Age, timing, and a variable environment affect double brooding of a long-lived seabird

Michael E. Johns[1],*, Pete Warzybok[2], Russell W. Bradley[2], Jaime Jahncke[2], Mark Lindberg[1], Greg A. Breed[1]

[1]Department of Biology and Wildlife and Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[2]Point Blue Conservation Science, 3820 Cypress Drive, Suite 11, Petaluma, CA 94954, USA

ABSTRACT: Differences in reproductive output for marine vertebrates are driven by a combination of environmental, physiological, and behavioral cues. Individuals use these cues when balancing the tradeoff between current reproductive investment and future survival, particularly when resources vary on spatial and temporal scales. A common strategy for maximizing fecundity in birds is to produce 2 broods in a single season, a behavior known as double brooding. Cassin's auklets *Ptychoramphus aleuticus* are among the relatively few seabirds that use this strategy; however, the proportion of breeding pairs that attempt double brooding is highly variable among years. We investigated the source of this variation using long-term monitoring data from Southeast Farallon Island off central California, USA. Double-brooding rates ranged from 0 to 90% over a 26 yr period, with an overall rate of 32% (95% CI ± 4.16%). Parameter estimates from generalized linear mixed models indicate that older females, earlier breeding initiation dates, stronger upwelling, and an interaction between age and upwelling strength increased the likelihood of double brooding in this population. Using a within-subject centering technique, the effects of age included both a within- and between-individual improvement in the likelihood of double brooding with age. Our findings indicate that females of higher quality and reproductive experience drive double brooding in this population and that these individuals are especially able to adopt a more flexible breeding regime in years characterized by high marine productivity.

KEY WORDS: Age-based demography · California Current · Cassin's auklet · Reproductive strategy · Seabird · Upwelling · Double brooding · Variable environment

INTRODUCTION

In order to maximize fitness, individuals must balance current reproductive investment against the odds of surviving to reproduce in the future (Pianka & Parker 1975), especially when resources vary on temporal and spatial scales. This is achieved by either delaying or abandoning breeding effort during years of sub-optimal conditions or by breeding early and producing the maximum number of offspring when conditions are favorable (Stearns 1992). Such decisions are influenced not only by environmental cues, but may also be shaped by age, inherent traits, body condition, breeding experience, and behavioral tendencies (Martin 1995, Pärt & Forslund 1996, Knape et al. 2011, Chambert et al. 2013). Individual differences in reproduction influence population level parameters, and there is much interest from both a management and theoretical perspective in understanding how these demographic and environmental factors interact (Weimerskirch 2001).

Life-history strategies flexible enough to allow extra investment in years of especially high productivity grant individuals the ability to adjust to variable environments (Cooch & Ricklefs 1994). In birds, a common strategy for making such adjustments is to

attempt 2 broods in a single season, known as double brooding. This allows species with high mortality risks and shorter lifespans to maximize fitness by investing in current reproduction at the cost of survival, a strategy that has been well documented in passerines (Norris 1993, Ogden & Stutchbury 1996, Nagy & Holmes 2005, O'Brien & Dawson 2013, Hoffmann et al. 2015). Double brooding is less common in long-lived species (>15 yr, e.g. many in the family Alcidae and order Procellariiformes), where, with low mortality risks, individuals are expected to invest more in future reproductive potential rather than immediate reproductive success (Stearns 1992, Reed et al. 2008). Environmental stochasticity, however, reduces the odds of producing offspring in some years and increases it in others (Newton 1989), so long-lived species able to adopt a more flexible breeding regime by opportunistically initiating a second brood are expected to achieve higher overall fitness.

At least 13 species of seabirds are known to double brood, most notably the silver gull *Chroicocephalus novaehollandiae* (Nicholls 1974), common tern *Sterna hirundo* (Wiggins et al. 1984), black noddy *Anous minutus* (Gauger 2000), and little penguin *Eudyptula minor* (Agnew et al. 2014), all of which inhabit temperate or tropical regions of the Southern Hemisphere. The only seabird in the Northern Hemisphere to regularly double brood is the Cassin's auklet *Ptychoramphus aleuticus.* This planktivorous member of the Alcidae breeds on offshore islands and isolated headlands from Baja California, Mexico, to the western Aleutian Islands of Alaska, USA. Double brooding only occurs in the southern portion of its range, with records from San Benito Island in Mexico (Wolf et al. 2009), the Channel Islands off southern California (Adams et al. 2014), and Southeast Farallon Island (SEFI) off central California (described here). Although double-brooding rates for Cassin's auklets are anecdotally highest during years of increased marine productivity, not all pairs will attempt a second brood, indicating such a behavior is driven by additional environmental, physiological, or behavioral parameters working in concert with resource abundance. It is unclear what demographic characteristics predict which individuals attempt double brooding.

Reproductive timing has been identified as one of the most important factors limiting double brooding in other species. Often females that breed earlier in the season are more likely to attempt a second brood than those that breed later (Geupel & DeSante 1990, Ogden & Stutchbury 1996, Agnew et al. 2014, Hoffmann et al. 2015, Béziers & Roulin 2016). In a

manipulative study of great tits *Parus major*, late-laying pairs that received early clutches from other nests double brooded at a higher rate than early-laying pairs that received late clutches (Verboven & Verhulst 1996), likely due to the timing of peak environmental conditions. In a similar manipulative study of mountain bluebirds *Sialia currucoides*, early breeders were more likely to double brood even when their clutches were switched with those from late breeders and hatch dates were delayed (O'Brien & Dawson 2013), indicating individual differences were more important than reproductive timing. In that same study, O'Brien & Dawson (2013) described an energetic limit to double brooding, confirming previous work on the influence of environmental conditions and timing of reproduction to match peak food availability (Moore & Morris 2005, Nagy & Holmes 2005, Grüebler & Naef-Daenzer 2008, Husby et al. 2009). Older females, however, generally have a higher propensity for double brooding and are more likely to attempt a second brood despite variable environmental conditions (Geupel & DeSante 1990, Nagy & Holmes 2005, Bulluck et al. 2013, Hoffmann et al. 2015). Such age effects on reproduction contain underlying within- and between-subject components, respectively representing a gain in breeding experience and a selection for individuals with advantageous traits over time (Forslund & Pärt 1995). Since the effects of experience and individual quality mask one another, separating them can be difficult when longitudinal data on individuals are lacking, leading most researchers to conclude that age effects are a confounded combination of the two.

