Ecology, 95(8), 2014, pp. 2077–2083

Longitudinal bio-logging reveals interplay between extrinsic and intrinsic carry-over effects in a long-lived vertebrate

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Abstract. Carry-over effects have major implications for individual fitness and population and evolutionary dynamics. The strength of these effects is dependent on an individual's intrinsic performance and the environmental conditions it experiences. However, understanding the relative importance of environmental and intrinsic effects underpinning seasonal interactions has proved extremely challenging, since they covary. A powerful approach is longitudinal measurement of individuals across a range of conditions, whereby each animal is effectively acting as its own control. We related time spent foraging during the nonbreeding period to subsequent breeding performance in European Shags *Phalacrocorax aristotelis*. By following individuals for up to six years, we could test simultaneously for extrinsic and intrinsic effects using random regression modeling. We detected significant annual and among-individual variation in daily foraging time during the late winter, and clear variation among individuals in the quadratic relationship between foraging time and date. Shorter foraging times were associated with earlier and more successful breeding, driven by differences among years and individuals, with no evidence of individual variation in the slope of these relationships. That both environmental and intrinsic variation shape carry-over effects has important implications for population responses to environmental change.

Key words: breeding phenology; data logger; downstream effects; European Shag; fitness; life-history trade-offs; random regression; reproductive success; seabird; seasonal interactions.

Introduction

Understanding the determinants of individual fitness is a central question in ecology because of the fundamental implications for population and evolutionary dynamics (Clutton-Brock 1988, Stearns 1992). That individuals may respond differently to the same environmental changes has been highlighted as an important, but underexplored possibility with consequences for population-level phenomena (Nussey et al. 2007, Grémillet and Charmantier 2010). Furthermore, fitness consequences of ecological variation may not be realized immediately, but instead have repercussions at a later life-history stage. Early life conditions, for example, can have long-term effects on individual fitness (Lindström 1999). Operating at shorter timescales, carry-over effects (COEs) are processes that affect an individual in one season that also affect its subsequent performance and are widely acknowledged to have an important impact on fitness (Norris and Marra 2007, Harrison et al. 2011). The strength of COEs varies because of differences in intrinsic performance or because individuals experience different environments. Establishing the interplay between environmental and intrinsic factors in determining COEs is critical for understanding the impacts of environmental change on populations (Harrison et al. 2011).

Quantifying the relative importance of extrinsic and intrinsic effects underpinning seasonal interactions has proved challenging because individuals may vary both in intrinsic performance and in the environmental conditions experienced, resulting in the two effects being confounded (Daunt et al. 2006, Harrison et al. 2011). Experimental manipulation has been useful in demonstrating causality in either intrinsic or extrinsic drivers of COEs (Betini et al. 2013, Catry et al. 2013). An alternative approach that can test extrinsic and intrinsic factors simultaneously involves longitudinal measurements across a range of environmental conditions, whereby individuals act as their own controls. Furthermore, this provides the opportunity to quantify the interaction between extrinsic and intrinsic effects, which is central to understanding a population's ability to respond to environmental change (Nussey et al. 2007).

We test for the interaction between extrinsic and intrinsic effects underpinning COEs from winter foraging to summer breeding performance in the European Shag *Phalacrocorax aristotelis* (hereafter, Shag) using longitudinal bio-logging of breeding individuals. A

Manuscript received 23 September 2013; revised 1 April 2014; accepted 16 April 2014. Corresponding Editor: J. Sauer.

