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Contrasting between- and within-individual trait effects on mortality risk in a long-lived seabird

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Abstract. Individual life span is the most important determinant of lifetime reproductive success and fitness across taxa. Identifying the relationships between life-history traits and survival therefore is fundamental to understanding the evolution of a species’ traits. Especially important in this respect is to separate the contributions of between- and within-individual trait effects, because only such an approach can identify markers of individual quality and expose within-individual processes such as aging or the occurrence of costs of reproduction. Here we report a rigorous cross-trait comparison in which we quantify effects of between- and within-individual variation in phenology, body mass, and reproductive performance on mortality risk in a long-lived seabird, the Common Tern *Sterna hirundo*. Between individuals, earlier arrival at the breeding colony, earlier egg-laying, greater body mass, and more successful reproduction are associated with a lower mortality risk, and are markers of individual quality. The standardized between-individual effects of arrival and laying date especially stand out, suggesting that phenology represents the best proxy for life span. In contrast, within individuals, earlier phenology, greater body mass, and more successful reproduction are associated with a higher mortality risk, as is a reduced probability of breeding. After correcting for changes in traits with age, within-individual effects of phenology, breeding probability, clutch size, and egg volume remain significantly associated with mortality risk, which reveals survival costs of early arrival and initial investment in reproduction, but suggests terminal effects in breeding probability. Overall, our study illustrates the usefulness of separating between- and within-individual trait effects on fitness measures to identify markers of individual quality and life-history trade-offs in natural populations.

Key words: aging; Common Tern; cost of reproduction; individual variation; life expectancy; life-history trade-offs; senescence; *Sterna hirundo*; time-dependent Cox model.

INTRODUCTION

Individual life span is the most important determinant of lifetime reproductive success and fitness across taxa (e.g., Clutton-Brock 1988, Newton 1989, Bennett and Owens 2002, Flatt and Heyland 2011). An individual’s life span is the outcome of its cumulative annual survival probabilities, and variation in life span therefore can be attributed to consistent between-individual variation in mortality risk (Vaupel et al. 1979), as well as variation in changes in within-individual risk of mortality over life (Tuljapurkar et al. 2009, Tuljapurkar and Steiner 2010). Neither the between- nor within-individual variation in mortality risk can be observed directly, but can be captured in the instantaneous rate of death (i.e., mortality risk) calculated in Cox models.

Pinpointing phenotypic traits that underlie variation in mortality risk is important for understanding trait evolution, as well as for predicting fitness for individuals in, for example, long-lived study species or populations of management interest. Especially important in this

respect is to separate the contributions of between- and within-individual trait effects on mortality risk, as they convey different biological information. Although between-individual trait effects arise through individual quality differences (van Noordwijk and de Jong 1986, Wilson and Nussey 2010), within-individual trait effects may arise through ontogenetic processes such as aging (improvement, as well as senescence) or through costs of reproduction (note that aging itself can also be a cost of reproduction; Kirkwood 1977). Each of these processes will differentially affect trade-offs and the evolution of life histories (e.g., Hamel et al. 2009, 2012).

Methods have recently become available to separate between- and within-individual age effects on traits (van de Pol and Verhulst 2006) or to separate between- and within-subject effects on traits in general (van de Pol and Wright 2009). Both methods have been employed successfully to reveal within-individual change with age in traits such as calving date or birth weight in red deer *Cervus elaphus* (Nussey et al. 2006), laying date in Mute Swans *Cygnus olor* (McCleery et al. 2008), reproductive success in Great Tits *Parus major* (Bouwuis et al. 2009, 2010), ornamentation in Collared Flycatchers *Ficedula albicollis* (Evans et al. 2011), or body mass in several species of ungulate (Nussey et al. 2011). Moreover, these

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methods have also been employed to study effects of single traits, such as hatching date in Barn Swallows *Hirundo rustica* (Saino et al. 2012), telomere length in Jackdaws *Corvus monedula* (Salomons et al. 2009) and Seychelles Warblers *Acrocephalus sechellensis* (Barrett et al. 2013), or fledging mass in Great Tits and Blue Tits *Cyanistes caeruleus* (Vedder et al. 2014), on survival or life span. We are now at a point where a rigorous cross-trait comparison of effects on mortality risk, taking into account the accumulating evidence for age effects on traits as well as mortality risk, is timely.

In this study, we therefore investigate effects of 10 phenotypic traits on mortality risk in a long-lived seabird, the Common Tern *Sterna hirundo* (Becker and Ludwigs 2004; see Plate 1). The traits measured capture aspects of phenology, body condition, and reproductive performance. Common Terns are particularly suitable for our purpose because individuals are known to display persistent individual differences in many traits related to fitness measures, while also undergoing within-individual change (Ezard et al. 2007, Becker et al. 2008, Rebke et al. 2010, Becker and Zhang 2011, Arnaud et al. 2013; H. Zhang, O. Vedder, P. H. Becker, and S. Bouwhuis, *unpublished manuscript*). We use Cox models to test for each of the 10 traits whether an individual's average phenotypic trait value, or its deviation from this average, is associated with mortality risk. Importantly, in a second analytical step, we correct for age effects on traits to specifically assess whether within-individual effects are due to aging, or a survival cost of trait expression independent from aging. Finally, we quantify the relative importance of life-history associations between the traits and mortality risk by assessing standardized effects. In doing so, we reveal and rank indicators of individual quality and elucidate the nature and importance of life-history trade-offs.

