

Inbreeding and experience affect response to climate change by endangered woodpeckers

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In recent decades, female red-cockaded woodpeckers (*Picoides borealis*) have laid eggs increasingly earlier in response to a changing climate, as has been observed in several other bird species breeding at north temperate latitudes. Within each year, females that lay earlier are more productive than females that lay later. However, inexperienced females, experienced females who change mates and inbred birds have not adjusted to the changing climate by laying earlier, and have suffered reproductive costs as a result. Failure to respond to global climate change may be a further example of the reduced ability of inbred animals to respond to environmental challenges.

Keywords: laying date; reproductive success; *Picoides borealis*; inbreeding; climate change

1. INTRODUCTION

Recent papers have described the impacts of global climate change on a variety of aspects of avian life histories. Examples include the influences of changes in sea-surface temperatures on the reproductive success of seabirds (Kitaysky & Golubova 2000) and of the increasing severity of the El Niño Southern Oscillation on the annual survival of migratory birds (Sillert *et al.* 2000). Only some species (Crick & Sparks 1999; Peñuelas & Filella 2001) and, in some cases, only some populations within a species (Visser *et al.* 1998), show responses to climate change. One of the most widely documented effects is an advance in egg-laying dates of some breeding bird species in response to warmer spring temperatures at north temperate latitudes (Crick *et al.* 1997; Winkel & Hudde 1997; McCleery & Perrins 1998; Crick & Sparks 1999). It is a common pattern in birds that early reproducing individuals are more successful than their conspecifics breeding later in the season (Perrins & McCleery 1989; Hochachka 1990; Svensson 1997), but whether this relationship remains true when the timing of nesting shifts, in response to a warmer climate, is unclear (Stevenson & Bryant 2000; Post *et al.* 2001). An advance in laying date may either help maintain the temporal relationship between reproduction and seasonal changes in critical factors, such as food availability, or it may disrupt this relationship, as has been demonstrated for great tits (*Parus major*) (Visser *et al.* 1998).

One study has shown that changes in the timing of egg laying in the collared flycatcher (*Ficedula albicollis*) in response to changes in the winter North Atlantic Oscillation are due to phenotypic plasticity, that is, adjustments made by individuals rather than microevolution within populations (Przybylo *et al.* 2000). It seems probable, however, that individuals of a population are not equally capable of adjusting the onset of breeding. The ability to handle environmental stresses is reduced in young,

inexperienced (Nol & Smith 1987) or inbred individuals (Keller *et al.* 1994; Bijlsma *et al.* 1999; Meagher *et al.* 2000). One might expect, therefore, that climate change produces differential effects not only at the species or population level, but also at the individual level.

We analysed long-term datasets from two red-cockaded woodpecker (*Picoides borealis*) populations in order to better understand reproductive behaviour in response to climate change. We address the following specific questions:

- (i) Is there a shift towards earlier breeding due to a changing climate?
- (ii) If so, what are the consequences of earlier breeding for reproductive success?
- (iii) Do individuals differ in their ability to adjust to a changing climate, due to breeding experience or level of inbreeding?

2. MATERIAL AND METHODS

(a) Study areas and populations

The red-cockaded woodpecker is an endangered, cooperatively breeding species that inhabits permanent territories, in groups consisting of a monogamous breeding pair and 0–4 adult helpers, most of which are previous male offspring (Walters 1990). We analysed reproductive data covering 19 years (1980–1998) from a population of 200 breeding groups in the Sandhills of south-central North Carolina, USA, and data spanning 13 years (1986–1998) from a population of 40 groups inhabiting Camp Lejeune Marine Base in coastal North Carolina. The methods used for monitoring reproduction, and the conduction of a census of the colour-banded woodpecker populations are described in detail elsewhere (Walters *et al.* 1988).

(b) Laying date

We analysed the laying date of the first egg of a group's first clutch of the year. We estimated this date based on the age of nestlings when first observed (Ligon 1971) and on incubation period or, for nests that did not hatch, on egg counts and the interval between them. The laying date of the first egg was

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estimated from the age of nestlings by backdating, assuming that one egg is laid per day, and that the interval between laying of the last egg and hatching is 11 days (Jackson 1994). Only 14% of nests failed before nestlings were aged in the Sandhills, and only 12% at Camp Lejeune. Egg-laying date could be estimated for some of these failed nests, because an incomplete clutch was observed during one check and a complete clutch during a subsequent check. In the remaining cases, we assumed that the clutch was halfway through the potential incubation period, since clutch completion, when observed, i.e. 5 days for clutches observed only once and one half (11 days minus the interval between checks) for clutches observed twice. Within a year, median laying date was the same whether or not clutches that failed before nestlings were aged were considered, so we included them in the analyses.