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number of studies have shown that winter diet, habitat, and distribution affect survival rate, timing of migration, and breeding phenology and success (e.g., Marra et al. 1998, Norris et al. 2004, Alves et al. 2013). We collected data on time spent foraging (hereafter, foraging time) during the nonbreeding period and subsequent breeding phenology and success. Foraging time in late winter may affect body condition or time spent on prebreeding activities, both of which relate to timing of breeding (Marra et al. 1998, Daunt et al. 2006). We followed individuals for up to six years that varied in environmental conditions, giving us sufficient power to address key questions. We used random regression models (Nussey et al. 2007) in a Bayesian framework (Hadfield 2010) because they enable the effects of extrinsic (i.e., environmental) and intrinsic (i.e., individual) variation to be estimated simultaneously. In particular, such models can test whether individuals vary in their average responses to extrinsic factors and in the shape (e.g., slope) of this relationship (an individual by environment interaction). We used this modeling approach to address the following questions: (1) Do seasonal patterns of foraging time in the nonbreeding period vary among years and individuals, and is there an individual by date interaction? (2) Are there COEs of foraging time on breeding phenology (laying date) and do these vary amongst years and individuals? (3) Does breeding phenology relate to breeding success (number of chicks fledged per pair), and is this relationship apparent among and within individuals?

METHODS

Logger deployment and fitness measures

The study was carried out on the Isle of May National Nature Reserve, southeast Scotland (56°11′ N, 02°33′ W). During chick rearing in the breeding seasons (May–July) of 2002, 2003, and 2006–2011 inclusive, adult Shags were fitted with a geolocation immersion logger (British Antarctic Survey; minimum $20 \times 9 \times 5.5$ mm, mass 1.5 g; maximum $22 \times 19 \times 12$ mm, mass 9 g; ~0.1–0.5% body mass) attached to a leg ring with cable ties. Loggers representing 0.23% body mass did not significantly affect diving ability in the closely related great cormorant *P. carbo* (Ropert-Coudert et al. 2009). Loggers were deployed on 81 individuals (45 males, 36 females), and birds were sexed on voice and behavior. Birds were relocated in subsequent breeding seasons and, where possible, were recaptured, the logger removed, and a new device deployed. In 7% of cases, loggers stopped recording between breeding seasons, and these data were discarded. The final sample size of data sets comprising complete year-round foraging data was 188 (2002–2003, $n = 19$ birds; 2003–2004, $n = 12$; 2006–2007, $n = 18$; 2007–2008, $n = 17$; 2008–2009, $n = 19$; 2009–2010, $n = 34$; 2010–2011, $n = 40$; 2011–2012, $n = 29$) from 71 individuals (40 males, 31 females; multiple years obtained as follows: six years from six birds, five from five birds, four from seven birds, three from nine birds, two from 28 birds, and one from 16 birds). Laying date (estimated directly or back calculated from hatching date) and breeding success (number of chicks fledged per pair) were recorded for individuals in all years as part of long-term monitoring of the population.

The loggers recorded immersion in sea water at 3 s intervals, integrated at 10-minute intervals. Because Shags have a wettable plumage, time spent in the water is a reliable proxy of foraging time ($r = 0.94$, $n = 48$ individuals, $P < 0.001$; Daunt et al. 2006). Shags spend the night on land, providing a natural break in foraging, so we calculated daily foraging time in hours. We defined the nonbreeding period as the period from offspring independence (90 days posthatching) to laying date in the following year (Daunt et al. 2006). Our two measures of extrinsic effects were date (days after 1 June, representing within-year variation in conditions) and nonbreeding period (representing among-year variation in conditions). We incorporated daily wind speed and direction in analyses, since we have shown that foraging time declines with increasing wind speed and is higher during easterly (onshore) winds (Daunt et al. 2006). We obtained wind data from Leuchars weather station (56°23′ N, 02°52′ W), which is near the center of the winter distribution (Barlow et al. 2013; wind data *available online*).[6] We took the sine of wind direction to remove circularity and give easterly winds the maximum value of 1.

Statistical modeling

We first modeled the effects of extrinsic and intrinsic factors on foraging time during the nonbreeding period. We then modeled the effects of extrinsic and intrinsic variation on the relationship between daily foraging time and laying date. Finally, we modeled the effects of extrinsic and intrinsic variation on the relationship between laying date and breeding success. In order to simultaneously estimate the effects of extrinsic and intrinsic variation in each case, we carried out random regression models in a Bayesian framework (Hadfield 2010). Full details of the statistical modeling can be found in the Appendix.

