be taken to match the timescale of evolutionary studies to the temporal variability of critical environmental conditions.

ACKNOWLEDGMENTS

LITERATURE CITED

Altwegg, R. A., A. Roulin, M. Kestenholz, and L. Jenni. 2006. Demographic effects of extreme winter weather in the barn owl. Oecologia 149:44–51.

Beukema, J. J., K. Essink, H. Michaelis, and L. Zwarts. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds. Neth. J. Sea Res. 31:319–330.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. Am. Nat. 161:1–28.

Caldow, R. W. G., J. D. Goss-Custard, R. A. Stillman, S. E. A. Le, V. dit. Durell, R. Swinfen, and T. Bregnballe. 1999. Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. J. Anim. Ecol. 68:869–878.

Camphuysen, C. J., B. J. Ens, D. Heg, J. B. Hulscher, J. Van Der Meer, and C. J. Smit. 1996. Oystercatcher *Haematopus ostralegus* winter mortality in The Netherlands: the effect of severe weather and food supply. Ardea 84A:469–492.

Caswell, H. 2001. Matrix population models. Construction, analysis and interpretation. 2nd edition. Sinauer Associates, Sunderland, MA.

Charmantier, A., R. H. McCleery, L. R. Cole, C. M. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–803.

Cooch, E. G., and G. C. White. 2008. Program MARK: analysis of data from marked individuals. 7th ed. Available at http://www.phidot.org/software/mark/docs/book/.

Durell, S. E. A. Le. V. dit. 2007. Differential survival in adult Eurasian oystercatchers *Haematopus ostralegus*. J. Avian Biol. 38:530–535.

———. 2000. Individual feeding specialisation in shorebirds: population consequences and conservation implications. Biol. Rev. 75:503–518.

Durell, S. E. A. Le. V. dit., J. D. Goss-Custard, and R. W. G. Caldow. 1993. Sex-related differences in diet and feeding method in the oystercatcher *Haematopus ostralegus*. J. Anim. Ecol. 62:205–215.

Durell, S. E. A. Le V.dit., J. D. Goss-Custard, R. W. G. Caldow, H. M. Malcolm, and D. Osborn. 2001. Sex, diet and feeding method-related differences in body condition in the Oystercatcher *Haematopus ostralegus*. Ibis 143:107–119.

Ens, B. J. 2006. The conflict between shellfisheries and migratory waterbirds in the Dutch Wadden Sea. Pp. 806–811 in G. C. Boere, C. A. Galbraith and D. A. Stroud, eds. Waterbirds around the world. The Stationery Office, Edinburgh, United Kingdom.

Ens, B. J., M. Kersten, A. Brenninkmeijer, and J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). J. Anim. Ecol. 61:703–715.

Ens, B. J., S. Dirksen, C. J. Smit, and E. J. Bunskoeke. 1996. Seasonal change in size selection and intake rate of oystercatchers *Haematopus ostralegus* feeding on the bivalves *Mytilus edulis* and *Cerastoderma edule*. Ardea 84A:159–176.

Fitzpatrick, M. J., E. Feder, L. Rowe, and M. B. Sokolwski. 2007. Maintaining a behaviour polymorphism by frequency-dependent selection on a single gene. Nature 447:210–213.

Frederiksen, M., F. Daunt, M. P. Harris, and S. Wanless. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. J. Anim. Ecol. 77:1020–1029.

Goss-Custard, J. D., and W. J. Sutherland. 1983. Feeding specializations in oystercatchers *Haematopus ostralegus*. Anim. Behav. 32:299–301.

Goss-Custard, J. D., and S. E. A. Le V.dit Durell. 1988. The effect of dominance and feeding method on the intake rates of Oystercatchers, *Haematopus ostralegus*, feeding on mussels. J. Anim. Ecol. 57:827–844.

Goss-Custard, J. D., A. D. West, and S. E. A. Le. V. dit. Durell. 1993. The availability and quality of the mussel prey *Mytilus edulis* of Oystercatchers *Haematopus ostralegus*. Neth. J. Sea Res. 31:419–439.

Goss-Custard, J. D., S. E. A. Le. V. dit. Durell, C. P. Goater, J. B. Hulscher, R. H. D. Lambeck, P. L. Meininger, and J. Urfi. 1996. How Oystercatchers survive the winter. Pp. 133–154 in J. D. Goss-Custard, ed. The Oystercatcher: from individuals to populations 1st. Oxford Univ. Press, Oxford.