(c) *Breeding experience*

We measured breeding experience in two ways: individual experience (female experience) and experience as a pair (pair experience). Females that had bred in the study area in a previous year were considered experienced. Pairs that had bred together in the study area in a previous year were considered experienced pairs. To separate the effects of individual and pair experience, inexperienced pairs included only females that had previous breeding experience with another partner in the study area.

(d) *Inbreeding coefficients*

We calculated inbreeding coefficients (Falconer 1989) from pedigree files containing all individuals that have been observed in the two study areas (Daniels & Walters 2000a). A brood was assigned an inbreeding coefficient greater than zero when either the female, or her mate, were inbred. In cases where both partners were inbred, we used the larger coefficient.

(e) *Climate data*

We obtained climate data from the US National Climatic Data Center (<http://www.ncdc.noaa.gov/>). Climate variables used were temperature, rainfall and departure from normal temperature in the months preceding breeding (December–March). We used the averages of the monthly means for temperature, and for departure from normal temperature, and averages of monthly sums for rainfall. The National Climatic Data Center defines departure from normal temperature as deviations from the average value of the preceding two decades. This average value is recalculated each decade. Thus, departure from normal temperature refers to the difference between the current temperature and average temperatures experienced in the previous two decades, depending on the year.

(f) *Statistical analysis*

We analysed the influence of laying date on reproductive success (number of fledglings) with a generalized linear mixed model (GLMM), while controlling for other factors known to influence fecundity of red-cockaded woodpeckers (Walters 1990). The model included female age, laying date (of the first egg of the first clutch), number of helpers and year as fixed effects, and individual as a random effect. All variables, except individual, were treated as continuous variables and the link function was linear. Covariance parameters were estimated by the residual maximum-likelihood method. Year was entered as a continuous variable because we were interested in changes over time, rather than annual variation, and this approach

allowed a stronger test of interaction between year and laying date. Number of helpers captures effects of both helpers and territory quality, as helpers both assist with care of offspring and are also associated with high-quality territories (Walters 1990; Heppell *et al.* 1994). Reproductive success increases with age to an asymptote at age four (Walters 1990; Conner *et al.* 2001). The study is of sufficient duration that this effect of age is not confounded with time (or with variables changing over time such as laying date and climate) in the analysis. We excluded climate from the model because of its correlation with laying date.

We analysed the effects of climate, age, year and individual on laying date, with another GLMM. We again treated individual as a categorical, random effect in a longitudinal analysis to control for potential pseudoreplication, and to avoid confounding differences between individuals with effects of other variables. This approach tested whether individual birds were adjusting to changes in climate over their lifetime (Kruuk *et al.* 1999). To capture any variation in laying date, related to variation in climate within individuals, we included in this analysis only females that bred at least twice in our study areas (Pryzybylo *et al.* 2000). Year was entered to account for non-independence of observations on different individuals in the same year. All variables, except individual, were treated as continuous variables and as fixed effects.

To further explore adjustments made by individuals, we compared median laying dates of novice breeding females to those of experienced females, and median laying dates of inexperienced pairs to those of experienced pairs, using Spearman rank correlations, correcting for tied values following Siegel (1987). For experienced females and experienced pairs that bred in multiple years, we randomly selected one year per individual and one year per pair to use in the analyses. Sample sizes differ among analyses of the same study area because not all categories were present in each year.

To examine the effects of inbreeding on the adjustment of laying date to climate, we added inbreeding terms to the GLMM used previously to measure the effects of climate on laying date, and included all individuals. We treated the inbreeding coefficient as a continuous variable for the Sandhills dataset, but as a binary variable (inbred versus not inbred) for Camp Lejeune, because sample size for inbred birds was small in this population. At Camp Lejeune, birds known to be inbred nested only in 1997 and 1998. Therefore, we included only these years in the analysis and discarded the variable year. Two experience variables were included in the analysis of the Sandhills data, to control for possible confounding of experience with inbreeding, because inbred birds might be short-lived (Coltman *et al.* 1998; Hedrick & Kalinowski 2000). Instead of having a continuous measure of experience, such as number of years, we used binary variables to avoid intercorrelation with age. Female experience was entered as a fixed effect with two levels (first-time breeder versus experienced breeder), as was pair experience (breeding together for the first time, but having breeding experience with other partners versus bred together previously). Because the analysis of the Camp Lejeune dataset comprised only two years, experience variables were not included in the Camp Lejeune model. All other variables were treated as in the previous GLMM on the effects of climate on laying date.

