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State-dependent environmental sensitivity of reproductive success and survival in a shorebird

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To understand the consequences of anthropogenic and environmental changes for wildlife populations, it is important to study how individuals differ in their sensitivity to environmental change, and whether this depends on individual characteristics. An individual's reproductive performance may provide an integrative, unidimensional proxy of an individual's characteristics. In this study, we define an individual's characteristics by three such reproductive states, namely successful-, failed-, and non-breeders in the previous year. We used a 16-year dataset of individually marked breeding Eurasian Oystercatchers *Haematopus ostralegus* to examine the inter-annual fluctuations in reproductive success and survival among breeding states, and their state-dependent sensitivity to environmental conditions. Environmental conditions included available biomass of the main prey species of breeding Oystercatchers (Ragworm, Baltic Tellin and Lugworm), tidal height which reflects one of the main causes of nest loss (flooding) and conditions that may impact the energetic requirements during incubation, such as temperature. We also included environmental variables measured in winter, including available biomass of the main winter prey species (Blue Mussel and Common Cockle) along with factors that may affect food availability and energetic requirements for homeostasis, namely bivalve weight loss, windchill, winter severity, and precipitation. Breeding birds that were successful the previous year had higher survival, and were more likely to remain successful, than failed- and non-breeders. The effects of environmental conditions acted in the same direction on reproductive success but had opposite effects on survival among the three breeding states, especially for windchill and Blue Mussel biomass. The contrasting state-dependent effects of the environment on survival thus averaged out when examining consequences for lifetime reproductive nest success (LRnS); instead LRnS was largely influenced by environmental conditions acting upon reproduction. Our study indicates that an individual's previous breeding state provides an integrative measure of heterogeneity in individuals' sensitivity of reproduction and survival to environmental change. Incorporating previous breeding state as a source of individual heterogeneity in population modelling may improve predictions of future population dynamics in a rapidly changing world.

Keywords: Individual quality, environmental change, life-history, traits

Anthropogenic environmental change has strong impacts on population dynamics and are the major contributing factors to biodiversity loss (Parmesan & Yohe 2003, Thomas *et al.* 2004, Jetz *et al.* 2007, Bellard *et al.* 2012, Urban 2015). Climate change effects, such as increasing temperatures, along with other anthropogenic changes like habitat degradation and exploitation may affect species vital rates, such as survival and reproduction, by changing inter alia resource availability or metabolic energy costs (Parmesan *et al.* 2000, van de Pol *et al.* 2010a, Reichert *et al.* 2012). For instance, climate change effects like warmer winters or prolonged droughts may result in lower reproductive performance and survival leading to declines in populations of birds (van de Pol *et al.* 2010b, Abadi *et al.* 2017), amphibians (McMenamin *et al.* 2008, Griffiths *et al.* 2010) and fish (Trape 2009).

The impact of environmental change may vary among individuals due to differences in individual sensitivity to stochastic weather conditions and to fluctuations in resource availability (Barbraud & Weimerskirch 2005). Individual heterogeneity in environmental sensitivity may be especially evident during adverse environmental conditions (Stearns 1992, Barbraud & Weimerskirch 2005, Tavecchia *et al.* 2005, Jenouvrier *et al.* 2015). Quantifying how individuals vary in their response to environmental change has often taken an individual quality perspective. In these studies, phenotypic characteristics of individuals like body mass, body size, telomere length or other physiological measurements were used to determine heterogeneity in individual sensitivity of survival and reproductive success to environmental change (Barbraud & Weimerskirch 2006, Weladji *et al.* 2008, Clark 2009, Hamel *et al.* 2009, Bauch *et al.* 2013, Le Vaillant *et al.* 2015, Angelier *et al.* 2019). However, defining individual quality is challenging, in part due to interactions between traits leading to opposing results when using only a single trait (Wilson & Nussey 2009, Lailvaux & Kasumovic 2011). In addition, it is challenging to measure all involved traits and advanced methods are required to combine these into an index that adequately defines individual quality (Wilson & Nussey 2009, Frauendorf *et al*. 2021).

Instead of defining individual quality by specific quantitative traits, an individual's previous breeding status may capture aspects of individual heterogeneity that phenotypic trait measures like body condition do not (e.g. Barbraud & Weimerskirch 2005). For instance, successful breeders may acquire and allocate more resources than unsuccessful or non-breeders and are therefore more likely to survive and successfully reproduce in a subsequent breeding season, independent of environmental conditions (van Noordwijk & de Jong 1986, Hamel *et al.* 2009, Jenouvrier *et al.* 2015, Kennamer *et al.* 2016, Dalessi *et al.* 2021). Given life history theories, one may expect a negative relationship between an individual's previous breeding status and its future survival or reproduction, as the cost of reproduction hypothesis predicts a negative trade-off among life-history variables (Williams 1966, Reznick 1985). However, subsequent research has indicated that trade-offs may be masked by individual heterogeneity (van Noordwijk & de Jong 1986, Hamel *et al.* 2009, Jenouvrier *et al.* 2015, Kennamer *et al.* 2016, Dalessi *et al.* 2021). The proportion of the population with consistently high reproductive performance, may thus have important implications for population growth rates under a changing frequency of unfavourable conditions induced by environmental change.

The Eurasian Oystercatcher *Haematopus ostralegus* is an example of a long-lived shorebird that exhibits individual heterogeneity in reproductive performance. Various characteristics of individual heterogeneity have been used to describe variation in reproductive performance of Oystercatchers, including territory quality (Ens *et al.* 1992, van de Pol *et al.* 2010b), laying date (Ens & Cayford 1996), age (van de Pol & Verhulst 2006), and pair-bond duration (van de Pol *et al.* 2006). Laying date and nest site choice show strong consistent individual heterogeneity that changes with age, breeding experience and pair-bond duration, and in turn help explain variation in nest success where the major causes of failure are flooding and predation, mainly by avian predators such as Common Gulls *Larus canus* and Herring Gulls *L. argentatus* on the Dutch Wadden Sea islands (Bailey *et al.* 2017, van de Pol *et al.* 2006, van de Pol & Verhulst 2006). Earlier nests have a lower flooding risk, as flooding mostly occurs late in the season whilst individuals choosing nest sites with higher elevation also have a lower flooding risk (Bailey *et al.* 2017). Predation risk is highest during the egg laying phase as both parents are regularly absent from the nesting site (van de Pol *et al.* 2014). Parents that can reduce time away from the nest can thus have higher nest survival, through for example foraging efficiently or occupying territories adjacent to the intertidal feeding grounds (Ens *et al.* 1992, Schwemmer *et al.* 2017). Given the suite of characteristics that define individual heterogeneity in reproductive performance, and its implications for population viability, it is important to understand how successful individuals are able to cope with environmental change. Understanding the sensitivity of Oystercatchers to changing environmental conditions is especially pertinent given that the species has experienced a dramatic decline in recent decades (Ens *et al.* 2011). Poor breeding success has been described as an important driver for the decline (van de Pol *et al.* 2014). In addition to poor breeding success, adult survival probability has also declined in recent years (Allen *et al.* 2019). Identified causes of the population declines are poor breeding success related to climate change impacts including increasing temperatures and sea level rise (van de Pol *et al.* 2010a,b), and low survival probability due to the loss of feeding resources from mechanical shellfisheries based on data from 1983–2008 (Smit *et al.* 1998, Ens *et al.* 2011). Despite a moratorium on mechanical shellfisheries in the Wadden Sea since 2004, Oystercatcher numbers have continued to decline (van de Pol *et al.* 2014). It is therefore imperative to understand how changing environmental conditions are impacting survival and reproduction and to understand individual heterogeneity in sensitivity to environmental change.

Based on data from 2002–17, we investigate how reproductive success and survival are affected by more recent changes in environmental conditions and importantly the individual heterogeneity in sensitivity to these changing conditions. Environmental conditions may not only have direct effects on Oystercatchers, for example due to weather conditions, but also indirectly by impacting the food stocks that Oystercatchers rely upon (van de Pol *et al.* 2010b). Previous research has shown how climate change negatively impacts fecundity but that these impacts may be offset by higher adult survival due to milder winters (van de Pol *et al.* 2010b). However, recent research indicates that adult survival has actually declined in recent years (Allen *et al.* 2019) and highlights the need for an up-to-date understanding of how reproduction and survival are being impacted by environmental change and investigate possible heterogeneity of individual sensitivity to environmental change. We incorporate individual heterogeneity in sensitivity to changing environmental conditions by using an individual's previous reproductive success, i.e. does survival and future reproductive success vary amongst non-breeders and failed or successful breeders, sensu Jenouvrier *et al.* (2015). We predict that successful breeders in the current year have a higher probability of breeding successfully in the next year and are less sensitive to changing environmental conditions, due to their possible dominance in acquiring food sources even during adverse conditions.