MATERIALS AND METHODS

Research colony and data collection

Data come from the Banter See Common Tern breeding colony near Wilhelmshaven on the German North Sea coast (53°36' N, 08°06' E), and have been collected following a consistent protocol since 1992 (Becker et al. 2001, Becker 2010). Common Terns spend winters in western Africa and migrate to the breeding colony in early spring, either to breed or to prospect potential sites for future breeding. Once birds establish themselves as breeders, the return rate is exceptionally high (90%; Szostek and Becker 2012). Each breeding season (April to August), all nests are visited three times a week to record clutch initiation date, clutch size, egg dimensions (measured with an accuracy of ± 0.1 mm), hatching date, brood size, and number of fledglings. All chicks are banded with uniquely numbered steel bands just after hatching, and are subcutaneously marked with passive integrated transponders (TROVAN ID 100; TROVAN, Köln, Germany) shortly prior to fledging. The sex of all successfully fledged individuals has been

determined by standard molecular methods since 1998 (Becker and Wink 2003) and by behavioral observations before that. Between 1992 and 2011, the number of breeding pairs fluctuated between 90 and 530.

The Banter See colony site consists of six rectangular concrete islands of equal size (10.7×4.6 m) surrounded by a 60 cm wall. Walls are equipped with 44 elevated platforms for terns to land and rest on. Each platform is equipped with an antenna that reads transponder codes at a distance of ≤ 11 cm, such that the presence of all locally fledged individuals, including subadults, nonbreeders, and breeders, is remotely and automatically recorded. Up to 22 platforms are additionally equipped with digital balances (Sartorius PT and BL series, Sartorius, Göttingen, Germany, accuracy ± 1 g) to weigh the identified terns. Data are read and recorded every five seconds. Transponder-marked breeders are additionally identified by placing an antenna around each clutch for at least 24 h during incubation. These methods enable highly accurate remote identification of individuals throughout their life (the resighting probability of breeders is almost 1.0; Szostek and Becker 2012), and therefore a highly accurate measurement of local survival. The average adult life span of Common Terns in our study population is 10 years.

We define all natal transponder-marked individuals that breed at the colony site as local *recruits* and the age of first breeding at the Banter See as the local *recruitment age* (RA), which could reliably be established for birds hatched after 1989. In our data set, 95% of breeders recruit between age 2 and 5 years, with 81% of individuals initiating reproduction at age 3 or 4 years. Average recruitment age is 3.70 ± 1.21 years (mean $\pm$ SD); following previous work from our population, we define four groups of RA: 2, 3, 4, and 5+ years (Ludwigs and Becker 2002, Becker et al. 2008; Zhang et al., *in press*).

In our analyses of mortality risk, we consider 10 phenotypic traits, for which descriptive statistics are reported in the Appendix: Table A1. *Arrival date* is defined as the day of the year (counting from 1 January) when an individual is first recorded at the colony site, as long as, for breeding birds, this is at least 10 days prior to that individual's laying date. Breeders that were not automatically recorded at resting platforms 10 days prior to laying ($n = 248$ bird-years, i.e., 5.7%), were not assigned an arrival date. *Arrival mass* is defined as the mean body mass calculated from arrival body mass in the first four days of colony attendance, for birds that were assigned an arrival date only. *Breeding probability* captures whether birds are observed breeding at the Banter See or not. Nonbreeding status includes observed skipped breeding (registration of nonbreeding individuals in the colony), as well as missing observations (458 bird-years in total), such that breeding probability, as RA, is a local measure. *Laying date* is defined as the day of the year when the first egg of a clutch is found. *Egg volume* is an average volume index of all eggs in a clutch, calculated as $\text{length} \times \text{width}^2 / 1000$, with length and width measured in millimeters. We define *clutch size* as

the number of eggs per clutch; *brood size* as the number of chicks hatched per clutch; *hatching success* as the proportion of hatched eggs per clutch; and *rearing success* as the proportion of hatchlings that reached a minimum age of 18 days per brood, for first clutches and broods only. *Annual number of fledglings* is defined as the annual number of chicks fledged per pair, including those from replacement (10.0%) and second (0.9%) clutches. Note that because egg volume and clutch size are affected by the males' courtship behavior in Common Terns (Nisbet et al. 2002, Becker and Ludwigs 2004), we analyze all traits for both sexes.

