POPULATION ECOLOGY - ORIGINAL PAPER

Causes of reduced clutch size in a tidal marsh endemic

**Brian J. Olsen · Joshua M. Felch · Russell Greenberg ·
Jeffrey R. Walters**

Abstract We tested three hypotheses of clutch size variation in two subspecies of the swamp sparrow (*Melospiza georgiana georgiana* and *M. g. nigrescens*). Swamp sparrows follow the pattern of other estuarine endemics, where clutch size is smaller among tidal salt marsh populations (*M. g. nigrescens*) than their closest inland relatives (*M. g. georgiana*). Our results support predation risk and temperature, but not adult survival, as explanations of this pattern in swamp sparrows. Coastal nests were twice as likely to fail as inland nests, and parental activity around the nest site was positively related to clutch size at both sites. When brood size was controlled for, coastal adults visited nests less often and females vocalized less frequently during visits than inland birds, which may decrease nest detectability to predators. Coastal parents waited longer than inland birds to feed offspring in the presence of a model nest predator, but there was no difference in their response to models of predators of adults, as would be expected if coastal birds possessed increased longevity. Additionally, coastal females laid more eggs than inland females over a single season, following a within-season bet-hedging strategy rather than reducing within-season investment. Coastal territories experienced ambient air temperatures above the physiological zero of egg development more often, and higher temperatures during laying correlated with smaller clutches and increased egg inviability among coastal birds. Similar effects were not seen among inland nests, where laying temperatures were generally below physiological zero. Both subspecies showed an increase in hatching asynchrony and a decrease in apparent incubation length under high temperatures. Coastal individuals, however, showed less hatching asynchrony overall despite higher temperatures. Both air temperatures during laying and predation risk could potentially explain reduced clutch size in not only coastal plain swamp sparrows, but also other tidal marsh endemics.

Keywords Egg viability · Predation · Survival · Swamp sparrow · Temperature

B. J. Olsen · R. Greenberg
Smithsonian Migratory Bird Center, National Zoological Park,
3001 Connecticut Ave. NW, Washington, DC 20008, USA

B. J. Olsen · J. R. Walters
Department of Biological Sciences, Virginia Polytechnic
Institute and State University, Blacksburg,
VA 24061-0406, USA

J. M. Felch
Department of Fisheries and Wildlife Sciences,
Virginia Polytechnic Institute and State University,
Blacksburg, VA 24061-0321, USA

Present Address:
B. J. Olsen (✉)
School of Biology and Ecology, University of Maine, Orono,
ME 04469-5751, USA
e-mail: brian.olsen@umit.maine.edu

Introduction

The study of clutch size variation in birds has significantly increased our understanding of vertebrate life histories. Food limitation (Lack 1948), nest predation (Ricklefs 1970; Skutch 1949; Slagsvold 1982), adult survivorship (Moreau 1944), and climate (Ashmole 1963; Cooper et al. 2005; Stoleson and Beissinger 1999) have all been purported to explain clutch size variation across latitudes and taxonomic groups, yet there is no consensus on a single

theoretical model. Clutch size is influenced by a number of phylogenetic and environmental constraints (Martin 2004), whose hierarchical organization (Ghalambor and Martin 2001) should allow for clutch size predictions in specific populations. To understand the interactions between these constraints, however, it is necessary to examine multiple, phylogenetically controlled pairs of species or populations in a variety of environments (Ferretti et al. 2005; Martin et al. 2000). Here we present a single such contrast between two subspecies of the swamp sparrow, *Melospiza georgiana*, at study sites 319 km apart at a similar latitude (39.6°N vs. 39.4°N), yet varying in elevation (800 m), predation risk, and climate.

In addition to patterns across latitude and elevation, clutch size increases predictably from tidal, salt marshes to inland habitats (Greenberg and Droege 1990). Relatively small clutches among tidal-salt-marsh birds suggest that the environment has selected for similar life histories across a diverse suite of bird species from rails to passerines. We tested for three possible causes of clutch size divergence between a population of coastal plain swamp sparrows (*M. g. nigrescens*) and a population of the nearest inland subspecies (*M. g. georgiana*) to elucidate factors behind the tidal-salt-marsh trend. The hypotheses tested include: (1) nest predation risk, (2) adult survival probability, and (3) ambient air temperature during laying.

Predation

The predation hypothesis predicts that females will lay small clutches when nest predation risk is high and that increased predation on eggs and nestlings should select for parental behaviors that decrease nest detectability. A reduced clutch size should decrease nestling provisioning demand, therefore decreasing parental activity near the nest (Ghalambor and Martin 2002; Skutch 1949). This scenario leads to a number of testable predictions (Table 1: P1–6). Within each subspecies, predation risk should be highest during the stage of offspring development with the most parental activity around the nest (P1), and parental activity should be higher around nests with more offspring (P2: Ferretti et al. 2005). Furthermore, nest attendance should be lower, on average, in the coastal population in order to reduce detection by predators (P3: Eggers et al. 2005; Fontaine and Martin 2006), which may in turn reduce nestling growth (Nolan et al. 2001) or increase the mass of food carried per provisioning trip (P4: Martin et al. 2000).

The influence of nest detectability on life history evolution may be larger in swamp sparrows than other passerine songbirds, as females utter distinctive calls near the nest during incubation and (albeit, less frequently) nestling provisioning. Although females of both subspecies give the nest-associated call (NAC) every time they leave the nest during the incubation stage, individuals vary in their use of the NAC when they return to the nest (personal observation). Under the predation hypothesis, therefore, we predict that females with the highest risk of nest predation should use the NAC less often during these return trips (P5). Females under conditions of high nest predation risk may further limit the nest's detection by decreasing the frequency of nest departures, thereby decreasing their use of the NAC (P6). The greatest decrease in nest visitation rate should occur during the incubation stage when females are more likely to use NAC and offspring development is constrained less by female visitation rate.

Finally, the predation hypothesis predicts that coastal populations should experience higher rates of nest predation (P7) and that coastal adults should show greater behavioral responses to nest predators than inland adults (P8: Ghalambor and Martin 2002).

Survivorship

Under the survivorship hypothesis, yearly adult survival probability explains clutch size through tradeoffs between current and future reproduction (Ghalambor and Martin 2001; Moreau 1944). Adults with a high probability of survival decrease clutch size to reduce energetic investment in current reproductive events, thereby maximizing their survival probability to the next breeding season. Adults with low survival probability, on the other hand, invest more energy in current reproduction, since there is a low chance of surviving to the next breeding season. Under this hypothesis, we predict that the smaller clutch size of coastal females will be accompanied by lower seasonal egg production (summed over all nesting attempts) to maximize survivorship in a given year relative to inland females (Table 1: S1). Also, yearly return rates should be higher in coastal adults (S2). Finally, to maximize adult survival, coastal birds should respond more strongly than inland birds to predators of adults (S3: Ghalambor and Martin 2001).