METHODS

Study area and studied species

Oystercatchers have been studied on Schiermonnikoog (53^{o}29' N, 06^{o}40' E) since 1983 (Ens *et al.* 1992) but our study focuses on the period of 2002–17. Schiermonnikoog is part of the Dutch Wadden Sea, which is an internationally protected intertidal area. Oystercatchers have been ringed with unique colour codes on Schiermonnikoog, which are identifiable at a range of ~200 m (Ens *et* *al.* 1992). Ongoing research projects and ringing operations mean that a high proportion of breeders have colour-rings (~90% of the breeding and ~10% of nonbreeding birds).

The Oystercatcher is a medium-sized long-lived shorebird with annual survival probability of ~90% (Durell 2007, Duriez *et al.* 2012), although survival probability may vary among seasons and areas (Allen *et al.* 2019). During the breeding season, both parents defend territories and equally share parental care. Individuals form long-term pair bonds and show high breeding site fidelity (Ens *et al.* 2014). Winter site fidelity is also high, however, during cold spells individuals may move to other regions (van de Pol *et al.* 2014). Oystercatchers on Schiermonnikoog are largely resident, i.e. the majority of the population tend to overwinter on Schiermonnikoog (Allen *et al.* 2019).

Reproduction and survival data

We used capture-mark-recapture and/or resighting data of 636 individual Oystercatchers breeding at least once between 2002–17. Nest searches were performed from start of May until late July and were checked approximately every three days, with daily checks around hatching. Each nest was given a unique ID and the geographical position was measured using GPS devices. Per nest, the clutch size and the number of hatchlings were recorded during the nest checks and the parents and fledged chicks were observed from hides; fledged chicks are dependent on their parents for food and are therefore easily observed when following their parents. Observational data of colour-ringed Oystercatchers were obtained from an online database portal (WaderTrack; www.wadertrack.nl). Dead recovery data (n = 77) were available from the Dutch Centre for Avian Migration and Demography.

Environmental covariate data

Environmental covariate data were collated for two principal time periods in relation to the annual cycle of the Oystercatcher. The winter period (December–March) spans a period when weather conditions and food availability may directly impact survival or have carry-over effects on reproduction. The incubation period (May–June) specifically considers the incubating phase when environmental conditions may directly influence nest success, i.e. eggs hatching. As described in the next section, our study defines an individual's reproductive success based on at least one egg hatching, i.e. nest success. We did not consider environmental conditions during the chick-rearing phase (June–July) due to the extremely low fledgling production during the study period.

During winter, we considered six environmental covariates that were related to weather conditions and food availability. Variables describing food availability included Common Cockle *Cerastoderma edule* and Blue Mussel *Mytilus edulis* biomass, which are among the principal food sources of Oystercatcher and may impact both survival and reproduction (Hulscher 1996, Table 1). Mussel and cockle data were obtained from survey data performed by Wageningen Marine Research (Troost *et al.* 2017). We also created an index, the bivalve weight loss (BWL) index, to account for how mussels and cockles may lose biomass during winter due to warm sea temperatures (Zwarts 1991). The bivalve weight loss index was based on the monthly percentage of ash-free dry biomass (AFDM) weight loss per increase of daily sea water temperature in degrees Celsius in the period November–February using the weight loss function for cockles and mussels (Zwarts 1991). The index was calculated by summing these monthly values, such that higher values indicate years during which bivalves lost more weight.

Variables describing the weather conditions included temperature and precipitation during winter given how these variables may influence food availability and directly affect the energy required for homeostasis of adult birds (Goss-Custard 1984, Camphuysen *et al.* 1996). Higher temperatures reduce the energy requirements for homeostasis, whilst bivalves will lose more weight due to warmer sea temperatures. Precipitation impacts energy requirements for homeostatis, but also food availability via bivalve larvae distribution and cockle mortality (Folmer *et al.* 2014, Kristensen 1958). Precipitation was included by calculating precipitation anomalies over the period 2002–17 from the average precipitation per month for the winter period over the period 1980–2010 (KNMI 2018a), whereas winter temperature was incorporated through a winter severity index. Winter severity has previously been described as an important environmental factor impacting survival of Oystercatchers (van de Pol *et al.* 2010a, b). We estimated winter severity based on the frequency of cold days between 1 December and 31 March, which was previously found to affect Oystercatcher survival (Camphuysen *et al.* 1996). In this index, days with mean temperatures below -10^{o}C counted for three points, days between -10^{o}C and -5^{o}C for two points and days between -5^{o}C and 0^{o}C for one point and tallied the total points per winter (IJnsen 1991). Additionally, we considered a windchill index to investigate the combined effects of low winter temperatures and high wind speeds given the additional energy requirements of high windchill (Wiersma & Piersma 1994). In this index, the daily wind speed in meters per second was divided by the minimum daily temperature in degrees Celsius and averaged over December–

February per winter. All weather data were collected from the weather station in Lauwersoog, eight kilometres south of Schiermonnikoog (53°41’ N, 06°20’ E).

During the incubation period, we considered five environmental covariates related to weather, flooding risk and food availability. Flooding risk has previously been described as important environmental factor impacting the reproduction of Oystercatchers (van de Pol *et al.* 2010a, b). Flooding risk was determined by estimating the maximum tidal height during the incubation period (May–June) using tidal height data from the Dutch Ministry of Infrastructure and Water Management (Rijkswaterstaat 2018). To describe the weather conditions, we calculated the average temperature for the incubation period (May–June) and precipitation was quantified by calculating precipitation anomalies over the period 2002–17 from the average precipitation per month during incubation over the period 1980–2010 (KNMI 2018a). Precipitation could increase the energetic cost for homeostasis and extreme precipitation events may inundate which may cause nest losses. Low temperatures increase the energetic requirements for homeostasis and reduce the foraging time as the incubated eggs cool more quickly.

We included two variables that describe food availability during the reproduction season, namely Ragworms *Hediste diversicolor,* and a combined variable of Baltic Tellin *Limecola balthica* and Lugworms *Arenicola marina* (van de Pol *et al.* 2010b). Oystercatchers heavily rely upon these prey species during the breeding season (Bunskoeke *et al.* 1996). Annual surveys of Ragworm, Baltic Tellin and Lugworm biomass were performed at the end of June by taking three samples every 50 m along a transect of 500 m perpendicular to the shoreline at the local intertidal flats. All food variables were converted into AFDM using standard flesh-to-shell ratios of 0.13 g/individual for Common Cockles (average 22.3 kJ g^{-1} AFDM), 0.05 g/individual for Blue Mussels (average 23.4 kJ g^{-1} AFDM, Zwarts and Wanink 1993, Zwarts *et al.* 1996), 0.04 g/individual for Ragworm (average 22.3 kJ g^{-1} AFDM), 0.04 g/individual for Baltic Tellin (average 22.0 kJ g^{-1} AFDM) and 0.06 g/individual for Lugworm (average 22.1 kJ g^{-1} AFDM, Zwarts & Wanink 1993).

State-dependent survival and reproduction

We investigated how survival to and reproductive success in year $t + 1$ were related to an individual’s breeding state in year t. We defined the breeding state according to the individual’s reproductive performance (Nichols *et al.* 1994). The three breeding states consisted of successful breeders (S), failed breeders (F), and non-breeders (N). The breeding states were determined from reproduction data and additional observational data from WaderTrack (www.wadertrack.nl). The classification was based on adult birds, i.e. birds above the age of three, that in year *t* either did not attempt to breed (N), and from those that bred, failed to hatch at least one egg (F) or successfully hatched at least one egg (S). The breeding state was based on nest success, i.e. nests hatching at least one egg, instead of whether any chicks fledged. The percentage of parents on Schiermonnikoog successfully fledging at least one chick has been low during the study period, averaging 9% in comparison to nest success which averaged 35%. In some years, 98% of breeders failed to fledge a chick meaning there would be no individual heterogeneity in reproductive success to analyse. In contrast, nest success was higher and never fell below 14%. In addition, low nest success has been shown to be one of the main drivers of population decline (Allen et al. *in press*) and the principal causes of nest failure (predation and flooding) occur during the incubation phase. Given the intense level of fieldwork and the high site fidelity of Oystercatchers, possible misclassification of non-breeders is expected to be very low.