Longitudinal studies following marked animals are useful for exploring how differential responses by individuals to variation in environmental conditions affect population-level reproductive parameters (Clutton-Brock & Sheldon 2010). Marked populations are also essential for testing whether age-specific patterns in reproduction are driven by inherent differences among individuals or by changes within individuals as they grow older. We used a 26 yr dataset on the breeding performance of known-age Cassin's auklets to identify specific demographic and environmental mechanisms that influence annual variability in double-brooding rates. Our objectives were to: (1) test the effects of female age, reproductive timing, and environmental variability on double-brooding decisions of a long-lived seabird; and (2) apply a within-subject centering technique to estimate the within- and between-subject effects of ageing on double-brooding patterns for this species.

MATERIALS AND METHODS

Field methods

SEFI is located at the southern end of a rocky archipelago within the Farallon Island National Wildlife Refuge (37° 42′ N, 123° 00′ W; Fig. 1) and contains some of the highest concentrations of breeding seabirds on the west coast of North America. Point Blue Conservation Science has maintained a continuous monitoring effort of the breeding performance of Cassin's auklets on SEFI since 1972 (Manuwal 1974, Ainley & Boekelheide 1990). Clutch size in this species is limited to a single egg, which is laid in excavated earthen burrows or natural rock crevices (Manuwal 1974). Beginning in 1983, 446 wooden nest boxes were distributed in 10 different locations throughout the island and subsequently monitored (Pyle 2001). Boxes were partially buried to simulate natural ground crevices in areas known to be suitable nesting habitat, and after 2008 they were given wooden shades to regulate temperature. Birds that recruited into these boxes were recaptured each spring to record band information and bill depth measurements, the latter used to determine sex (Nelson 1981). Boxes containing a breeding pair were visited every 5 to 15 d to determine lay date, then left alone for 25 d until returning to determine whether the egg had hatched or failed. If hatched, chicks were
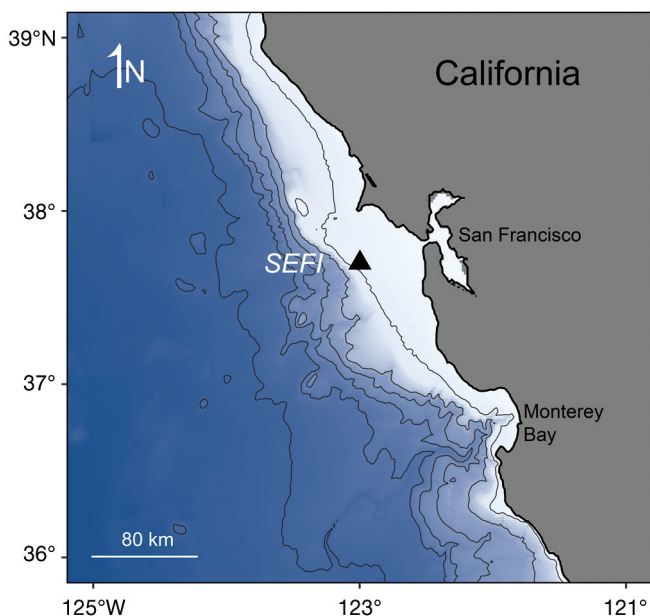

Fig. 1. Location of Southeast Farallon Island (SEFI; black triangle), highlighting its proximity to the productive waters of the continental shelf break off the central coast of California, USA. Bathymetric contours shown at 100 m intervals

measured every 5 d until fledged or lost. If the chick survived to fledge, boxes were again monitored every 5 d to note lay date of a potential second brood. Chicks that reached fledging age (>35 d or fully feathered) were marked with a numeric United States Geological Survey (USGS) stainless steel leg band. Birds banded as chicks represent the pool of known-aged individuals for this population, some of which were banded from natural crevices prior to the installation of nest boxes in 1983. Use of nest boxes on SEFI by known-age recruits first occurred in 1989, with 1981 as the earliest hatch year for these recruits.

Probability of double brooding

A total of 2079 breeding records from 919 known-age Cassin's auklets were compiled between 1989 and 2015. We chose to focus only on known-age female breeders, since egg production and the decision to lay depends primarily on the abilities and condition of the female. Only breeding records with confirmed sex and age were used for the double-brooding analysis, excluding records where the difference in bill depth measurements between parents was too small (<0.4 mm) to discern sex (Nelson 1981) and where females were not banded as chicks. Double brooding is defined as a second nesting attempt following the successful fledging of the first chick. Only breeding records where the first chick was absent from the box after reaching fledgling age were used for this study to exclude second broods that were actually a continuation of an initial nest failure.

Generalized linear mixed models (GLMM, binomial with logit link) were constructed to estimate the probability of attempting a second brood as a function of combinations of predictor variables considered important for reproduction. All models contained fixed predictors female age (AGE) and lay date of the first clutch (LAY). A quadratic age term (AGE^2) was included to model a possible decline in double-brooding attempts in older individuals. To characterize environmental conditions linked to primary production, 3 average seasonal (March–August) oceanographic parameters were included: sea surface temperature (SST), multivariate El Niño Southern Oscillation index (MEI), and upwelling index (UPW). SST was measured from daily water samples collected directly from SEFI. Pacific basin-wide MEI data, a more comprehensive measure of El Niño Southern Oscillation (Wolter & Timlin 1993), were obtained from the National Oceanographic and Atmospheric Administration (NOAA) website (www.esrl.noaa.gov). Upwelling in-

dices for the region surrounding 36° N, 122° W, defined as the average volume of water upwelled through the Ekman Layer every second along 100 m of coastline ($m^3 \times s^{-1} \times 100\ m^{-1}$ of coastline), were obtained from the NOAA Pacific Fisheries Environmental Laboratory website (www.pfeg.noaa.gov). An interaction term for age and each environmental predictor was included to test the possibility that environmental variability has a differential effect on specific age classes. All models contained individual female and year as random intercept terms to account for variation among individuals and annual variation not explained by the environmental parameters tested, consistent with previous studies of repeated measures over time. Fifteen candidate models were fitted in R (R Core Team 2015) using the package lme4 (Bates et al. 2015) and ranked using Akaike information criteria with sample size adjustments (AIC_c; Anderson & Burnham 2002).

