

Article

Causes of seasonal decline in reproduction of the cooperatively-breeding acorn woodpecker

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Clutch size and reproductive success decline seasonally in a wide range of temperate avian taxa. Two competing hypotheses have been proposed to explain such declines: the ‘timing’ hypothesis, which states that conditions affecting reproduction decline intrinsically with date, and the ‘quality’ hypothesis, which proposes that high-quality individuals or individuals in high-quality situations breed earlier. We contrasted the relative importance of these two hypotheses using a long-term dataset of the cooperatively-breeding acorn woodpecker *Melanerpes formicivorus* in central coastal California (USA). This population exhibits an 11% seasonal decline in clutch size, a 60% seasonal decline in fledging success, and a 77% seasonal decline in fledgling overwinter survival. Clutch size tracks seasonal availability of flying insects, which are a likely ecological driver of the seasonal decline in reproduction and, because of the nonlinear relationship of flying insects with date, constitute a likely factor constraining even earlier nesting. By parsing lay date data into within-female and between-female components, we found that only the within-female component had a statistically significant direct effect on clutch size, supporting the timing hypothesis. For both fledging success and overwinter survival, however, both within- and between-female effects were highly significant, with between-female effects (differences in female quality) being stronger than within-female effects. These results suggest that timing per se is a key factor affecting the seasonal decline in clutch size, but that both differences in female quality and an intrinsic seasonal decline in conditions drive the even more dramatic seasonal declines in fledging success and overwinter survivorship of fledglings.

Keywords: clutch size, laying date, phenology

Introduction

A seasonal decline in reproductive output is one of the most ubiquitous patterns found in temperate birds and has been studied extensively for over 70 years (Lack 1947, Klomp 1970, Rowe et al. 1994, Pärt et al. 2017, Weiser et al. 2018). Conclusions from these studies, which include both empirical and experimental approaches, have varied widely, but have in several cases provided evidence for both the hypotheses that earlier-breeding birds are of higher quality (the ‘quality’



hypothesis; Christians et al. 2001), and that conditions intrinsically decline seasonally independent of bird quality (the ‘timing’ hypothesis; Verhulst and Nilsson 2008, Karagicheva et al. 2016).

Despite the sustained focus on this pattern, numerous questions remain. First, what is the mechanism underlying the apparent seasonal decline in environmental conditions found within seasons? Second, what are the relative contributions of quality vs timing to the seasonal trends in reproductive output (Öberg et al. 2014)? Third, given that early-season breeding birds are often more successful, what factors constrain the earliest breeding date (Gienapp et al. 2006)? Fourth, how will climate change affect seasonality of performance, and will selection on the phenology of breeding be able to track climate change to avoid potentially detrimental phenological mismatches with food supply (Visser et al. 1998, Walther et al. 2002)?

Here we determine the seasonal patterns of clutch size, number of young fledged per nest, and juvenile overwinter survival in the acorn woodpecker *Melanerpes formicivorus*, a cooperatively breeding, resident species, addressing some of these unresolved questions. We first document in greater detail the observed seasonal decline in reproductive output previously reported in this species (Koenig and Walters 2012), focusing on the overall relationship between timing of reproduction and abundance of flying insects and testing for long-term changes in the timing of reproduction over the 36 years of the study. We then examine the seasonal decline within years with the goal of contrasting the relative importance of the quality and timing hypotheses.

Hypotheses and predictions

Overall timing of reproduction

Timing of reproduction in several nidicolous bird species has been shown to be related to food supply, with peak fledging occurring when relevant food sources are at their maximum (Lack 1955, Klomp 1970) and seasonal declines in offspring quality and survival being mediated by food (Harriman et al. 2017). Critical food for acorn woodpeckers consists of stored acorns and flying insects, both of which are consumed during the breeding season (Koenig and Mumme 1987). Insects, however, are more nutritionally valuable and are particularly important for rapidly growing nestlings (Koenig et al. 2008). We thus predicted that reproduction should be timed such that fledging and flying insect abundance should peak about the same time. To the extent that there has been a change in phenology of reproduction over the course of the study, such changes are likely attributable to climate change, with warmer spring temperatures potentially advancing the spring breeding season (Walther et al. 2002).

The timing hypothesis

This hypothesis predicts that the decline in productivity is driven by an intrinsic seasonal decline in environmental conditions that is unrelated to the condition or quality of the breeding birds themselves (Verhulst and Nilsson 2008).

We tested this hypothesis statistically by quantifying seasonal trends in within-female variation in clutch size and reproductive success. Such within-female variation focuses on the degree to which these metrics decline seasonally while controlling for differences among females (Christians et al. 2001).