In all models, we controlled for possible autocorrelation over time by specifying the covariance matrix within individuals as decaying exponentially over time. We first ran the models with all possible interactions, and then produced a final model by

eliminating statistically insignificant ($p > 0.05$) interactions. Goodness of fit was assessed by residual analyses (McCullagh & Nelder 1989), and when assumptions of mixed models were not met, we log-transformed variables where appropriate (Sokal & Rohlf 1995). We tested for individual effects by the likelihood-ratio test for nested models (Self & Lian 1987). The model is run with and without the factor 'individual', and the corresponding values of $-2 \times \log$ -likelihoods are subtracted. The resulting value follows a χ^2 distribution with 1 d.f. and hence indicates a significant effect if greater than 3.84 ($p = 0.05$). This procedure is more reliable than the Wald Z-statistic (Self & Lian 1987). All calculations were done using SAS 8.1 (SAS Institute 1999–2000).

3. RESULTS

(a) Advance of laying date

In both populations, the median laying date of the first egg of first clutches advanced over the study period (figure 1). In the Sandhills, median laying date was significantly correlated with departure from normal temperature ($r_s = -0.43$, $p < 0.05$, $n = 19$), but not with temperature or rainfall. Departure from normal temperature increased over time, indicating that temperatures became increasingly warmer relative to the average temperature measured during the previous two decades ($r_s = 0.50$, $p < 0.05$, $n = 19$). Departure from normal temperature, and mean monthly temperature, were highly correlated ($r_s = 0.97$, $p < 0.01$, $n = 19$), whereas neither temperature variable was correlated with rainfall ($r_s = 0.13$, $p < 0.50$, $n = 19$, in both cases). Results of subsequent analyses (see below) were the same using either temperature variable. We use departure from normal temperature because it is significantly correlated with laying date and it generally produced a better model fit.

No warming trend was evident at Camp Lejeune, and median laying date was not correlated either with temperature or departure from normal temperature at this site. Instead, median laying date was correlated with rainfall in the months preceding breeding ($r_s = -0.61$, $p < 0.05$, $n = 13$), which increased during the study ($r_s = 0.57$, $p < 0.05$, $n = 13$). Again, rainfall was not correlated with the two temperature variables ($|r_s| < 0.04$, $p < 0.80$, $n = 13$, in both cases). Thus, the inland birds responded to higher temperatures, and the coastal birds to higher rainfall, by laying earlier.

(b) Reproductive success

In both populations, females that laid earlier, and females assisted by helpers, produced more fledglings from their first broods (table 1). A logarithmic transformation of laying date was used, so these results suggest that the effects of laying date were strongest early in the season. Year did not interact with laying date, indicating that the advantage of laying early persisted as laying date advanced over the years, in response to changing climate. A significant effect of year was indicated by a slight decline in reproductive success over the study period in both populations (table 1). In both populations, older females were more productive (table 1; figure 2). A logarithmic transformation was used for age, reflecting the asymptotic relationship of reproductive success and age. There was also an interaction between female age and laying date in

