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RELATIVE CONSISTENCY IN SIZE, SHAPE, AND COLORATION OF SAVANNAH SPARROW EGGS WITHIN AND BETWEEN BREEDING SEASONS

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Abstract. Within bird populations, eggs vary extensively in size, shape, and color, but individual females tend to lay eggs that are relatively consistent in most traits. We measured all eggs laid by individual female Savannah Sparrows (*Passerculus sandwichensis*) breeding on Kent Island, New Brunswick, comparing subsequent clutches within the same year and in successive years. Repeatability was high for egg size and shape (0.78 and 0.72, respectively). Conversely, the repeatability of intensity of spotting was only moderate (0.46), and the background color of eggs varied from clutch to clutch and even within a clutch. Egg size increased slightly within a year from a female's first to subsequent clutch, but egg size was independent of the female's body size, the age or size of her mate, or weather conditions during clutch formation. Ranking of individual females' eggs by size and shape remained almost the same from clutch to clutch. Although laying eggs that are relatively consistent and individually distinctive in size, shape, and spotting could be an adaptation to allow females to discriminate their own eggs from those of brood parasites, this explanation does not apply on Kent Island, where neither intra- nor interspecific brood parasitism occurs. We found no evidence of short-term effects of egg size on the size of 7-day-old nestlings or of long-term effects on adults' survival or lifetime reproductive success. High repeatabilities suggest a substantial genetic component to variation in certain egg traits, which could limit females' ability to modify their eggs in response to environmental changes.

Key words: allometry, heritability, *Passerculus sandwichensis*, repeatability.

Consistencia Relativa en Tamaño, Forma y Coloración de los Huevos de *Passerculus sandwichensis* dentro y entre Estaciones Reproductivas

Resumen. Dentro de las poblaciones de aves, los huevos varían enormemente en cuanto a tamaño, forma y color, pero las hembras individualmente tienden a poner huevos relativamente consistentes entre sí para la mayoría de los rasgos. Medimos todos los huevos puestos por hembras individuales de *Passerculus sandwichensis* que anidan en la Isla Kent, New Brunswick. Comparamos las nidadas subsecuentes dentro del mismo año y entre años sucesivos. El tamaño y la forma del huevo presentó una alta repetibilidad (0.78 y 0.72, respectivamente). De modo contrario, la intensidad del manchado presentó una repetibilidad moderada (0.46) y el color de fondo de los huevos varió de una nidada a otra e incluso dentro de una nidada. El tamaño del huevo aumentó ligeramente dentro de un año desde la primera nidada de una hembra hacia las nidadas subsecuentes, pero el tamaño del huevo fue independiente del tamaño corporal de la hembra, de la edad y del tamaño de su pareja o de las condiciones meteorológicas durante la formación de la nidada. El ordenamiento de los huevos de las hembras individuales por tamaño y forma permaneció casi invariable de una nidada a otra. Aunque la puesta de huevos que son relativamente consistentes e individualmente distintivos en cuanto a tamaño, forma y manchado podría ser una adaptación que permita a las hembras discriminar sus propios huevos de los de las aves parásitas, esta explicación no es válida para la Isla Kent, donde no existe parasitismo ni intra- ni inter-específico. No encontramos evidencia de efectos de corto plazo del tamaño del huevo en el tamaño del pichón de siete días de vida o efectos de largo plazo en la supervivencia del adulto o en el éxito reproductivo de toda la vida. La alta repetibilidad sugiere que existe un componente genético importante de la variación en ciertos rasgos de los huevos, lo que puede limitar la capacidad de las hembras de modificar sus huevos en respuesta a los cambios ambientales.

INTRODUCTION

Within a bird species, eggs can vary extensively in size (Christians 2002). Larger eggs tend to lead to greater hatching success, offspring size, immunocompetence, and juvenile growth rate, and possibly long-term survival and fecundity (Williams 1994, Krist 2011). Several hypotheses have been put forth to explain the extent, causes, and consequences of egg-size variation within and between clutches laid by the same female. Egg-size variation may be adaptive, arising when females benefit by modifying the sex ratio of offspring and when egg size is sex-specific (Magrath et al. 2003), or

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when brood reduction is advantageous and is facilitated by laying eggs of different sizes (Slagsvold et al. 1984). Alternatively, variation may be nonadaptive and simply reflect proximate factors such as weather or food availability during egg laying (Saino et al. 2004, Ardia et al. 2006, Whittingham et al. 2007). Costs of reproduction, developmental history, and aging may also explain variation in egg size within and between females (Wheelwright and Schultz 1994, Potti 1999, Beamonte-Barrientos et al. 2010, Robinson et al. 2010).

In addition to size, shape and color are two other egg traits whose variation is likely to influence fitness and be shaped by phylogeny, the female's condition, diet, and other constraints (Arendt 2004, Kilner 2006, Avilés et al. 2007, Cassey et al. 2010, Lopez de Hierro and De Neve 2010). Studying variation in egg traits can yield insights about the genetic basis of phenotypic variation and the likelihood of evolutionary responses to changed environmental conditions. A key question is the degree to which females are flexible in terms of different egg traits. Compared to other traits, egg size tends to vary less within a female, and repeatability and heritability are high in most species studied (Christians 2002). In contrast, variation in egg color is often greater with a larger environmental component (García-Nava et al. 2011, Riehl 2011).