The quality hypothesis

This hypothesis predicts that earlier breeding birds are in better physical condition and that the seasonal decline is due to birds of lower quality initiating reproduction later (Verhulst et al. 1995). We tested this hypothesis by quantifying seasonal trends in among-female variation in clutch size and reproductive success. Among-female variation focuses on the degree to which these metrics vary among females independent of seasonality per se (Pettifor et al. 1988). Significant among-female effects could be attributable to other factors associated with females such as age, differences in social group size or prior group history, or differences in territory quality, however.

Material and methods

Field study

We studied a color-banded population of acorn woodpeckers located at Hastings Reservation, central coastal California (USA). The habitat consists of oak woodland and savanna and is subject to a Mediterranean climate in which 84% of precipitation falls between 1 Nov and 31 Mar. The population has been under continuous study since 1972 (MacRoberts and MacRoberts 1976, Koenig and Mumme 1987), but here we restrict analyses to the 36 yr of 1981–2016.

Acorn woodpeckers are cooperative breeders that live in territorial groups of up to 15 individuals (mean = 4.5; Koenig et al. 1995a). Groups consist of a variable number of breeders and non-breeding helpers of both sexes, who are offspring from prior nesting attempts that participate in most or all group activities including territoriality, food storage, and feeding of offspring (Mumme and de Queiroz 1985). In addition to helpers, joint-nesting by two (rarely more) breeder females occurs in approximately 20% of groups (Koenig and Mumme 1987). Joint-nesting females typically engage in egg-destruction often lasting for days at the start of egg-laying (Mumme et al. 1983, Koenig et al. 1995b). For this reason, along with the difficulty of assigning maternity to eggs in joint nests, we restricted our analyses to groups with a single breeder female, for which maternity is unambiguous (Dickinson et al. 1995).

During the period covered by the analyses reported here, we followed the breeding success of 762 breeding attempts by groups of known social composition with a single breeder female. We recorded clutch size (for 602 of the attempts), hatchability (the proportion of eggs surviving to hatching that actually hatch; Koenig 1982), the number of young fledged (assumed to be equal to the number of young banded, which

was generally on day 21 of the 32-day nestling period), and the number of young surviving to February of the year following fledging, after which natal dispersal often takes place (Koenig et al. 2000). Many nests were found after hatching, precluding an accurate assessment of clutch size or hatching success. Consequently, we used the estimated date on which the last egg was laid (last egg date; LED) rather than the more commonly used first egg date for nesting phenology (Mumme et al. 1983, Koenig et al. 1995b).

To compare phenology of nesting with flying insect abundance, we used the annual mean LED of the first nests of all groups with a single breeder female that attempted reproduction that year. Groups often re-nested after nest failure ($n=78$ nests) or attempted second nests within the spring season ($n=117$ nests). We therefore performed two sets of analyses. The first included all spring nesting attempts and the second included only the LED of the first nesting attempt of each group, the latter in order to avoid confounds related to prior reproductive effort within a season. For the analysis of within- vs among-female effects, we only present results using all nesting attempts, as results were unchanged using first nests only. Birds in this population also sometimes nest in the autumn, but such attempts (LED after 15 July; Koenig and Stahl 2007) are relatively rare and thus not considered further here.

Environmental factors examined for their relationship with breeding phenology included rainfall, mean maximum and minimum temperatures during the prior winter (the wet season prior to the main breeding season from 1 Nov – 31 Mar), and mean maximum and minimum temperature during early spring (just prior to the main breeding season, 1 Mar – 30 Apr). Weather data were obtained from the Hastings weather station located near the center of the study area. We also investigated the effects of several other variables on breeding phenology, including female age (dividing birds into those known to be in their second year and older), social group size, territory quality (dividing groups into low-quality territories with < 1000 acorn storage holes and high-quality territories with > 1000 acorn storage holes), and whether or not there had been a turnover in the breeder composition of the group from the prior year (0=no turnover; 1=turnover in either breeder males, breeder females, or both).

Analyses were divided into two sets. The first included female age, group size, territory quality, and turnovers as fixed effects and the second included the prior autumn's acorn crop and the weather variables as fixed effects. In all cases, year was included as a random effect in order to control for annual variability.

Acorn woodpeckers are insectivorous whenever weather conditions are favorable (MacRoberts 1970). Nonetheless, they are highly dependent on the size of the local acorn crop (Koenig and Haydock 1999, Koenig et al. 2015). Thus, in some of the analyses, we included an estimate of the acorn crop of the study area the prior autumn based on visual surveys of oaks at Hastings conducted each autumn between 1980 and 2015 (Koenig et al. 1994a). Surveys consisted of

two observers counting as many acorns as possible for 15 s on each of 250 tagged trees (Koenig et al. 1994b); values for the two observers were summed (N_{30}), ln-transformed (LN_{30}) to reduce non-normality, and then averaged across all trees (xLN_{30}) to yield an index of the overall acorn crop available to birds during the winter prior to the subsequent spring breeding season.