Temperature

Under the temperature hypothesis, ambient air temperatures control clutch size through developmental effects on unincubated eggs (Ardia et al. 2006; Cooper et al. 2005, 2006; Stoleson and Beissinger 1999). Swamp sparrows, like many passerine cup-nesters, typically lay one egg per day and begin incubation (and hence thermoregulation) upon the completion of the clutch (Mowbray 1997). All eggs except for the last egg are, therefore, subject to variation in ambient temperatures. Assuming that physiological zero is between 24° and 26°C (Webb 1987), development is suspended for eggs that are laid in ambient

Table 1 Predictions of three hypotheses of avian clutch size variation

Hypothesis	Prediction	Supported
Predation risk (P)	P1: Predation risk is highest in the development stage with the most parental activity around the nest	N
	P2: Adult activity around the nest correlates with clutch size	Y
	P3: Adult activity around the nest is lower overall where predation risk is high	Y
	P4: Reduced adult activity may result in slower nestling growth or larger food loads per trip	Indirect evidence
	P5: Nest arrival calls, if more plastic, are used less frequently where predation risk is high	Y
	P6: Nest departure calls are more infrequent during incubation due to decreased nest departures where predation risk is high	Y
	P7: Lower clutch sizes where predation risk is highest	Y
	P8: Coastal adults show greater latency in nest attendance than inland adults in the presence of a nest predator	Y
Adult survival probability (S)	S1: Egg production per female per season is negatively associated with return rate (thus positively with clutch size)	N
	S2: Higher yearly adult return rates associated with lower clutch sizes	N
	S3: Coastal adults show greater feeding latency than inland adults in the presence of an adult predator	N
Temperature during laying (T)	T1: Controlling for clutch size, nests with inviable eggs experience more suboptimal laying temperatures	Y
	T2: Inviable eggs are more common in subspecies with more suboptimal laying temperatures	Y
	T3: More days with ambient temperatures in suboptimal zone (24–36°C) in subspecies with smaller clutch size	Y
(a) Reduced laying period	T4: Incidence of daily suboptimal temperatures predicts lower clutch sizes within subspecies	Coastal only
(b) Early onset of incubation	T5: Hatching asynchrony is greater in subspecies where laying temperatures are higher	N
	T6: Apparent incubation length is smaller in subspecies with more suboptimal temperatures	N
	T7: Hatching asynchrony is positively related to ambient temperatures during laying	Y
	T8: Apparent incubation length is positively related to ambient temperatures during laying	Y

Y, Yes; N, no

temperatures below 24°C. For eggs that are laid in conditions above this critical limit and below optimal incubation temperatures (36°C: Cooper et al. 2005; Stoleson and Beissinger 1999), partial, slowed development can lead to abnormalities and inviable eggs (Deeming and Ferguson 1992). The temperature hypothesis thus predicts that the first laid egg is the most vulnerable to defects, and among clutches laid in similar conditions, larger clutches should possess more inviable eggs (Cooper et al. 2005). Stated another way, among clutches of the same size, those with inviable eggs should have experienced more suboptimal temperatures during laying (Table 1: T1). Regardless of clutch size, the incidence of inviable eggs should be higher along the coast, due to its warmer temperatures (T1).

Females that lay eggs in these suboptimal temperatures can follow two possible strategies. First, they can decrease clutch size to limit the length of the laying period, resulting in lower clutch sizes in more suboptimal climates. Following this scenario, we predict that coastal birds will experience suboptimal temperatures more frequently during laying (T3) and that in both environments, suboptimal ambient temperatures will result in reduced clutch sizes (T4).

Following a second strategy, females can begin incubation during laying yet prior to clutch completion, thereby raising the temperature of the first-laid eggs above the suboptimal zone. This strategy results in asynchronous starts of embryonic development within a clutch and thereby increases hatching asynchrony. Following this second scenario, we predict that hatching asynchrony will be greater in coastal populations (T5) or apparent incubation length (the time from clutch completion to the start of

hatching) will be shorter in coastal birds due to the earlier onset of incubation (T6). Under this scenario, both hatching asynchrony (T7) and apparent incubation length (T8) will be correlated with ambient temperatures during laying within each subspecies.

Materials and methods

Study site

We investigated the coastal *M. g. nigrescens* at sea level on two plots of Spartina marsh, each approximately 15 ha, located within state game lands near Woodland Beach, Delaware (75.6°W, 39.4°N); the study period was from May to August 2002–2005. The *Melospiza g. georgiana* studies were conducted 319 km inland at 800 m a.s.l. on two plots in cranberry fens on the Allegheny Plateau in Garrett County, Maryland (79.3°W, 39.6°N); the study period was from May to August 2004–2005. Wetlands at both sites are not shaded by trees and are thus subject to large variations in daily temperatures. Nests, however, are typically placed in thick vegetation (mean distance from modal vegetation height to nest lip ± standard error, controlling for plot differences within subspecies: coastal = 0.57 ± 0.03 m; inland = 0.54 ± 0.03 m) and are therefore not often warmed by sunlight directly.

Nest monitoring

To calculate nest success and failure rates (Table 1: P1, P7), we located nests using the NAC of female sparrows (McDonald and Greenberg 1991) and rechecked nests daily to ascertain hatching and fledging dates until fledging or failure. We assigned failure to one of four categories: predation, flooding, abandonment, and other/unknown. Flooding failures were synchronized across the coastal marsh and coincided with the new or full moons or storm-related tidal surges. We assigned flooding as the cause of failure to nests on these days when the high tide mark (seen as mud on standing vegetation) was higher than the nest, eggs were displaced from the nest bottom without other noticeable harm, or nestlings were dead in the nest, wet, and otherwise uninjured. We labeled nests as abandoned when all eggs in clutches with more than one egg did not hatch after 15 days of observed incubation (3 days longer than the mean species incubation length; Mowbray 1997), or when vegetation placed in the nest was not removed by the female after 24 h. Other/unknown causes of failure were rare, but we assigned failures to this category when adults with active nests died or disappeared, single egg clutches did not hatch, or all chicks died without obvious external injury or evidence of high water. We assigned predation as the cause of failure when all chicks or eggs disappeared, often accompanied (but not always) by egg or nestling fragments, disturbed nest material, disturbed vegetation around the nest, or mammalian footprints in the mud. Territories with nests that failed near their predicted fledging dates were checked repeatedly in subsequent days for evidence of adults feeding fledglings. We called nests that fledged at least one nestling successful and used color bands to ascertain within-season nest success and total egg and fledging production for each adult pair.

We tested for differences in mean clutch size between the subspecies using a repeated-measures analysis of variance (ANOVA), controlling for year and for nesting attempts within territories. We calculated daily probabilities of nest predation and survival using a modified Mayfield (1975) method, partitioning failure risk into predation events and non-predation events (which included flooding, abandonment, and other/unknown) via the method described by Etterson et al. (2007). We calculated stage (incubation or brooding), and clutch-specific maximum likelihood estimates (MLE) of daily predation probabilities within subspecies using

$$\hat{M}_p = \frac{N_p}{N_s + N_p + N_o} \qquad (1)$$

where $\hat{M}_p$ is the MLE for daily predation probability for each development class and each clutch size within subspecies, N_p is the number of days nests were observed that resulted in a predation event, N_s is the number of days observed that resulted in the survival of the chicks to the next interval, and N_o represents the number of days that resulted in failure that was not due to predation. Stage- and clutch-specific variances were calculated similarly using

$$\sigma^2 = \frac{M_p \cdot (1 - M_p)}{N_s + N_p + N_o} \qquad (2)$$

We modeled the daily predation rate using a logistic exposure model (Rotella et al. 2004; Shaffer 2004a, b) in Proc GENMOD of SAS (SAS Institute 2005), modifying Shaffer's (2004b) SAS macros to model daily predation rate (Eq. 1) instead of survival rate. Candidate predictors included subspecies, development stage (laying, incubation, or brooding), clutch size, Julian date, and study year nested within site (coastal or inland). Models were ranked using the small-sample corrected version of the Akaike information criterion (AICc) scores, and models with ΔAICc values ≤ 2.0 were considered equivalent.

Nestling measurements

To test for a predicted tradeoff between nest attendance and nestling growth under the predation hypothesis (P4), we weighed nestlings every 3 days in all active nests. Final

pre-fledging measurements were taken at every nest when nestlings reached 7 days of age (2005 only), and we gathered no further measurements on older nestlings to prevent premature fledging. Nestling growth slopes were calculated by plotting all chick weights for each territory against a logistic growth curve via the method described by Ricklefs (1967). We combined all nesting attempts for each territory to reduce the impact of short-term weather events. We tested for subspecies differences in growth rate with ANOVA, controlling for year within site. We also tested for subspecies and brood size differences in the pre-fledging weights of 7-day nestlings using a repeated-measures ANOVA, subsampling multiple nesting attempts within each territory (again controlling for year within site).