In total, our data, based on locally hatched and transponder-marked individuals that bred at least once between 1993 and 2011, contain up to 423 males and 359 females of known age and RA with 2305 and 2068 observed bird-years for males and females, respectively. Sample sizes for each of the 10 phenotypic traits whose effect on mortality risk we study, however, vary and are reported in Table 1. For each of the 10 phenotypic traits, we calculate a between-individual component, *B*, by averaging all trait values for each individual. We also calculate a within-individual component, *W*, as the year-specific deviation between the actual value and the average value (i.e., $W = \text{trait value} - B$; van de Pol and Wright 2009).

Survival analysis

Cox proportional hazard models, in general, are used to quantify the effect of a covariate on the time it takes for an event, in our case death, to occur via a hazard function (Cox 1972). The hazard rate at time *t*, given the observed covariate *X* (a vector representing a set of input variables, X_1, X_2 , and so forth) is formulated as

$$h(t, \mathbf{X}) = h_0(t) \exp \left(\sum_g \beta_g X_g \right)$$

where $h_0(t)$ describes how the hazard changes with time at baseline levels of the covariates (when the input covariates are zero), X_g is the *g*th time-independent or fixed covariate (where *g* is an index of the input variables that may influence mortality risk or of the corresponding coefficient; $g = 1, 2, \dots$) and β_g is the coefficient of the covariate X_g (Kleinbaum and Klein 2012). In order to quantify the effects of both time-independent between- and time-varying within-individual trait components on mortality risk, we here use an extended Cox model with time-varying covariates, for which the assumption of proportional hazard is no longer made (Kleinbaum and Klein 2012). This model is formulated as

$$h(t, \mathbf{X}(t)) = h_0(t) \exp \left(\sum_g \beta_g X_g + \sum_p \delta_p X_p(t) \right)$$

where the additional term $X_p(t)$ represents the *p*th time-varying covariate ($p = 1, 2, \dots$), and δ_p is its coefficient. We run all Cox models using the procedure *coxph* in the

package *survival* in the R program (version of 3.0.1, Fox 2002).

In our study, the “time to event” for each individual is defined as the number of years since recruitment age to death ($n = 499$) or to the end of the study (i.e., 2011) if no death event occurred within the study period ($n = 283$, right-censoring). We assign a death event to an individual if it did not appear in any of the years following an observation until the end of the breeding season in 2013, or for at least two consecutive years if it was observed in 2011. Although we thus assume death, rather than directly observe it, we assess the reliability of this assumption to be high, because 96% of breeders do not skip observation for two or more consecutive years since first reproduction (Appendix: Table A2). Note, however, that the estimated mortality risk is local and may include permanent emigration from the study area, but we assume permanent emigration to be rare, since estimates of local survival are very high (i.e., ranging between 0.9 and 0.7 between age 2 and 25 years; Zhang et al., *in press*). Overall, the “time to event” in this study represents the local individual life expectancy from the onset of reproduction, and averages 6.8 ± 0.24 years (mean $\pm$ SE).

Individuals that did not die during our study period contribute to right-censoring cases, which are implemented in the extended Cox models with a variable “status,” which has two levels: 0 indicates no death for a time interval, whereas 1 indicates that death has occurred. Right-censoring cases therefore are defined by having status 0 for all age intervals of that individual. Both assigned death and right-censoring cases contribute to the parameter estimates in a Cox model by being involved in the construction of a partial likelihood function (Kleinbaum and Klein 2012). We expect right-censoring cases to be unlikely to bias the estimates of mortality risk in our study, because the unobserved events are caused by a time limitation of the study rather than subjective exclusion of individuals.

In a first analytical step, we run extended Cox models in which we consider sex and RA as categorical covariates or as strata, while testing for between- and within-individual trait component effects on mortality risk, and select the final form based on Akaike's information criterion (AIC) obtained using the *extractAIC* function. Specifically, we consider four forms of each model: (1) only between- and within-individual trait components as covariates, i.e., $B + W$; (2) between- and within-individual trait components as covariates, with sex and RA as additional categorical covariates, as well as an interaction between sex and RA, i.e., $B + W + \text{sex} \times \text{RA}$; (3) between- and within-individual trait components as covariates, with sex and RA as additional categorical covariates, as well as interactions between numerical and categorical covariates, i.e., $B \times \text{sex} \times \text{RA} + W \times \text{sex} \times \text{RA}$; and (4) between- and within-individual trait components as covariates, with a combination of sex and RA as strata,

TABLE 1. Between- and within-individual effects of 10 phenotypic traits on mortality risk in Common Terns (*Sterna hirundo*).