To compare timing of reproduction in the population with that of insect abundance, we used an index of flying insect abundance acquired from nine yellow dish-pan traps filled with soapy water (Southwood 1978) set out to sample the study area and run annually starting at the beginning of April through the end of June. Traps were emptied weekly and insects caught were sorted, dried, weighed, and standardized to gms day^{-1} . Flying insect abundance within a season was estimated by averaging data across all years (April through the end of June) from 1981 to 2007.

Statistical analyses

Overall, the timing of reproduction within years was analyzed using mixed-effects models of LED on clutch size; in all cases, female identity (FEMID) was included as a random effect. Gaussian distributions were assumed, as analyses with poisson distributions failed to converge. We included both linear (LED) and squared (LED^2) terms as fixed effects, but dropped the latter when it was not statistically significant. Relationships between environmental conditions and timing of reproduction were quantified by means of a mixed-effects model in which LED was the dependent variable, the weather variables and the mean acorn crop were considered fixed effects, and year (YEAR) was included as a random effect. Trends through time for LED, clutch size, and young fledged were analyzed with linear regressions; relationships between statistically significant environmental variables and YEAR were analyzed with Pearson correlations. We tested for significant quadratic effects by comparing AIC_c values of regression models that did and did not include the squared year term ($YEAR^2$) as fixed effects.

In the analysis comparing the timing of reproduction relative to flying insect abundance, only first nesting attempts were included. The rationale for this is that only the timing of first nesting attempts can potentially be coordinated with the subsequent expected food supply, whereas subsequent nesting attempts are dependent on unpredictable factors such as predation or other factors leading to nest failure.

Distinguishing the quality and timing hypotheses was accomplished by separating within- from among-female effects on clutch size and fledging success. This was done by within-subject centering, a procedure that involves subtracting each female's mean LED (averaged across all years she nested) from the LED of each of her individual nesting attempts, thereby separating within-female variation (timing effects) in LED from among-female variation (quality effects; van de Pol and Wright 2009). Data were available for 257 females, with a mean (\pm standard deviation) number of

nests per female of 2.96 ± 2.53 (range 1 to 13). We considered three sets of mixed-effects model analyses, described in detail below, following the protocol of van de Pol and Wright (2009) and including additional analyses derived from Westneat et al. (2009).

Analysis 1: In the first set of models, mean-centered values of LED (within-female effects), mean LED for each female (among-female effects), and YEAR were included as fixed effects, while female identity (FEMID) was included as a random effect. This tested the significance of the timing (the within-female effects) and quality (the among-female effects) hypotheses, controlling for year effects. Statistical significance of female identity was tested using log-likelihood ratio tests (Pinheiro and Bates 2000) where the difference between models ($-2 \times \log$ -likelihood) is distributed according to a χ^2 distribution with degrees of freedom equal to the number of constrained parameters. We conducted parallel analyses in which group size, territory quality, and breeder turnovers from the prior year were included as fixed effects in order to control for some of the confounding variables that potentially contribute to differences among females.

Analysis 2: The non-centered LED values (within- and among-female effects combined), mean LED for each female (among-female effects), and YEAR were included as fixed effects. Because the non-centered composite variable was included in the model, the among-female effect tested the statistical significance of the difference between the among- and within-female effects. That is, the value of the difference was expected to be non-significant when the within- and among-female effects were effectively the same (van de Pol and Wright 2009). Parallel analyses that included group size, territory quality, and breeder turnovers from the prior year as fixed effects were also conducted.

Analysis 3: This set of analyses compared four mixed models. The complete model included centered values of LED, mean LED for each female, and YEAR as fixed effects along with both random intercepts and slopes of the FEMID \times mean-centered LED interaction. The three models we compared to the full model differed as follows: 1) YEAR was excluded as a fixed effect; 2) random slopes of the FEMID \times LED interaction were excluded (variance in slopes constrained to zero; van de Pol 2012); and 3) random intercepts of the FEMID \times LED interaction were excluded (variance in intercepts constrained to zero). Models were compared to one including both random intercepts and slopes of the FEMID \times LED interaction using log-likelihood ratio tests. The goal of these comparisons was to determine the statistical significance of among-year variation and whether among-female phenotypic differences could be attributed to differences in the rate at which clutch size of females varied with date (random slopes) or to differences in the mean clutch size of females at the mean laying date (random intercepts). This latter term is of particular importance as it may incorporate many of the ways in which female quality could be affecting performance that are potentially missed by the set of models described in analysis 1.

Although ideally the above protocol clearly distinguishes quality vs timing effects on clutch size and fledging success, at least two caveats are worth noting. First, differences in female quality may have effects on reproductive performance without affecting laying date; thus, female quality may be important even if no among-female variation in LED is detected. Second, among-individual variance in laying date can arise from causes other than differences in quality. Although we attempt to capture some of these effects by quantifying the random intercepts of female clutch size at the mean laying date (described above) and by the analyses of among-female effects controlling for group size, territory quality, and breeder turnovers (described in analysis 1), it remains likely that among-individual variance in LED may be affected by other unmeasured factors.