We used a multi-state live-dead recovery model (Lebreton *et al.* 1992, Brownie *et al.* 1993) to estimate how survival varied among the three breeding states, and how reproductive success in year *t* + 1 depended upon the breeding state in year *t*, which is estimated by the transition probabilities of the multi-state model (Nichols *et al.* 1994). We subsequently investigated how inter-annually varying environmental conditions may influence the state-dependent survival and transition probabilities. Given the high site fidelity, we assumed that the birds were exclusively breeding on Schiermonnikoog, and the intensive level of fieldwork meant that if an individual was breeding then it was assumed to always be observed (van de Pol *et al.* 2006, 2007). This was confirmed when estimating the resighting probability of breeders, which was close to one in most years (average resighting probability of 0.97 for breeders). We therefore fixed the resighting probability of breeders to one to avoid issues of parameter identifiability resulting from parameter estimates being near the boundary, i.e. 0/1 (White & Burnham 1999). Colour-ringed Oystercatchers that had no territory record in year *t* but were seen on a high-tide roost during the breeding season, were assumed to be not breeding and were classified as a non-breeder (N) in year *t*. The sampling period for resightings of breeding and non-breeding birds was March–July, while the time interval of the model was one year. Non-instantaneous sampling may bias model outputs, however previous research has indicated that non-instantaneous sampling (including more observations) may actually improve the precision of model estimates (O'Brien *et al.* 2005). The period for dead recoveries was from the start of the breeding season to the start of the next breeding season, which is also the period when Oystercatchers experience the highest mortality, especially Oystercatchers breeding in coastal areas (Camphuysen *et al.* 1996, Allen *et al.* 2019).

Model selection

We first investigated time-based model structures to identify how survival and reproduction varied during the study period and thus determine the best performing temporal linear model structure for survival, resighting, dead recovery, and transition probabilities, and how these varied across the three breeding states. We considered three temporal variables: a) an intercept only model, i.e. no temporal variation, b) a trend of time (T), and c) time-dependent estimates for each year (t). Model selection was based on the Akaike Information Criterion (AIC), with a weighted penalty for smaller sample sizes (AICc). We used the change in AICc to evaluate whether other models significantly improved the data fit (Lebreton *et al.* 1992).

Once we had identified the top performing model using time-based variables, we identified the best performing model that contained environmental covariates for survival and transition probabilities. We formed a-priori hypotheses about which environmental variables may influence survival or transitions among the breeding states (Table 1). Given the number of years in our study (15 years), we limited the number of environmental variables to a maximum of three (Table 1). We also considered simpler models that included a single variable or a combination of two variables from those shown in Table 1. An interaction term for breeding state (i.e. stratum) was included with the environmental covariate to determine if the effect of environmental covariates differed among breeding states (Table 2). Prior to the multi-state mark-recapture analysis, we determined the collinearity between all environmental covariates using a Pearson Correlation matrix for multi-model selection (Grueber *et al.* 2011). The correlation between winter severity index and bivalve weight loss, winter severity index and precipitation during winter and the correlation between precipitation during winter and bivalve weight loss was above or close to 0.70 ($R = 0.71$, $R = 0.61$, and $R = 0.67$, respectively) and therefore these variables were never included within the same model to avoid issues with collinearity.

To estimate state-dependent transition probabilities to $t + 1$ for an individual with breeding state t, the reproductive success at time $t + 1$ may depend on its breeding state at time t and upon the environmental conditions it experiences during the incubation period at $t + 1$. Breeding state transition probabilities from t to $t + 1$ were therefore related to environmental conditions during the incubation period at $t + 1$. All three a-priori chosen models for the incubation period included tidal height and temperature. High tides may strongly impact population viability of Oystercatchers (van de Pol *et al.* 2010a, b) and temperature during incubation may affect the time spent incubating and foraging, as during lower temperatures the eggs lose more heat when the adults are foraging whilst the adult requires more energy for homeostasis (Goss-Custard 1984, Camphuysen *et al.* 1996). The other variables included in the incubation period were two variables related to food availability (Ragworm and Baltic Tellin/Lugworm) and one related to weather (precipitation; Table 1). Incubation variables (May–June) were only related to transition probabilities amongst breeding states. These include the non-breeding state, given that the average laying date of the populations is in the latter part of May and therefore conditions during this period could impact breeding probability (van de Pol *et al.* 2010a, b; Table 1).

All five a-priori chosen models for the winter period included the principal food source of Oystercatchers during this period, Common Cockles, given its previously described importance for survival and reproduction (Hulscher 1996; Table 1). Each of the five a-priori chosen models also included a variable describing the severity of the winter (winter severity, windchill, bivalve weight loss; Table 1). The final variables in the models for the winter period alternated between a secondary weather variable (precipitation) or a variable related to food availability (Blue Mussels). Winter period variables (December–March) were related to survival, and also transitions among breeding states given possible carry-over effects from the winter to the breeding season (Ens *et al*. 2014; Table 1). State-dependent transitions from time t to $t + 1$ were therefore also related to environmental covariates measured in the winter between t and $t + 1$. Survival was only related to environmental variables in the winter period because Oystercatchers experience the highest mortality in this period, especially Oystercatchers breeding in coastal areas (Camphuysen *et al.* 1996, Allen *et al.* 2019; Table 1).

We ranked models using AICc to identify which of the two key periods (Winter, Incubation), and associated weather and food variables, provided the best model fit for explaining variation in survival, and the probability of transitioning among breeding states. In the case of survival model selection, a number of models provided support, i.e. several models were within ΔAICc = 10. We extracted the beta estimates and standard error from each model and model-averaged these using the R-Package *MuMIn* (Barton 2018). We estimated full model-averaged coefficients, such that if a parameter did not appear in a model then it was assigned a zero. The models were averaged based on the Akaike weights. The model averaged parameters were used in later analyses to assess population level effects of environmental change (see below). Given the influence of territory quality on reproductive success, we also replicated the analysis above, but included an individual covariate signifying whether an individual bred in a low- or high-quality territory. Territory quality did not influence results, but are available in Supporting Information Appendix S1.

To compare the performance of environmental covariates in relation to the top performing time-based model, we used the AIC difference and additionally calculated the amount of variation (R^2) explained by the covariates as:

$$R^2 = \frac{DEV(constant) - DEV(covariate)}{DEV(constant) - DEV(time)} \qquad \text{Equation 1}$$

where DEV is the deviance, covariate represents model structures containing either the time-based models or those with environmental covariates, constant is a constant model without covariates and time is the full time-dependent model (Skalski *et al.* 1993, Grosbois *et al.* 2008). The constant model was an intercept-only model for survival and transition probabilities, but we kept the time-based structure for resighting probabilities and dead recoveries. In this way, we only examine explained variation for the survival and transition probabilities of the multi-state model. Goodness-of-fit was not tested, as there is no goodness-of-fit test developed for multi-state mark-recapture models in MARK (White & Burnham 1999).

The multi-state mark-recapture models were constructed in R-Package *RMark* (Laake 2013) and were run in program MARK version 6.2 (White & Burnham 1999). For descriptive purposes, the average transition probability per breeding state over our study period, based on the top performing time-based model, was estimated using function *par.avg* of the R-Package *MuMIn* (Barton 2018), which estimates the average coefficient over the yearly transition estimates and standard errors based on the model averaging theory by Burnham and Anderson (2002). The analyses were performed in R version 3.4.1 (R Core Team 2017).

Population-level effects of environmental changes

We ran iterative simulations to study the consequences of the fitted multi-state mark-recapture models for the lifetime reproductive nest success (LRnS), which is based on the model predictions of nest success (at least one egg hatching), rather than the more commonly used lifetime reproductive success (LRS), which is the number of offspring produced. We identified the stable state distribution (Successful-, Failed-, Non-breeder) of the combined survival and transition parameters which we applied to a starting population of 500 individuals. Each of 1000 stochastic simulations started with this initial population size, and each simulated year consisted of (breeding) state-specific survival and transition probabilities given the state of the environment, which were based upon the model coefficients and their standard errors, i.e. the model predictions. We identified the average number of times that an individual was successful within its lifetime independent of environmental conditions, i.e. a baseline scenario. We then re-ran the simulations but incorporated the influence of environmental covariates on either survival or reproduction rates, in which we used the range for a particular covariate whilst including the mean value for other covariates. In each case, we extracted the mean LRnS to compare how environmental conditions influence LRnS in comparison to the baseline scenario. Population simulations of LRnS were performed using the R-Package *popbio* (Stubben & Milligan 2007).