Trait	Between-individual effect		Within-individual effect		Age-corrected within-individual effect	
	Estimate	P	Estimate	P	Estimate	P
Arrival date	0.062 (0.006)	<0.001	−0.034 (0.007)	<0.001	−0.031 (0.008)	<0.001
Arrival mass	−0.031 (0.011)	0.005	0.037 (0.014)	0.009	0.025 (0.014)	0.087
Breeding probability	0.256 (0.234)	0.270	−1.150 (0.179)	<0.001	−0.949 (0.183)	<0.001
Laying date	0.057 (0.007)	<0.001	−0.091 (0.009)	<0.001	−0.058 (0.009)	<0.001
Egg volume	−0.091 (0.025)	<0.001	0.138 (0.029)	<0.001	0.099 (0.029)	0.001
Clutch size	−1.038 (0.136)	<0.001	0.574 (0.114)	<0.001	0.308 (0.112)	0.006
Brood size	−0.540 (0.088)	<0.001	0.206 (0.061)	<0.001	0.050 (0.061)	0.400
Hatching success	−0.889 (0.250)	<0.001	0.250 (0.171)	0.140	0.021 (0.171)	0.900
Rearing success	−1.470 (0.305)	<0.001	0.660 (0.183)	<0.001	0.034 (0.188)	0.860
No. fledglings	−0.828 (0.150)	<0.001	0.275 (0.080)	0.001	0.006 (0.081)	0.940

Notes: Within-individual effects (estimated coefficients for input variables, with SE in parentheses) are shown without and with age correction, and significant effects are presented in bold. In addition, the variance and significance of year as a frailty term are presented, with sample sizes in the last two columns.

i.e., $B + W + \text{strata (sex, RA)}$. In the latter case, the extended Cox model is formulated as $h(t, \mathbf{X}(t)) = h_j(t) \exp(\beta X_1 + \delta X_2(t))$, where $h_j(t)$ is the baseline hazard for the j th stratum ($j = 1, 2, \dots$) specified by each of eight combinations of sex and RA, X_1 represents the between-individual trait component, and $X_2(t)$ represents the within-individual trait component. In this stratified Cox model, the effects of sex and RA are not of direct interest, but indicate different baseline hazards for different sex–RA combinations that depend only on time (Kleinbaum and Klein 2012; see also Zhang et al., *in press*). In the best-performing model for each phenotypic trait, to test whether between- and within-individual trait effects on mortality risk differ significantly, the within-individual values are replaced by the actual values of the trait (also a time-varying covariate), which causes the between-individual term to represent the difference (van de Pol and Wright 2009).

Second, we consider unobserved heterogeneity by including a shared frailty term in the best-performing model from the previous step, which is equivalent to adding a random effect to the Cox model. We consider individual identity and year as two alternative frailty terms to account for individual heterogeneity and various environmental conditions, respectively, and again select the best-performing model based on AIC values. In this case, the extended Cox model with a shared frailty term is defined as $h(t, \mathbf{X}(t)) = \alpha_k h_j(t) \exp(\beta X_1 + \delta X_2(t))$, where α_k denotes the shared frailty term for the k th group ($k = 1, 2, \dots$) specified by individual identity or year, which adjusts the hazard rate by assigning a common value with a mean of 1 to individuals from the same group (Kleinbaum and Klein 2012).

Third, again using the best-performing model from the previous step, we examine to what extent the within-individual trait effects on mortality risk are caused by both the trait values and mortality risk changing with age by correcting for the age effect on the trait, because all traits investigated were strongly age dependent (H. Zhang, O. Vedder, P. H. Becker, and S. Bouwhuis, *unpublished manuscript*). Age-corrected trait values are

residuals obtained by running generalized additive mixed models (GAMMs; Wood 2006, Ezard et al. 2007) with each trait as a dependent variable and between- and within-individual age effects (i.e., a mean age for each individual and a deviation of the actual age and the mean; van de Pol and Wright 2009) as independent variables to account for selective disappearance and within-individual age effects, respectively. In these GAMMs, individual identity and calendar year are included as random effects.

All models described are run for each of the 10 phenotypic traits separately for three reasons. First, this preserves sample size because data for all traits are not always available for all individuals. Second, both the between- and within-individual components of the phenotypic traits are all strongly intercorrelated (Appendix: Table A3), causing single-trait analyses to be more appropriate than multi-trait analyses (i.e., multiple independent variables tested in one model). Third, because our aim is to establish whether there is individual heterogeneity for each trait, and whether increased performance in a trait is associated with survival costs, instead of determining exact causal pathways that lead to the observed effects, our objectives do not require multi-trait analyses. However, in order to compare trait effects on mortality risk across our correlated traits, in our final analytical step, we rerun the best-performing models with standardized input values for between- and within-individual trait components. These standardized values are obtained by calculating a Z score (trait value minus the mean trait value, divided by its standard deviation) for raw data, between- and within-individual trait values, as well as age-corrected trait, and age-corrected between- and within-individual values, respectively (cf. Vedder et al. 2014).

RESULTS

Sex, recruitment age, and frailty

For all traits, the best-performing models are the ones in which sex and RA are used as strata (Appendix: Table

TABLE 1. Extended.