Analyses were conducted in R 3.2.0 (R Development Core Team) using the 'lme4' package (Bates et al. 2015).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.232k9q5>> (Koenig and Walters 2018).

Results

Overall timing of reproduction

Last egg dates for all spring nests ranged from 20 Mar to 15 July; the LED of the latest first nest was 20 June. Significant declines were evident in all measures of reproduction; specifically, clutch size declined 11% over the course of the season (4.63 to 4.13 eggs), young fledged declined 60% (3.25 to 1.30), and number of young surviving to Feb declined a dramatic 77% (1.80 to 0.41) (Fig. 1). Relationships were significantly quadratic for clutch size (Fig. 1 a, d); for all other metrics of reproduction, the quadratic term was non-significant. Hatchability also declined seasonally (mixed-effects model including YEAR as a random effect; mean \pm standard error effect size of LED on hatchability = -0.0034 ± 0.0008 , $t = -4.47$, $df = 1012$, $p < 0.001$).

Relationships between reproduction and female age, group size, turnovers in group composition, territory quality, and environmental factors are summarized in Table 1. Last egg date was significantly influenced by the mean acorn crop and mean maximum early spring temperature: birds initiated clutches earlier following larger acorn crops and when temperatures during early spring were warmer. In contrast, clutch size was unaffected by either the acorn crop or any of the weather variables but was significantly larger when groups were larger, territories contained more storage facilities and were thus of higher quality, and when there had not been a turnover in breeder composition from the prior year. Significantly more young fledged following years of good acorn crops and when there had not been a turnover in breeder composition.