Effects of age

We used a within-subject centering method described by Van de Pol & Wright (2009) to separate and test the between- and within-subject variation underlying the effect of age on the probability of double brooding. To isolate and interpret these age effects alone, any quadratic or interaction terms in the top-performing GLMM were removed for this analysis. We found that leaving the quadratic and interaction terms in the model masked the between- and within-subject effects, making it difficult to interpret the coefficients (see Appendix). A reduced example model for predicting the probability of double brooding (DB_{it}) for individual female i at time t is:

$$\text{logit}(DB_{it}) \sim \mu + AGE_{it} + LAY_{it} + ENV_t \\ + (1 \mid YEAR_t) + (1 \mid ID_i) + \varepsilon_{it} \tag{1}$$

with mean μ and fixed predictors AGE_{it} for female age, LAY_{it} for lay date of first clutch, and ENV_t for the environmental variable (SST, MEI or UPW) identified as most important through the model selection process. Random intercept terms are $(1 \mid YEAR_t)$ for year of breeding record and $(1 \mid ID_i)$ for the unique band number of each female. To separate the between- and within-subject components of age, the term AGE_{it} in the reduced model was decomposed into its between- and within-subject components:

$$\text{logit}(DB_{it}) \sim \mu + B_i + W_{it} + LAY_{it} + ENV_t \\ + (1 \mid YEAR_t) + (1 \mid ID_i) + \varepsilon_{it} \tag{2}$$

B_i for the between-subject variation calculated as the mean age of subject i across all records ($\overline{AGE_i}$), and W_{it} for the within-subject variation calculated as the mean age of subject i subtracted from the age at time of observation ($AGE_{it} - \overline{AGE_i}$). Parameter estimates for these new terms and the original age term in Model 1 were estimated and compared in R (R Core Team 2015) using the package lme4 (Bates et al. 2015). A positive estimate for B_i would indicate females that persist in the population longer through a selection for higher-quality individuals, or those that begin breeding later in life, are more likely to double brood (individual quality). A positive estimate for W_{it} would indicate females increase their odds of double brooding as they age, regardless of whether they only breed for a few years while young or breed many years over a lifetime (gain in experience). We tested for difference in the slopes of B_i and W_{it} with:

$$\text{logit}(DB_{it}) \sim \mu + AGE_{it} + (B_i - W_{it}) + LAY_{it} + ENV_t \\ + (1 \mid YEAR_t) + (1 \mid ID_i) + \varepsilon_{it} \tag{3}$$

where no difference between the estimates for B_i and W_{it} would indicate that female age alone as a fixed predictor in the final model represents equal between-subject effects of quality and within-subject effects of experience (Van de Pol & Wright 2009).

RESULTS

Probability of double brooding

A total of 483 breeding records from 193 known-age females with successful first broods were identified. From these records, the annual proportion of females that went on to produce a second brood varied from 0 to 90% over a 26 yr period (Fig. 2A), with an overall double-brooding rate of 32% (95% CI ± 4.16%). Female ages ranged from 2 to 18 yr, with double brooding confirmed in all age classes excluding 2 yr olds (Fig. 2B). Similarly, success rates of second broods varied substantially by year (Fig. 3A) but generally increased with female age (Fig. 3B). The mean age of females that double brooded (8.5 ± 0.27; mean ± SE) was higher than those that did not double brood (5.8 ± 0.17). Lay dates of the first clutch for females that attempted double broods ranged from March 11 to April 28, with an average lay date of April 3 (ordinal day 93 ± 0.86 d) for double-brooded females and April 23 (ordinal day 113 ± 1.04 d) for single-brooded females. Mean seasonal MEI (0.02 ± 0.04) and SST (11.78 ± 0.05) were both lower for re-
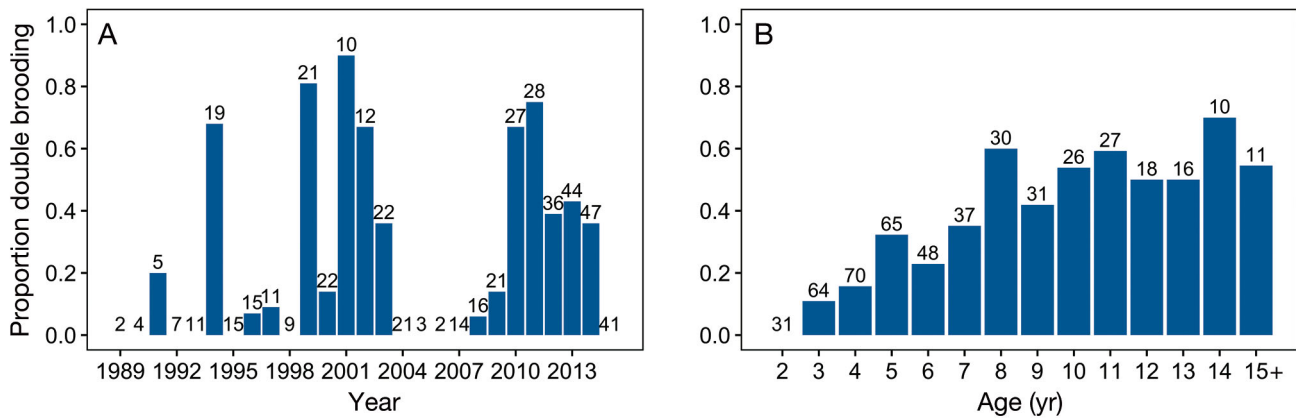
Fig. 2. Proportion of known-age female Cassin's auklets with successful first clutches that attempted double brooding by (A) year (1989–2015) and (B) age (2–18 yr). Sample sizes displayed above bars. Ages 15–18 were combined for illustrative purposes due to small sample sizes for those age classes
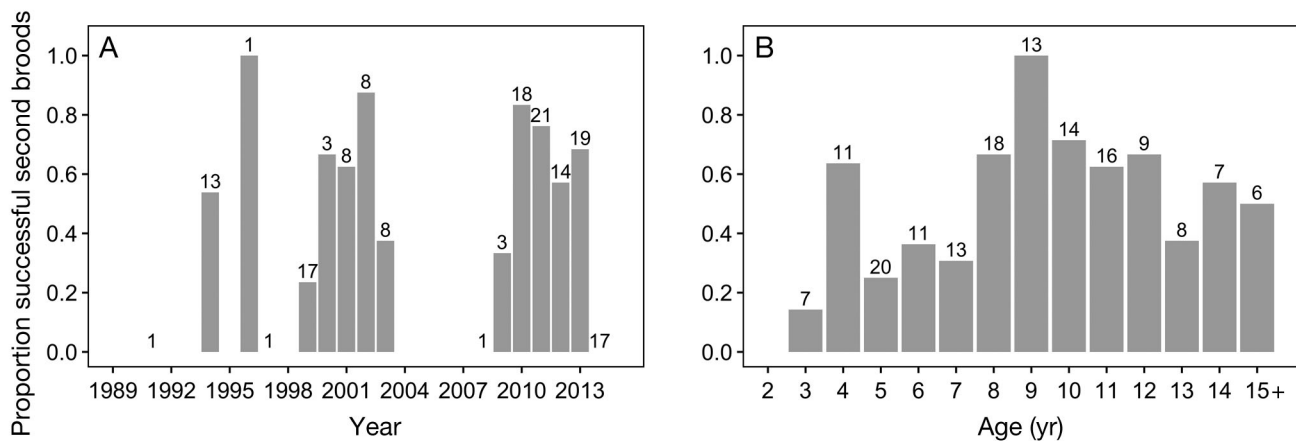