In this study, we used data collected in multiple years over a two-decade period from an isolated population of Savannah Sparrows to examine phenotypic plasticity in egg size, shape, and color across different time scales and over a range of environmental conditions. We predicted that egg size would be positively correlated with female body size, condition, and age, and negatively correlated with clutch size. We also predicted that egg size would decline in successive clutches if egg size is affected by previous reproductive expenditures. Alternatively, if egg size, shape, and coloration are mainly inflexible and determined by genetic differences between females or by permanent environmental effects, they should vary little with respect to clutch size or female size, condition, age, or previous reproductive effort. Because cloacal diameter ultimately limits egg size, we expected a negative allometric relationship between egg breadth and length (i.e., large eggs should be disproportionately elongated) (Mazer and Wheelwright 1993). Although egg color is likely to be under very different controls than are size or shape, we predicted that coloration would differ as a function of habitat and season, assuming that spatial and temporal variation in prey availability could affect females' diets and the pigments incorporated into eggshells. Finally, assuming that the effectiveness of cryptic coloration depends upon light conditions, we expected differences in egg coloration between nests that were open or covered (García-Nava et al. 2011).

METHODS

STUDY SITE AND SPECIES

Since 1987 we have studied Savannah Sparrows breeding on Kent Island, an 80-ha island in the Bay of Fundy, New Brunswick, Canada (44° 35′ N, 66° 46′ W). The study site consists of three fields totaling 10 ha in area, within which all adults are uniquely color-banded, all nests are located, and all nestlings are banded. Savannah Sparrows breeding on Kent Island spend the winter in the mid- and southern United States. Several weeks after their return, females lay clutches of 3–5 eggs in cryptic open-cupped or grass-covered nests on the ground in open habitats. If the first brood successfully fledges, most females lay a second clutch 1–2 weeks later. If the first clutch is preyed upon, females start laying replacement clutches within 1–5 days; replacement clutches that are destroyed may also be replaced. Because almost all females lay more than one clutch per season, we were able to compare egg traits in subsequent clutches within a year. In this population, natal and breeding philopatry are much higher than in most migratory passerines, with about 11% of nestlings and 50% of adults returning the following year to breed on the island (Wheelwright and Mauck 1998), so we could also compare traits between years and generations. Neither intraspecific nor interspecific brood parasitism have been observed in this population (Freeman-Gallant et al. 2005), which allowed us to assign eggs to incubating females with confidence. For more detailed descriptions of the study species, field methods, and study site, see Wheelwright and Mauck (1998) and Wheelwright and Rising (2008).

EGG MEASUREMENTS

In 1989, we used an electronic balance and dial calipers to measure the mass (to 0.1 g) and maximum length and breadth (to 0.1 mm) of eggs from 60 clutches laid by 39 different females (Wheelwright and Schultz 1994). Five clutches from two additional females were measured in 1992–94. Eggs were measured within several days after clutches were complete. In 2009 and 2010, to minimize handling and risk of breakage as well as to quantify coloration, we photographed eggs early in incubation and measured images digitally (to 0.01 mm) in Adobe Photoshop CS5. Eggs were placed flat on a tray next to a ruler and neutral-density gray card, and photographed with a Canon digital SLR and flash from directly above within a closed box (to ensure consistent light conditions) with the long axis of each egg perpendicular to the plane of the photograph. Shutter speed, aperture, ISO, flash output, and camera distance from the eggs were kept constant between images. Using digital photography and interpreting JPEG files to analyze color can introduce biases (Dale 2000, Stevens et al. 2007, Stoddard and Stevens 2010). We minimized such problems by capturing images in RAW format, where proper white balance was calibrated from the neutral-density gray card and color measurements were taken. Because entire clutches were photographed together, color variation between eggs from the same clutch is unlikely to have been affected by some of the other issues raised by Stevens et al. (2007) (e.g., corrected color curves). Images were later converted to JPEG for measurements of size and shape.

The 2009–10 sample included 70 clutches laid by 46 different females, including four mother–daughter pairs. Combining all years, we measured two or more successive clutches from the same breeding season for 45 females, and we measured eggs of eight females in two different years. To estimate egg volume, we used the formula $\text{volume}_{\text{est}} = 0.51 \text{ length} \times \text{breadth}^2$ (Hoyt 1979, Coe and Rotenberry 2003), which was strongly correlated with mass in the 1989 sample (mass = 0.98 volume + 0.5; $r^2 = 0.70$, $n = 280$, $P < 0.0001$). We calculated various measures of egg shape; here we present data on breadth:length ratios.