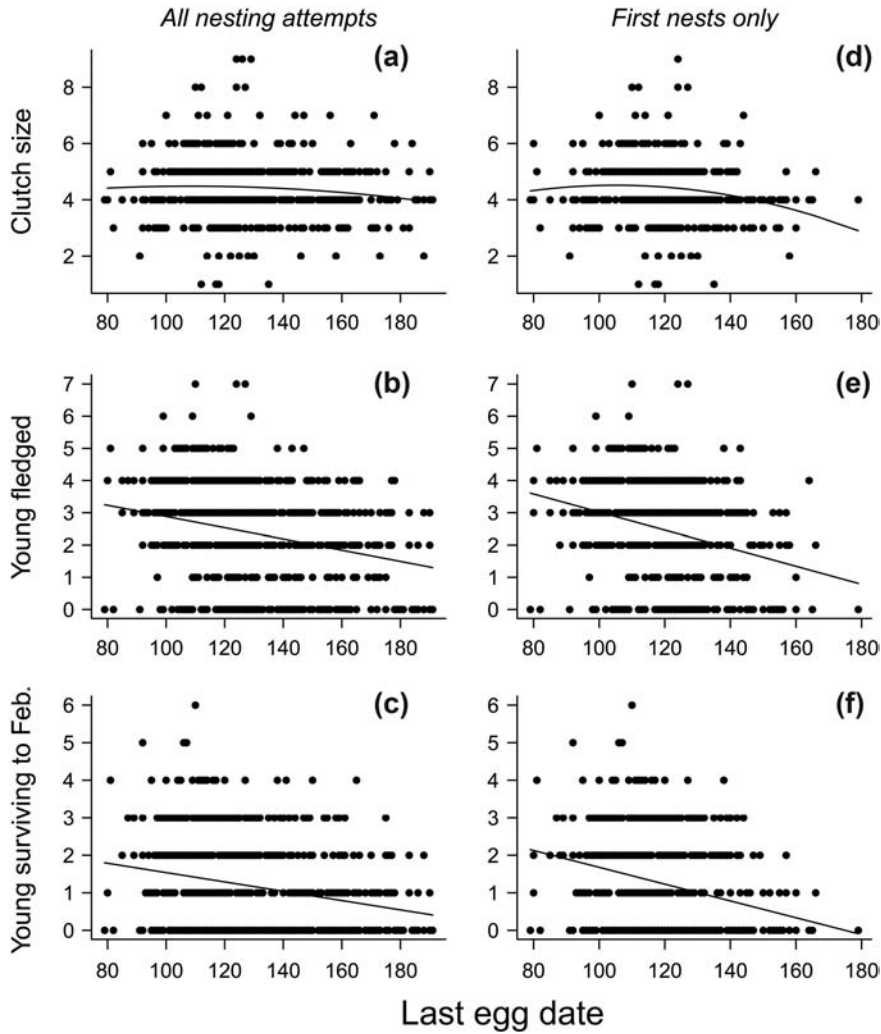


Figure 1. Scatterplots of clutch size, young fledged, and young surviving to February for all nests (left column) and for first nesting attempts only (right column) by day-of-year. All factors are linear (i.e. polynomial term not significant) except for clutch size (panels a and d), for which the quadratic term was significant. Coefficients from mixed models including FEMID as a random effect: (a) clutch size = $0.045 \pm 0.018 \times \text{LED} - 0.0002 \pm 0.0001 \times \text{LED}^2$, $t=2.53$ [LED], -2.85 [LED²], $df=369$, $p=0.01$ [LED], 0.005 [LED²]; (b) young fledged = $-0.015 \pm 0.002 \times \text{LED}$, $t=-6.6$, $df=500$, $p < 0.001$; (c) young surviving to February = $-0.011 \pm 0.002 \times \text{LED}$, $t=-6.1$, $df=500$, $p < 0.001$; (d) clutch size = $0.067 \pm 0.030 \times \text{LED} - 0.0003 \pm 0.0001 \times \text{LED}^2$, $t=2.3$ [LED], -2.6 [LED²], $df=241$, $p=0.02$ [LED], 0.01 [LED²]; (e) young fledged = $-0.027 \pm 0.004 \times \text{LED}$, $t=-6.6$, $df=322$, $p < 0.001$; (f) young surviving to February = $-0.022 \pm 0.003 \times \text{LED}$, $t=-6.6$, $df=322$, $p < 0.001$.

Considering first nesting attempts only (Fig. 1d), the predicted values of clutch size exhibited a quadratic peak at LED (day-of-year) 109 (= 19 Apr; Fig. 1d). This compares to the predicted flying insect biomass based on the yellow pan traps, which was also quadratic in shape, peaking at day-of-year 159 (= 7 June), 50 d later. Given an 11-day incubation and 32-day nestling period (Koenig et al. 1995a), the insect peak comes seven days after the expected fledging date of eggs from a nest completed on 19 Apr (Fig. 2).

We detected no significant long-term trends (1981–2016) in mean LED ($r=-0.07$, $p=0.70$), mean clutch size ($r=0.26$, $p=0.13$), mean young fledged ($r=0.32$, $p=0.06$), the mean acorn crop ($r=0.03$, $p=0.85$), or any of the weather variables tested (correlations with YEAR; all $p \geq 0.08$; df for all

tests=34). Models testing for non-linearity in these long-term trends failed to garner greater support than linear models (Supplementary material Appendix 1 Table A1).

Within-female versus among-female effects

Models testing the within- and among-female effects are summarized in Table 2; results of parallel analyses including group size, territory quality, and breeder turnovers are in Supplementary material Appendix 1 Table A2. For clutch size, the effect of within-female LED was statistically significant but the among-female effect was not, although the random effect of female identity was highly significant and the test comparing the within- and among-female effects

Table 1. Results of mixed-effects models testing 1) breeder female age (second year or older), group size, territory quality (low or high based on storage facilities), whether there was a turnover in breeder composition or not as fixed factors, and 2) environmental factors (the prior autumn's acorn crop, winter weather, and early spring weather) as fixed effects on last egg date, clutch size, and young fledged. Values are mean \pm standard error of the effect size for each fixed effect; p-value in parentheses. Year was included as a random effect in all analyses. Significant values in bold.

Analysis	Fixed factors	Dependent variable		
		Last egg date	Clutch size	Young fledged
1	Female age	-0.47 \pm 3.39 (0.89)	-0.16 \pm 0.18 (0.38)	-0.18 \pm 0.22 (0.43)
	Group size	-0.46 \pm 0.39 (0.25)	0.04 \pm 0.02 (0.04)	0.03 \pm 0.03 (0.23)
	Territory quality	6.31 \pm 3.87 (0.10)	0.63 \pm 0.22 (0.004)	-0.03 \pm 0.26 (0.92)
	Turnover in breeder composition	3.67 \pm 1.98 (0.06)	-0.31 \pm 0.11 (0.004)	-0.56 \pm 0.13 (< 0.001)
2	Mean acorn crop	-8.59 \pm 1.09 (< 0.001)	0.09 \pm 0.08 (0.28)	0.22 \pm 0.10 (0.04)
	Mean maximum winter temperature	1.19 \pm 0.95 (0.22)	-0.10 \pm 0.07 (0.18)	-0.16 \pm 0.09 (0.08)
	Mean minimum winter temperature	0.69 \pm 1.21 (0.57)	-0.07 \pm 0.09 (0.47)	-0.01 \pm 0.11 (0.91)
	Winter rainfall	0.04 \pm 0.05 (0.50)	0.00 \pm 0.01 (0.56)	-0.00 \pm 0.01 (0.82)
	Mean maximum early spring temperature	-2.09 \pm 0.75 (0.01)	0.03 \pm 0.06 (0.60)	-0.07 \pm 0.07 (0.29)
	Mean minimum early spring temperature	-0.34 \pm 1.37 (0.80)	-0.01 \pm 0.11 (0.91)	0.00 \pm 0.13 (0.99)
	Early spring rainfall	-0.12 \pm 0.15 (0.41)	0.01 \pm 0.01 (0.65)	0.01 \pm 0.01 (0.41)