Fig. 3. Proportion of double-brooding known-age female Cassin's auklets with successful second clutches by (A) year (1989–2015) and (B) age (2–18 yr). Sample sizes displayed above bars. Ages 15–18 were combined for illustrative purposes due to small sample sizes for those age classes

cords with double broods compared to single broods (0.48 ± 0.04, 12.13 ± 0.04, respectively). Mean *UPW* was higher for records with double broods (200.8 ± 2.6) compared to single broods (173.2 ± 1.9).

The model including *AGE, AGE²*, *LAY, UPW*, and an interaction between *AGE and UPW* out-performed all other models based on AIC$_c$ selection (Tables 1 & 2). With an age-specific response to seasonal upwelling conditions, older females were more likely to double brood regardless of upwelling strength, whereas younger females showed a much lower chance of double brooding in weak upwelling years compared to average or strong upwelling years (Fig. 4). Controlling for lay date and upwelling, the probability of double brooding increased as females aged, with the quadratic age term describing an asymptote in middle-aged birds followed by a slight decline in double brooding for the oldest individuals.

Across all age groups, the probability of double brooding increased with high upwelling strength (Fig. 5A) and early lay dates of the first clutch (Fig. 5B).

Effects of age

There was a positive trend in the likelihood of double brooding with increasing female age at time of reproduction, mean age across all breeding records, and centered age (Fig. 6). The raw data showed a slight curvature in the proportion of double-brooding attempts with increasing female age (Fig. 6A) and mean age (Fig. 6B) which was not captured by the exclusion of the quadratic age term in this reduced linear model. The within-individual variation was significant, indicating that the likelihood of double brooding increased with each additional year of

Table 1. Generalized linear mixed model) selection results for the probability of attempting double brooding in Cassin's auklets as a function of important predictor variables. *AGE*: female age; AGE^2: quadratic age term; *LAY*: lay date of the first clutch; *UPW*: upwelling index; *MEI*: multivariate El Niño Southern Oscillation index; *SST*: sea surface temperature. Models ranked from best (lowest corrected Akaike information criteria, ΔAIC_c) to worst, with AIC_c weights (ω_i), and number of parameters (K). Marginal R^2 (R^2m) values show model fit for fixed effects only. All models contained random intercept terms: (1|*YEAR*) and (1|*ID*), i.e. year of breeding record and unique band number of each female, respectively

Model	K	ΔAIC_c	ω_i	R^2m
$AGE + AGE^2 + LAY + UPW + AGE{:}UPW$	8	0.0	0.54	0.74
$AGE + AGE^2 + LAY + UPW$	7	2.1	0.19	0.72
$AGE + LAY + UPW + AGE{:}UPW$	7	4.5	0.06	0.72
$AGE + AGE^2 + LAY + MEI$	7	5.1	0.04	0.72
$AGE + LAY + UPW$	6	5.3	0.04	0.70
$AGE + AGE^2 + LAY + SST + AGE{:}SST$	8	5.3	0.04	0.68
$AGE + AGE^2 + LAY$	6	5.8	0.03	0.68
$AGE + AGE^2 + LAY + MEI + AGE{:}MEI$	8	7.0	0.02	0.72
$AGE + LAY + MEI$	6	7.4	0.01	0.71
$AGE + AGE^2 + LAY + SST$	7	7.8	0.01	0.68
$AGE + LAY$	5	8.2	0.01	0.66
$AGE + LAY + SST + AGE{:}SST$	7	8.7	0.01	0.67
$AGE + LAY + MEI + AGE{:}MEI$	7	9.4	0.00	0.71
$AGE + LAY + SST$	6	10.2	0.00	0.66
(Intercept only)	3	145.8	0.00	0.00

breeding (Model 2, $\beta_W = 0.32 \pm 0.09$, p < 0.001). The same was true for the between-individual variation, indicating females that persisted in the population longer, either by breeding over many years or recruiting late in life, were more likely to double brood (Model 2, $\beta_B = 0.27 \pm 0.08$, p < 0.001). While the effect sizes for the within- and between-subject variation were both positive, they were not significantly differ-

Table 2. Direction and magnitude of the fixed effects in the top-performing GLMM for predicting the probability of a double brooding attempt by female Cassin's auklets, with coefficient estimate (β) and standard error (SZ), z-score (*Z*) and p-value (p). Parameters in the top model are considered important predictors based on model selection results. The top model contained random intercept terms: (1|*YEAR*) and (1|*ID*). See Table 1 for parameter definitions

Predictor	β	SE	Z	p
Intercept	0.151	5.113	0.030	0.976
AGE	1.689	0.532	3.178	0.001
AGE^2	−0.040	0.017	−2.399	0.016
LAY	−0.171	0.032	−5.284	<0.001
UPW	0.058	0.021	2.782	0.005
AGE:UPW	−0.003	0.002	−1.946	0.052

ent (Model 3, $\beta_{(B - W)} = -0.05 \pm 0.13$, p = 0.67), suggesting that using age as a predictor in the model is an accurate portrayal of a gain in double-brooding experience while accounting for individual heterogeneity among subjects (Table 3).