Savannah Sparrow eggs vary in background eggshell color and dark spotting (maculation). We assigned each egg visually to one of four categories of background color (light brown, brownish-blue, bluish-white, blue; mean corresponding red/green/blue channels were quantified in Adobe Photoshop: see Table 1). We ranked intensity of spotting visually on a scale of 1 to 5, with 5 being most heavily spotted (Lopez de Hierro and De Neve 2010). We also measured two other aspects of spotting, mean spot size (diameter <2 mm, 2–4 mm, >4 mm) and uniformity of spotting (spots concentrated on the blunt end of the egg vs. evenly distributed, on a scale of 1 to 5). Results for spot size and uniformity were similar to those for spotting intensity so we describe only the latter in this paper. Visual assignments of color patterns were done by a single individual (ESG) without reference to the identity of each egg; repeated measurements of the same eggs yielded identical values. Some of the variation in egg size, shape, and color was likely to have been due to factors such as the order in which they were laid or offspring sex (Slagsvold et al. 1984, Styrsky et al. 2002, Bowers et al. 2011). However, because finding Savannah Sparrow nests before the clutch is complete is difficult and can provoke nest desertion, we were unable to test for laying-order effects. Likewise, because of the risks of brood abandonment we did not attempt to monitor hatching closely enough to associate individual nestlings with the eggs from which they hatched. Instead, we indirectly assessed how egg size affects subsequent survival and body size by testing for associations between mean egg volume within a clutch and the mean size of fledglings and recruits, as well as the longevity and lifetime reproductive success of recruits (Krist 2011).

STATISTICAL ANALYSES

To identify the factors affecting egg size, shape, and spotting, we used univariate tests (paired *t*-tests, ANOVA, linear regressions) and linear mixed models, applying standard model-selection procedures based on AIC*c* values (Demidenko 2004). To avoid pseudoreplication due to the inclusion of an average of 6.6 eggs per female, we treated the female's identity as a random effect. Fixed effects included clutch size (1–5 eggs), the female's age and the age of her mate (1–6 years), Julian date of laying of the first egg within a clutch, nest type (open cup vs. grass-covered), weather conditions preceding egg laying (mean temperature, total precipitation, and mean wind speed 5–10 days and 0–5 days before the first egg was laid), and several measures of body size and condition of females and males (tarsus length, wing length, bill length, bill depth; mass was used for males but not females because during the breeding season a female's mass can vary from 16 to 24 g, depending upon the stage of egg laying and time of day). We also included clutch number (first vs. subsequent clutch) as well as a more fine-grained measure of clutch number (first, replacement of the first, replacement of the replacement of the first, or second clutch). Repeatability, the proportion of phenotypic variance caused by genetic and permanent non-genetic differences among individuals (Falconer and Mackay 1996), was calculated according to Lessells and Boag (1987). We give descriptive statistics (mean ± 1 SD [± 1 SE for slopes and repeatability estimates]) for the 1989 and 2009–10 samples separately because of different methods of measurement.

TABLE 1. Mean values for color components for visually assigned categories of background colors of Savannah Sparrow eggs. Measurements were done on images captured in RAW format, where proper white balance was calibrated from the neutral-density gray card in Adobe Photoshop CS5 ($n = 5$ eggs per category). ANOVAs and Tukey's multiple-comparison tests showed that each category differed significantly from all others in one or more luminosity channels as well as in hue, saturation, or brightness.

	Background color category			
	Blue	Bluish-white	Brownish-blue	Light brown
Red channel	193.6	207.0	182.8	196.2
Green channel	183.4	195.4	163.0	174.8
Blue channel	165.0	181.8	143.4	153.6
Hue	39.0	32.4	30.0	30.0
Saturation	14.8	12.0	21.4	21.8
Brightness	75.6	82.0	71.6	77.0

P values are two-tailed. All statistical analyses were run in PASW Statistics 18.0.

RESULTS

EGG SIZE

Eggs showed extensive size variation within the population. In terms of volume, the largest egg in the population was 1.74 times the smallest, and the coefficient of variation (SD/mean × 100) was 10.1% ($n = 297$). Within a clutch, however, females tended to be consistent in the size of eggs they laid: 95.3% of the population variation in egg volume occurred among clutches (ANOVA: $F_{34,109} = 19.07$, $P < 0.0001$). On average, the largest egg laid by a female was 1.13 times as big as her smallest ($n = 39$ females). Between subsequent clutches laid during the same breeding season, the mean volume of a female's eggs was strongly correlated, regardless of her age or clutch number (Fig. 1A, 2A; linear regression slopes: 1989: 1.07 ± 0.16; $r^2 = 0.70$, $P < 0.0001$; 2009-10: 1.02 ± 0.11; $r^2 = 0.81$, $P < 0.0001$). Between years, the mean volume of a female's eggs was also highly consistent (Fig. 3A; linear regression slope = 0.98 ± 0.18; $r^2 = 0.84$, $P = 0.001$; paired *t*-test: $t_7 = 1.38$, $P = 0.21$). Repeatability of egg volume was 0.78 ± 0.04. (Egg length and breadth, which we used to estimate volume, had repeatabilities of 0.79 ± 0.04 and 0.74 ± 0.05, respectively.)