The aim of the foraging time model was to establish whether the relationship with date varied among nonbreeding periods (the extrinsic effect) and individuals (the intrinsic effect). Visual inspection of daily foraging time against date showed that the relationship was well represented by a quadratic model, supporting earlier findings (Daunt et al. 2006, 2007). We therefore fitted a model with daily foraging time as the response variable and date, date squared, nonbreeding period, wind speed, sine wind direction, sex, and the interactions between nonbreeding period and date plus date squared and between sex and date plus date squared as fixed

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effects. The random effect of individual was modeled using five polynomial functions of date: (1) zero-order polynomial, which models variation among individuals in average daily foraging time (i.e., the individual intercept); (2) first-order polynomial, which models variation among individuals in average daily foraging time and the linear relationship with date; (3) second-order polynomial, which models variation among individuals in average daily foraging time and the quadratic relationship with date; and (4) first-order polynomial and (5) second-order polynomial, both with fitting of covariances between random effects to test whether regression coefficients varied independently among individuals or not (Kirkpatrick and Heckman 1989).

Model selection proceeded as follows. First, the most appropriate fixed effects to include in the model were determined by starting with a full model, including all main effects and two-way interaction terms. Nonsignificant terms were then dropped sequentially from the full model. During this model simplification process, the random effects structure was always a simple zero-order polynomial. The most appropriate random effects were determined by fitting a series of increasingly complex random effects structures (i.e., the five polynomial functions of date listed above) to the minimum adequate fixed effects model and comparing them using the deviance information criterion (DIC; Spiegelhalter et al. 2002). To illustrate the pattern of variation among nonbreeding periods and individuals graphically, we calculated, respectively, the mean and coefficient of variation (CV) of individual monthly means.

The aims of the model of laying date were to establish (1) whether there was a relationship with winter foraging time, such that an increase in foraging time was associated with a delay in laying, as shown previously in one year (Daunt et al. 2006); (2) whether this relationship was driven by intrinsic differences between individuals, the environmental conditions experienced in different years, or both; and (3) in which period outside the breeding season was foraging time most closely associated with subsequent laying date. We therefore divided the foraging time data into seven nonoverlapping windows of 30 d commencing on 1 September, approximating to successive months from September to March. For each of the 188 data sets, we calculated the mean daily foraging time in each window. We did not model the effects in April because the majority of individuals laid during this month. We used within-subject centering of the fixed effects (van de Pol and Wright 2009), a useful method of partitioning variation into differences among individuals (intrinsic effect) and within individuals (extrinsic effect) in situations where there is among-individual variation in the predictor (i.e., *x*-axis) variable of interest. For each 30-d window, we calculated the mean daily foraging time across nonbreeding periods for each individual (hereafter, foraging time mean), the between-individual effect. We then calculated foraging time minus foraging time mean (hereafter, foraging time anomaly), the within-individual effect. These two variables were then fitted as fixed effects in the model, together with sex, a sex by foraging time mean interaction, and a sex by foraging time anomaly interaction. Visual inspection of the data suggested that relationships were linear, so we tested zero-order and first-order polynomials, the latter with and without covariances between random effects estimated. The model selection procedure was the same as for the foraging time model.

The aim of the model of breeding success was to test whether laying date was linked to breeding success and whether this was evident within and among individuals. As with the laying date model, we used within-subject centering. We calculated mean laying date across years for each individual (laying date mean, the between-individual effect) and laying date minus laying date mean (laying date anomaly, the within-individual effect). Nonbreeding period, linear and quadratic laying date mean and laying date anomaly, and interactions between each and nonbreeding period were fitted as fixed effects, where the response variable was number of chicks fledged per pair with Gaussian errors. A random effect of individual ID was included. The model selection procedure was the same as in the laying date and foraging time models.