As a relative measure of nestling satiation, we shook the vegetation lightly approximately 20 cm above each nest during daily checks and recorded the duration of nestling begging up to a maximum of 2 min. We tested for differences in nestling begging rates between subspecies using a doubly repeated-measures ANOVA for multiple measures of each nest attempt within each territory, controlling for nestling age, Julian date, brood size, and the time of day of our observation.

Adult behavioral observations and survival estimates

During all breeding seasons we captured adults in mist-nets and juveniles in the nest and attached unique color-band combinations for subsequent identification during behavioral observations or for resighting to estimate yearly return probability.

To determine if adults changed the frequency of their NAC in response to predation risk (P5, P6), we observed incubating females during 2004 and 2005 from a distant location (>15 m) for four consecutive cycles of departure and arrival (ranging in time from 70 to 160 min of observation). We noted the time intervals between each NAC and the direction of female movement (departing from the nest or arriving at the nest) based on directional auditory cues and visual confirmation. For each female, we then calculated (1) the average time between two nest departures (since females do not always call during nest arrivals) and (2) the ratio of calls given during nest arrivals versus nest departures. We never witnessed an incubating female leave a nest without giving a NAC. We tested for subspecific differences in each measure of the NAC using ANOVA, controlling for year within site, Julian date, and clutch size.

To determine the relative adult activity near nests with chicks (P2, P3), we observed nests with nestlings of at least 3 days of age in 2005 from a camouflaged location and recorded the number of feeding trips made by adults (males

and females were differentiated by color bands). We tested for subspecific differences in nestling feeding rates using ANOVA, controlling for nestling age, Julian date, brood size, and time of day.

After three feeding trips by each parent or 2 h (whichever came first), we placed a predator model in a clearly visible location, 5–10 m from the nest and above the modal vegetation height. Following methodology modified from Ghalambor and Martin (2002), we then recorded the length of time until the first provisioning event by either parent (P8, S3). We removed the model after 1 h if no visits had occurred. We chose the predator for each trial randomly from three models, including an adult sparrow predator (taxidermied Cooper's Hawk, *Accipiter cooperii*), a nest predator (Flambeau crow decoy; Flambeau, Middlefield, OH), and a white, plastic milk jug used to control for neophobia (Greenberg 1989). To determine the relative behavioral response of coastal versus inland sparrows to nest versus adult predators, we compared the length of time it took for the first parent to visit the nest in the presence of the models. Specifically, we tested for the effect of a predator-model-by-subspecies interaction on the latent feeding time using ANOVA, controlling for baseline provisioning rate, Julian date, brood size, time of day, and nestling age. Given the relatively large number of levels of the interaction and the number of controlled independent variables, *a priori* power analysis (using expected effect sizes extrapolated from Ghalambor and Martin 2002) indicated an appropriate increase in α to 0.10. Latency values for each subspecies-by-treatment combination were determined *post hoc* using least-squares means controlling for all independent variables.

Subspecific differences in the total number of eggs laid, and in the number of renests per season were tested with ANOVA, controlling for year within site (S1). The short time period of our inland study (two seasons) prohibited mark-recapture analysis of survival, so we instead report between-year resighting rates (either by targeted, mist-net capture or visual identification of unique color combinations) (S2). Efforts were made in all years to band all adults and nestlings greater than 5 days of age within the plots. Inter-annual estimates of the return rate for coastal birds were determined for each year of return (2002–2003, 2003–2004, and 2004–2005) for comparison to the single year of return (2004–2005) in the inland site. We only calculated adult return rates among birds that were confirmed breeders in at least 1 year to exclude floaters or birds intruding from off the plots. For juveniles we calculated return rates for any nestlings that were detected as adults. Across all years and sites we identified the territorial male for 94.8% of our territories (275 males out of 290 territories) and the breeding female for 79.0% of our territories (229 females).

Temperature correlates

Daily high temperatures were obtained from the Maryland/Delaware/DC chapter of the Atlantic Coast Observer Network (ACON 2006). Daily high temperatures for Delaware laying periods were assigned from those recorded at the Bear, DE station (75.6°W, 39.6°N), 22 km from the coastal plots, and inland temperatures were assigned from the Frostburg, MD station (79.9°W, 39.6°N), 51 km from the inland plots. Daily highs during the laying period were averaged across all days prior to and including the day of clutch completion (T1, T4). To test for a subspecific difference in the probability of encountering suboptimal temperatures, we used a repeated-measures logistic regression to see if subspecies explained whether or not nests experienced temperatures above 26°C during the laying period, subsampling nesting attempts within territories. We tested for site differences in mean daily high temperatures using ANOVA controlling for year within site.

To test for subspecific differences in egg viability, we first used a repeated-measures ANOVA to test for differences in the percentage of inviable eggs per clutch, controlling for year within site and Julian date and subsampling nesting attempts within territory (T2). Second, to test for the effect of temperature on the presence or absence of inviable eggs within a clutch (T1), we used a repeated-measures logistic regression, subsampling nesting attempts within territories. Candidate variables included subspecies, the presence of suboptimum temperatures on the first day of laying (above 26°C or not), the presence of suboptimum temperatures on the last day of laying (above 26°C or not), the number of days with temperatures above 26°C, the mean daily high temperature during the entire laying period, clutch size, year within site, and Julian date. For this test we excluded all one-egg clutches, since we could not differentiate between inviability and abandonment in these cases.

We tested for subspecific differences in hatching asynchrony (T5, T7) by comparing the number of days each nest took to complete hatching based on their progress at daily checks. Our value is a maximum estimate of the time it took a brood to completely hatch, since nests were only checked once per day. If there was no evidence of hatching on a given day, and the clutch was completely hatched on the next day, we assumed that the brood took that entire 24-h period to hatch. In broods where we assumed hatching occurred over 2 or 3 days, the last chick was not completely out of the shell until 2 or 3 days after the first nest check showing evidence of hatching.

We assigned incubation start dates based on the last day of laying. In cases where clutch completion was not observed, incubation start dates were back-calculated from the date of hatching based on population-specific averages for incubation length. We excluded these nests when testing predictions about apparent incubation length (T6, T8). We tested a number of possible effects of temperature on breeding, including the effect of mean daily high temperatures during laying on clutch size (by subspecies), the effect of laying temperature on apparent incubation length (by subspecies and clutch size), and the effect of mean high laying temperatures on hatching asynchrony. For all these tests, we used repeated-measures ANOVA, controlling for Julian date and year within site and subsampling nesting attempts within territory.

Statistical procedures

For all ANOVAs we performed model selection among all possible combinations of candidate predictors. Final models were constrained so that all independent variables were significant at $P < 0.10$, and all final models had AIC values lower than the next best model by >2.0 ΔAIC. For logistic regression (excepting the logistic exposure model of predation rate), we performed model selection using Scaled Pearson χ^2 values controlling for the degrees of freedom. Final models were those where χ^2/df was closest to 1.0.

All subspecies means were determined post hoc using least-squares means. Means reported are these model-specific, corrected means $\pm$ standard error (SE). For the predator model experiment, treatment-level independent contrasts are reported along with full model results. All residuals met assumptions of normality and homogeneity of variance where appropriate, and all statistical tests were conducted using SAS ver. 9.1.3 (SAS Institute 2005).

Results

Like Greenberg and Droege (1990), we found that the salt marsh population of swamp sparrows had a significantly smaller clutch size (3.25 $\pm$ 0.04; $F_{1,302} = 23.6$, $P < 0.001$) than the interior population (3.61 $\pm$ 0.06) ($n = 313$ territory-years: 211 coastal, 102 inland). Inclusion of the effect of year within site did not improve the model.

The predation hypothesis

In the coastal population, 79% of failures were due to predation (228 events out of 288 failures among 408 nests monitored), 14% of failures (40 nests) were due to flooding, and the remaining 7% of failures (20 nests) were due to abandonment and other unknown causes. In contrast, in the inland subspecies, 98% of nest failures were due to predation (62 events of 63 failures among 149 nests monitored), only a single nest was abandoned, and no nests were flooded.