No measure of female body size or condition (mass divided by tarsus or wing length), alone or in combination with other factors, had a significant effect on egg volume in univariate tests or increased absolute AIC*c* in mixed-model analyses. The same was true for the size, condition, and age of a female's social mate, and for all weather variables. Once clutch number (first vs. replacement or second) was incorporated into the model, date of laying and clutch size had no effect.

Based on AIC_c, the mixed models that most powerfully explained variation in egg volume included the random effect of female but only clutch number (first vs. subsequent) in 1989, and only female age and/or clutch number in 2009–10. Akaike weights, w_i, which estimate the probability in favor of a given model from the set of models considered, were 0.99 for the best model in 1989 and 0.68 for the best model in 2009–10 (w_i for the next best model for 2009–10 = 0.18; see Tables 2 and 3). Eggs of first clutches were slightly smaller than eggs of subsequent clutches within the same year (paired *t*-tests: 1989: $t_{21} = 3.76$, $P = 0.001$; 2009–10: $t_{22} = 2.28$, $P = 0.03$). The 2% difference in egg volume between first and subsequent clutches was virtually identical in all years of the study, despite different measurement techniques (Figs. 1, 2; 1989: first: 2.10 ± 0.15 cm^3, $n = 138$; subsequent: 2.14 ± 0.17 cm^3, $n = 143$; 2009–10: first: 2.10 ± 0.21 cm^3, $n = 144$; subsequent: 2.14 ± 0.21 cm^3). The effect of the female's age in 2009–10 was mainly due to a decline in egg size in birds older than 2 years (especially the small sample of 5-year-olds). The mean volume of eggs was 2.13 ± 0.20 cm^3 ($n = 112$) for 1-year-olds, 2.18 ± 0. 20 cm^3 ($n = 138$) for 2-year-olds, and 1.93 ± 0.20 cm^3 ($n = 47$) for females 3 years old and older. Egg volume appeared to vary with clutch size (means for clutches with 1–5 eggs = 2.36, 2.12, 2.11, 2.14, and 1.99 cm^3, respectively). However, because clutch size was confounded with clutch number (replacement clutches have the most eggs, whereas second clutches and replacements of replacements have the fewest), the effect of clutch size on egg volume was not significant once clutch number was included in the model.

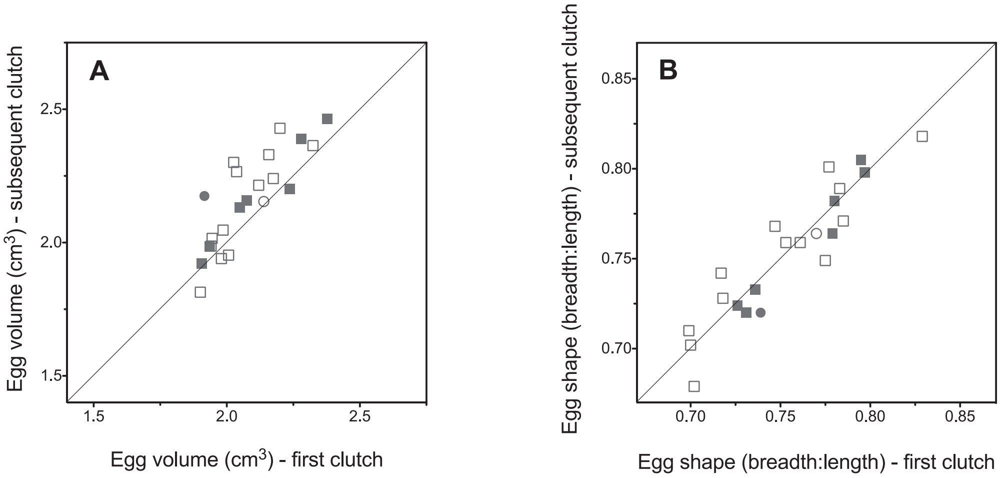

FIGURE 1. Consistency of relative egg size and shape between successive clutches within a single breeding season in 1989. (A) Mean egg volume (cm^3), (B) mean egg shape (breadth:length). Each point represents a pair of clutches laid by the same female in the same year ($n = 22$). Solid symbols = 1-year-old females, open symbols = older females, circles = successful first clutches followed by second clutches, squares = first clutches that were preyed upon followed by replacement clutches. Diagonal line designates 1:1 relationship between successive clutches. Linear regressions for size and shape (see text): $P < 0.0001$.