DISCUSSION

At SEFI, double brooding by Cassin's auklets was common over a 26 yr period; however, inter-annual rates were highly variable (Fig. 2A). Older females, early first clutch lay dates, and strong upwelling led to an increased likelihood of double brooding. Furthermore, older females were less affected by differences in upwelling strength than younger females (Fig. 4), indicating females become better able to cope with environmental uncertainty as they age. Females
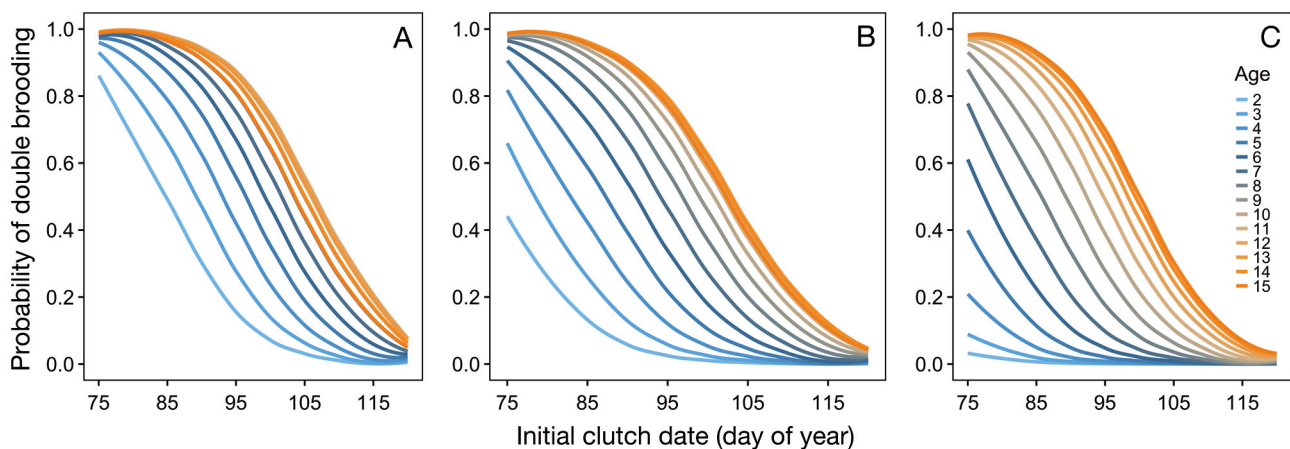

Fig. 4. Final GLMM response curves for the probability of a double-brooding attempt in Cassin's auklets as a function of female age (yr) and lay date of first clutch varied by (A) strong, (B) average, and (C) weak seasonal upwelling conditions. Strong upwelling was defined as 220, average as 200, and weak as 120 (m^3 s^{-1} 100 m^{-1} of coastline) based on data monthly averages near the Farallon Islands from 1989–2015
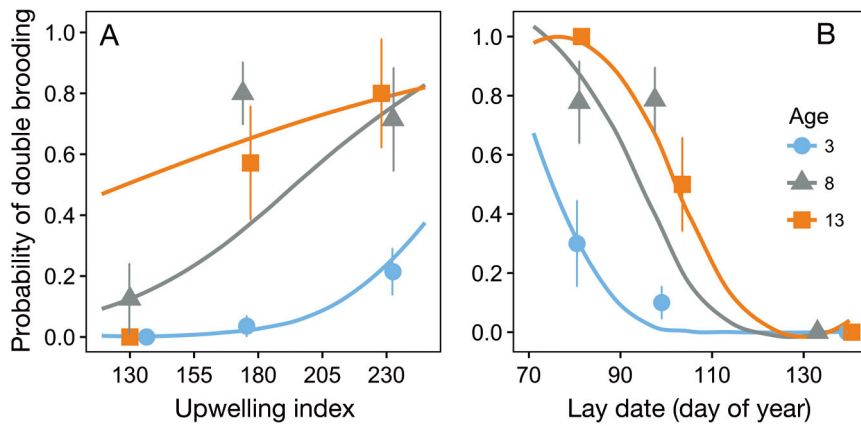
Fig. 5. Final GLMM response curves for the probability of a double-brooding attempt in Cassin's auklets as a function of young (3 yr), middle-aged (8 yr), and old (13 yr) females varied by (A) seasonal upwelling and (B) lay date of the first clutch. Mean and SE of the proportion of females that attempted second broods for each age group were binned into early, middle, and late categories of upwelling and lay date to illustrate model fit
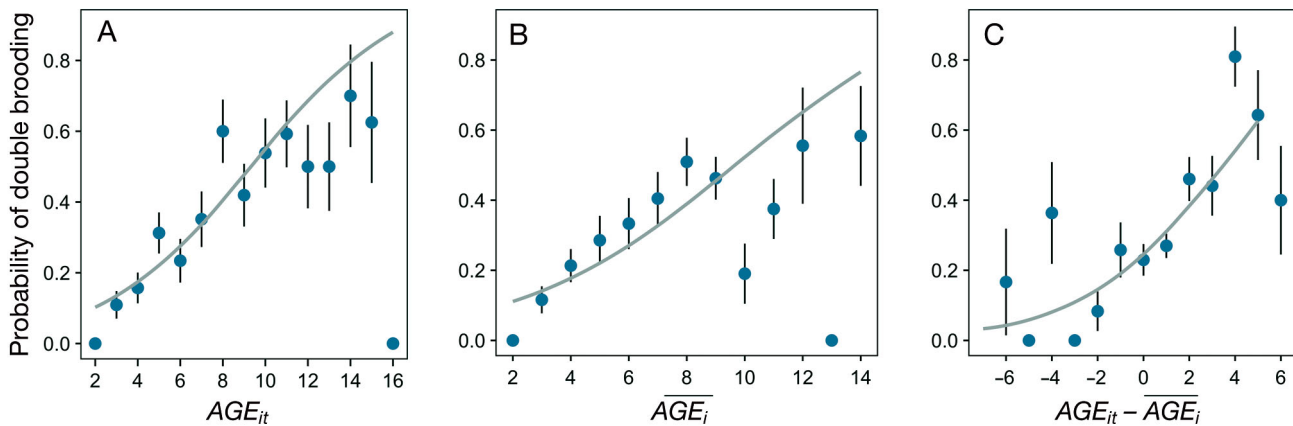