In accordance with our prediction (Table 1: P7), the coastal population, with its lower clutch size, experienced more than twice the daily nest predation risk ($M_p \pm \sigma = 0.063 \pm 0.004$) of the inland population (0.029 ± 0.004) across all years, clutch sizes, and nest stages. The highest ranked model predicting a predation event during a nest observation was the full model (AICc $= 2272.0$, $n = 5{,}629$, likelihood-ratio $\chi^2 = 368.5$, $P < 0.0001$), which included the effects of subspecies ($\chi^2 = 101.6$, $P < 0.001$), clutch size ($\chi^2 = 22.3$, $P < 0.001$), nest development stage ($\chi^2 = 25.8$, $P < 0.001$), year within site ($\chi^2 = 256.6$, $P < 0.001$), and the Julian date of the observation ($\chi^2 = 2.7$, $P = 0.10$). Three models were equivalent to the full model: the full model without the effect of subspecies (ΔAICc $= 0.0$, likelihood-ratio $\chi^2 = 368.5$, $P < 0.0001$), the full model without the date of observation (ΔAICc $= 0.7$, likelihood-ratio $\chi^2 = 371.8$, $P < 0.0001$), and the full model with neither date nor subspecies (ΔAICc $= 0.7$, likelihood-ratio $\chi^2 = 371.8$, $P < 0.0001$). In these top four models, nests were significantly more likely to be depredated when the population was coastal (P7), when the clutch size was smaller, and when the nest was in the egg stage versus the nestling stage (contrary to P1) and in the nestling stage over the building stage (Fig. 1). The fifth ranked model (without clutch size and date) performed less well than the first four (ΔAICc $= 18.8$), and the null model representing constant survivorship was the lowest ranked model (ΔAICc $= 356.5$).

Nest detectability

The absolute time between nest visits by adults was less in the nestling phase (from one arrival to the next) than in the egg stage (from one departure to the next) for both coastal (nestlings $= 11.2 \pm 1.0$ min; eggs $= 29.6 \pm 1.5$ min) and inland nests (nestlings $= 6.0 \pm 0.9$ min; eggs $= 26.6 \pm 1.5$ min). Despite this, and contrary to our prediction (P1), predation risk was higher at the egg stage, but only for small clutch size in the coastal population (Fig. 1)

The best model ($n = 52$, $r^2 = 0.15$, $f_{3,48} = 2.7$, $P = 0.05$) explaining female movement near the nest during incubation (determined by nest departure frequency) included subspecies ($t = 4.7$, $P = 0.04$), clutch size ($t = 4.5$, $P = 0.04$), and Julian date ($t = 4.6$, $P = 0.04$). As predicted by the predation hypothesis (P3, P6), coastal females waited longer between nest departures (31.0 ± 1.7 min) than did inland females (25.7 ± 1.6 min), when clutch size and Julian date were controlled (Fig. 2). Females of both subspecies waited longer between departures in nests with smaller clutch sizes, controlling for state and Julian date.

The best model ($n = 52$, $r^2 = 0.39$, $f_{4,47} = 7.4$, $P = 0.0001$) of female vocalization frequency near the nest
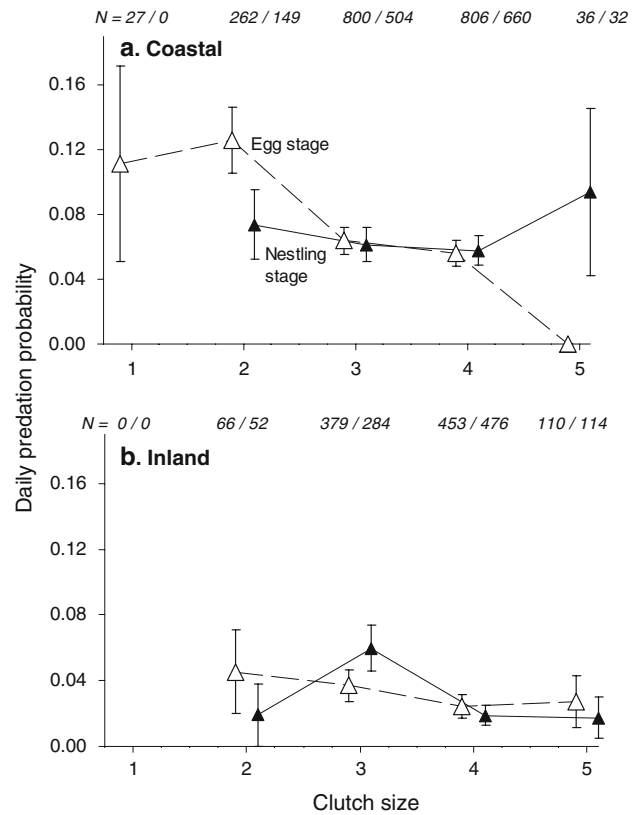

Fig. 1 The maximum likelihood estimates ($\pm$ standard deviation, SD) of the daily probability of nest failure due to predation for coastal *Melospiza georgiana nigrescens* (**a**) and inland *M. g. georgiana* nests (**b**) in the egg stage (*open triangles*) and the nestling stage (*filled triangles*) by clutch size. Data points are offset for visibility. *Italicized values above* each panel indicate sample size (egg/nestling) for each point. We sampled no nests with only a single egg for *M. g. georgiana*, and among *M. g. nigrescens* no single-egg nests and all five-egg nests survived to hatching

during the incubation period (determined by the ratio of calls given during nest arrivals vs. nest departures) included subspecies ($f = 3.2$, $P = 0.08$), clutch size ($f = 5.3$, $P = 0.03$), and year ($F = 9.9$, $P = 0.0003$). As predicted by the predation hypothesis (P5), coastal females called a lower percentage of the time during arrivals ($40.5 \pm 5.9\%$ of arrivals) than inland females ($54.4 \pm 5.7\%$ of arrivals), controlling for clutch size and year (Fig. 3). Furthermore, among inland females, there was a positive relationship between clutch size and vocalization frequency (P2), such that those females that had invested more in egg production called more often (Fig. 3). Although clutch size is also tied to calendar date, this does not account for the relationship between clutch size and the NAC ratio, as Julian date was not significant in the full model ($F = 0.1$, $P = 0.73$). No similar trend between clutch size and vocalization frequency was evident among coastal females (Fig. 3).

The best model ($n = 52$, $r^2 = 0.39$, $f_{3,48} = 10.1$, $P < 0.0001$) explaining parental activity around nests with
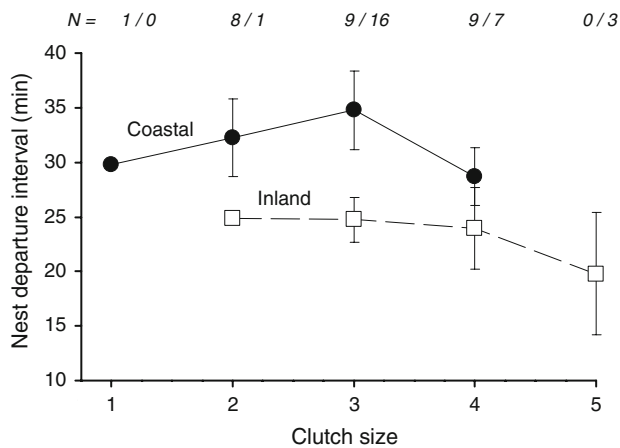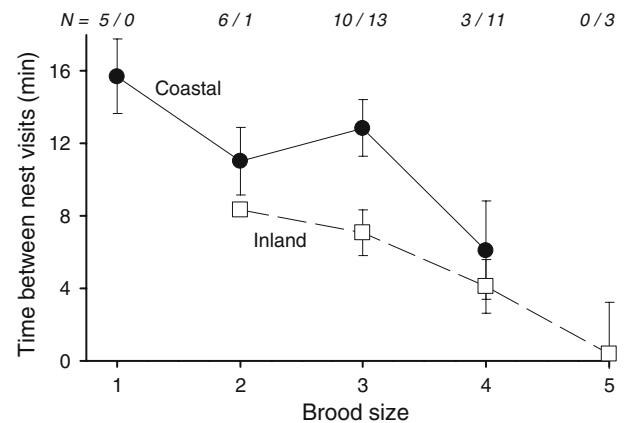
Fig. 2 Time between successive nest departures (mean ± SE) for each clutch size of incubating coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*) as determined by the nest departure call. *Italicized values above* the panel indicate sample size (coastal/inland) for each point. Values are least squares means controlling for Julian date. Sampling was not performed for nests with five eggs for *M. g. nigrescens* nor for nests with only a single egg for *M. g. georgiana*
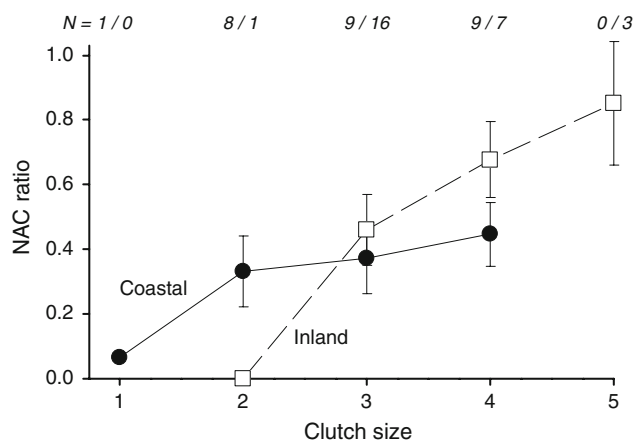