RESULTS

Breeding population

During the entire study period (2002–17), the breeding status was known for an average 264 (sd = ± 58.96) Oystercatchers per year (min = 120, max = 317). Approximately 70% of these were breeders, whilst the remaining 30% were non-breeders. Nest success averaged 29% (sd = ± 5.64) during the study meaning that almost two in every three nests failed to hatch at least one egg.

Breeding state specific survival and reproduction

Reproductive success varied considerably among years and the breeding state in time $t + 1$ was strongly linked to the breeding state at time t (Table 2 & Table S1 in Supporting Information Appendix S2), as suggested by the top time-based capture-mark-recapture multi-state model. Although the probability of breeding successfully varied over time (Fig. S1 in Supporting Information Appendix S2), successful breeding birds at time t tended to have a higher probability of breeding successfully at time $t + 1$ compared with failed breeders and non-breeders (Fig. 1 & Table 2). Once a failed breeder, the probability to transition back to the successful breeding state was also lower compared to successful breeders ($\psi_{FS} = 0.25 < \psi_{SS} = 0.42$; Fig. 1). Individuals that did not breed in year t had a low probability of entering the breeding population in year $t + 1$ (Fig. 1). When these individuals did attempt to breed, the attempt usually failed ($\psi_{NF} = 0.22 > \psi_{NS} = 0.08$; Fig. 1). Breeding birds had similar annual survival probabilities (Fig. 2; $\Phi_S = 0.95 \pm 0.04$ se,

$\Phi_F = 0.93 \pm 0.05$ se), whilst non-breeder survival was lower ($\Phi_N = 0.90 \pm 0.09$ se) as suggested by the top time-based capture-mark-recapture multi-state model (Model 6 in Table 2 & Table S2 in Supporting Information Appendix S2). The lower non-breeder survival is in part due to a declining non-breeder survival from 2011 onwards (Fig. 2).

Environmental effects on reproduction

Reproductive success was most sensitive to Ragworm biomass, average temperature over May and June, and tidal height which together explained 68% of the variation (Model 13 in Table 2). Any combinations of these three environmental variables were always more important than other models that were considered, and also the effects of each variable singularly or a combination of two environmental variables (Table 2 & Table S1 in Supporting Information Appendix S2). The direction of the effect of all environmental variables on the transition probability to the successful state (conditional on survival) was similar for individuals in different previous states, but the effect size and statistical significance varied for non-, failed, and successful breeders (Fig. 3 & Table S3 in Supporting Information Appendix S2). Average temperature in May and June decreased the probability of subsequent breeding success of successful breeders and non-breeders (Fig. 3 & Table S3in Supporting Information Appendix S2), but did not significantly affect the probability of breeding success of failed breeders (Table S3 in Supporting Information Appendix S2). Ragworm biomass significantly increased probability of becoming successful for all breeding states (Fig. 3). Whilst tidal height increased the probability of becoming successful for all breeding states, these effects were not significant (Fig. 3). The results for how environmental conditions affect all other transitions are shown in Figs. S2-S4 and Table S3 in Supporting Information Appendix S2.

Environmental effects on survival

Two models explaining variation in survival received significant support (Models 7 & 8 in Table 2), which contained the variables of windchill, Blue Mussel and Common Cockle (Fig. 4). However, several models were within ΔAICc = 10 and could thus be considered (Models 9–19 in Table 2 & Table S2 in Supporting Information Appendix S2). After model averaging, none of the environmental variables were significantly impacting any of the breeding state-specific survival probabilities, i.e. the confidence intervals overlapped zero (Fig. 4 & Table S3 in Supporting Information Appendix S2). Despite the large confidence intervals, model selection results provided clear support for breeding state-specific relationships between survival environmental conditions: including an interaction term between breeding state and the environmental covariates always provided an improved model fit compared with a model that did not include the interaction (Table 2 & Table S2 in Supporting Information Appendix S2). Some of the variables showed contrasting effects on survival among the breeding states, which were mainly attributed to Common Cockle and Blue Mussel biomass, and windchill (Models 7 & 8 in Table 2), the effect sizes of windchill and Blue Mussel biomass being largest on survival of non-breeders, and of Common Cockle biomass on survival of successful breeders (Fig. 4 & Table S3 in Supporting Information S2).

Population-level effects of environmental change

Integrating the environmental covariates affecting survival and transitions among breeding states into simulations of LRnS revealed that conditions during the incubation period acting upon reproduction had the strongest standardized effects on the per capita LRnS (Fig. 5A), whilst environmental covariates acting upon survival in winter had a smaller effect (Fig. 5B). The LRnS increased with increasing Ragworm biomass, higher tides and Blue Mussel biomass, but decreased with increasing average temperature in May and June (Fig. 5). Effects of Common Cockle biomass in winter and windchill on LRnS were near zero (Fig. 5B).

DISCUSSION

Quantifying differences in individual sensitivity to environmental change has been challenging, in part due to complex interactions between phenotypic traits leading to opposing results and the difficulty of measuring all involved traits (Wilson & Nussey 2009, Frauendorf *et al.* 2021). Our study suggests that previous breeding state provides an integrated measure of these traits defining individual heterogeneity in sensitivity to environmental change that are not only linked to reproductive success but also survival. Successful breeders had the highest breeding success and survival in the next year, regardless of environmental conditions. Furthermore, the effect and the magnitude of the effects of environmental conditions differed among breeding states and environmental effects on survival even contrasted among breeding states. Classifying an individual according to its breeding state therefore helps the quantification of heterogeneity in individual sensitivity to environmental change, which may be missed when using only a single or few phenotypic traits.

Individual variation in reproductive performance

Individuals with a successful previous breeding state had a higher probability of reproductive success and survival, which is in accordance with other studies suggesting that vital rates are affected by heterogeneity in individual quality (Weimerskirch *et al.* 2001, Hamel *et al.* 2009, Jenouvrier *et al.* 2015, Kennamer *et al.* 2016). However, nest success was low during the study period meaning that despite successful birds having a higher probability of being successful than failed or non-breeders, this was only marginally higher than successful breeders failing in the next year. Traits such as territory quality (Ens *et al.* 1992, van de Pol *et al.* 2010b), laying date (Ens & Cayford 1996), age (van de Pol & Verhulst 2006), and pair-bond duration (van de Pol *et al.* 2006) had been described as important traits impacting reproductive performance in Oystercatchers. That said, using previous breeding state is linked to approaches that use phenotypic traits, for example successful breeding birds are likely to have earlier laying dates and higher nest elevations but it may also capture phenotypic traits that are not (easily) measured. However, our results suggest that individual breeding success changes with inter-annual variation in environmental conditions. During optimal conditions the majority of the population has high reproductive success, whilst during adverse conditions only a limited selection of individuals are able to breed successfully. Hence, the proportion of successful breeders will vary depending on the environmental conditions, supporting the incorporation of interactions between environmental covariates and the previous breeding state as a measure of inter-individual quality differences.

Individual heterogeneity in environmental sensitivity of vital rates

During the incubation period (May–June), higher Ragworm biomass and tidal height, and lower temperatures would increase the probability of nest success for all three breeding states. However, the magnitude of these effects depended on previous breeding state, for example, increasing temperatures significantly reduced the probability of non-breeders becoming successful but not so for successful or failed breeders. Unexpectedly, tidal height had a significant positive correlation with the probabilities of successful bird remaining successful. A potential explanation is that successful birds may both lay earlier and nest higher, which both reduce flooding risks, and in years with high tides, the flooding of low elevation nests reduces competition for resources thus increasing nest success further, through for example parents having more time to defend their nests (Bailey *et al.* 2017, van de Pol *et al.* 2006, 2014).

The negative effect of temperature in May and June may be related to the availability of feeding resources. Higher temperature reduces the accessibility of prey items, such as worms, due to deeper burying depths of these species (Evans 1987), which may impact the energy acquisition for breeding birds. Similar to previous research (Bunskoeke *et al.* 1996, van de Pol *et al.* 2010b), our results emphasise the importance of Ragworm biomass over other prey species given the significant positive effects to reproductive success for all three breeding states, which may be due to the higher availability of Ragworms during the breeding season compared to other prey species such as Baltic Tellin and Lugworms (Bunskoeke *et al.* 1996). High food availability may reduce the time spent foraging and therefore increases the available time defending the nest against predators increasing the probability of successfully hatching the eggs. The temporal model (Model 4 in Table 2) outperformed the equivalent environmental covariate models for transitions (Model 6 in Table 2), suggesting that transitions showed a linear trend over time that is not accounted for by the included environmental covariates. The temporal model may also indicate that some of the environmental conditions may be changing systematically over time, although our study period of 15 years is likely too short to explore the systematic changes of environmental conditions in a robust way.