RESULTS

We found that foraging time increased in the early part of the nonbreeding period and then declined (Fig. 1a). The pattern of increasing foraging time early in the period was relatively consistent across years, but thereafter marked differences became apparent from January onwards and continued to diverge until March (range among nonbreeding periods: September, 4.09–5.04 h; December, 5.64–6.40 h; March, 3.95–7.76 h), resulting in a significant interaction between nonbreeding period and date plus date squared ($P < 0.001$ in all pairwise comparisons; see Table 1). There was also a significant main effect of nonbreeding period (difference from the intercept, corresponding to the nonbreeding period 2002–2003, ranging from −0.765 h to 0.553 h; six out of seven pairwise comparisons statistically significant; see Table 1). We also found significant effects of wind speed and direction, such that foraging time decreased by 0.015 1 − sm/4 wind speed and was 0.015 h/d longer during easterly winds (Table 1). We found no effect of sex or the interaction between sex and date on foraging time ($P > 0.05$).

Individuals differed in average daily foraging time and in the quadratic relationship with date (second-order polynomial preferred on the basis of DIC; covariance = 0; see Appendix). However, there was no evidence that these parameters covaried across individuals (no additional support for second-order polynomial; covariance ≠ 0; see Appendix). Accordingly, the coefficient of variation (CV) followed a strong seasonal pattern in all

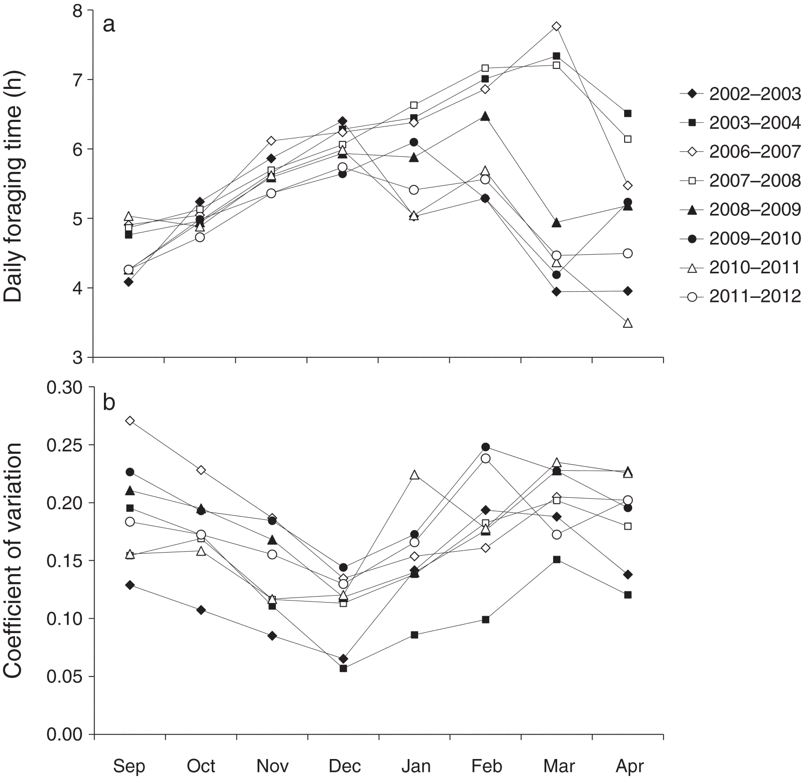

FIG. 1. (a) Daily foraging time for the eight nonbreeding periods studied, shown as mean of individual monthly means; (b) coefficient of variation of individual monthly means of daily foraging time.

nonbreeding periods, with CV highest at the start and end of the nonbreeding period and lowest in December (range among nonbreeding periods: September, 0.13–0.27; December, 0.06–0.14; March, 0.15–0.23; see Fig. 1b).

There was no evidence that foraging time between September and December was linked to laying date, but there were significant relationships between laying date and foraging time in January, February, and March (Table 2). Foraging time mean (the intrinsic effect) was an important determinant of laying date in these three months, such that an increase of 1 h in January, February, and March led to a delay in laying date of 4.0, 3.7, and 4.9 d, respectively (Table 2; Fig. 2a, c, e; $P < 0.001$ in all cases). Similarly, an increase of 1 h in foraging time anomaly (the extrinsic effect) in January, February, and March led to a delay in laying date of 6.2, 4.2, and 5.0 d respectively (Table 2; Fig. 2b, d, f; $P < 0.001$ in all cases). We detected no significant effect of sex or an interaction between sex and foraging time mean or anomaly ($P > 0.05$). Individuals varied in average laying date, but there was no evidence of among-individual variation in the relationship between foraging time and laying date (no additional support for first-order polynomial with or without covariance; see Appendix).