Fig. 3 Ratio (mean ± SE) of the incidence of nest associated calls (NAC) given during nest arrival versus departure for incubating coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*), calculated for each clutch size. *Italicized values above* the panel indicate sample size (coastal/inland) for each point. Values are least squares means controlling for year within site. Sampling was not performed for nests with five eggs for *M. g. nigrescens* nor for nests with only a single egg for *M. g. georgiana*

nestlings (determined by the rate of provisioning trips) included subspecies ($F = 6.0$, $P = 0.02$), brood size ($F = 10.6$, $P = 0.002$), and Julian date ($F = 4.3$, $P = 0.04$). As predicted by the predation hypothesis (P3), coastal parents waited longer between provisioning trips (10.6 ± 1.1 min) than inland parents (6.6 ± 1.0 min), and both subspecies were more active around nests with larger broods (P2; Fig. 4).

Fig. 4 Time between successive nestling provisioning trips (mean ± SE) by coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*) parents, calculated for each clutch size. *Italicized values above* the panel indicate sample size (coastal/inland) for each point. Values are least squares means controlling for Julian date. Sampling was not performed for nests with five eggs for *M. g. nigrescens* nor for nests with only a single egg for *M. g. georgiana*

Tradeoffs in nestling growth

The decreased nestling visitation of coastal parents (for a given brood size relative to inland pairs) could result in reduced nestling growth (P4). The full model explaining nestling growth slopes ($n = 144$, $r^2 = 0.19$, $f_{4,139} = 8.2$, $P < 0.0001$) did indeed include subspecies ($F = 13.9$, $P = 0.0003$) as well as year within site ($F = 9.7$, $P < 0.0001$). However, when yearly effects within each population was controlled for, the mean maximum growth rate was actually faster in coastal nestlings (6.98 ± 0.06 g/day) than it was in inland nestlings (6.67 ± 0.06 g/day) where provisioning trips were more frequent. Further, there was no effect of subspecies ($n = 83$, $f_{1,78} = 0.08$, $P = 0.78$) on the mass of coastal (12.0 ± 0.2) and inland (12.1 ± 0.2) nestlings at 7 days after hatching, and year alone was the best predictor of 7-day-old nestling mass ($n = 83$, $f_{1,78} = 2.8$, $P = 0.03$). These results suggest that coastal adults bring larger food loads than inland birds or, alternatively, loads of higher quality per trip (P4).

Coastal nestlings begged over twice as long (28.0 ± 2.8 s) as inland nestlings (12.7 ± 1.7 s). The best model for begging intensity ($n = 113$, $f_{2,397} = 11.4$, $P < 0.0001$) included the effects of subspecies ($f_{1,111} = 19.9$, $P < 0.0001$) and brood size ($f_{1,284} = 10.9$, $P = 0.001$). In the coastal population, where provisioning rate was lower, nestlings in larger broods tended to beg longer than those in smaller broods. Among inland broods, however, begging length was relatively constant across all broods (Fig. 5).

Finally, as predicted by the predation hypothesis (P8), coastal parents waited longer ($n = 48$, $df = 38$, $t = 1.7$,
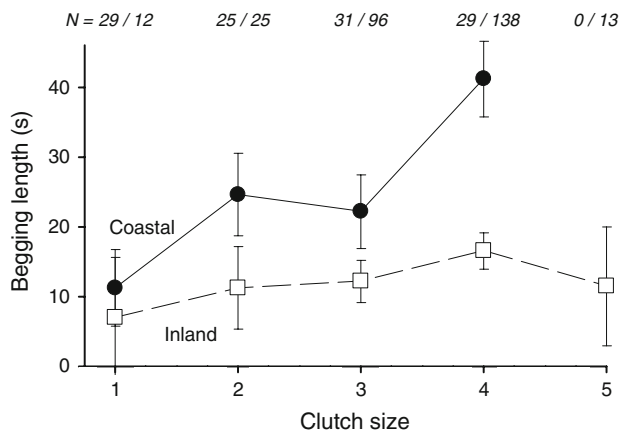
Fig. 5 Begging length time (mean ± SE) for coastal *Melospiza georgiana nigrescens* (*filled circles*) or inland *M. g. georgiana* (*open squares*) nestlings when the vegetation was disturbed approximately 20 cm above the nest, calculated for each clutch size. *Italicized values above* the panel indicate sample size (coastal/inland) for each point. Sampling was not performed for nests with five eggs for *M. g. nigrescens*
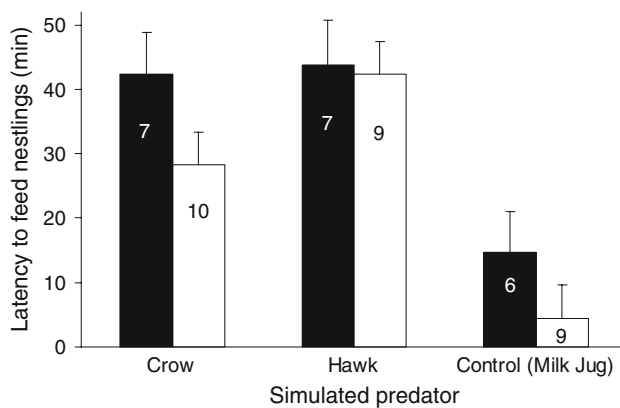
Fig. 6 Latency to feed nestlings (mean ± SE) by coastal *Melospiza georgiana nigrescens* (*filled bars*) and inland *M. g. georgiana* (*open bars*) in the presence of a simulated predator within 10 m of the nest. Values are least squares means controlling for baseline visitation rate, Julian date, and time of day. *Values within bars* indicate the sample size for each subspecies for each treatment

$P = 0.09$; Fig. 6) to feed offspring in the presence of a nest predator (42.6 ± 6.2 min) than did inland adults (28.3 ± 4.8 min), controlling for baseline provisioning rates.

The survivorship hypothesis

Contrary to the survivorship hypothesis, coastal females made more nesting attempts per season (2.4 ± 0.1 attempts, maximum of five nests) than inland females (1.8 ± 0.1 attempts, maximum of three nests) and, despite their reduced clutch size, laid more eggs over a season (8.1 ± 0.4 eggs, maximum of 19 eggs) than inland females

(6.5 ± 0.4 eggs, maximum of 11 eggs). The best model for nesting attempts ($n = 164$, $r^2 = 0.18$, $f_{5,158} = 6.8$, $P < 0.0001$) included both subspecies ($f = 17.4$, $P < 0.0001$) and year within site ($f = 1.7$, $P = 0.16$). The final model for eggs produced ($n = 164$, $r^2 = 0.11$, $f_{5,158} = 4.1$, $P < 0.002$) was structured similarly (subspecies $f = 8.9$, $P = 0.003$; year $f = 1.4$, $P = 0.25$).