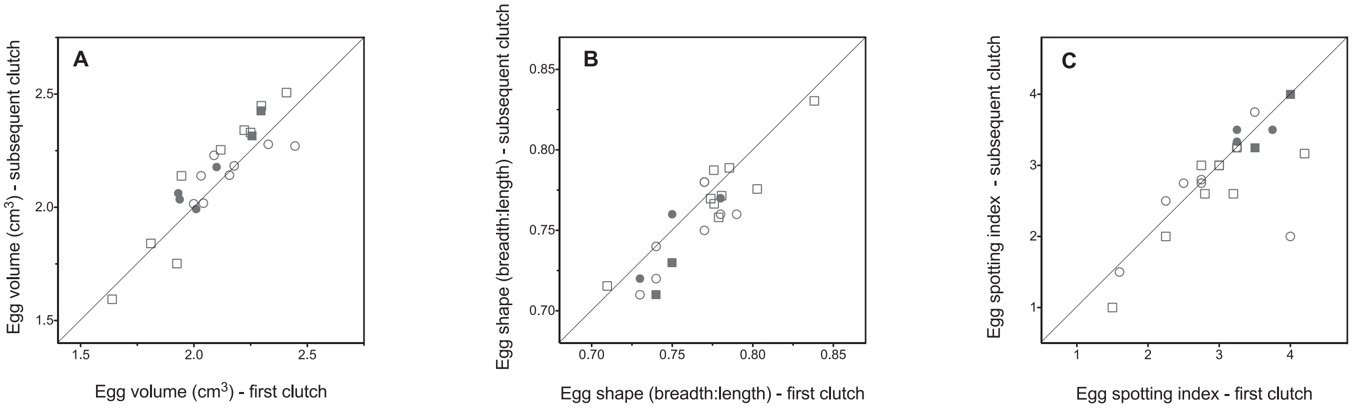

FIGURE 2. Consistency of relative egg size, shape, and spotting between successive clutches within a single breeding season in 2009. (A) Mean egg volume (cm^3), (B) mean egg shape (breadth:length), (C) mean spotting index. Each point represents a pair of clutches laid by the same female in the same year ($n = 23$). Symbols and lines as in Fig. 1. Linear regressions for size, shape, and spotting (see text): $P < 0.0001$.

LONG-TERM CONSEQUENCES OF EGG SIZE

As noted above, we did not mark individual eggs. To estimate the size of the egg from which a particular nestling hatched, we used the mean egg size of the clutch from which it hatched, using data from 1989. Given the high repeatability and low variance of egg traits within clutches, this provided a sense of the possible long-term consequences of variation in egg size on traits such as lifetime reproductive success. The nine nestlings that hatched in 1989 and survived to be recruited into the breeding population were no more likely to have come from clutches with large mean egg volumes than were nonsurvivors ($t_{14} = 0.87$, $P = 40$). Similarly, there was no correlation between the mean egg volume of a clutch and the mean (or maximum) size of fledglings from that nest ($n = 16$ broods that fledged young). Nor was there a correlation with any measure of adult body size or fitness for those fledglings from that nest that survived to reproduce (longevity, lifetime production of fledglings or recruits) (linear regressions: all $P > 0.5$).

EGG SHAPE

Eggs ranged in shape from nearly round (breadth:length = 0.89) to relatively elongated (0.64), with a coefficient of variation of 4.9% ($n = 297$). As with egg volume, the shape of a female's eggs tended to be relatively consistent between clutches (Figs. 1B, 2B; linear regression: 1989 slope = 0.95 ± 0.09; $r^2 = 0.85$, $P < 0.0001$; 2009–10 slope = 0.93 ± 0.11; $r^2 = 0.77$, $P < 0.0001$). Eggs from a female's first clutch were slightly rounder than eggs of subsequent clutches in the 2009–10 sample (paired t-test: $t_{22} = 2.90$, $P = 0.008$; Fig. 2B) but not in 1989 ($t_{21} = 0.21$, $P = 0.84$; Fig. 1B). Between years the shape of a female's eggs was strongly correlated (Fig. 3B; slope = 0.84 ± 0.21; $r^2 = 0.73$, $P = 0.007$), and there was no difference in mean shape (paired t-test: $t_7 = 1.30$, $P = 0.24$). Repeatability of egg shape was 0.72 ± 0.05.

In mixed-model analyses of the 1989 sample, egg shape appeared not to be influenced by the size of the female or her mate, or by the male's age, year, date of laying, clutch size, nest characteristics, clutch number, or weather. In the 2009–10 sample, the best model included only clutch number and the female's age.