Breeding success was negatively related to laying date, such that an increase in laying date mean (the intrinsic effect) of 1 d led to a decline in breeding success of 0.04 chicks fledged per pair (Table 3; Fig. 2g; $P < 0.001$) and an increase in laying date anomaly (the extrinsic effect) of 1 d led to a decline in breeding success of 0.04 chicks fledged per pair (Table 3; Fig. 2h; $P < 0.001$). Breeding success also varied among years (difference from the intercept, corresponding to 2003, ranging from –0.801 to 1.303 chicks fledged per pair; two out of seven pairwise comparisons statistically significant; see Table 3). However, there was no evidence of a quadratic effect of laying date mean or laying date anomaly (both $P > 0.1$) nor for an interaction between year and laying date mean or laying date anomaly (both $P > 0.1$).

DISCUSSION

Understanding the relative importance of environmental and intrinsic effects in driving seasonal COEs has proved challenging in correlational studies. We analyzed a longitudinal bio-logging data set using advanced modeling approaches to provide the first demonstration of a COE of foraging time in the late winter on breeding performance that results from both environmental and intrinsic effects. These findings are important because they show that both intrinsic and extrinsic factors need to be considered when quantifying COEs on individual fitness, in particular amongst long-lived species that breed in multiple years and therefore are likely to experience a range of environmental conditions.

TABLE 1. Output for fixed effects in minimum adequate model of foraging time.

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	*P*
Intercept	6.481	6.239	6.724	<0.001
2003–2004	0.553	0.408	0.695	<0.001
2006–2007	0.552	0.309	0.798	<0.001
2007–2008	0.289	0.016	0.531	0.022
2008–2009	−0.076	−0.345	0.174	0.558
2009–2010	−0.742	−1.021	−0.509	<0.001
2010–2011	−0.765	−1.021	−0.529	<0.001
2011–2012	−0.552	−0.791	−0.286	<0.001
Date	−0.394	−0.648	−0.172	<0.001
Date^2	−2.286	−2.541	−2.039	<0.001
Wind speed	−0.015	−0.019	−0.010	<0.001
Wind direction	0.015	0.012	0.018	<0.001
2003–2004 × date	1.501	1.355	1.675	<0.001
2006–2007 × date	1.369	1.097	1.625	<0.001
2007–2008 × date	1.397	1.136	1.697	<0.001
2008–2009 × date	0.819	0.566	1.119	<0.001
2009–2010 × date	0.455	0.198	0.753	0.002
2010–2011 × date	0.114	−0.131	0.406	0.422
2011–2012 × date	0.513	0.243	0.790	<0.001
2003–2004 × date^2	1.608	1.377	1.838	<0.001
2006–2007 × date^2	0.934	0.665	1.267	<0.001
2007–2008 × date^2	1.244	0.956	1.605	<0.001
2008–2009 × date^2	0.813	0.477	1.124	<0.001
2009–2010 × date^2	0.944	0.665	1.265	<0.001
2010–2011 × date^2	1.077	0.784	1.377	<0.001

Notes: The intercept corresponds to the posterior mean in 2002–2003, at the mean date (because date was first mean centered, the mean is 23 December). The most parsimonious model involved a second-order polynomial with covariance set to zero (see the Appendix for outputs of random effects structures).

We recorded striking interannual variation in foraging time in the latter part of the winter. Late winter is when peak mortality typically occurs (Frederiksen et al. 2008). We could not carry out a survival analysis since all data were from surviving birds, but years in which late winter foraging time was high were associated with lower survival rates in the population as a whole (*unpublished data*; correlation between foraging time in March and proportion of adults returning from the previous year: *r* = −0.88). Individuals differed in average foraging time in the nonbreeding period and in the quadratic relationship with date, resulting in a higher CV at the start and end of the nonbreeding period. However, the lack of covariance amongst parameters in the random model structure indicated no link between mean foraging time

TABLE 2. Output for fixed effects in minimum adequate models of laying date for each month where foraging time mean or foraging time anomaly were significant (all effects shown significant at $P < 0.001$).