Small sample sizes precluded a definitive test of predictions on annual survival related to the survivorship hypothesis (S1, S2), but the trends in return rates did not support the hypothesis. All (i.e., male, female, and juvenile) coastal return rates were either similar to or lower than inland return rates. Of all males banded in the inland population in 2004, 55% returned in 2005 (21 of 38 banded birds); in comparison, the 3-year average in the coastal population was 50% (2002–2003, 52% of 23 banded males; 2003–2004, 38% of 77 males; 2004–2005, 60% of 57 males). Between 2004 and 2005, 39% of females returned in the inland population (11 of 28 banded birds), which was a higher rate than that observed in any of the 3 study years for the coastal population (2002–2003, 15% of 13 females; 2003–2004, 16% of 45 females; 2005–2006, 30% of 20 females). Likewise, juvenile return was higher inland in 2005 (eight returned as adults, 7% of 141 nestlings banded) than for any year for the coastal population (2002–2003, 0% of 35 nestlings; 2003–2004, 0.7% of 150 nestlings; 2005–2006, 4% of 125 nestlings).

The predator model experiment also did not support the survivorship hypothesis (but it did support the predation hypothesis, see above). The best model of feeding rates in the presence of a model predator ($n = 48$, $r^2 = 0.61$, $f_{9,38} = 6.7$, $P < 0.0001$; Fig. 6) included baseline provisioning rate ($f = 4.1$, $P = 0.05$), Julian date ($f = 9.4$, $P = 0.004$), time of day ($f = 2.7$, $P = 0.08$), and the interaction between model type and subspecies ($f = 9.5$, $P < 0.0001$). All adults responded stronger to either predator mount than they did to the milk-jug controls ($n = 48$, $df = 1$, $f = 40.8$, $P < 0.0001$). Contrary to the survivorship hypothesis (S3), however, coastal birds did not wait longer ($t_{38} = 0.3$, $P = 0.75$) to feed in the presence of a predator of adults (45.0 ± 6.8 min) than did inland adults (42.1 ± 5.1 min).
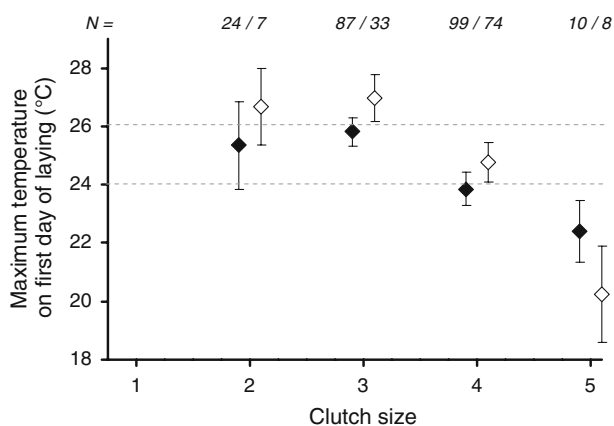
The temperature hypothesis

In concordance with the temperature hypothesis (T3), more coastal nests (75.6%) than inland nests (40.2%) experienced temperatures above the range of physiological zero reported by Webb (1987) during laying ($n = 413$, Wald $\chi_1^2 = 44.4$, $P < 0.001$). This is a direct result of the significantly higher mean daily high temperatures during the breeding season ($n = 1102$, $r^2 = 0.13$, $f_{5,1096} = 32.8$, $P < 0.0001$) in coastal Delaware (26.0 ± 0.2°C) than in

inland Maryland ($21.4 \pm 0.3°C$), controlling for year ($f = 10.7$, $P < 0.001$).

Further supporting the temperature hypothesis (T2), subspecies was a significant predictor ($f_{1,228} = 5.1$, $P = 0.02$) of the percentage of viable eggs within clutches ($n = 265$, $f_{5,228} = 2.9$, $P = 0.01$), controlling for year ($f_{4,228} = 2.2$, $P = 0.07$). The coastal population had lower egg viability overall ($84.6 \pm 1.5\%$ of eggs hatch) than the cooler inland population ($90.1 \pm 1.9\%$ of eggs hatch).
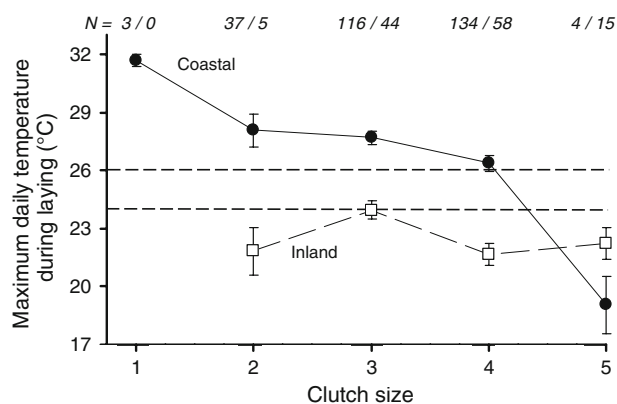
Controlling for clutch size ($\chi^2_1 = 13.9$, $P = 0.0002$), the best model predicting whether or not nests with a similar egg number possessed inviable eggs ($n = 266$, Wald $\chi^2_{8,303} = 26.9$, $P = 0.0004$) included the effects of subspecies ($\chi^2_1 = 4.7$, $P = 0.03$), year ($\chi^2_3 = 8.7$, $P = 0.03$), Julian date ($\chi^2_1 = 3.4$, $P = 0.06$), the presence of suboptimal temperatures on the first day of incubation ($\chi^2_1 = 9.3$, $P = 0.002$), and the mean high daily temperatures across the laying period ($\chi^2_1 = 6.6$, $P = 0.01$). Suboptimal temperatures on the first day of laying (Fig. 7) and higher temperatures throughout the laying period increased the probability that at least one egg in the clutch was inviable (T1). The addition of the presence of suboptimal temperatures on the last day of laying ($\chi^2_1 = 0.03$, $P = 0.87$) or the number of days of suboptimal temperatures during the entire laying period ($\chi^2_1 = 0.5$, $P = 0.46$) did not improve the model. These results support the proposal that first laid eggs are most at risk of improper development due to suboptimal temperatures.

Clutch size was affected by ambient temperature during laying in a manner consistent with the temperature hypothesis (T4). The best model for clutch size ($n = 247$, $r^2 = 0.34$, $f_{7,508} = 28.0$, $P < 0.001$) included Julian date ($f_1 = 146.7$, $P < 0.001$) and year within site ($f_4 = 2.9$, $P = 0.02$). When we controlled for these effects, there was a significant interaction between subspecies and the mean temperature during laying ($f_2 = 5.5$, $P = 0.005$), such that the temperature was negatively related to clutch size among coastal territories but unrelated among inland ones. The effect of nesting attempt number (i.e., the first to fifth nest of a given female), which is well known to correlate with clutch size, was not significant when added to this final model ($f_1 = 0.7$, $P = 0.42$). The mean high temperatures during the laying period of inland nests fell below the range of physiological zero for egg development outlined by Webb (1987), while the mean temperatures during laying among coastal nests fell above this range in all but the largest clutches (Fig. 8).