(analysis 2) was non-significant. Despite a statistically significant effect of breeder turnovers, results for the within- and among-female factors were unchanged in analyses including group and territory variables (Supplementary material

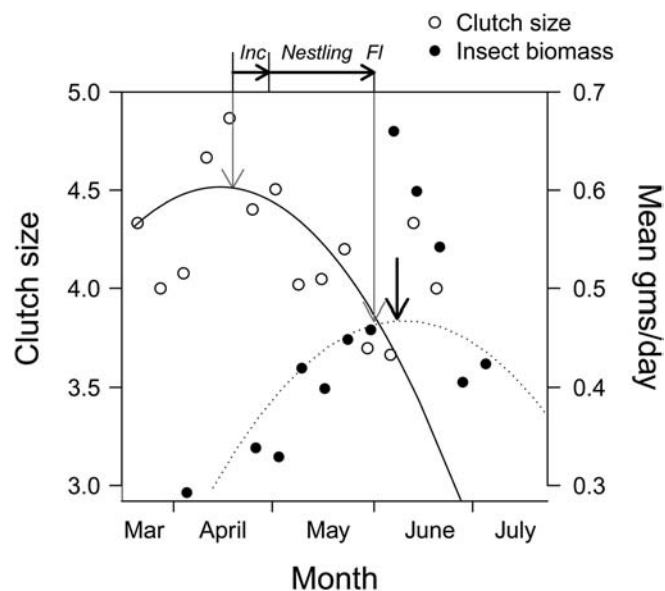


Figure 2. Observed and predicted clutch size and biomass of flying insects (the latter indexed by the yellow pan traps), using quadratic regressions of clutch size on LED and dry weight of flying insect biomass on LED including both linear and quadratic terms. For clutch size, the regression is $\text{clutch size} = 0.1286 + 0.0932 \times \text{LED} - 0.0004 \times \text{LED}^2$; the values peak at day-of-year 109 (19 Apr; marked by an arrow). Both linear and quadratic terms are significant ($p < 0.05$). For flying insect biomass, the regression is $\text{insect biomass} = -0.0375 + 0.0707 \times \text{LED} - 0.0025 \times \text{LED}^2$; the values peak at day-of-year 159 (9 June; marked by the bold arrow). Both linear and quadratic terms are significant ($p < 0.001$). Also marked is the expected fledging date (FI) for eggs laid in a nest with a LED date at the peak of 19 Apr given an 11-day incubation (Inc) and 32-day nestling period.

Appendix 1 Table A2). Model comparisons indicated that the random intercepts of FEMID \times LED interaction, but neither YEAR nor the random slopes of the FEMID \times LED interaction, were statistically significant (Table 3).

For young fledged and juvenile overwinter survivorship, both within- and among-female effects were highly significant, with the latter being considerably greater based on the effect sizes and the results of analysis 2. Female identity was again highly significant as a random effect. As with clutch size, these results were unchanged in analyses that included potentially confounding factors, despite group size and turnovers in breeder composition being significant (Supplementary material Appendix 1 Table A2). The random intercepts of the FEMID \times LED interaction were statistically significant for both young fledged and young surviving to February (Table 3). YEAR was also a significant factor affecting young surviving to February, while the random slopes of the FEMID \times LED interaction were marginally significant as a factor affecting young fledged.

Discussion

Acorn woodpeckers in central coastal California exhibit significant seasonal declines in reproductive success (Fig. 1). Thus, this species exhibits the typical temperate pattern of a seasonal decline in clutch size and reproductive success (Klomp 1970, Rowe et al. 1994), with the effect being more pronounced as the nesting stage advances from eggs through fledging and juvenile survivorship. Other variables influencing reproductive success included the prior autumn's acorn crop (for last egg date and young fledged), mean maximum early spring temperature (for last egg date), group size and territory quality (for clutch size), and turnovers in breeder composition (for clutch size and young fledged).

We detected no long-term changes in mean clutch size, reproductive success, mean acorn crop, or any of the environmental factors examined for their potential effects on

Table 2. Effect size (\pm standard error) and p-values (in parentheses) of variables testing within- and among-female effects on clutch size, young fledged, and young surviving to February using mixed-effects models; for additional details, see text. Statistically significant values in bold.