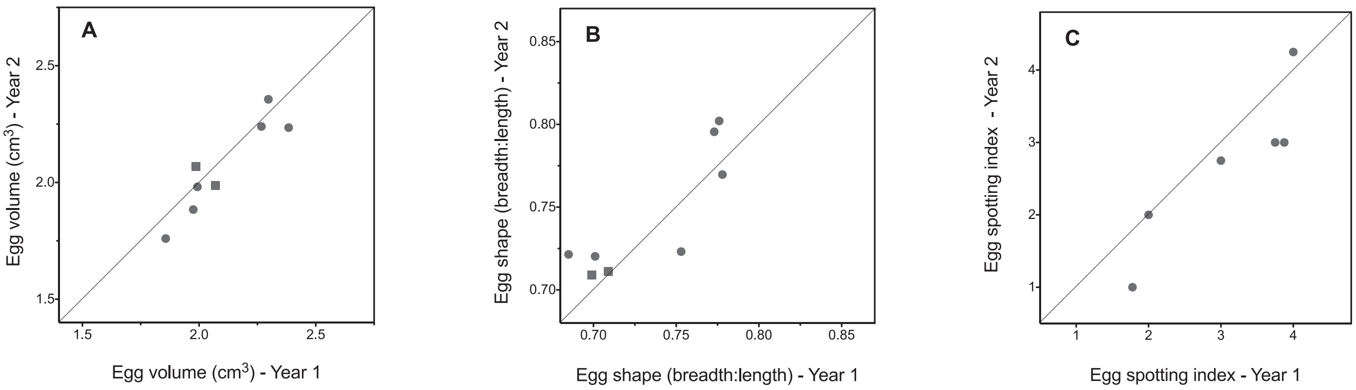

FIGURE 3. Consistency of egg size, shape, and spotting between years. (A) Mean egg volume (cm^3), (B) mean egg shape (breadth:length), (C) mean spotting index. Each point represents a pair of clutches laid by the same female in different years ($n = 8$). Circles = 2009–10 clutches; squares = 1992–94 clutches. Diagonal line designates 1:1 relationship between successive clutches. Linear regressions for size, shape, and spotting (see text): $P = 0.001$, 0.007, and 0.01, respectively.

TABLE 2. Akaike's information criterion (AIC_c) for competing linear mixed effects models to explain variation in volume of Savannah Sparrow eggs on Kent Island, New Brunswick. Eggs were measured by different methods in 1989 and 2009–10 (see text).

	1989		2009–10	
Model[a]	ΔAIC_c[b]	w_i[c]	ΔAIC_c	w_i
Clutch number, female age, female wing, male age, male wing	33.275	0.00	36.935	0.00
Clutch number, female age, female wing, male age	28.050	0.00	21.300	0.00
Clutch number, female age, female wing	21.930	0.00	16.146	0.00
Clutch number, female age	7.831	0.00	0.18	0.18
Clutch number	0[d]	0.99	4.276	0.08
Female age	40.638	0.00	0[e]	0.68
Female wing	29.124	0.00	9.853	0.00
Male age	39.028	0.00	6.197	0.03
Male wing	13.331	0.00	13.331	0.00

[a] All models also included the female's identity as a random effect.

[b] Difference for model relative to smallest AIC_c in the model set.

[c] Approximate probability in favor of the given model from the set of models considered.

[d] $AIC_c = -380.606$.

[e] $AIC_c = -339.968$.

TABLE 3. Akaike's information criterion (AIC_c) for competing linear mixed-effects models to explain variation in shape (breadth/length) of Savannah Sparrow eggs on Kent Island, New Brunswick, in 2009–10 (see Table 2). No variables, alone or in combination, had a significant effect on egg shape in the 1989 sample.

Model	ΔAIC_c	w_i
Clutch number, female age, female wing, male age, male wing	54.432	0.00
Clutch number, female age, female wing, male age	51.359	0.00
Clutch number, female age, female wing	27.489	0.00
Clutch number, female age	4.044	0.12
Clutch number	43.574	0.00
Female age	0[a]	0.88
Female wing	69.415	0.00
Male age	35.518	0.00
Male wing	54.477	0.00

[a] $AIC_c = -1019.543$.

Yearling females and 2-year-olds tended to lay relatively elongated eggs, whereas older females tended to lay rounder eggs.

Egg shape showed negative allometry, with large eggs being disproportionately elongated, as indicated by slopes of linear regressions of egg breadth on length being <1 (1989: 0.07 ± 0.03, $P = 0.03$; 2009–10: 0.22 ± 0.03, $P < 0.001$; Fig. 4). Regressions of log-transformed variables gave equivalent results.

EGG COLOR

As with egg size and shape, spotting intensity was relatively consistent between clutches within the same year (Fig. 2C; linear regression: slope = 0.78 ± 0.14; $r^2 = 0.58$, $P < 0.0001$; paired t-test: $t_{22} = 1.57$, $P = 0.13$) as well as between years (Fig. 3C; slope = 1.01 ± 0.24; $r^2 = 0.82$, $P = 0.01$; paired t-test: $t_5 = 2.10$, $P = 0.09$). Repeatability of egg spotting (0.46 ± 0.07) was substantially lower than repeatability of egg volume or shape. The best model to explain variation in egg spotting included only clutch number and nest type, but neither was significant.

About half (49%) of all eggs had a background color of brownish blue, about a quarter (29%) of bluish-white, about 10% of blue, and about 10% of light brown. In contrast to the high consistency of other egg traits, background color was surprisingly variable even within a clutch. In only 22% of clutches (10/46) did all eggs have the same background color. Between clutches, only about a third of females (7/23) were consistent in terms of the proportions of eggs of different background colors, whereas nearly half (10/23) laid clutches with background colors quite distinct from those of their first clutch. Within a clutch, however, eggs of different background color were similar in size and shape (ANOVA: $F_3 = 1.37$, $F_1 = 0.35$, respectively; $P > 0.25$). Spotting intensity was not associated with background color or nest type (ANOVA: $F_3 = 0.09$, $F_1 = 0.24$, $P > 0.62$). Although our three study sites differed in plant composition and microhabitat structure (factors that could affect crypsis of eggs of different colors) and predominant prey species (e.g., seaweed flies in territories close to the shore, lepidopteran larvae in spruce-enclosed fields, differences that could affect pigments incorporated into eggshells), frequencies of the four background colors were similar at all sites, and there were no differences in spotting intensity ($\chi^2_6 = 4.8$, $P = 0.57$; ANOVA: $F_2 = 2.71$, $P = 0.07$).