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI
January			
Intercept	81.339	64.424	95.943
Foraging time mean	4.000	1.265	6.775
Foraging time anomaly	6.153	4.075	8.263
February			
Intercept	82.350	70.858	94.887
Foraging time mean	3.682	1.541	5.530
Foraging time anomaly	4.190	2.153	6.268
March			
Intercept	79.283	72.357	86.419
Foraging time mean	4.899	3.567	6.193
Foraging time anomaly	4.990	3.781	6.215

Note: In all cases, the most parsimonious model involved a zero order polynomial (see Appendix for outputs of random effects structures).

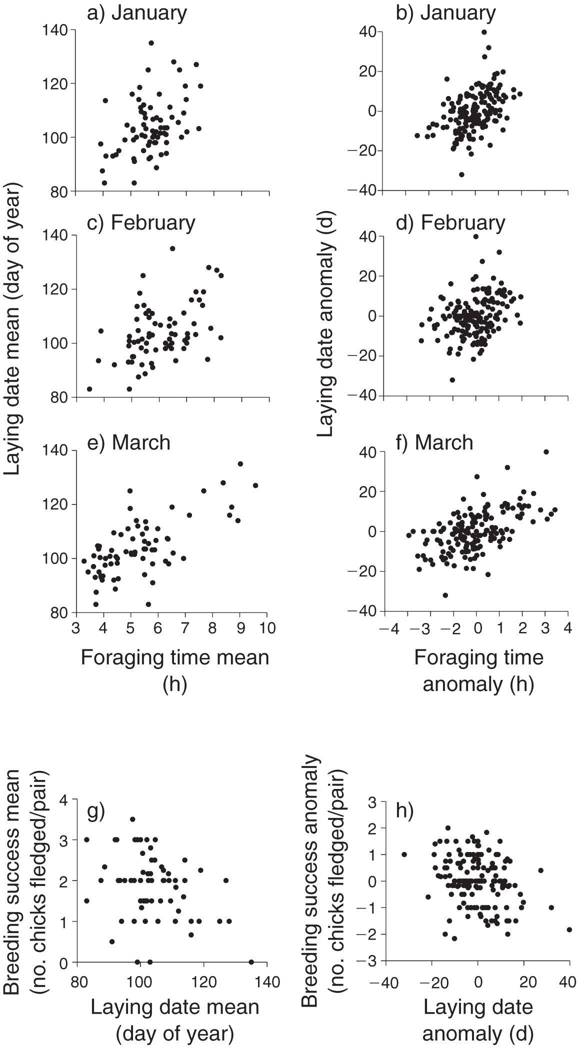

FIG. 2. Relationship between foraging time mean and laying date, representing between-individual (i.e., intrinsic) effects in (a) January, (c) February, and (e) March, respectively; relationship between foraging time anomaly and laying date, representing within-individual (i.e., extrinsic) effects in the same months (b) January, (d) February, and (f) March; relationship between (g) laying date mean and breeding success, representing between-individual effects; and (h) laying date anomaly and breeding success, representing within-individual effects. To illustrate these relationships to match how the statistical models are testing the two components, laying date mean and laying date anomaly (for panels a–f) and breeding success mean and breeding success anomaly (for panels g and h) are plotted on the *y*-axes.

TABLE 3. Output for fixed effects in minimum adequate model of breeding success.

Fixed effect	Posterior mean	Lower 95% CI	Upper 95% CI	*P*
Intercept	5.831	3.567	7.811	<0.001
2003–2004	−0.801	−1.874	0.103	0.126
2006–2007	0.431	−0.288	1.125	0.244
2007–2008	1.303	0.471	1.958	<0.001
2008–2009	−0.047	−0.644	0.542	0.864
2009–2010	0.914	0.379	1.503	0.002
2010–2011	0.262	−0.265	0.775	0.308
2011–2012	−0.182	−0.754	0.355	0.492
Laying date mean	−0.040	−0.060	−0.018	<0.001
Laying date anomaly	−0.040	−0.061	−0.024	<0.001