Fig. 6. Reduced GLMM response curves for the probability of a double-brooding attempt in Cassin's auklets as a function of (A) female age, (B) between-subject age term, and (C) within-subject age term, controlling for lay date of first clutch and seasonal upwelling strength. AGE_{it}: female age of subject i at time t; $\overline{AGE_i}$: mean age of subject i across all records. Mean and SE of the proportion of females that attempt a second brood for female age, and the between- and within-subject components of age, were calculated from equally spaced bins and plotted to show model fit

that tended to live longer likely gained experience in double brooding with successive breeding attempts, suggesting that females of higher quality and with

Table 3. Parameter estimates, standard errors, Z-scores and p-values of fixed predictors for 3 variations of the reduced GLMM for predicting the probability of a double-brooding attempt in Cassin's auklets, describing the between- and within-subject effects of age. B_i: between-subject variation calculated as the mean age of subject i across all records; W_{it}: within-subject variation calculated as the mean age of subject i subtracted from the age at time of observation. Remainder of equation indicated by ψ is: + LAY_{it} + UPW_t + $(1|YEAR_t)$ + $(1|ID_i)$ + ε_{it}. See Table 1 for other parameter definitions

	Predictor	β	SE	Z	p
(1) AGE_{it} + … ψ	AGE	0.295	0.063	4.711	<0.001
(2) B_i + W_{it} + … ψ	B	0.271	0.082	3.311	0.001
	W	0.325	0.097	3.362	0.001
(3) AGE_{it} + B_i + W_{it} + … ψ	AGE	0.325	0.097	3.362	0.001
	(B–W)	–0.054	0.129	–0.420	0.675

more reproductive experience drive double brooding in this population, specifically during years of high marine productivity.

Timing of breeding initiation was a major factor determining whether a female would attempt a second brood. This is consistent with double-brooding behavior in other studies where lay dates varied among individuals (Geupel & DeSante 1990, Ogden & Stutchbury 1996, Husby et al. 2009, Agnew et al. 2014, Hoffmann et al. 2015, Béziers & Roulin 2016), with only highly synchronous species showing no effects of reproductive timing on double brooding (Cornell & Williams 2016). Although age and upwelling strength explained some of the variation, even older females breeding in years of optimal upwelling conditions were less likely to double brood when lay dates were delayed, and none attempted double brooding if the

first clutch was laid after April 28. Parents that breed early have additional time to fledge the first chick and rear a second before upwelling subsides and resources become more scarce (Manuwal 1979). This could explain why double brooding in Cassin's auklets is not observed at higher latitudes, such as in other well-studied northern colonies like Triangle Island in British Columbia, Canada, where a brief upwelling season might prevent even early breeders from attempting a second brood.

Along with matching peak environmental conditions, age-specific differences in timing may also be contributing to the success of early breeders. Female Cassin's auklets with energetically rich prey in their pre-breeding diet lay earlier in the season than those that target energetically poor prey items (Sorensen et al. 2009). The interaction between age and upwelling reported here suggests that, for these birds, understanding the conditions that lead to increased productivity, or potentially locating spatially dispersed areas of high prey abundance, requires a certain level of experience only acquired with age. Thus, older females may simply be more capable foragers, enabling them to breed earlier than less experienced younger females, which in turn allows for additional time to second brood. Reproductive timing may also be correlated with individual heterogeneity, where females of higher quality choose to lay earlier in the season (Hipfner et al. 1999, Blums et al. 2005). Females paired with males of higher quality or experience, or females that have bred with the same male over many years, might also have an increased likelihood of double brooding. This effect, however, is likely reflected more in greater chick success rather than whether or not a female decides to attempt a second brood. Incubation and chick-rearing duties are shared equally between both sexes in this species (Manuwal 1974), so females would need to invest the same amount of energy in reproduction regardless of the males' performance.

Age-specific effects on reproduction and survival for birds have been well documented (Martin 1995). For Cassin's auklets, older parents tend to have greater reproductive success (Pyle et al. 2001) and produce chicks with higher survival and recruitment rates (Lee et al. 2012) than younger parents. Our study adds double brooding as another measure of increased reproductive performance with age for this species, similar to findings from other taxa (Geupel & DeSante 1990, Nagy & Holmes 2005, Bulluck et al. 2013). We found that females that attempted second broods had longer lifespans than single-brooded females, despite the added physiological stresses of increased breeding effort and subsequent risk of reduced survival for double-brooded parents (Verhulst 1998, Hoffmann et al. 2015). Our results also suggest a decline in the likelihood of double brooding for the oldest females in this population; however, this might be attributable to decreased survival for birds of extreme age (Lee et al. 2012).

Variable environmental conditions have a considerable effect on a range of life-history parameters in seabirds, including survival, abundance, growth, and phenology (Sydeman et al. 2012), but few studies outside of passerines have linked its effects to double brooding. Of the 3 climate-related environmental indices we tested, upwelling strength best described the variation in double brooding rates. During the summer breeding season, Cassin's auklets on SEFI forage within the California Current System (CCS), a wind-driven upwelling region that extends from British Columbia to Mexico. They rely on the most abundant prey locally available while on colony (Abraham & Sydeman 2006), switching between the 2 dominant North Pacific krill species *Euphausia pacifica* and *Thysanoessa spinifera*. The presence and abundance of these key prey items are directly related to local upwelling conditions (Dorman et al. 2015), underscoring the importance of summer upwelling strength to Cassin's auklet diet (Black et al. 2011, Manugian et al. 2015). Strong upwelling leads to higher prey abundance well into the later months of the breeding season, giving birds extended access to high-energy resources necessary to attempt a second brood. Warm water associated with El Niño Southern Oscillation (ENSO) as measured by MEI causes greater stratification of the water column, which reduces transport of nutrients essential for phytoplankton production to the surface and makes krill less available to shallow-diving planktivores (Di Lorenzo et al. 2005, Polovina et al. 2008, Dorman et al. 2011, Manugian et al. 2015), yet our analysis did not select this as an important predictor. Reproductive success in Cassin's auklets has become less influenced by ENSO in recent years and appears to be more correlated with North Pacific Gyre Oscillation strength (Schmidt et al. 2014), possibly explaining why *MEI* had little predictive power in our study. It may also be that, because foraging occurs close to the breeding colony during the summer, local phenomena such as regional upwelling are more correlated with reproductive parameters than basin-wide phenomena described by *MEI*. We did not address winter oceanographic conditions experienced during the non-breeding season. Although pre-breeding season environmental condition may influence the

phenology of Cassin's auklets on SEFI and limit the potential for double brooding, virtually nothing is known about the winter distribution and habitat use of this population. A better understanding of their winter movements would help identify specific non-breeding environmental parameters that may explain additional variation in double brooding.