Frailty		No. observations	No. death events/ no. individuals
Variance	<i>P</i>		
0.079	0.001	3898	434/759
0.169	0.008	2021	215/659
0.093	<0.001	4373	499/782
0.143	<0.001	3912	416/782
0.075	0.006	3874	414/782
0.067	0.011	3915	416/782
0.068	0.009	3899	415/782
0.074	0.009	3899	415/782
0.045	0.058	3250	340/726
0.056	0.016	3899	415/782

A4). Although different sex–RA groups of birds therefore are characterized by different baseline hazards of mortality, we have no evidence that trait effects on mortality risk are modulated by sex or RA. Moreover, models that include calendar year as a frailty term outperform models that include individual identity as a frailty term, or that exclude frailty terms altogether, so that between-individual mortality risk not associated with the traits that we study is overruled by significant yearly variation in mortality risk (Appendix: Table A4).

Between-individual effects on mortality risk

We find significant relationships between mortality risk and individual average values of each trait, except

breeding probability (Table 1). More specifically, between individuals, a lower mortality risk is significantly associated with earlier and heavier arrival at the colony; earlier egg laying; larger egg volume, clutch size, and brood size; greater hatching and rearing success; and a greater annual number of fledglings (Table 1, Fig. 1). Comparison of between-individual effects across traits reveals that one unit increase in the standardized input variable for arrival and for laying date has the largest influence on mortality risk, followed, in order, by the standardized effects of clutch size, annual number of fledglings, brood size, rearing success, arrival mass, egg volume, and hatching success (Fig. 1; Appendix: Table A5).

Within-individual effects on mortality risk

Within individuals, all phenotypic traits have opposite effects on mortality risk compared to the between-individual effects of the same traits (Table 1), and for all traits the between- and within-individual effects on mortality risk are significantly different (all $P < 0.001$). Earlier egg-laying, earlier arrival at the colony, larger clutch size, lower probability of breeding, larger egg volume, greater rearing success, larger annual number of fledglings, larger brood size, and heavier mass at arrival at the colony, ordered by their standardized effects, are all significantly associated with a higher mortality risk

FIG. 1. Standardized effects on mortality risk in Common Terns of between-individual (B), within-individual (W), and age-corrected within-individual components (W_AC) of 10 phenotypic traits. Shown are estimated coefficients and their standard errors, which quantify the trait effects on mortality risk due to one unit increase in the standardized input variable. The upper row of five panels includes traits with significant W_AC effects; the lower row of five panels includes traits for which the W_AC effects are nonsignificant.

(Appendix: Table A5). However, the within-individual effect of hatching success is nonsignificant (Table 1).

Age-corrected within-individual effects on mortality risk

After correcting for age effects on within-individual trait expression, earlier laying and arrival, decreased breeding probability, greater egg volume, and larger clutch size, ordered by their standardized effects, remain significantly associated with a higher mortality risk, whereas the effects of arrival mass, brood size, hatching success, rearing success, and annual number of fledglings become, or remain, nonsignificant (Table 1, Fig. 1; Appendix: Table A5).

DISCUSSION

Costs of reproduction are central to life histories, because they require individuals to trade off limited resources among life-history traits (Williams 1966, Stearns 1992). However, if, in a population, variation in resource acquisition between individuals is greater than variation in allocation strategy, life-history trade-offs may be masked by heterogeneity in individual quality (van Noordwijk and de Jong 1986, Wilson and Nussey 2010). This may explain why similar traits have been found to be oppositely associated with annual survival or life span across species. For example, an early onset of reproduction in Mute Swans (McCleery et al. 2008), increased breeding probability in bighorn sheep *Ovis canadensis*, mountain goats *Oreamnos americanus*, and roe deer *Capreolus* (Hamel et al. 2009), and greater reproductive success in Great Tits (Bouwhuis et al. 2009, 2010) and Storm Petrels *Hydrobates pelagicus* (Sanz-Aguilar et al. 2008) have been found to be associated with greater survival and therefore have been explained by heterogeneity in individual quality, whereas these same traits have been found to be associated with lower survival in Cliff Swallows *Petrochelidon pyrrhonota* (Brown and Brown 1999), Black-legged Kittiwakes *Rissa tridactyla* (Aubry et al. 2011), and red deer (Proaktor et al. 2008), respectively, and have been explained by life-history trade-offs.

In our study, we correct for heterogeneity in individual quality by estimating the effect of deviations in trait expression from an individual's long-term average on its mortality risk. Assuming that such within-individual trait variation is not largely driven by resource acquisition, this should reveal trade-offs with survival. Indeed, within individuals, we find earlier and heavier arrival at the breeding colony, earlier egg-laying, larger egg volume, larger clutch and brood size, greater rearing success, and a larger annual number of fledglings to all be significantly associated with a higher mortality risk. Theoretically, these associations could have arisen because annual survival in adult Common Terns is age dependent and declines from the age of 2 years onward (Zhang et al., *in press*), whereas fledgling production, for example, increases within individuals to

the age of 14 years (Rebke et al. 2010), causing older birds to perform comparably well in traits associated with reproduction, but less well in survival. This may already constitute an optimal resource allocation strategy following the disposable soma model of senescence (Kirkwood 1977), but may also result from resource-independent effects, for example if late-life expression of deleterious genes (Medawar 1952, Williams 1957) affects survival more than it does reproduction.