Analysis	Variable	Dependent variable		
		Clutch size	Young fledged	Young surviving to February
1	Within-female lay date (\pm SE)	-0.006 \pm 0.002 (0.005)	-0.011 \pm 0.003 (< 0.001)	-0.010 \pm 0.002 (< 0.001)
	Among-female mean lay date (\pm SE)	-0.004 \pm 0.005 (0.38)	-0.032 \pm 0.006 (< 0.001)	-0.017 \pm 0.004 (< 0.001)
	Female identity random effects (variance)	0.258 (< 0.001)	0.198 (< 0.001)	0.125 (< 0.001)
	Residual random effects (variance)	0.758	1.761	1.100
	N observations (N females)	602 (228)	762 (257)	762 (257)
2	Difference between within- and among-female lay date	0.001 \pm 0.005 (0.80)	-0.021 \pm 0.006 (0.001)	-0.007 \pm 0.005 (0.15)

reproductive performance. This long-term consistency in breeding phenology was not necessarily expected given that there have been significant changes in the forest community of the study area over this time period and a concomitant increase in the acorn woodpecker population (McMahon et al. 2015), almost entirely because of an increase in the number of social groups rather than any increase in group size (Hagemeyer et al. unpubl.).

Our results provide strong support for timing of reproduction being an important determinant of reproductive success independent of among-female variation (quality effects), as within-female effects were highly significant in all analyses (Table 2). Interestingly, we failed to find support for among-female differences in reproductive phenology playing a direct role in driving differences in clutch size independent of within-female effects, although differences due to female identity were significant in all analyses and are likely to be important in ways other than through LED. Female quality (or some other difference associated with females) was highly significant and considerably more important than timing as a factor directly affecting fledging success and the number of young surviving to February.

What drives these patterns? There are numerous potential factors that may contribute to the intrinsic seasonal decline in conditions – the timing effect – including the greater thermal inertia of larger clutches laid earlier in the season (the clutch-cooling hypothesis; Reid et al. 2000), the reduction of egg

viability as temperatures increase seasonally (the egg-viability hypothesis; Veiga 1992), a seasonal increase in nest predation (Slagsvold 1982), and the strong seasonality of flying insects, a critical food source for nestlings (Koenig et al. 2008).

Critical tests of these hypotheses are outside the scope of this paper, but all – with perhaps the exception of nest predation – potentially play a role in the observed seasonal decline in conditions found here. The relationship between clutch-cooling and clutch size remains to be determined, but the energetic consequences of communal cavity roosting are considerable (du Plessis et al. 1994), suggesting that seasonal differences in the thermal qualities of different clutches could be important. Other factors such as the effects of temperature and microbes on egg viability are plausible mechanisms but have not been implicated as a strong driver of seasonal clutch size declines in other temperate species (Wang et al. 2011).

Although a role for predation cannot be totally eliminated, nest predation is relatively low in cavity-nesting species (Martin and Li 1992, Koenig et al. 1995a), making other factors more likely to be important in driving the observed seasonal decline in clutch size (Slagsvold 1982). Of these other factors, the strong seasonality of flying insects exhibiting a peak in abundance a few days after the expected fledging date of nests with the largest predicted clutch size (Fig. 2) suggests that nesting later becomes progressively more difficult as the season unfolds and food sources – both flying insect biomass and stored acorns – decline. Regardless of the

Table 3. Comparison of full mixed models including centered values of LED, mean LED for each female, and YEAR as fixed effects and female identity (FEMID) as a random effect (both random slopes and intercepts) with models eliminating (and thus testing the significance) one variable or aspect of the full model. The aspects being tested were 1) the fixed YEAR effect, 2) the effect of the random slopes of the FEMID \times LED interaction, and 3) the effect of the random intercepts of the FEMID \times LED interaction. Listed are log-likelihood values for all models and their associated degrees of freedom (df) along with χ^2 and p-values for the log-likelihood difference between the full model and the models eliminating the particular variable or aspect of the full model. Significant differences in bold.

Model		Dependent variable		
		Clutch size	Young fledged	Young surviving to February
Full	Log-likelihood (df)	-836.9 (41)	-1328.3 (41)	-1151.0 (41)
Excluding year	Log-likelihood (df)	-858.5 (5)	-1351.9 (5)	-1196.9 (5)
	χ^2 (p-value)	43.2 (0.19)	47.3 (0.10)	91.8 (< 0.001)
Excluding random FEMID \times LED slopes	Log-likelihood (df)	-837.1 (39)	-1331.3 (39)	-1152.5 (39)
	χ^2 (p-value)	0.4 (0.81)	6.0 (0.05)	3.1 (0.21)
Excluding random FEMID \times LED intercepts	Log-likelihood (df)	-857.0 (39)	-1337.9 (39)	-1158.4 (39)
	χ^2 (p-value)	40.2 (< 0.001)	19.2 (< 0.001)	14.7 (< 0.001)

combination of factors contributing to the seasonal decline in clutch size, the seasonal decline in food availability – at least until the acorn crop begins to mature in late summer – is likely to be the key factor determining the seasonal decline in conditions driving the within-female component of the seasonal decline in young fledged and subsequent juvenile survivorship.