Whilst the dependency of reproductive success on environmental conditions was in the same direction for all three states, we found opposite effects of environmental conditions acting upon survival among breeding states, especially with regards to windchill and Blue Mussel biomass. Survival of non-breeders showed an increasing trend with increasing Blue Mussel biomass, whilst successful breeders and failed breeders showed an opposite trend. Although the effect sizes were not significant, model selection provided significant support for breeding-state specific sensitivity to environmental conditions, i.e. including an interaction of the environmental variable with breeding state. These differences in dependency on prey species among individuals may arise through density-dependence effects and social dominance (Ens *et al.* 2014). Oystercatchers are known to exhibit differences in feeding dominance among individuals, whereby individuals breeding in high-quality habitats tend to win conflicts over non-breeders and breeders in low-quality habitats (Bruinzeel *et al.* 2006). A previous study indicated that the dominant individuals tend to occupy mussel beds (Goss-Custard *et al.* 1982) hence years with higher mussel biomass may release competition for foraging resources elsewhere and thus benefit survival of non-breeders.

Interestingly, all three breeding states had higher survival during colder and windier winters, especially non-breeding birds, indicating that warmer winters may actually negatively impact Oystercatcher survival and this result is opposite with previous findings on this same population (van de Pol *et al.* 2010b, 2011). Cold winters increase mortality rates in Oystercatchers as the energy required for homeostasis increases whilst icing of the feeding ground reduces prey availability (Camphuysen *et al.* 1996) and stronger winds reduces feeding time as water levels rise with strong winds (Hulsher *et al.* 1993). Cold winters are expected to become less frequent and average winter temperatures are predicted to increase due to climate change (van de Pol *et al.* 2010b) and indeed during our study period severe winters have been infrequent. This suggests that winter temperatures may have a parabolic effect on Oystercatcher survival, with suboptimal conditions for survival during either warm winters or extreme cold winters. The availability of Common Cockles and Blue Mussels depends on winter temperature, as large reproductive events of bivalves are more likely following cold winters (Beukema *et al.* 2009). Furthermore, sea temperatures remain high during warm winters leading to increased metabolic rates of bivalves that increases weight loss (Zwarts 1991) and warm temperatures may also increase spat predation by crabs and shrimps (Zwarts 1991, Beukema 1992, Honkoop & Beukema 1997, Honkoop *et al.* 1998, Beukema & Dekker 2014). These combined factors indicate that the warmer winters, in combination with a relative lack of extreme cold spells, are impacting Oystercatcher survival through their food resources rather than the direct impacts of temperature alone.

The observed decline in non-breeder survival during the latter part of the study reflects their apparent survival, i.e. permanent emigration and mortality are not distinguishable in our model. The decline in non-breeder survival thus suggests recent increased emigration or mortality of non-breeders in the study population. Our study shows a tendency for decline in the number of breeding birds on Schiermonnikoog, which may indicate that the breeding habitat quality declined. However, resighting probability of non-breeders remained the same over the course of the study period (mean = 0.52 ± 0.26 sd and over the last 6 years mean = 0.70 ± 0.10 sd; Fig. S5 in Supporting Information Appendix S2). Furthermore, a previous study conducted on a national scale, thus providing estimates closer to true survival, also detected a similar trend in declining survival of Oystercatchers in the east Wadden Sea (Allen *et al.* 2019). Given the intensive resighting effort nationwide (over 40.000 resightings annually), non-breeding individuals would have a high probability to be observed in the Netherlands, unless they would go to areas with low resighting probabilities, i.e. leaving the Netherlands to the German Wadden Sea or going to specific inland areas where no volunteer observers are active. The large probability of detection outside the study area thus suggests that survival of non-breeders has been declining in recent years, as opposed to increased rates of emigration.

We may have overestimated the statistical significance of the effects of environmental conditions on reproduction or survival, as the response of pair members may be non-independent. Non-independence is challenging to take into account, as our models are not easily extended with complex random effect structures that account for such non-independence. However, we note that ignoring non-independence typically results in overestimating the precision and should not systematically bias the estimation of effect sizes. Furthermore, pair members typically split up in winter, and thus the survival estimates of pair members are expected to be largely independent of each other.

In addition, our approach of analysing nest success as opposed to productivity, i.e. number of chicks reared, may influence some results. For instance, rearing chicks requires additional energy expenditure and hence successful birds may subsequently have a lower survival probability. However, Oystercatchers are long-lived species that are more likely to invest in annual survival than annual reproductive success (Stearns 1992). In addition, we show that adults that successfully hatch at least one egg tend to have higher survival than those that do not hatch an egg, meaning that individual heterogeneity in quality may be masking potential costs of reproduction (van Noordwijk & de Jong 1986). The Oystercatcher population on Schiermonnikoog is also largely resident (Allen *et al.* 2019) meaning there is ample time to build reserves before the harsh winter months, in contrast to some Oystercatcher populations, such as Iceland, where the cost of reproduction may be higher given that migrants in the population need to build reserves before completing a 700 km ocean crossing (Méndez *et al.* 2020).

Population-level effects of environmental changes

Our simulations indicated that LRnS was most strongly influenced by environmental effects on reproduction rather than on survival. Population growth rates in long-lived species, like the Oystercatcher, are thought to be more sensitive to changes in annual adult survival rather than reproductive rates (Stearns 1992). A potential explanation about why LRnS was more sensitive to environmental effects on reproduction rather than survival is that environmental effects on reproductive success were unidirectional across breeding states, i.e. all individuals benefited or suffered albeit at varying degrees to environmental change (Fig. 5). In contrast, environmental effects on survival would often contrast whereby non-breeders and breeders responded in opposing ways to environmental change. Although relationships with survival were quite strong for specific states (Fig. 4), these opposing effects on survival dampened out at the population level in a given year when averaging over all states (Fig. 5), an effect also known as the portfolio effect (Figge 2004, Schindler *et al.* 2015). The portfolio effect thus indicates that ecological heterogeneity of winter conditions actually spreads risks among survival of breeders and non-breeders in a given year, meaning that conservation actions could instead be prioritised on the reproductive period where improving environmental conditions would ultimately lead to higher LRnS. Our analyses provide clear indications how previous breeding state interact with environmental conditions to influence reproduction and survival, and finally influence LRnS. Our results thus provide indications of the key environmental factors that contribute to the declining population.

The Oystercatcher has continued to decline despite a moratorium on mechanical shellfisheries in the Wadden Sea since 2004 (van de Pol *et al.* 2014). Furthermore, a concerning result was that the probability of nest success declined during our study period, and the number of failed- and non-breeders increased – a pattern that is consistent with previously detected trends (Ens *et al.* 2014). The worsening breeding success may be further compounded by climate change predictions, whereby our results indicate that temperature increases will not only influence over-winter survival of non-breeders but also carry-over to impact the probability of reproductive success for all individuals. Our study suggests that including a metric that captures individual heterogeneity in sensitivity to environmental change may improve predictions of population models, as the performance and response to the environment of the mean individual may not be representative of all individuals. Improving environmental conditions related to the reproductive period would yield the highest increases in LRnS, and may result in increased breeding success as the condition of individual increases and therefore improves the breeding success and survival. Understanding how the complex interactions between abiotic conditions and individual variation in sensitivity to these abiotic conditions may impact species reproductive success and survival is crucial to predict the impacts of changing environmental conditions on population growth rates and achieving effective conservation management.

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DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: The results and discussion of the multi-state live-dead recovery analysis for Oystercatchers with territory quality included.

Appendix S2: Supplementary tables and figures to provide additional results that are not presented in the main text.

Tables

Table 1. Combinations of three environmental covariates used per period in the multi-state mark-recapture model selection. Winter covariates were measured during the winter between the two reproductive periods of *t* and *t* + 1, whilst incubation covariates were measured during the reproductive season of *t* + 1. Survival (Φ) was only related to winter covariates whereas the transition probability (ψ) was related to environmental covariates from both winter and the incubation period, as shown by *Par*. For descriptive purposes, the combination of three covariates were assigned a name in column *Combination name* which we refer to in the results.