When repeating our analyses with age-corrected trait values, we find qualitatively similar results for arrival date, laying date, egg volume, and clutch size, whereas the effects of arrival mass, brood size, rearing success, and annual number of fledglings become nonsignificant. Hence, age-independent performance in traits associated with the timing and initial investment in reproduction comes with an increased mortality risk, providing strong evidence for life-history trade-offs. At present we can only speculate regarding the proximate mechanisms underlying the costs of reproduction that we find, but perhaps faster migration, increased competition for fast territory establishment, and increased investment in egg production are energetically costly at a time when resource availability cannot compensate for these costs, leading to somatic wear, for example as seen in telomere length in Common Terns (Bauch et al. 2013). Establishing the physiological nature of the trade-offs that we find, as well as establishing whether costs of reproduction in the Common Tern are immediate or cumulative (e.g., Moyes et al. 2006, Aubry et al. 2009, 2011), are foci of our ongoing work.

Although we find that traits associated with the timing and initial investment in reproduction (egg volume, clutch size) come with an increased mortality risk, we find that traits more strongly associated with the success of a reproductive attempt are either not correlated with mortality risk (hatching success) or are correlated only without correcting for age (brood size, rearing success, and annual number of fledglings), while they are often considered the most energetically expensive traits and therefore also most likely to be involved in trade-offs (Lack 1947). Possibly, these traits are under a stronger influence of environmental variation in resource availability, rather than parental allocation strategies, which masks life-history trade-offs. Strong year-to-year variation of those reproductive parameters is well known in many species, including the Common Tern, in which it is caused by the interplay of food availability and weather, and occasionally predation (Nisbet et al. 2002, Becker and Ludwigs 2004, Dänhardt and Becker 2011).

Although within-individual effects of phenology and reproductive output are coherent for nine out of 10 phenotypic traits, results for the trait "breeding probability" are the opposite. Reduced, rather than increased, breeding probability is associated with an increased mortality risk, which suggests that breeding is the default state in Common Terns and that completely foregoing a reproductive attempt reflects a sudden

PLATE 1. Banter See Common Tern with two chicks. Photo credit: S. Bouwhuis.

senescent decline in physiological state that is followed by death. Such a “terminal decline” in performance has been observed in various species (e.g., see Coulson and Fairweather 2001, Rattiste 2004, Nussey et al. 2011, Hayward et al. 2013).

We find between-individual variation in traits to be associated markedly differently with mortality risk than within-individual variation. Individuals that, on average, arrive early and heavy at the breeding colony, start laying early, have a large egg volume, large clutch and brood size, high hatching and rearing success, and a high annual number of fledglings, are least likely to die. The standardized between-individual effects of arrival and laying date especially stand out, suggesting

that an advanced phenology represents the best proxy for a long life span and thus indicates high individual quality. This reinforces a common notion about avian timing of reproduction; early reproduction has fertility benefits (e.g., Arnold et al. [2004] for Common Terns), but entails survival costs, such that only high-quality individuals are able to (arrive and) reproduce early (Verhulst and Nilsson 2008). It also fits well with previous findings in our study population that phenology is a persistent individual trait canalized during individuals’ lives (Ezard et al. 2007, Arnaud et al. 2013) that is related to fitness (Stearns and Kawecki 1994).

In conclusion, by separating within-individual effects from between-individual effects of a multitude of

phenotypic traits on survival, we reveal the survival costs of early phenology and initial investment in reproduction, independent of average age-specific allocation patterns. In addition, our study reinforces the notion that individuals vary in levels of resource acquisition, which is similarly allocated to a multitude of traits (Wilson and Nussey 2010), with early breeding phenology being the best between-individual proxy of life expectancy. Overall, our study illustrates the usefulness of separating within-individual processes from heterogeneity in individual quality to identify life-history trade-offs in natural populations.