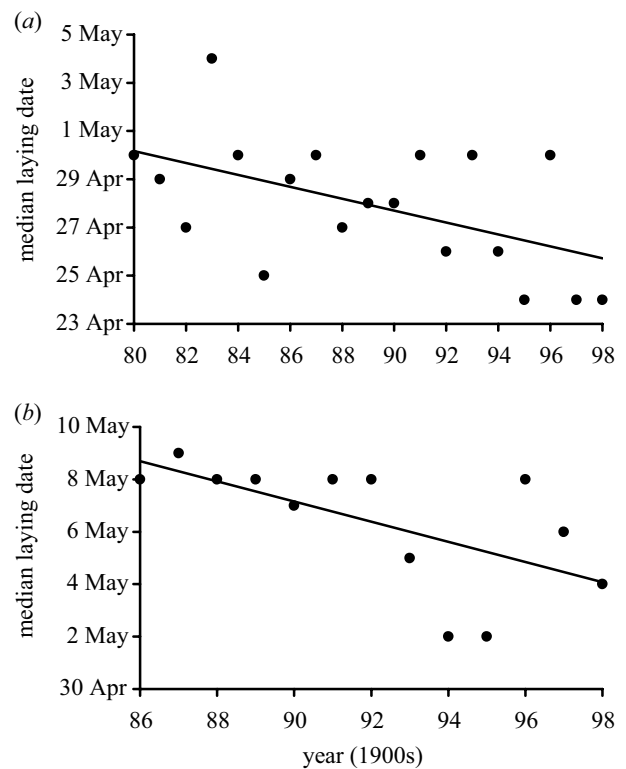


Figure 1. The median laying date in two populations of red-cockaded woodpeckers. Laying dates have advanced over time in both the Sandhills (a) and Camp Lejeune (b) population. One randomly selected entry for individual was used to calculate median laying date. (a) $r_s = -0.52$, $p < 0.05$, $n = 19$; (b) $r_s = -0.77$, $p < 0.01$, $n = 13$. r_s , Spearman rank correlation coefficient corrected for tied values (Siegel 1987). n , number of years.

the Sandhills data (table 1), indicating that the advantage of laying early was stronger in older females (figure 2). In both populations, the same patterns emerged even more strongly when number of fledglings produced per breeding season was used as a measure of reproductive success, instead of fledglings from the first nest (data not shown).

(c) Phenotypic plasticity and breeding experience

Individuals differed in how they altered laying date in response to climate (individual effect; table 2). Climate significantly affected laying date within individuals in both populations (climate effect), indicating that females adjusted laying date during their lifetime and hence exhibited phenotypic plasticity for this trait (table 2). There was also a strong effect of age (again using a log transformation) in both populations, with individuals laying earlier as they grew older. Year effects were weak (Sandhills) or absent (Lejeune), indicating that the other factors included in the models accounted for changes over time in laying date (table 2).

Breeding experience affected adjustment of laying date. In both populations, median laying date of novice female breeders did not change significantly over the study period (Sandhills: $r_s = -0.29$, $p > 0.20$, $n = 19$ yr, 623 females; Camp Lejeune: $r_s = 0.08$, $p > 0.50$, $n = 12$ yr, 70 females), whereas median laying date of experienced females advanced (Sandhills: $r_s = -0.50$, $p > 0.05$, $n = 18$ yr, 895 females; Camp Lejeune: $r_s = -0.69$, $p > 0.02$, $n = 13$ yr,

Table 1. General linear mixed models of reproductive success, measured as the number of fledglings produced from first nests. (Independent variables are laying date (fixed effect, log-transformed), female age (fixed effect, log-transformed), number of helpers (fixed effect), year (fixed effect) and individual (random effect). Sandhills: $n = 2866$ observations of 1053 breeding females, Camp Lejeune: $n = 389$ observations of 125 breeding females. b , coefficient. Statistics are F -ratios except for individual effects where χ^2 is given (likelihood-ratio test for nested models). Only effects significant in one or both populations are shown.)

source	Sandhills			Camp Lejeune		
	$b \pm \text{s.e.}$	statistic	p	$b \pm \text{s.e.}$	statistic	p
laying date	-0.02 ± 0.00	23.11	<0.001	-0.56 ± 0.24	7.51	0.006
age	0.12 ± 0.03	15.77	<0.001	0.05 ± 0.03	2.91	0.090
year	-0.01 ± 0.00	8.10	0.005	-0.04 ± 0.01	8.31	0.005
number helpers	0.29 ± 0.03	83.38	<0.001	0.32 ± 0.08	16.30	<0.001
laying date \times age	-0.01 ± 0.00	6.91	0.009	—	—	—
individual	—	50.20	<0.001	—	0.01	0.920