The best model ($n = 191$, $f_{10,507} = 6.4$, $P < 0.0001$) explaining the number of days between the first piped egg and the fully hatched brood (a measure of hatching asynchrony) included year ($f_3 = 2.6$, $P = 0.06$), Julian date ($f_1 = 3.2$, $P = 0.08$), brood size ($f_4 = 5.9$, $P = 0.001$), subspecies ($f_1 = 8.3$, $P = 0.005$), and the mean daily high temperatures during laying ($f_1 = 15.2$, $P = 0.0003$). Contrary to what we expected if coastal females began incubation early to escape suboptimal laying temperatures (T5), hatching asynchrony was lower overall (Fig. 9) among eggs laid in coastal territories (1.4 ± 0.06 days until hatch completion) than in those laid inland (1.7 ± 0.07 days until hatch completion). However, asynchrony was positively related to mean temperature during

Fig. 7 The maximum ambient temperature on the first day of laying (mean ± SE) for broods of *Melospiza georgiana* where all eggs successfully hatched (*filled diamonds*) or where one or more eggs were inviable (*open diamonds*), calculated for clutch size. The *dashed lines* indicate the temperature range of the lower limit for embryonic development outlined by Webb (1987). Values are least squares means controlling for Julian date and the mean daily maximum temperatures for the entire laying period. Data points are *offset* for visibility. *Italicized values above* the panel indicate sample size (no inviable eggs/inviable eggs) for each point. Data for a clutch size of one are not shown as we could not differentiate between inviable and abandoned eggs

Fig. 8 The relationship between the daily maximum ambient temperature during laying (mean ± SE) and clutch size in coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*), controlling for Julian date and year. The *dashed lines* indicate the range of the lower limit for embryonic development outlined by Webb (1987). *Italicized values above* the panel indicate sample size (coastal/inland) for each point
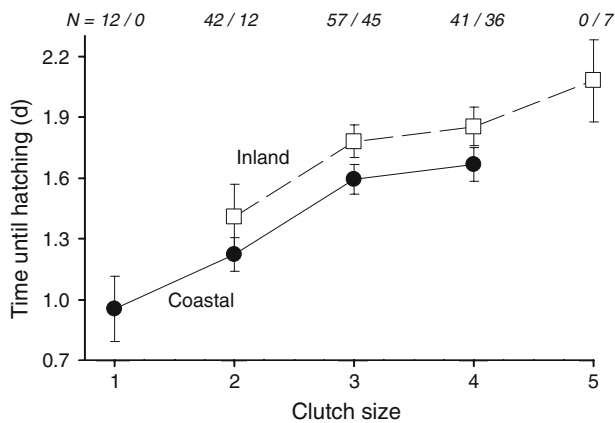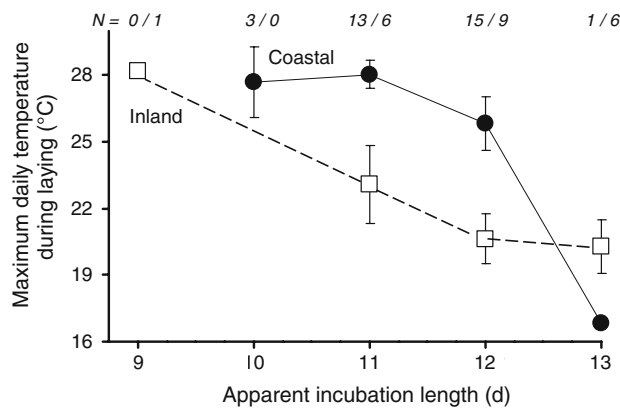
Fig. 9 The number of days taken to hatch (mean ± SE) as a function of brood size among coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*), controlling for mean high ambient temperatures during the laying period, Julian date, and year. *Italicized values above* the panel indicate sample size (coastal/inland) for each point
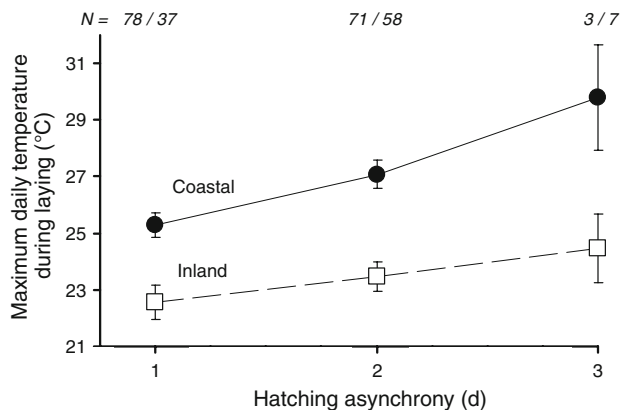
Fig. 10 Hatching asynchrony (the number of days taken to complete hatch) relative to the daily maximum ambient temperature during laying (mean ± SE) experienced by coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*), controlling for brood size, Julian date, and year. *Italicized values above* the panel indicate sample size (coastal/inland) for each point

laying within each subspecies (T7). This relationship is more easily visualized if the mean temperature during laying is depicted by subspecies for all nests that share the same hatching duration, controlling for brood size, year, and Julian date (Fig. 10).

Consistent with the temperature hypothesis (T8), mean ambient temperature during laying was the best predictor of apparent incubation length ($n = 54$, $f_{1,45} = 4.9$, $P = 0.03$), with the full model ($n = 54$, $r^2 = 0.44$, $f_{12,41} = 2.7$, $P = 0.008$) controlling for clutch size ($f_{6,41} = 2.3$, $P = 0.06$) and year within site ($f_{5,41} = 2.6$, $P = 0.04$). Adding the Julian data of the start of incubation did not improve the model ($\Delta AIC = 7.1$) and Julian date was not a significant factor ($f_{1,40} = 0.5$, $P = 0.48$).

Fig. 11 Daily maximum air temperature during laying (mean ± SE) calculated for each apparent incubation length (days from last laid egg to first hatched chick) for coastal *Melospiza georgiana nigrescens* (*filled circles*) and inland *M. g. georgiana* (*open squares*) controlling for year. *Italicized values above* the panel indicate sample size (coastal/inland) for each point. No *M. g. georgiana* broods took 10 days to hatch and no *M. g. nigrescens* broods took 9 days to hatch

Contrary to our prediction (T6), however, there was no difference between coastal and inland birds; subspecies was not significant when added to the full model ($n = 54$, $F_{1,41} = 0.1$, $P = 0.75$). These results are easily visualized if the mean laying temperatures are plotted for all nests of each apparent incubation length within each subspecies (Fig. 11).

Discussion

No support for survivorship

Our results do not support the survivorship hypothesis. Adults of the coastal subspecies, with their smaller clutches, did not exhibit the behavioral signs of a more iteroparous life history between years. That provisioning behavior in the presence of an adult predator did not differ between the subspecies suggests that—on the scale of the breeding season—both populations possess similar trade-offs between current and future reproduction (Ghalambor and Martin 2001). More importantly, coastal females actually laid more eggs than inland females over the length of the season and thus expended more energy than inland females each breeding season, despite their smaller investment in each nesting attempt.

Our limited data on return rates also do not support the survivorship hypothesis. The observed lower return rates of coastal juveniles and females are inconclusive because they might be due to differences in dispersal rather than survival. Delaware Bay is lined with contiguous, suitable habitat for miles (Beadell et al. 2003), whereas the wetlands on the Allegheny Plateau occur as small, disjunct

pockets of marsh and swamp with miles of unsuitable habitat in between (Fenwick and Boone 1984). Under these circumstances it is likely that dispersal is easier between coastal habitats. In addition, females in many bird species are more likely to disperse following a failed nesting attempt (Gowaty and Plissner 1997; Greenwood and Harvey 1982; Haas 1998; Powell and Frasch 2000; Winkler et al. 2004), and nest failure rates are higher in the coastal population. However, breeding males are likely much more site-faithful, and the fact that our data do not indicate higher return rates among coastal males suggests that survival rates are not substantially higher on the coast than inland.

A strong case for predation

Predation had consistent support as an explanation of low clutch sizes in the tidal salt marsh. Coastal territories experienced a much higher predation risk, and coastal females had a greater cumulative seasonal investment in eggs. This investment pattern follows a within-season, bet-hedging strategy—as expected under conditions defined by a high probability of failure (Eggers et al. 2006; Slagsvold 1984).