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LITERATURE CITED

- Arnaud, C. M., P. H. Becker, F. S. Dobson, and A. Charmantier. 2013. Canalization of phenology in common terns: genetic and phenotypic variations in spring arrival date. *Behavioral Ecology* 24:683–690.
- Arnold, J. M., J. J. Hatch, and I. C. T. Nisbet. 2004. Seasonal declines in reproductive success of the Common Tern *Sterna hirundo*: timing or parental quality? *Journal of Avian Biology* 35:33–45.
- Aubry, L. M., E. Cam, D. N. Koons, J.-Y. Monnat, and S. Pavard. 2011. Drivers of age-specific survival in a long-lived seabird: contributions of observed and hidden sources of heterogeneity. *Journal of Animal Ecology* 80:375–383.
- Aubry, L. M., D. N. Koons, J.-Y. Monnat, and E. Cam. 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. *Ecology* 90:2491–2502.
- Barrett, E. L. B., T. A. Burke, M. Hammers, J. Komdeur, and D. S. Richardson. 2013. Telomere length and dynamics predict mortality in a wild longitudinal study. *Molecular Ecology* 22:249–259.
- Bauch, C., P. H. Becker, and S. Verhulst. 2013. Telomere length reflects phenotypic quality and costs of reproduction in a long-lived seabird. *Proceedings of the Royal Society B* 280: 20122540.
- Becker, P. H. 2010. Populationsökologie der Flussseseschwalbe: Das Individuum im Blickpunkt. Pages 137–155 in F. Bairlein and P. H. Becker, editors. 100 Jahre Institut für Vogelforschung "Vogelwarte Helgoland." Aula-Verlag, Wiebelsheim, Germany.
- Becker, P. H., T. Dittmann, J.-D. Ludwigs, B. Limmer, S. C. Ludwig, C. Bauch, A. Braasch, and H. Wendeln. 2008. Timing of initial arrival at the breeding site predicts age at first reproduction in a long-lived migratory bird. *Proceedings of the National Academy of Sciences USA* 105:12349–12352.
- Becker, P. H., and J.-D. Ludwigs. 2004. *Sterna hirundo* Common Tern. BWP Update: *Journal of Birds of the Western Palearctic* 6:91–137.
- Becker, P. H., H. Wendeln, and J. González-Solís. 2001. Population dynamics, recruitment, individual quality and reproductive strategies in common terns *Sterna hirundo* marked with transponders. *Ardea* 89:241–252.
- Becker, P. H., and M. Wink. 2003. Influences of sex, sex composition of brood and hatching order on mass growth in common terns *Sterna hirundo*. *Behavioral Ecology and Sociobiology* 54:136–146.
- Becker, P. H., and H. Zhang. 2011. Renesting of Common Terns *Sterna hirundo* in the life history perspective. *Journal of Ornithology* 152:213–225.
- Bennett, P. M., and I. P. F. Owens. 2002. Evolutionary ecology of birds: life history, mating system and extinction. Oxford University Press, Oxford, UK.
- Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing old: selective disappearance and the partitioning of senescence to stages within the breeding cycle. *Proceedings of the Royal Society B* 276:2769–2777.
- Bouwhuis, S., A. J. Van Noordwijk, B. C. Sheldon, S. Verhulst, and M. E. Visser. 2010. Similar patterns of age-specific reproduction in an island and mainland population of great tits *Parus major*. *Journal of Avian Biology* 41:615–620.
- Brown, C. R., and M. B. Brown. 1999. Fitness components associated with laying date in the Cliff Swallow. *Condor* 101: 230–245.
- Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.
- Coulson, J. C., and J. A. Fairweather. 2001. Reduced reproductive performance prior to death in the Black-legged Kittiwake: senescence or terminal illness? *Journal of Avian Biology* 32:146–152.
- Cox, D. R. 1972. Regression models and life tables. *Journal of the Royal Statistical Society B* 34:187–220.
- Dänhardt, A., and P. H. Becker. 2011. Herring and sprat abundance indices predict chick growth and reproductive performance of Common Terns breeding in the Wadden Sea. *Ecosystems* 14:791–803.
- Evans, S. R., L. Gustafsson, and B. C. Sheldon. 2011. Divergent patterns of age-dependence in ornamental and reproductive traits in the collared flycatcher. *Evolution* 65: 1623–1636.
- Ezard, T. H. G., P. H. Becker, and T. Coulson. 2007. Correlations between age, phenotype, and individual contribution to population growth in Common Terns. *Ecology* 88: 2496–2504.
- Flatt, T., and A. Heyland. 2011. Mechanisms of life history evolution: the genetics and physiology of life history traits and trade-offs. Oxford University Press, Oxford, UK.
- Fox, J. 2002. An R and S-PLUS companion to applied regression. SAGE Publications, Thousand Oaks, California, USA.
- Hamel, S., S. D. Côté, J.-M. Gaillard, and M. Festa-Bianchet. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. *Journal of Animal Ecology* 78:143–151.
- Hamel, S., J. M. Craine, and E. G. Towne. 2012. Maternal allocation in bison: co-occurrence of senescence, cost of reproduction, and individual quality. *Ecological Applications* 22:1628–1639.
- Hayward, A. D., A. J. Wilson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2013. Reproductive senescence in female Soay sheep: variation across traits and contributions of individual ageing and selective disappearance. *Functional Ecology* 27:184–195.
- Kirkwood, T. B. L. 1977. Evolution of ageing. *Nature* 270:301–304.
- Kleinbaum, D. G., and M. Klein. 2012. Survival analysis. A self-learning text. Third edition. Springer, New York, New York, USA.
- Lack, D. 1947. The significance of clutch-size. *Ibis* 89:302–352.
- Ludwigs, J.-D., and P. H. Becker. 2002. The hurdle of recruitment: Influences of arrival date, colony experience and sex in the common tern *Sterna hirundo*. *Ardea* 90:389–399.