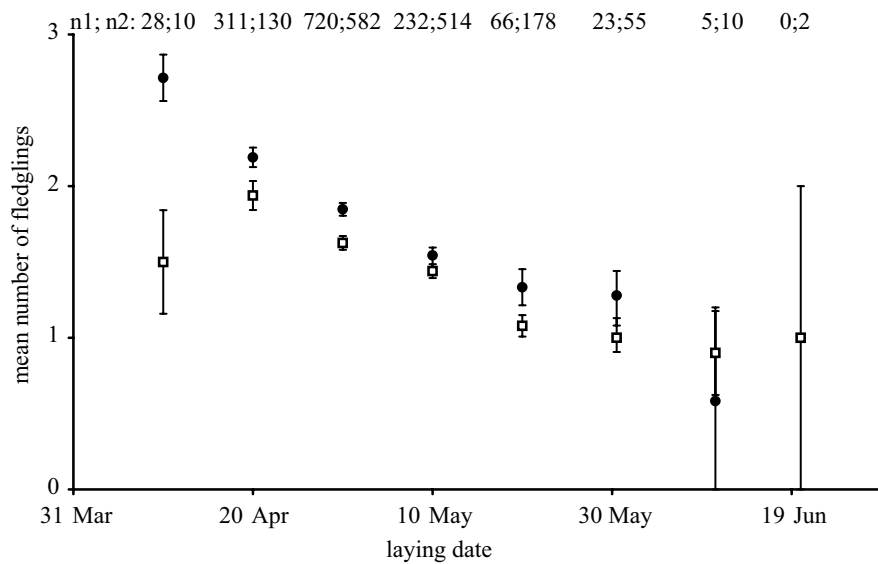


Figure 2. The effects of laying date (grouped into 10-day categories) and age on reproductive success (mean \pm s.e.) of red-cockaded woodpeckers in the Sandhills population. Circles indicate birds less than 2 years of age (n1); squares indicate birds less than 3 years of age (n2). One randomly selected observation was used per individual.

Table 2. General linear mixed models of laying date.

(Independent variables are female age (fixed effect, log-transformed), number of helpers (fixed effect), year (fixed effect), climate (fixed effect) and individual (random effect). Sandhills: $n = 2659$ observations of 812 breeding females, Camp Lejeune: $n = 367$ observations of 103 breeding females. b , coefficient. Statistics are F -ratios except for individual effects where χ^2 is given (likelihood-ratio test for nested models). Only effects significant in one or both populations are shown.)

source	Sandhills			Camp Lejeune		
	$b \pm \text{s.e.}$	statistic	p	$b \pm \text{s.e.}$	statistic	p
climate	-3.90 ± 0.91	18.52	<0.001	-0.29 ± 0.15	3.85	0.044
age	-4.75 ± 0.30	255.33	<0.001	-5.28 ± 0.78	23.73	<0.001
year	-0.09 ± 0.04	4.74	0.030	-0.01 ± 0.16	0.20	0.985
number helpers	-1.52 ± 0.26	33.65	<0.001	0.63 ± 0.67	0.00	0.766
individual	—	71.53	<0.001	—	12.00	<0.001

103 females). Similarly, median laying date of experienced pairs advanced (Sandhills: $r_s = -0.64$, $p < 0.01$, $n = 18$ yr, 787 pairs; Camp Lejeune: $r_s = -0.57$, $p = 0.05$, $n = 12$ yr, 104 pairs), but median laying date of newly formed pairs of experienced birds did not (Sandhills: $r_s = -0.29$, $p > 0.20$, $n = 18$ yr, 681 pairs; Camp Lejeune: $r_s = -0.02$, $p > 0.90$, $n = 13$ yr, 107 pairs).

(d) Inbreeding

In the Sandhills, 182 out of 1086 broods (16.8%) involved at least one inbred partner with inbreeding coefficients ranging from 0 to 0.25. The GLMM confirmed the effects of female experience and pair experience on laying date (table 3). In addition to effects of climate, female age, number of helpers and individual, both

Table 3. Expanded general linear mixed models of laying date.

(Independent variables are female age (fixed effect, log-transformed), number of helpers (fixed effect), year (Sandhills only, fixed effect), climate (fixed effect, log-transformed for Sandhills), inbreeding (fixed effect), female experience (fixed effect, Sandhills only), pair experience (fixed effect, Sandhills only) and individual (random effect). Sandhills: $n = 2930$ observations of 1086 females, 182 inbred or paired with an inbred mate (1980–1998), Camp Lejeune: $n = 80$ observations of 53 females, five inbred or paired with an inbred mate (1997–1998). b , coefficient. Statistics are F -ratios except for individual effects where χ^2 is given (likelihood-ratio test for nested models). Only effects significant in one or both populations are shown.)