At the population level, the added reproductive output of double-brooded individuals may be an important buffer against years of low marine productivity. Cassin's auklets on SEFI have experienced a steep decline in population size since the 1970s (N. Nur et al. unpubl., P. Warzybok et al. unpubl.) and have shown a marked decrease in reproductive success during strong ENSO events and warm water anomalies (Dorman et al. 2011, N. Nur et al. unpubl.). This apparent vulnerability to shifting oceanographic patterns highlights the importance of understanding the demographic and environmental processes that impact double brooding. A logical next step will be to determine to what extent double brooding contributes to the overall population size, by measuring survival and recruitment rates of chicks from second broods, and producing a survival analysis of females that attempt multiple second broods within a lifetime. We suspect the likelihood of survival for chicks from second broods depends more on the availability of late-season resources and less on parental age effects since, as we report here, parents that attempt second broods are generally already of higher quality and experience.

Simple life-history models predict a negative correlation between current reproductive investment and survival to the next year (Stearns 1992), yet, in some iteroparous species, this pattern may be nuanced by the counteracting effects of individual quality and experience (Beauplet et al. 2006, Weladji et al. 2008, Hamel et al. 2009). For animals living in habitats characterized by a high degree of environmental uncertainty, such as in many marine systems, the costs associated with reproduction vary depending on seasonal environmental quality (Stearns 1992). Individuals with enough physiological plasticity to invest in double brooding likely do so when the odds of second-brooded offspring survival are high and the costs of increased breeding effort are low, postponing somatic maintenance costs to years when offspring survival might be lower. Often such individuals are of higher quality and show little evidence of reproductive costs. Our results indicate Cassin's auklets fit this model of plastic reproductive investment, where females that live longer are more likely to double brood when marine productivity is high,

and show a positive correlation between increased reproductive investment and longevity. This adds further evidence to the benefit of a more flexible breeding regime for marine species inhabiting highly variable environments.

LITERATURE CITED

Abraham CL, Sydeman WJ (2006) Prey-switching by Cassin's auklet *Ptychoramphus aleuticus* reveals seasonal climate-related cycles of *Euphausia pacifica* and *Thysanoessa spinifera.* Mar Ecol Prog Ser 313:271–283

Adams J, Mazurkiewicz D, Harvey AL (2014) Population monitoring and habitat restoration for Cassin's auklets at Scorpion Rock and Prince Island, Channel Islands National Park, California: 2009−2011. Interim data summary report. US Geological Survey, Western Ecological Research Center, Santa Cruz Field Station, Pacific Coastal Marine Science Center, Santa Cruz, CA and Channel Islands National Park, Ventura, CA

Agnew P, Houston D, Lalas C, Wright J (2014) Variation in reproductive performance of little penguins (*Eudyptula minor*) attributable to double brooding. J Ornithol 155: 101−109

Ainley DG, Boekelheide RJ (1990) Seabirds of the Farallon Islands. Ecology, dynamics, and structure of an upwelling-system community. Stanford University Press, Stanford, CA

Anderson DR, Burnham KP (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York, NY

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1−48

Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C (2006) Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. Oikos 112:430−441

Béziers P, Roulin A (2016) Double brooding and offspring desertion in the barn owl (*Tyto alba*). J Avian Biol 47: 235−244

Black BA, Schroeder ID, Sydeman WJ, Bograd SJ, Wells BK, Schwing FB (2011) Winter and summer upwelling modes and their biological importance in the California Current Ecosystem. Glob Change Biol 17:2536−2545

Blums P, Nichols JD, Hines JE, Lindberg MS, Mednis A (2005) Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia 143:365−376

Bulluck L, Huber S, Viverette C, Blem C (2013) Age-specific responses to spring temperature in a migratory songbird: older females attempt more broods in warmer springs. Ecol Evol 3:3298–3306

Chambert T, Rotella JJ, Higgs MD, Garrott RA (2013) Individual heterogeneity in reproductive rates and cost of reproduction in a long-lived vertebrate. Ecol Evol 3: 2047–2060

Clutton-Brock T, Sheldon BC (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. Trends Ecol Evol 25:562–573

Cooch EG, Ricklefs RE (1994) Do variable environments significantly influence optimal reproductive effort in birds? Oikos 69:447–459

Cornell A, Williams TD (2016) Individual quality and double-brooding in a highly synchronous songbird population. Auk 133:251–260

Di Lorenzo E, Miller AJ, Schneider N, McWilliams JC (2005) The warming of the California Current System: dynamics and ecosystem implications. J Phys Oceanogr 35: 336–362

Dorman JG, Powell TM, Sydeman WJ, Bograd SJ (2011) Advection and starvation cause krill (*Euphausia pacifica*) decreases in 2005 Northern California coastal populations: implications from a model study. Geophys Res Lett 38:L04605

Dorman JG, Sydeman WJ, Garcia-Reyes M, Zeno RA, Santora JA (2015) Modeling krill aggregations in the central-northern California Current. Mar Ecol Prog Ser 528: 87–99

Forslund P, Pärt T (1995) Age and reproduction in birds – hypotheses and tests. Trends Ecol Evol 10:374–378

Gauger VH (2000) Double brooding in the black noddy (*Anous minutus*): incidence and effect of an unusual seabird reproductive strategy. PhD dissertation, Universtiy of Hawaii, Mānoa, Honululu, HI

Geupel GR, DeSante DF (1990) Incidence and determinants of double brooding in wrentits. Condor 92: 67–75

Grüebler MU, Naef-Daenzer B (2008) Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. Ecology 89:2736–2745

Hamel S, Cote S, Gaillard JM, Bianchet-Festa M (2009) Assessing the accuracy of species distribution models to predict amphibian species richness patterns. J Anim Ecol 78:143–151