- McCleery, R. H., C. M. Perrins, B. C. Sheldon, and A. Charmantier. 2008. Age-specific reproduction in a long-lived species: the combined effects of senescence and individual quality. *Proceedings of the Royal Society B* 275:963–970.
- Medawar, P. B. 1952. An unsolved problem of biology. H. K. Lewis, London, UK.
- Moyes, K., T. Coulson, B. J. T. Morgan, A. Donald, S. J. Morris, and T. H. Clutton-Brock. 2006. Cumulative reproduction and survival costs in female red deer. *Oikos* 115:241–252.
- Newton, I. 1989. Lifetime reproduction in birds. Academic Press, Toronto, Canada.
- Nisbet, I. C. T., J. P. Montoya, J. Burger, and J. J. Hatch. 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among common terns *Sterna hirundo* in breeding and wintering grounds. *Marine Ecology Progress Series* 242:267–274.
- Nussey, D. H., T. Coulson, D. Delorme, T. H. Clutton-Brock, J. M. Pemberton, M. Festa-Bianchet, and J.-M. Gaillard. 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. *Ecology* 92:1936–1947.
- Nussey, D. H., L. E. B. Kruuk, A. Donald, M. Fowlie, and T. H. Clutton-Brock. 2006. The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecology Letters* 9:1342–1350.
- Proaktor, G., T. Coulson, and E. J. Milner-Gulland. 2008. The demographic consequences of the cost of reproduction in ungulates. *Ecology* 89:2604–2611.
- Rattiste, K. 2004. Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proceedings of the Royal Society B* 271:2059–2064.
- Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement and senescence in a long-lived bird. *Proceedings of the National Academy of Sciences USA* 107:7841–7846.
- Saino, N., M. Romano, R. Ambrosini, D. Rubolini, G. Boncoraglio, M. Caprioli, and A. Romano. 2012. Longevity and lifetime reproductive success of barn swallow offspring are predicted by their hatching date and phenotypic quality. *Journal of Animal Ecology* 81:1004–1012.
- Salomons, H. M., G. A. Mulder, L. van de Zande, M. F. Haussmann, M. H. K. Linskens, and S. Verhulst. 2009. Telomere shortening and survival in free-living corvids. *Proceedings of the Royal Society B* 276:3157–3165.
- Sanz-Aguilar, A., G. Tavecchia, R. Pradel, E. Mínguez, and D. Oro. 2008. The cost of reproduction and experience-dependent vital rates in a small petrel. *Ecology* 89:3195–3203.
- Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, UK.
- Stearns, S. C., and T. J. Kawecki. 1994. Fitness sensitivity and the canalization of life-history traits. *Evolution* 48:1438–1450.
- Szostek, K. L., and P. H. Becker. 2012. Terns in trouble: demographic consequences of low breeding success and recruitment on a common tern population in the German Wadden Sea. *Journal of Ornithology* 153:313–326.
- Tuljapurkar, S., and U. K. Steiner. 2010. Dynamic heterogeneity and life histories. *Annals of the New York Academy of Sciences* 1204:65–72.
- Tuljapurkar, S., U. K. Steiner, and S. H. Orzack. 2009. Dynamic heterogeneity in life histories. *Ecology Letters* 12: 93–106.
- van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to separate within- and between-individual effects. *American Naturalist* 167:766–773.
- van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. *Animal Behaviour* 77:753–758.
- van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* 128:137–142.
- Vaupel, J. W., K. G. Manton, and E. Stallard. 1979. The impact of heterogeneity in individual frailty on the dynamics of mortality. *Demography* 16:439–454.
- Vedder, O., S. Bouwhuis, and B. C. Sheldon. 2014. The contribution of an avian top predator to selection in prey species. *Journal of Animal Ecology* 83:99–106.
- Verhulst, S., and J.-A. Nilsson. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. *Philosophical Transactions of the Royal Society B* 363:399–410.
- Williams, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100:687–690.
- Wilson, A. J., and D. H. Nussey. 2010. What is individual quality? An evolutionary perspective. *Trends in Ecology and Evolution* 25:207–214.
- Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.
- Zhang, H., M. Rebke, P. H. Becker, and S. Bouwhuis. *In press*. Fitness prospects: effects of age, sex and recruitment age on reproductive value in a long-lived seabird. *Journal of Animal Ecology*. <http://dx.doi.org/10.1111/1365-2656.12259>

SUPPLEMENTAL MATERIAL

Ecological Archives

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