HERITABILITY OF EGG TRAITS

Our sample included only four mother–daughter pairs, too small a sample for reliable estimates of heritability of egg traits based on single parent–offspring regressions (Falconer

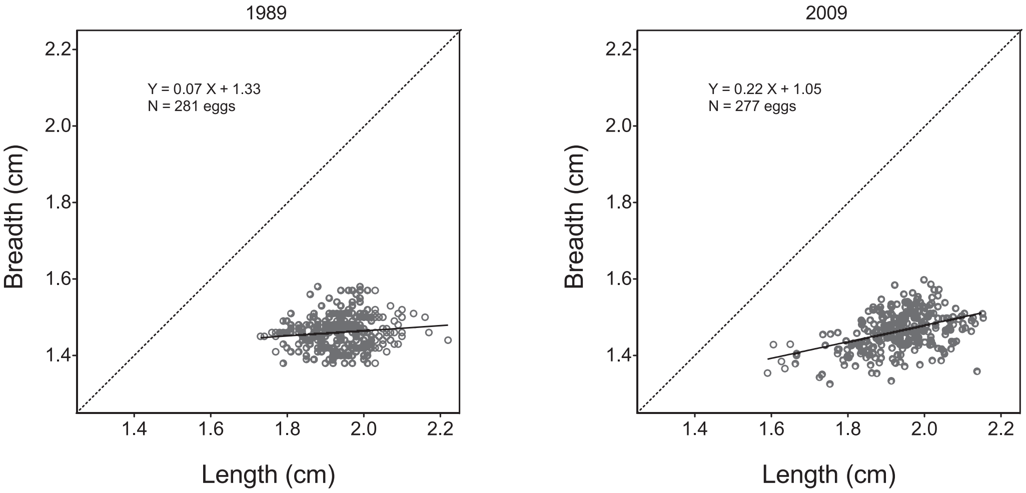

FIGURE 4. Negative allometric relationship between length and breadth (cm) of individual eggs in 1989 and 2009. Dashed diagonal lines designate isometry, solid lines indicate slope of linear regression. Eggs were measured with calipers in 1989 and from digital photographs in 2009 (see text).

and Mackay 1996). Nonetheless, the fact that all regression slopes were positive was consistent with the high estimates of repeatability reported above (especially for volume and shape) and suggest a heritable basis for variation in egg traits, although only the slope for egg shape was significantly different from 0 (regression slopes: volume: 0.15 ± 0.16; shape: 1.85 ± 0.25; spotting: 0.93 ± 0.44).

DISCUSSION

Individual female Savannah Sparrows tend to lay eggs of the same size, shape, and spotting in subsequent clutches. Consistency is especially notable relative to other females, but even in absolute terms most egg traits show high repeatability and little phenotypic variation within females. In this respect, egg traits differ from other aspects of reproduction such as date of laying, clutch size, and interval between clutches, which vary with the female's age and condition, time of year, and environmental factors (Wheelwright and Schultz 1994). Our study supports the conclusions of a recent survey showing that individual females of a broad range of taxa show little flexibility in egg size (Christians 2002). It also provides one of the few case histories from a natural population of a migratory passerine that does not rely on nest boxes, whose uniformity might be expected to reduce phenotypic variance in egg traits.

Repeatability provides an upper-limit estimate of a trait's narrow-sense heritability, h^2 (Falconer and Mackay 1996, Dingemanse et al. 2002). Heritability, in turn, is important to understand because it can constrain a trait's evolutionary response to selection (breeder's equation: $R = h^2S$, where S = the selection differential) (Falconer and Mackay 1996). However, even though the high repeatability of egg size and shape and moderate repeatability of egg spotting found in this study are consistent with a substantial genetic component to variation in egg traits, single parent–offspring regressions (a more direct way of estimating h^2) provided only weak support for high heritability. Moreover, an analysis of 103 phenotypic traits in the same population, taking advantage of a full pedigree spanning up to 12 generations and applying a more powerful animal-model approach (Wilson et al. 2010), found little additive genetic variance and only modest h^2 values for morphological traits (mean $h^2 = 0.21 \pm 0.17$, $n = 50$), and even lower values for traits closely associated with fitness (Wheelwright et al., unpubl. data). As emphasized by Styrsky et al. (2002), a trait can have high repeatability but low heritability if variation among females is due mainly to permanent environmental effects (e.g., developmental history) (Potti 1999). The fact that the females we studied renested in the same general location and, in most cases, with the same mate also raises the possibility that other nongenetic effects could partly explain consistency in egg traits between clutches. Nonetheless, we found no evidence that weather, habitat, mate characteristics, or female size influenced egg traits, which indicates that females may have limited flexibility in modifying their eggs in response to different environmental conditions.