Heg, D., B. J. Ens, T. Burke, L. Jenkins, and J. P. Kruijt. 1993. Why does the typically monogamous oystercatcher (*Haematopus ostralegus*) engage in extra-pair copulations? Behaviour 126:247–289.

Heg, D., N. J. Dingemanse, C. M. Lessells, and A. C. Mateman. 2000. Parental correlates of offspring sex ratio in Eurasian oystercatchers. Auk 117:980–986.

Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. Science 260:216–219.

Hulscher, J. B. 1985. Growth and abrasion of the Oystercatcher bill in relation to dietary switches. Netherl. J. Zool. 35:124–154.

———. 1988. Mussel kills oystercatcher (*Haematopus ostralegus*). Limosa 61:42–45.

———. 1996. Food and feeding behaviour. Pp. 7–29 in J. D. Goss-Custard, ed. The Oystercatcher: from individuals to populations. Oxford Univ. Press, New York.

Hulscher, J. B., and B. J. Ens. 1991. Somatic modifications of feeding system structures due to feeding on different foods with emphasis on changes in bill shape in Oystercatchers. Pp. 889–896 in B. D. Bell, ed. Acta XX Congressus Internationalis Ornithologici. New Zealand ornithological congress trust board, Wellington, New Zealand.

———. 1992. Is the bill of the male Oystercatcher a better tool for attacking mussels than the bill of the female? Netherl. J. Zool. 42:85–100.

Kingsolver, J. G., H. E. Hoekstra, J. M. Hoekstra, D. Berrigan, S. N. Vignieri, C. E. Hill, A. Hoang, P. Gibert, and P. Beerli. 2001. The strength of phenotypic selection in natural populations. Am. Nat. 157:245–261.

Lande, R. C., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population dynamics in ecology and conservation. Oxford Univ. Press, Oxford, UK.

Łomnicki, A. 1978. Individual differences between animals and the natural regulation of their numbers. J. Anim. Ecol. 47:461–475.

Lynch, M., and B. Walsh. 1998. Genetics and analysis of quantitative traits. 1st ed. Sinauer, Sunderland, MA.

Meyer, A. 1989. Cost of morphological specialization: feeding performance of the two morphs in the trophically polymorphic cichlid fish, Cichlasoma citrinellum. Oecologia 80:431–436.

Norris, K. 1999. A trade-off between energy intake and exposure to parasites in oystercatchers feeding on a bivalve mollusc. Proc. R. Soc. Lond. B 266:1703–1709.

Norton-Griffiths, M. 1967a. A study of the feeding behaviour of the Oystercatcher (Haematopus ostralegus). D.Phil. thesis, Oxford Univ., Oxford.

———. 1967b. Some ecological aspects of the feeding behaviour of the Oystercatcher Haematopus ostralegus on the edible Mussel Mytilus edulis. Ibis 109:412–424.

Nussey, D. E., E. Postma, P. Gienapp, and M. E. Visser. 2005. Selection on heritable phenotypic plasticity in a wild bird population. Science 310:304–306.

Partridge, L., and P. Green. 1985. Intraspecifc feeding specialization and population dynamcis. Pp. 207–226 in R. M. Sibly and R. H. Smith, eds. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell Scientific Publications, Oxford.

Pfennig, D. W. 1992. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionarily stable strategy. Evolution 46:1408–1420.

Rasbash, J., F. Steele, W. Browne, and B. Prosser. 2004. A user's guide to MLwiN—version 2.0. Centre for Multilevel Modelling, London.

Rutten, A. J., K. Oosterbeek, B. J. Ens, and S. Verhulst. 2006. Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers. Behav. Ecol. 17:297–302.

Safriel, U. N. 1985. 'Diet dimorphism' within an oystercatcher Haematopus ostralegus population—adaptive significance and effects on recent distribution dynamics. Ibis 127:287–305.

Salomonsen, F. 1930. Remarks on the European forms of Haematopus ostralegus L. Ibis 6:55–56.

Schindler, D. E., J. R. Hodgson, and J. F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia 110:592–600.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64:419–461.

Sinervo, B., E. Svensson, and T. Comendant. 2000. Density cycles and an offspring quantity and quality game driven by natural selection. Nature 406:985–988.