Coastal individuals also exhibited numerous behavioral adaptations to increased predation risk. For all clutch sizes, coastal sparrows had lower rates of movement in the vicinity of nests in all development stages (Figs. 2, 4), and females vocalized less frequently during the incubation period (Fig. 3). Both of these adaptations likely limit nest detection by predators (Ghalambor and Martin 2000; Skutch 1949). Within both populations, larger broods required more visitations (Fig. 4). A lower clutch size thus nets coastal individuals an additional decrease in activity near the nest during provisioning.

Aside from these clutch-size dependent and independent decreases in nest-related activity, coastal parents exhibited more plastic behavioral reaction norms. After we controlled for baseline provisioning rates (clutch-size-independent decreases in behavior) and brood size (clutch-size-dependent decreases in behavior), coastal adults still responded more strongly to a nest predator model than inland pairs. These plastic responses during periods of acute predation risk have been noted in other bird species (Eggers et al. 2005) and are likely to be less costly in terms of nestling growth and condition if clutch size is low. Indeed, nestlings in larger coastal broods exhibited the highest begging intensities of any nestling of either subspecies (Fig. 5). This result suggests that coastal parents may be limited in their ability to increase clutch size and still satiate offspring at the same level accomplished by inland parents because of a tradeoff between provisioning rate and predation risk. Only one prediction of the

predation hypothesis was not upheld—that predation risk would be higher in the nestling stage. Poorly placed nests, however, are predated quickly, elevating predation rates in the incubation stage. Thus, this effect may balance any effect of parental activity at the nestling stage.

North American tidal marsh sparrows as a group (including three *Ammodramus*, two *Melospiza*, and a single *Passerculus* species) experience high rates of nest loss from predation relative to their closest inland relatives. Variation in clutch size among populations of these species is strongly predicted by predation rates (Greenberg et al. 2006). Both bet-hedging and nest detection tradeoffs thus may account for the ecosystem-wide pattern.

The case for temperature

Our results provide some support for temperature as a cause of the clutch size difference between the subspecies. Coastal nests frequently experienced suboptimal temperatures during egg-laying, and both subspecies exhibited sensitivity to ambient temperature. Clutches were more likely to possess inviable eggs if they experienced suboptimal temperatures on the first day of laying and high mean temperatures throughout the laying cycle. Although we did not mark eggs to determine laying order, the importance of temperature on the first day of laying and not the last day of laying suggests that it is exposure to ambient temperature that leads to inviability. If this were true, however, we would expect this effect would be the strongest in the largest clutches where exposure is greater; however, the opposite was true (Fig. 7).

Among coastal territories, mean daily high ambient air temperatures during laying correlated with smaller clutches (Fig. 8). This effect was not seen among inland nests, where laying temperatures were typically below physiological zero. Under suboptimal thermal conditions coastal females were able to decrease their exposure by beginning incubation earlier, which can either (1) inhibit further egg laying, thereby decreasing clutch size, or (2) result in a greater degree of hatching asynchrony and a decrease in apparent incubation length. Clutch sizes are of course smaller in the coastal population, but both subspecies showed an increase in hatching asynchrony and a decrease in apparent incubation length under high temperature conditions, thereby providing support for the occurrence of the second effect as well. Decreased apparent incubation lengths could also result from a lower cooling rate of eggs and thus faster development in higher temperature conditions (Magrath et al. 2000; O'Connor 1984; Skutch 1976). The presence of increased hatching asynchrony as well under these conditions argues against this as the only cause. Furthermore, the subspecies-specific reaction norms were shifted in the coastal population, such that asynchrony

among coastal broods was lower than that in inland broods of each clutch size (Fig. 9), despite the greater temperatures coastal nests experienced (Fig. 10). This suggests an additional adaptation to predation, as coastal pairs would benefit by decreasing the time offspring spend in the nest, and might involve changes in nestling growth patterns or female incubation patterns (coastal nestlings did have faster growth rates after hatching). The evolution of a new reaction norm also explains why the coastal population does not exhibit a shorter apparent incubation length and larger hatching asynchrony on average despite the higher incidence of suboptimal temperatures (T5 and T6). Overall, therefore, females both decreased clutch sizes under suboptimal temperature conditions and began incubation earlier to limit the exposure of clutches to developmental abnormalities.

Previous investigations of the effect of temperature on clutch size have been conducted on cavity-nesting birds (Cooper et al. 2005, 2006; Stoleson and Beissinger 1999). Since cavities can buffer environmental conditions, it is reasonable to presume that open-cup nesters, like swamp sparrows, would be more affected by ambient air temperatures. Air temperatures during laying remain a strong, relatively untested, hypothesis of clutch size variation, and the concept deserves further investigation with this and other non-cavity-nesting species. In order to establish a more convincing case for temperature effects on clutch sizes of coastal plain swamp sparrows, it will be necessary to confirm that it is indeed the first laid eggs that are inviable under high temperature conditions as well as to measure temperatures at individual nests whose fates are tracked rather than relate regional temperature patterns to nest success patterns as we have done.

Other possibilities: food limitation

A fourth hypothesis explaining clutch size variation that was not tested explicitly in this study is Lack's (1948) classic explanation invoking food limitation. At a cursory level, it does not appear that food limitation can explain the difference in clutch size between the environments, as starvation of nestlings was equally rare in both populations. Of 507 nests over four seasons in the coastal population, we witnessed 21 nests (4.1%) with dead nestlings that did not appear to be injured or did not perish during a known high water event. Of the 149 inland nests, six (4.0%) were found over two seasons that possessed dead chicks under similar circumstances. Partial brood loss was also the same between the sites (t test $n = 166$, $t_{161} = -0.7$, $P = 0.47$) with 95 and 97% of hatched chicks surviving until fledging in successful coastal and inland nests, respectively.

Although longer begging by coastal nestlings could indicate reduced food availability in the coastal population,

the increased hunger response may instead be caused by an increase in the variance of hunger due to decreased nest attendance. The equal pre-fledging size of young and faster growth rates in the coastal population support this idea and suggest that coastal adults may be partitioning their feeding behavior towards times that present less risk for detection by predators (Eggers et al. 2005). Coupled with the fact that provisioning trips per offspring were less frequent among coastal broods, these observations suggest that coastal parents are provisioning young with either higher quality food or more food during each provisioning trip than inland adults are. Arguing for quality over quantity, coastal adults typically bring single items to the nest, while we have often witnessed inland sparrows bring multiple items to the nest in a single trip (personal observation). A decrease in clutch size due to food limitation, however, may alleviate many symptoms of the root cause. Experimental manipulation of clutch size is necessary to fully eliminate or accept food limitation as an additional cause.

Conclusions

The difference in clutch size between coastal (*M. g. nigrescens*) and inland (*M. g. georgiana*) swamp sparrows was consistent with both the predation and temperature hypotheses of life history variation, but we found no support for the survivorship hypothesis. Survivorship has been posited as a higher order determinant of clutch size in birds, explaining gross patterns among latitudes (Martin 2002). Within latitudes, however, where survival probabilities may be more similar, predation has been found to predict clutch size more closely (Martin 1995; Martin et al. 2000). Under similar higher order survival constraints, temperature and predation should interact to select for specific parental life histories and behavioral tactics. In this system, we found that adaptations for high nest predation shape the solution to suboptimal laying temperatures (reduced clutch size instead of increased hatching asynchrony).

Clutch size is an adaptable life history trait that reflects tradeoffs by individuals in a number of areas. To understand which factors play the greatest role in specific circumstances, it is necessary to compare closely related species or populations under a variety of selection regimes. The clutch size of tidal salt marsh endemics is an ideal candidate for life history convergence due to environmental constraints. For one species pair, we found that two environmental variables, predation risk and ambient temperature, explained clutch size. This supports the reported correlation between predation risk and clutch size found across populations of all the North American tidal sparrows (Greenberg et al. 2006) and may represent an explanation for the convergence in clutch size within this group.

Further study should address whether temperature can explain the divergence among other tidal marsh endemics and within additional ecosystems.

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