Combination name	**Time period**	**Covariates**			**Par**
Winter1	December–March	Winter severity index	Cockle	Precipitation	Φ/ψ
Winter2	December–March	Windchill	Cockle	Precipitation	Φ/ψ
Winter3	December–March	Winter severity index	Cockle	Mussel	Φ/ψ
Winter4	December–March	Bivalve weight loss	Cockle	Mussel	Φ/ψ
Winter5	December–March	Bivalve weight loss	Cockle	Precipitation	Φ/ψ
Incubation1	May–June	Precipitation	Temperature	Tidal height	ψ
Incubation2	May–June	Ragworm	Temperature	Tidal height	ψ
Incubation3	May–June	Baltic tellin+lugworm	Temperature	Tidal height	ψ

Table 2. Results of the model selection for survival and transition parameters in relation to environmental conditions, and in models 1, 2 and 6, a time structure for either survival, transitions or both. Models 7 to 19 are the top performing models with environmental covariates within ΔAICc < 10 of the top model with environmental covariates. Models 20 to 24 show the change in ΔAICc when the transition structure is changed. *Wi* is the weight of the model, *k* is the number of parameters and *R2* is the variance explained by the model. The AICc of the top model (Model 7) was 12685.4. Note that the DeltaAICc has been modified to relate to the top covariate model (hence the time model has a negative DeltaAIC). In all cases the models contained the same structure for resighting probability (p = stratum:time) and dead recoveries (r = time). Exception is the NULL model, in which all parameters are set to 1. Note that all transitions models included the interaction of stratum:tostratum, and all survival models included an interaction with stratum, with each environmental covariate, but these are not shown to save space.

Nr	**Survival**	**Transition**	***k***	**ΔAICc**	***Wi***	**Deviance**	**R^2**
1	time	Time	169	-120.40	0.00	12215.6	
2	mussel+cockle+WSI	Time	133	-109.70	0.00	12305.9	0.92
3	stratum	Time	124	-96.74	0.00	12333.1	0.89
4	time	Time	91	-87.12	0.00	12586.5	0.65
5	Time	time	127	-77.82	0.00	12345.6	0.88
6	time	Ragworm+tide+temp	103	-7.60	0.00	12466.6	0.77
7	mussel+windchill	Ragworm+tide+temp	64	0	0.37	12555.4	0.68
8	cockle+windchill	Ragworm+tide+temp	64	0.35	0.31	12555.7	0.68
9	BWL+mussel	Ragworm+tide+temp	64	3.50	0.06	12558.9	0.68
10	mussel	Ragworm+tide+temp	61	4.46	0.04	12566.0	0.67
11	WSI+mussel	Ragworm+tide+temp	64	4.62	0.04	12560.0	0.68
12	precip+cockle+windchill	Ragworm+tide+temp	67	4.67	0.04	12553.8	0.69
13	mussel+cockle+WSI	Ragworm+tide+temp	67	4.94	0.03	12554.1	0.68
14	cockle+mussel	Ragworm+tide+temp	64	5.37	0.03	12560.7	0.68
15	precip+cockle+WSI	Ragworm+tide+temp	67	5.46	0.02	12554.6	0.68
16	cockle	Ragworm+tide+temp	61	5.94	0.02	12567.5	0.67
17	WSI+cockle	Ragworm+tide+temp	64	6.50	0.01	12561.9	0.68
18	BWL+cockle+mussel	Ragworm+tide+temp	67	7.04	0.01	12556.2	0.68
19	precip+mussel	Ragworm+tide+temp	64	8.44	0.01	12563.8	0.68
20	mussel+cockle+WSI	precip+temp+tide	67	37.86	0.00	12587.0	0.65
21	mussel+cockle+WSI	Ragworm+temp	61	41.92	0.00	12603.5	0.64
22	mussel+cockle+WSI	temp+tide	61	50.15	0.00	12611.7	0.63
23	mussel+cockle+WSI	Baltic/Lug+temp+tide	67	48.08	0.00	12597.3	0.64

24	mussel+cockle+WSI	ragworm+tide	61	66.68	0.00	12628.2	0.62
25	time	Stratum:tostratum	85	106.1	0.00	12618.0	0.63
26	mussel+cockle+WSI	Constant	33	665.72	0.00	13289.5	0.00
27	~NULL		4	1034.84	0.00	13685.2	

Figure Legends

Figure 1. Average annual transition probabilities for successful- (S), failed- (F), and non-breeders (N) to all other states including the mortality probability (cross symbol; Model 1 in Table 2). The mortality estimate (1- Φ) for each state is based upon the survival parameter in the model, whilst transition probabilities among successful-, failed- and non-breeder state are based upon the mlogit transition parameters and hence sum to 1. For visualisation purposes, the annual transition and survival estimates were averaged for the 2002–17 study period using the values of the top performing time-based model. The transition probability for remaining in the same state was calculated by subtraction, i.e.1 - transitions to other states.

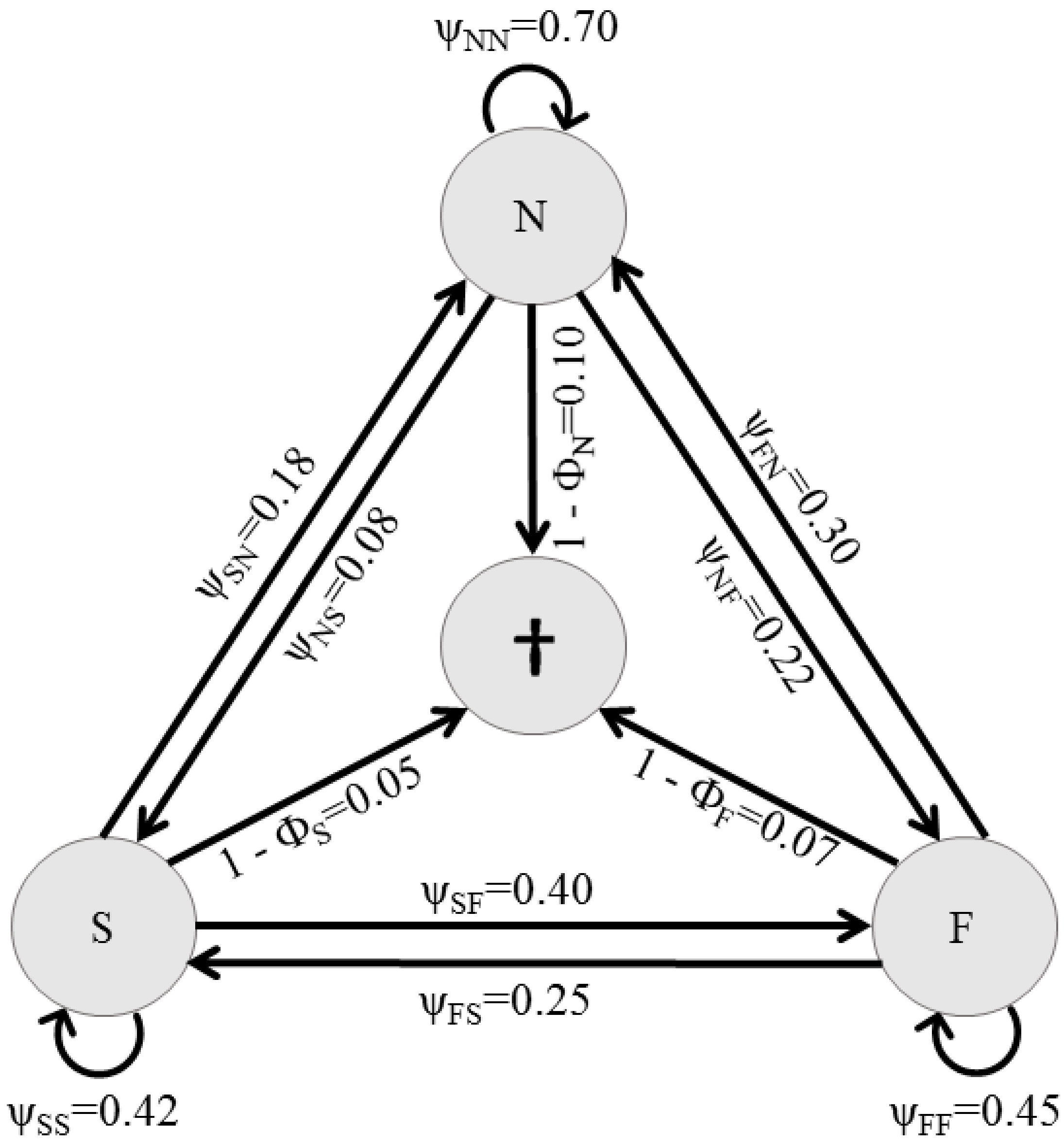
Figure 2. Survival probabilities and standard errors of successful- (S; red circle), failed- (F; orange triangle), and non-breeders (N; blue square) over the period 2002–17 of the top performing time-based model (Model 1 in Table 2). Points in the graph are horizontally jittered for visualisation purposes.