source	Sandhills			Camp Lejeune		
	$b \pm \text{s.e.}$	statistic	p	$b \pm \text{s.e.}$	statistic	p
climate	-2.69 ± 0.85	9.90	0.002	-1.64 ± 1.04	1.79	0.187
age	-1.98 ± 0.43	20.81	<0.001	-5.99 ± 1.12	28.63	<0.001
inbreeding	449.02 ± 218.45	4.22	0.041	-33.29 ± 17.76	2.05	0.157
number helpers	-1.19 ± 0.27	19.48	<0.001	0.27 ± 0.99	0.07	0.789
female experience	-2.10 ± 0.63	10.26	0.001	—	—	—
pair experience	-4.20 ± 0.43	93.29	<0.001	—	—	—
individual	—	83.60	<0.001	—	4.43	0.032
inbred. \times climate	-95.63 ± 46.62	4.14	0.042	1.86 ± 0.92	2.98	0.089

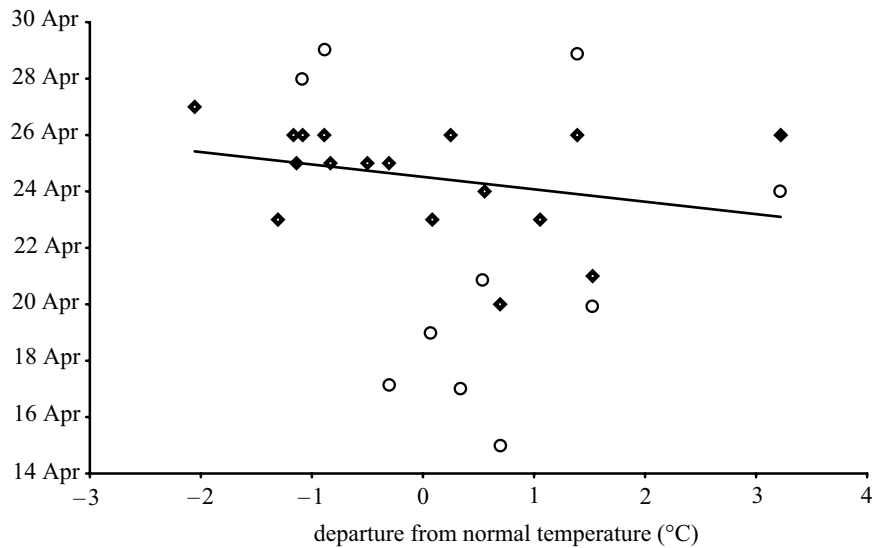


Figure 3. The effects of inbreeding on the relationship of laying date of red-cockaded woodpeckers (Sandhills population) to climate. Circles represent inbred birds (kinship coefficient less than 0, $n = 182$); diamonds represent non-inbred birds (trend line, $n = 1004$). One randomly selected observation per individual was used to calculate the median laying date.

inbreeding and the interaction between inbreeding and climate affected laying date (table 3). Inbred birds did not adjust laying date to climate, whereas non-inbred birds did (figure 3). The main effect of inbreeding was weak and hard to interpret (table 3). Median laying dates of inbred birds were highly variable, rather than consistently early or late; in some years they were remarkably early (figure 3). Inbred birds produced fewer fledglings than their non-inbred conspecifics (GLMM on the effects of female age, number of helpers, year and inbreeding on reproductive success, inbreeding effect: $F_{1,549} = 4.55$, coefficient $b \pm \text{s.e.} = -2.5 \pm 1.2$, $p = 0.0331$, $n = 2737$). There was no significant interaction between inbreeding and either experience variable, or between inbreeding and age. When inbreeding was entered as a two-level factor (inbred versus not inbred), the effects were even stronger (inbreeding: $F_{1,528} = 11.80$, $b \pm \text{s.e.} = 57.2 \pm 16.6$, $p = 0.0006$;

inbreeding \times climate: $F_{1,528} = 12.67$, $b \pm \text{s.e.} = -12.8 \pm 3.6$, $p = 0.0004$, $n = 2930$). In both models, a logarithmic transformation of climate produced a better fit. The weak year effect of the previous model (table 2) was not found, indicating that the factors included in the expanded model account for observed changes in laying date over time in the Sandhills.