Notes: Breeding success is number of chicks fledged per pair. The intercept corresponds to the posterior mean in 2002–2003 at the mean laying date. Individual was included in the model as a random effect (see Appendix for random effects structure).

and the quadratic relationship with date. Among-individual variation in foraging time and the relationship with date may reflect variation in resource acquisition (Stearns 1992), which could be related to intrinsic foraging efficiency underpinned by factors such as genetic differences, age, experience, or parasite load. Alternatively, resource acquisition may be dependent on winter habitat choice, since Shags winter up to a few hundred kilometers from the colony (Barlow et al. 2013).

Our results support recent studies demonstrating the importance of COEs of winter conditions on breeding phenology and performance (e.g., Marra et al. 1998, Norris et al. 2004, Daunt et al. 2006, Alves et al. 2013). COEs on breeding phenology were driven by between- and within-individual effects, but individuals did not vary in the slope of their relationship between foraging time and breeding phenology. This suggests that when conditions in late winter are favorable, individuals obtain their daily food requirements in less time and may, therefore, be able to return to the colony and attain breeding condition sooner or allocate more time to breeding activities, such as territorial defense. Similarly, intrinsic differences may result in individuals with low foraging time (e.g., due to above-average resource acquisition abilities) benefiting from a physiological or temporal advantage, which carries over to earlier breeding. If these intrinsic differences are relatively stable throughout an individual's lifetime, then such high-quality foragers would breed relatively early regardless of the environmental conditions, consistent with the patterns documented in Fig. 2a, c, and e. However, we cannot discount the possibility that the within-individual patterns observed (i.e., Fig. 2b, d, and f) are due to temporal covariance. That is, associations between extrinsic effects in late winter and breeding phenology may result from temporal autocorrelation in the environment that affects both winter foraging and breeding phenology, for example, related to cyclical environmental variation with long periodicity. Similarly, performance in terms of both foraging and breeding proficiency may be consistent within individuals, without there necessarily being any causal (e.g., physiological) link. However, the overall relationship between foraging time and laying date was determined by both between- and within-individual effects, suggesting that environmentally driven variation in foraging time (the within-individual effect) has a causal effect on breeding phenology, over and above any associations due to intrinsic differences among individuals (the between-individual effect). Crucially, the association with breeding phenology had fitness implications, since earlier breeders were more successful, as previously recorded in many species (Clutton-Brock 1988).

It is widely recognized that both extrinsic and intrinsic effects may shape COEs, and experimental manipulation has been successful in demonstrating causality (Betini et al. 2013, Catry et al. 2013). By establishing to what extent these extrinsic and intrinsic factors interact, our approach is complementary to experimental evidence, and we hope will provide impetus to others possessing similar longitudinal data or planning new studies. Between-individual variation in responses to environmental conditions is a common phenomenon in wild vertebrate populations with important consequences for population and evolutionary dynamics (Nussey et al. 2007, Grémillet and Charmantier 2010). We identified complex relationships whereby both intrinsic and extrinsic effects were important in explaining links between winter foraging and breeding parameters, such that individuals varied in the strength of the effect of date on foraging time in the nonbreeding period, but not in the carry-over effect from foraging time to breeding phenology. Understanding the interactions between these effects is important in quantifying drivers of individual fitness variation and eco-evolutionary dynamics, and thus the ability of populations to adapt to environmental change.

ACKNOWLEDGMENTS

We are grateful to Debbie Russell, Hanna Granroth-Wilding, and Katherine Herborn for help in the field; Mike Harris, Emma Cunningham, and Dan Nussey for useful discussions; and Adam Butler for statistical advice. We are grateful to Jon Green and an anonymous referee for valuable comments on the manuscript. We thank Scottish Natural Heritage for access to the Isle of May and Natural Environment Research Council for funding. T. E. Reed was funded by the Beaufort Marine Research Award in Fish Population Genetics funded by the Irish Government under the Sea Change Programme.

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SUPPLEMENTAL MATERIAL

Appendix

Statistical models (*Ecological Archives* E095-185-A1).