Figure 3. Transition probabilities and confidence intervals of successful- (S; solid red line) failed- (F; orange dashed line) and non-breeders (N; blue dotted line) towards the successful breeding state in relation to a) Ragworm biomass, b) average temperature, and c) tidal height during the incubation period. The transition probabilities are based on averaging models 7–19 (Table 2). The estimates were calculated by setting the non-estimated environmental covariates effects to zero. The transition of S to S (solid red line) are estimated by subtraction and hence the confidence intervals were calculated using the function *deltamethod* in R-Package *msn* (Jackson 2021). The covariates were standardised before being used in the model.

Figure 4. Survival probability and confidence intervals of successful- (S; solid red line), failed- (F; orange dashed line) and non-breeders (N; blue dotted line) in relation to a) Common Cockle biomass, b) Blue Mussel biomass, c) windchill, d) bivalve weight loss, e) precipitation and f) winter severity index. The estimates are based on averaging models 7–19 (Table 2). The estimates

were calculated by setting the non-estimated environmental covariates effects to zero. The covariates were standardised before they were included in the model.

Figure 5. The per capita lifetime reproductive nest success in relation to environmental conditions acting upon a) reproductive success and b) survival. The influence the environmental conditions a) Ragworm biomass (7.70 ± 3.37 sd; red square), average temperature during incubation (14.28 ± 0.97 sd; orange circle) and tidal height during incubation (166.38 ± 16.57 sd; blue triangle) through reproductive success and the influence of b) winter severity (WSI; 18.38 ± 15.15 sd; blue diamond), Common Cockle (48.37 ± 42.72 sd; red square cross) and Blue Mussel biomass (1139.36 ± 616.11 sd; orange circle) through survival. The horizontal dashed line represents the average per capita lifetime reproductive nest success (2.59).



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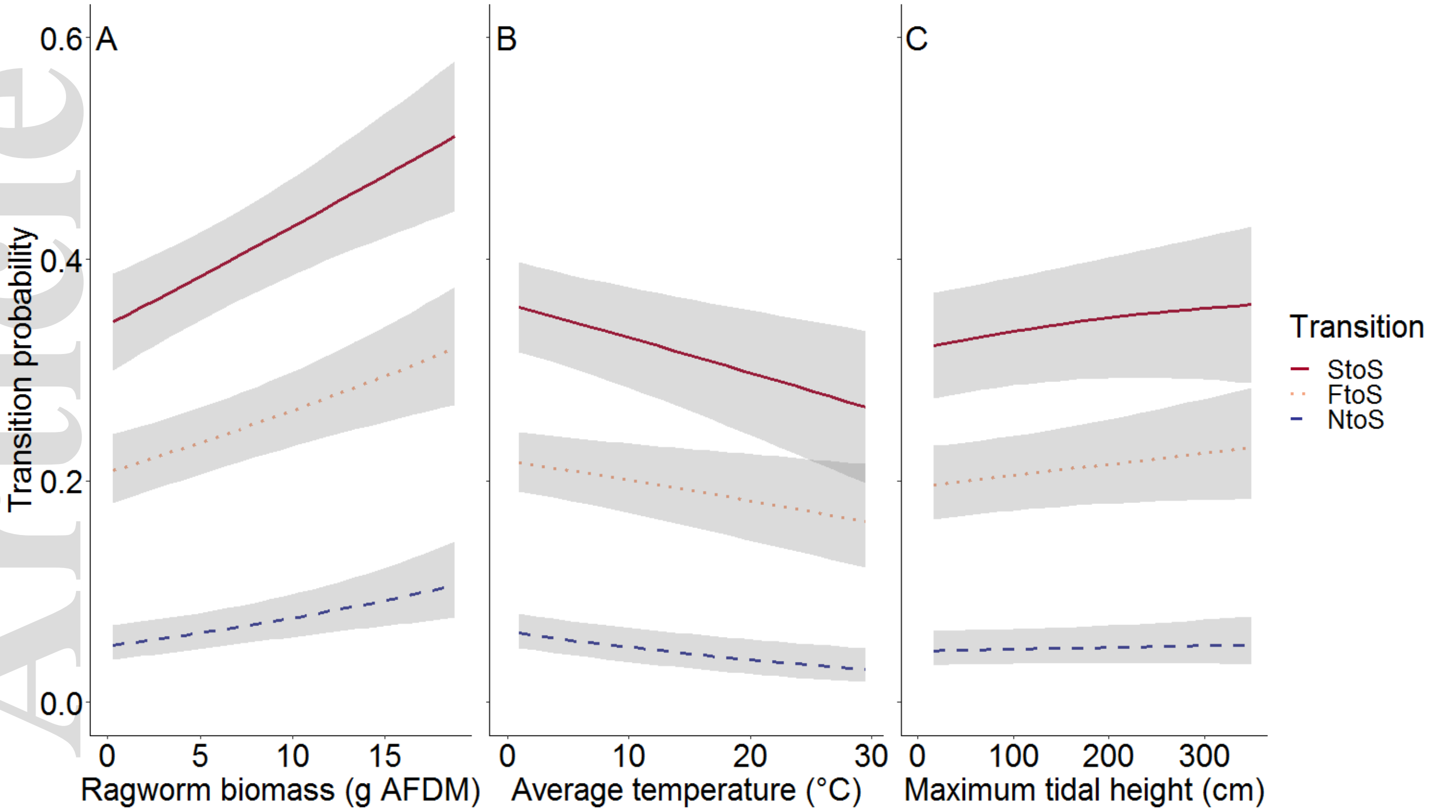

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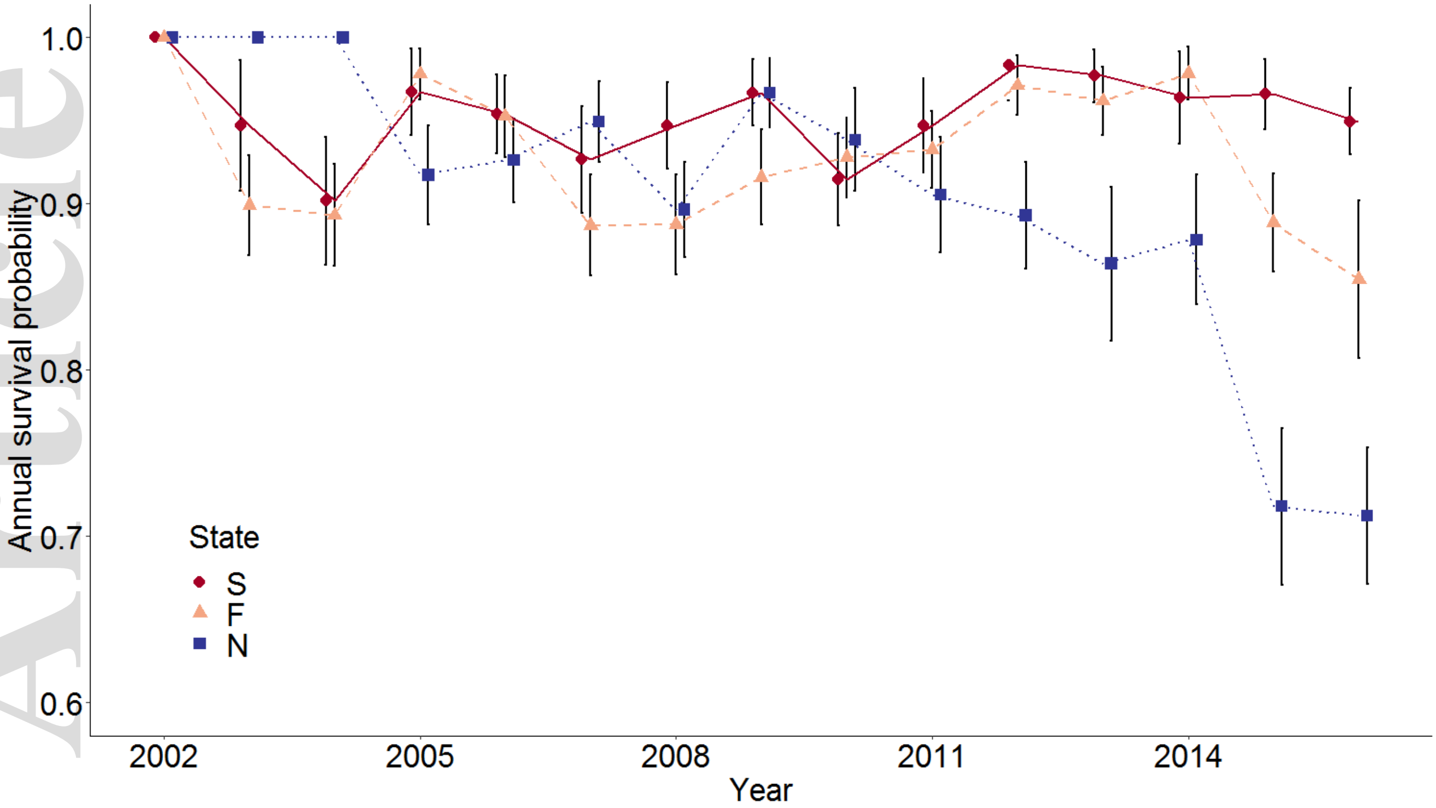