At Camp Lejeune, 5 out of 53 broods (9.4%) involved an inbred bird, with inbreeding coefficients ranging from 0 to 0.125. In the limited sample available for this population, the interaction between inbreeding and climate was marginally significant (table 3) and no significant interaction between inbreeding and age occurred. Although the sample size was reduced by nearly 80% compared with the previous Camp Lejeune model (table 2), effects of female age and individual differences were again detected (table 3). We did not test for an effect of inbreeding on reproductive success due to the small sample size.

4. DISCUSSION

In the past two decades, egg laying has occurred increasingly earlier in two red-cockaded woodpecker populations as the climate has changed. Because different climatic variables (i.e. departure from normal temperature and rainfall) were correlated with this shift in laying date in the two populations, we suspect that neither is the actual variable to which the birds are responding, or the actual cue used to time breeding. Temperature and rainfall may instead be surrogates for other, causal variables linked to the, as yet unknown, process governing onset of breeding. Our findings indicate that climate change has not disrupted the relationship between the cues used to time breeding, and temporal variation in factors that influence reproductive success, such as food availability or nest predator activity. It would be premature to conclude, however, that the red-cockaded woodpecker actually profits from climate change due to the benefits of breeding earlier. On the contrary, overall reproductive output decreased slightly in both populations over the study period. Whether this is due to climate change is unclear, because our models do not include other factors potentially influencing reproductive success, such as changes in habitat quality (James *et al.* 1997).

The seasonal decline in productivity we observed is commonly reported from other bird species (Perrins 1965; Verhulst & Tinbergen 1991). Our data indicate that adjustments in laying date in response to climate change result from phenotypic plasticity in this trait, as has also been reported in earlier studies (Nager & van Noordwijk 1995; Przybylo *et al.* 2000). Our data further indicate that inexperienced females, experienced females breeding with new mates and inbred birds are shifting egg-laying dates less than other birds, or not at all. Other studies suggest that, in birds, coordinated interaction with the breeding partner is essential in responding properly to environmental cues (Coulson 1966). Regardless of why novice breeders and experienced females breeding with new mates are unable, or less able, to make adjustments in timing of breeding, climate change may accentuate the effects of age on reproductive success (Walters 1990) and increase selection against changing mates, which female red-cockaded woodpeckers sometimes do (Daniels & Walters 2000b).

Perhaps laying early is advantageous only for some individuals, and these are the ones that respond to climate change. The interaction between female age and laying date we observed does indeed indicate that older females profit more from laying early than do younger females. However, young females that lay early are more productive than young females that lay late (figure 2). We think it more probable that some individuals are less able, rather than less willing, to adjust the timing of their egg laying, and suffer reproductive costs as a result.

The inability of inbred birds to adjust laying dates to changes in climate may represent a third adverse effect of inbreeding on reproduction in red-cockaded woodpeckers, in addition to reduced hatching success and reduced survival of fledglings to age one (Daniels & Walters 2000a). Inbred birds produced fewer fledglings than non-inbred individuals, but we do not have sufficient data to separate the effects of laying date from other effects of inbreeding

depression. Inbreeding depression has been reported to affect various traits in other species (see Hedrick & Kalinowski 2000 for a review), and impacts seem to be greater on life history than on morphological traits (DeRose & Roff 1999). Inbred individuals are more susceptible to parasitic infections (Coltman *et al.* 1999; Cassinello *et al.* 2001), perhaps due to a less effective immune system resulting from low genetic variation (O'Brian & Evermann 1988; Hughes 1991; Paterson 1998). Immunocompetence accounts for differences in egg-laying dates among female tree swallows (*Tachycineta bicolor*), with less competent birds laying later in the season than their conspecifics (Hasselquist *et al.* 2001). Perhaps the failure of inbred red-cockaded woodpeckers to alter their laying dates, in response to climate change, is a manifestation of a reduced immunocompetence. Our findings provide another example of the reduced ability of inbred animals to handle environmental challenges by extending this pattern to global climate change (Keller *et al.* 1994; Bijlsma *et al.* 1999; Coltman *et al.* 1999; Dahlgard & Hoffmann 2000; Meagher *et al.* 2000). By unequally affecting inbred and non-inbred individuals, global climate change may represent an additional, previously unknown threat to endangered species, such as the red-cockaded woodpecker, that are largely restricted to small, isolated populations (Azevedo *et al.* 2000).

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