Hipfner JM, Gaston AJ, Martin DL, Jones IL (1999) Seasonal declines in replacement egg-layings in a long-lived, Arctic seabird: costs of late breeding or variation in female quality? J Anim Ecol 68:988–998

Hoffmann J, Postma E, Schaub M (2015) Factors influencing double brooding in Eurasian hoopoes (*Upupa epops*). Ibis 157:17–30

Husby A, Kruuk LEB, Visser ME (2009) Decline in the frequency and benefits of multiple brooding in great tits as a consequence of a changing environment. Proc R Soc B 276:1845–1854

Knape J, Jonzén N, Sköld M, Kikkawa J, McCallum H (2011) Individual heterogeneity and senescence in silvereyes on Heron Island. Ecology 92:813–820

Lee DE, Warzybok PM, Bradley RW (2012) Recruitment of Cassin's Auklet (*Ptychoramphus aleuticus*): individual age and parental age effects. Auk 129:124–132

Manugian S, Elliott ML, Bradley R, Howar J and others (2015) Spatial distribution and temporal patterns of Cassin's auklet foraging and their *Euphausiid* prey in a variable ocean environment. PLOS ONE 10:e0144232

Manuwal DA (1974) The natural history of Cassin's auklet (*Ptychoramphus aleuticus*). Condor 76:421–431

Manuwal DA (1979) Reproductive commitment and success of Cassin's auklet. Condor 81:111–121

Martin K (1995) Patterns and mechanisms for age-dependent reproduction and survival in birds. Am Zool 35:340–348

Moore DJ, Morris RD (2005) The production of second clutches in the common tern: proximate effects of timing and food supply. Waterbirds 28:458–467

Nagy LR, Holmes RT (2005) To double-brood or not? Individual variation in the reproductive effort in black-throated blue warblers (*Dendrioca caerulescens*). Auk 122:902–914

Nelson DA (1981) Sexual differences in measurements of Cassin's auklet. J Ornithol 52:233–234

Newton I (1989) Lifetime reproduction in birds. Academic Press, London

Nicholls CA (1974) Double-brooding in a Western Australian population of silver gull, *Larus novaehollandiae.* Aust J Zool 22:63–70

Norris K (1993) Seasonal variation in the reproductive success of blue tits: an experimental study. J Anim Ecol 62:287–294

O'Brien EL, Dawson RD (2013) Experimental dissociation of individual quality, food and timing of breeding effects on double-brooding in a migratory songbird. Oecologia 172: 689–699

Ogden LJE, Stutchbury BJM (1996) Constraints on double brooding in a neotropical migrant, the hooded warbler. Condor 98:736–744

Pärt T, Forslund P (1996) Age and breeding performance in monogamous birds: the influence of mate experience. Trends Ecol Evol 11:220

Pianka ER, Parker WS (1975) Age-specific reproductive tactics. Am Nat 109:453–464

Polovina JJ, Howell EA, Abecassis M (2008) Ocean's least productive waters are expanding. Geophys Res Lett 35: L03618

Pyle P (2001) Age at first breeding and datal dispersal in a declining population of Cassin's auklet. Auk 118:996–1007

Pyle P, Sydeman WJ, Hester M (2001) Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's auklets. J Anim Ecol 70:1088–1097

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reed TE, Kruuk LEB, Wanless S, Frederiksen M, Cunningham EJA, Harris MP (2008) Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. Am Nat 171:E89–E101

Schmidt AE, Botsford LW, Eadie JM, Bradley RW, Di Lorenzo E, Jahncke J (2014) Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. Mar Ecol Prog Ser 499:249–258

Sorensen MC, Hipfner JM, Kyser TK, Norris DR (2009) Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. J Anim Ecol 78:460–467

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. Mar Ecol Prog Ser 454:107–117

Van de Pol M, Wright J (2009) A simple method for distinguishing within- versus between-subject effects using mixed models. Anim Behav 77:753–758

Verboven N, Verhulst S (1996) Seasonal variation in the incidence of double broods: the date hypothesis fits better than the quality hypothesis. J Anim Ecol 65:264–273

Verhulst S (1998) Multiple breeding in the great tit, II. The costs of rearing a second clutch. Funct Ecol 12:132–140

Weimerskirch H (2001) Seabird demography and its relationship with the marine environment. In: Schreiber EA, Burger J (eds) Biology of marine birds. CRC Press, Boca Raton, FL, p 115–132

Weladji RB, Loison A, Gaillard JM, Holand Ø and others (2008) Heterogeneity in individual quality overrides costs of reproduction in female reindeer. Oecologia 156:237–247

Wiggins DA, Morris RD, Nisbet ICT, Custer TW (1984) Occurrence and timing of second clutches in common terns. Auk 101:281–287

Wolf SG, Sydeman WJ, Hipfner JM, Abraham CL, Tershy BR, Croll DA (2009) Range-wide reproductive consequences of ocean climate variability for the seabird Cassin's auklet. Ecology 90:742–753

Wolter K, Timlin MS (1993) Monitoring ENSO in COADS with a seasonally adjusted principal component index. In: Procedings 17th Climate Diagnostics Workshop. NOAA/NMC/CAC, NSSL, Oklahoma Climate Survey, CIMMS and the School of Meteorology, University of Oklahoma, Norman, OK, p 52–57

Appendix.

Parameter estimates, standard errors, Z-scores and p-values of fixed predictors of the top GLMM for predicting the probability of a double brooding attempt in Cassin's auklets, with the age term decomposed into the between- (B) and within-subject (W) components. Both the interaction and quadratic terms for the 2 components of age are non-significant and appear to mask the main effects of predictors W and B. The quadratic and interaction terms were ultimately removed in the final analysis for the between- and within-subject effects of female age for ease of interpretation. Random intercept terms were: (1|$YEAR$) and (1|ID). See Table 1 for parameter definitions

Predictor	β	SE	Z	p
Intercept	3.308	6.118	0.541	0.589
W	1.542	0.653	2.362	0.018
B	1.273	0.728	1.750	0.080
W^2	0.008	0.029	0.281	0.778
B^2	−0.521	0.027	−1.921	0.055
LAY	−0.168	0.032	−5.259	<0.001
UPW	0.041	0.024	1.706	0.088
W:UPW	−0.006	0.003	−1.949	0.051
B:UPW	−0.001	0.002	−0.440	0.660