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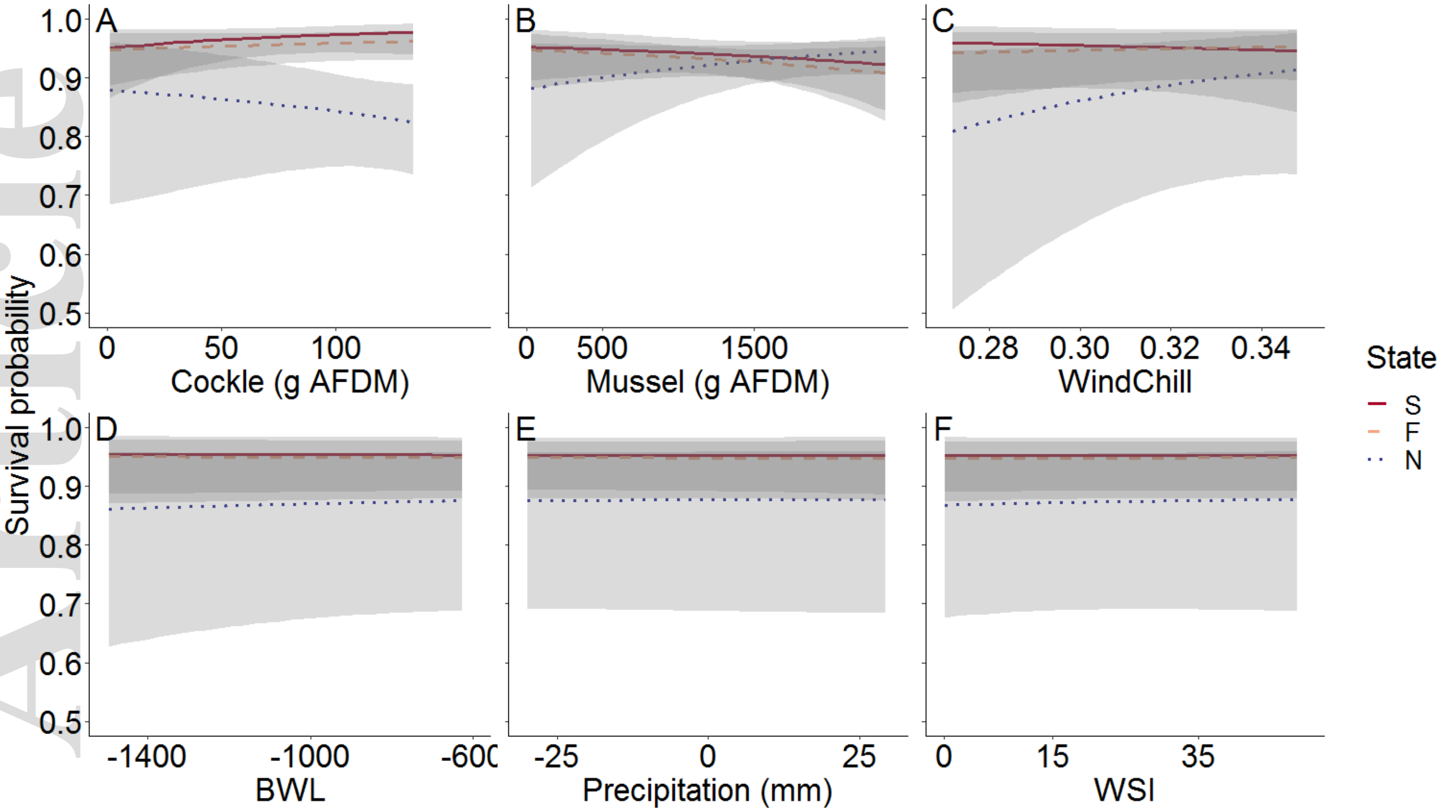

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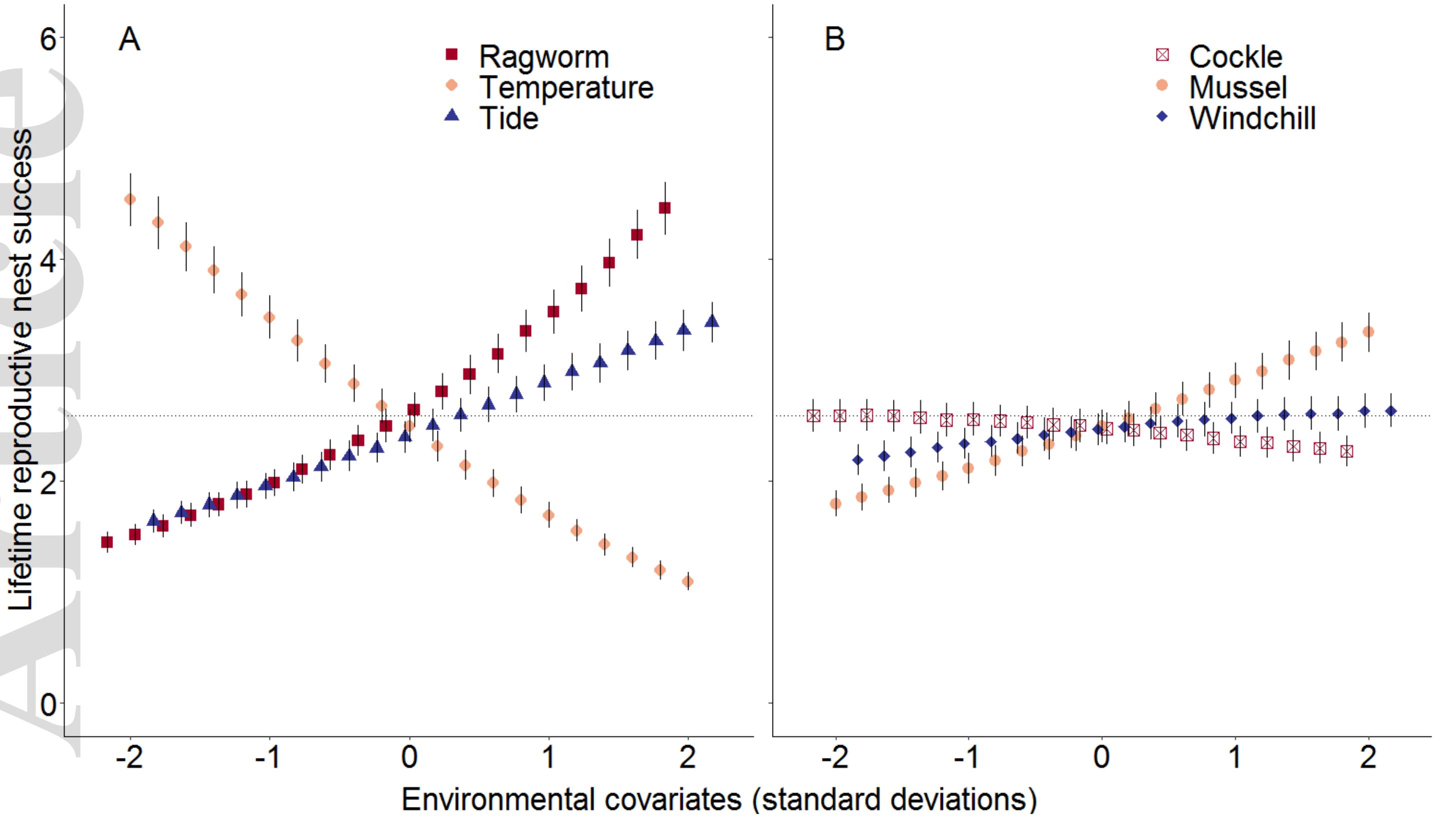

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