Skulason, S. L., and T. B. Smith. 1995. Resource polymorphisms in vertebrates. Trends Ecol. Evol. 10:366–370.

Stillman, R. A., J. D. Goss-Custard, R. T. Clarke, and S. E. A. Le. V. dit. Durell. 1996. Shape of the interference function in a foraging vertebrate. J. Anim. Ecol. 65:813–824.

Sutherland, W. J., and C. W. Anderson. 1987. Six ways in which a foraging predator may encounter options with different variances. Biol. J. Linn. Soc. 30:99–144.

Sutherland, W. J., B. J. Ens, J. D. Goss-Custard, and J. B. Hulscher. 1996. Specialization. Pp. 56–76 in J. D. Goss-Custard, ed. The Oystercatcher: from individuals to populations. Oxford Univ. Press, Oxford.

Svanbäck, R., and L. Persson. 2009. Population density fluctuations change the selection gradient in Eurasian perch. Am. Nat. 173:507–516.

Swennen, C., L. L. M. De Bruijn, P. Duiven, M. F. Leopold, and E. C. L. Marteijn. 1983. Differences in bill form of the Oystercatcher Haematopus ostralegus; a dynamic adaptation to specific foraging techniques. Neth. J. Sea Res. 17:57–83.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc. Natl. Acad. Sci. USA 105:560–565.

van de Hurk, B., A. K. Tank, G. Lenderink, A. van Ulden, G. J. van Oldenborgh, C. Katsman, H. van den Brink, F. Keller, J. Bessembinder, G. Burgers, et al. 2006. Climate Change Scenarios 2006 for the Netherlands. Royal Netherlands Meteorological Institute, De Bilt, The Netherlands.

van de Pol, M. 2006. State-dependent life-history strategies: a long-term studies on Oystercatchers. Ph.D. thesis, Univ. of Groningen, Groningen.

van de Pol, M., L. W. Bruinzeel, D. Heg, H. P. van der Jeugd, and S. Verhulst. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of Oystercatchers. J. Anim. Ecol. 75:616–626.

van de Pol, M., I. Pen, D. Heg, and F. J. Weissing. 2007. Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? Am. Nat. 170:530–541.

van de Pol, M., K. Oosterbeek, B. J. Ens, L. Brouwer, A. J. Rutten, S. Verhulst, J. M. Tinbergen, and M. de Jong. 2009a. Using Oystercatchers' bill shapes as a proxy for feeding specialization: more differentiation than meets the eye? Ardea 97:335–347.

van de Pol, M., K. Oosterbeek, A. J. Rutten, B. J. Ens, J. M. Tinbergen, and S. Verhulst. 2009b. Biometric sex discrimination is unreliable when sexual dimorphism varies within and between years: an example in Eurasian Oystercatchers Haematopus ostralegus. Ibis 151:171–180.

van de Pol, M., Y. Vindenes, B.-E. Sæther, S. Engen, B. J. Ens, K. Oosterbeek, and J. M. Tinbergen. 2009c. Effects of climate change and variability on population dynamics in a long-lived shorebird. Ecology, In press.

Verhulst, S., K. Oosterbeek, A. J. Rutten, and B. J. Ens. 2004. Shellfish fishery severely reduces condition and survival of oystercatchers despite creation of large marine protected areas. Ecol. Soc. 9:17

Wanink, J. H., and L. Zwarts. 1996. Can food specialization by individual Oystercatchers Haematopus ostralegus be explained by differences in prey specific handling efficiencies? Ardea 84A:177–198.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl.):120–138.

White, E., and J. C. Gittins. 1964. The value of measurements in the study of wader migration, with particular reference to the oystercatcher. Bird Study 11:257–261.

Whittingham, M. J., P. A. Stephens, R. B. Bradbury, and R. P. Freckleton. 2006. Why do we still use stepwise modelling in ecology and behaviour? J. Anim. Ecol. 75:1182–1189.

Wilson, A. J., J. M. Pemberton, J. G. Pilkington, T. H. Clutton-Brock, and L. E. B. Kruuk. 2009. Trading offspring size for number in a variable environment: selection on reproductive investment in female Soay sheep. J. Anim. Ecol. 78:354–364.

Zwarts, L., and R. H. Drent. 1981. Prey depletion and the regulation of predator density: oystercatchers (Haematopus ostralegus) feeding on mussels (Mytilus edulis). Marine Science 15:193–216.

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