In contrast, among-female differences are significantly more important than the (still significant) timing effects when it comes to fledging success and juvenile survivorship. Specifically, among-female quality accounted for 74% of the seasonal decline in young fledged and 63% of the seasonal decline in fledglings surviving to February based on the relative effect sizes (Table 2). These results support the conclusion that clutch size is primarily determined by ecological factors affecting all females more or less equally, whereas the success of fledging and post-fledging survivorship is a product of both ecological factors and, more importantly, differences in female quality.

We detected (marginally) significant among-female variation in the slopes of the FEMID \times LED interaction (within-subject effects of lay date) only in the analysis of young fledged (Table 3), and thus our data fail to support the existence of important phenotypic differences among females in terms of the rate at which their clutch sizes decline seasonally (van de Pol and Wright 2009). In contrast, we found highly significant differences in the intercepts of the FEMID \times LED interaction, indicating that there were significant differences in mean laying dates among females, presumably related to their age, quality, and condition.

What factors determine differences in female quality remain to be determined. Obvious candidates include group size (including the number of helpers), female age, and prior female experience, all of which vary not only among females but from year to year for the same female. Results of the within- and among-female effects remained unchanged, however, in analyses that included, and thus controlled for, group size, breeder turnovers, and territory quality as indexed by the size of a group's facilities for storing acorns (Supplementary material Appendix 1 Table A2). This suggests that among-female differences in quality are apparently important irrespective of differences among these factors. Another element that could potentially vary importantly among females is egg size; however, prior analyses of egg size failed to find any significant relationship between clutch size and egg volume (Koenig et al. 2009).

How do these results illuminate the other issues raised in the introduction? Initiation of nesting attempts in the spring is, like the seasonal decline itself, plausibly limited by flying insect abundance, which is relatively low early in the season and peaks after young begin to fledge near the end of May (Fig. 2). Only when the acorn crop is particularly large in the autumn does it appear to be possible for birds to attempt to nest in the absence of being able to rely on a high abundance of flying insects to feed their young (Koenig and Stahl 2007).

How climate change in the future may affect these relationships is unclear. Thus far, no long-term trends have been detected at our study site, despite considerable annual variation, particularly in the acorn crop and its subsequent effects on reproduction. Interestingly, we have observed no relationship between the timing of budburst of valley oaks *Quercus lobata*, a key species for acorn woodpeckers in the study site, and mean last egg date of the population (data from 2003 to 2017; $r = -0.09$, $df = 13$, $p = 0.75$). Moreover, 2015, an unusually warm, dry year in which budburst of the deciduous oaks was strikingly early (M. Pesendorfer and W. Koenig, unpubl. data), was not accompanied by earlier nesting by the woodpeckers (mean last egg date of first nests across all years was 9 May; mean last egg date of first nests in 2015 was 10 May). Whether this suggests that acorn woodpeckers will fail to respond appropriately to phenological changes accompanying future climate change remains to be seen.

Prior studies have yielded variable results in terms of the relative importance of the quality and timing hypotheses. In experimental studies manipulating the timing of nesting attempts, Christians et al. (2001) found that the seasonal decline in clutch size of European starlings *Sturnus vulgaris* was due entirely to differences between females, whereas Wiggins et al. (1994), Verhulst et al. (1995), and Karagicheva et al. (2016) concluded that timing effects were primarily responsible for declines in clutch size observed in collared flycatchers *Ficedula albicollis*, great tits *Parus major*, and tree swallows *Tachycineta bicolor*, respectively. In a notably thorough and thoughtful analysis, Westneat et al. (2009) showed that clutch size in house sparrows *Passer domesticus* was affected by both lay date (timing) and differences among females (female quality) along with other factors, including attempt order and the interaction between attempt order and lay date.

Verhulst and Nilsson (2008) suggested that, in contrast to the results reported for European starlings (Wiggins et al. 1994), timing – but not quality – should always be important in cases where a significant seasonal decline is observed, since only if timing by itself is important is there an incentive for high-quality birds to breed earlier. Our results are consistent with this hypothesis: timing per se was significant in all analyses, whereas quality (among-female effects) was not. It does not follow that quality is necessarily less important than timing; this was not the case in our analyses of young fledged and young surviving to February. But female quality, as suggested by Verhulst and Nilsson (2008), was only significant in situations when timing per se was important as well. Additional studies using the statistical approach employed here to test the relative importance of these two drivers of the seasonal decline in reproduction observed so commonly are clearly desirable.

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Conflict of interest – The authors declare no conflicts of interest.

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Supplementary material (Appendix JAV-01784 at <www.avianbiology.org/appendix/jav-01784>). Appendix 1.