Despite high repeatability of most egg traits, Savannah Sparrows showed intriguing variation in several aspects of their eggs. As in other species (Christians 2002), egg size increased slightly (<3%) from the age of 1 to 2 years, although it appeared to decline again in females older than 2 years and especially in the few 5-year-olds in the sample, suggesting an effect of senescence. Unexpectedly, within the same breeding season, females laid slightly bigger eggs in replacement clutches than in their first clutches, despite the fact that the number of eggs in replacement clutches was slightly larger (4.31 eggs ± 0.69 vs. 4.21 eggs ± 0.55, respectively; n = 1424). If the energetic and material expense of producing a first clutch—nest-building, egg-laying, incubation—was appreciable and carried over, one would have expected a decline in egg size with each subsequent clutch. Styrsky et al. (2002) also found House Wren (*Troglodytes aedon*) eggs laid later in the season were larger, a result due mainly to increasing breadth, whereas in our study the effect was due mainly to increasing length (unpubl. data).

More favorable weather conditions or food availability could conceivably explain the seasonal increase in egg size: on Kent Island, ambient temperatures rise an average of 1.7° C between first and replacement clutches, and 4.0° C between first and second clutches. If females can lay larger eggs when conditions are more favorable (Saino et al. 2004), one would expect an increase in egg size as the season progresses despite the accumulated costs of reproduction. However, the fact that no weather variable proved significant in our mixed-model analyses weakens support for the hypothesis that improving environmental conditions enable females to lay bigger eggs. An alternative explanation is that female Savannah Sparrows withhold reproductive investments at the beginning of the breeding season because first clutches have a substantially higher risk of being preyed upon or abandoned (37%) than do replacement clutches (24%) or second clutches (9%) (n = 1560 nests) (Wheelwright and Schultz 1994). The small but significant increase in clutch size as well as egg size between first and replacement clutches is consistent with the hypothesis that females hedge their bets in the face of higher predation risk for early clutches. We found no support for the prediction that females invest in larger eggs when mated to an older or bigger male. As in other bird species (Christians 2002), egg size was not correlated with clutch size once clutch number was controlled for.

Krist (2011) lamented the absence of studies relating egg size to offspring fitness. Because we did not mark individual eggs, we could only estimate the size of the egg from which an individual bird hatched by using the mean egg size of the clutch from which it hatched. Nonetheless, we found no evidence that the influence of egg size extended into adulthood or affected longevity or lifetime reproductive success, or even mass at fledging.

Results for egg shape were similar to those for egg size: females were highly consistent in the shape of their eggs, both within and between seasons, and repeatability was high. Egg shape would not necessarily be expected to be influenced by the female's age, size, or condition, or the age, size, or condition of her mate, or by weather. None of these factors was associated with egg shape in the 1989 sample, and only the female's age and clutch number appeared to influence egg shape in the 2009–10 sample (which, as noted above, was measured by a different method). In the entire sample, egg shape was negatively allometric, with increasing size being due mainly to greater egg length. Presumably, cloacal diameter constrains the upper limit of egg breadth more than it does egg length.

By consistently laying eggs of the same size, shape, and spotting, females should be better able to recognize and eject foreign eggs laid by interspecific and intraspecific brood parasites (Kilner 2006). However, given that Brown-headed Cowbirds (*Molothrus ater*) do not occur on Kent Island and Savannah Sparrows do not dump eggs in other females' nests, recognition of individual eggs is unlikely to explain the high consistency in egg traits in this population. Furthermore, the background color of eggs was so variable even within clutches that, were it not for the uniformity of size and shape of eggs within clutches and molecular paternity analyses (Freeman-Gallant et al. 2005), one could have concluded that egg dumping was widespread. Another indication that Savannah Sparrows on Kent Island do not use egg color as a cue to recognize eggs is that females do not reject model cowbird eggs, even when they are painted bright red or blue to maximize their distinctiveness (Wheelwright and Rothstein, unpubl. data). Although background color is probably influenced by diet (Morales et al. 2011), we found no difference in the colors of eggs laid by females in territories near the shore vs. inland, or between clutches laid early vs. late in the breeding season, despite the fact that Savannah Sparrows' diets vary by habitat and time of year (Wheelwright, unpubl. data). Variation in background color within clutches and a lack of difference between open vs. covered nests also argues against the hypothesis that in this population variation in color is an adaptation to increase crypsis and reduce predation (Kilner 2006).

In conclusion, Savannah Sparrows breeding on Kent Island show substantial variation in egg traits but very little variation (other than in background color) within a female's clutches, even between years. To the degree that high repeatabilities of egg traits reflect high heritabilities, the challenge will be to determine the factors maintaining genetic variation and the causes and consequences of variation of egg traits in natural populations.

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