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INTRA- AND INTER-CLUTCH PATTERNS IN EGG MASS IN THE SPOTTED SANDPIPER

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Abstract.—We looked for patterns in egg mass in the Spotted Sandpiper (*Actitis macularia*) within and across clutches, and for heritability of egg dimensions. Measurements of egg length, width, and mass were collected for 6 yr. Females laid from 1–5 clutches in a year. Egg mass was measured for 343 eggs from 98 clutches of 44 females. Of these, laying sequence was known for 337 eggs. Mean egg mass was 9.5 g (SD = 0.64), length was 3.2 cm (SD = 0.10), and width was 2.4 cm (SD = 0.06) (n = 547 for egg dimensions). We compared female mass to (1) mean egg mass of all clutches, (2) mean egg mass of first clutch, (3) summed egg mass of all clutches, (4) summed egg mass of first clutch, (5) summed egg mass of last clutch, and (6) number of clutches. We also compared mean egg mass with (7) laying date for first clutches, (8) clutch number, (9) laying order within a clutch, for all clutches, (10) laying order within first clutch, (11) female identity, and (12) egg length and width. In addition, we compared mean egg masses of females in their first year of laying with their second year for (13) all clutches combined, and for (14) first clutches only. Finally, we compared (15) mean egg mass of females to mean egg mass of their daughters. Only egg dimensions and female identity resulted in significant relationships to egg mass.

PATRONES INTRA- Y INTER-CAMADA EN MASA DE HUEVOS EN *ACTITIS MACULARIA*

Sinopsis.—Investigamos la presencia de patrones en la masa de los huevos de *Actitis macularia* dentro de y entre camadas, y evidencia de herencia de dimensiones de huevos. Medidas del largo del huevo, ancho, y masa se coleccionaron por seis años. Las hembras pusieron entre 1 y 5 camadas al año. La masa de huevos se midieron para 343 huevos provenientes de 98 camadas de 44 hembras. De estos, se conoce la secuencia de deposición para 337 huevos. La masa promedio de los huevos fue de 9.5 g (SD = 0.64), el largo 3.2 cm (SD = 0.10) y el ancho 2.4 cm (SD = 0.06) (n = 547 para dimensiones de huevos). Comparamos la masa de hembras a (1) promedio de masa de huevos para todas las camadas, (2) promedio de la masa de huevo de la primera camada, (3) la suma de todas las masas de huevos de todas las camadas, (4) la suma de masas de huevos de la primera camada, (5) la suma de las masas de huevos de la última camada, y (6) el número de camadas. También comparamos el promedio de las masas de huevos con (7) la fecha de deposición para las primeras camadas, (8) el número de camada, (9) el número de orden en la deposición en una camada, para todas las camadas, (10) el número de orden en la deposición en la primera camada, (11) la identidad de la hembra, y (12) el largo y el ancho del huevo. Además comparamos el promedio de las masas de huevos de hembras en su primer año de poner con su segundo año para (13) todas las camadas combinadas, y (14) para las primeras camadas. Finalmente, (15) comparamos el promedio de las masas de huevos de hembras con el promedio de masa de huevo de sus hembras. Solamente las dimensiones del huevo y la identidad de la hembra indicaron relación significativa con la masa del huevo.

Research on egg size in birds has focused on patterns within and among clutches, with the intent of identifying evolutionary and ecological forces regulating these patterns (e.g., Drent and Daan 1980, Väisänen et al. 1972). Parental investment into an egg reflects resources available to parents and the probability of hatch (Birkhead and Nettleship 1982, Järvinen and Ylimaunu 1984, Rofstad and Sandvik 1985, Slagsvold et al. 1984, Smith and Fretwell 1974). Studies of variation in egg size have shown several patterns, including a small first egg (Forbes and Ankney 1988), small terminal egg (Slagsvold et al. 1984), large middle eggs (Coleman and Whittall 1990, Leblanc 1987, Stokland and Amundsen 1988), and increase in egg size during the laying sequence (Howe 1976, Slagsvold et al. 1984). The relative size of the terminal egg also can vary negatively with clutch size (Slagsvold et al. 1984). Interclutch patterns have been less well studied, but observations include heavier eggs in late clutches (Redmond 1986) and small eggs in replacement clutches in poor habitat (Galbraith 1988).

We looked for patterns in egg size in the Spotted Sandpiper (*Actitis macularia*). Spotted Sandpipers do not exhibit brood reduction and they lay a determinate clutch of four eggs. Egg production at our study area is not limited by nutrient availability, and variability in food abundance does not appear to affect egg mass (Lank et al. 1985). Spotted Sandpipers are sex-role reversed; the male is the primary incubator and brooder (Maxson and Oring 1980, Oring 1982, Oring and Lank 1986). When females do help with egg and chick care, female reproductive success is unaffected (Oring et al. 1991); rather, females increase their lifetime reproductive success by increasing the number of clutches they lay and their laying rate (Oring et al. 1991). No relationship has been found between female mass and egg mass in Spotted Sandpipers (Lank et al. 1985). Because Spotted Sandpiper females do not appear to be food limited in reproductive output, we expected individual differences in egg size to be based on differences among females and on chance environmental events (cf. Slagsvold and Lifjeld 1989). Specifically, we compared (1) female mass to egg mass patterns of first clutches and yearly egg production, (2) egg mass with laying date, laying order within clutches, clutch number, female identity, and egg dimension, (3) egg mass between the same females in their first and second years of breeding, and between (4) females and their female offspring.

METHODS

Measurements of egg length, width, and mass were collected for 6 yr, 1976–1977 and 1979–1982, from a color-marked population of Spotted Sandpipers on Little Pelican Island, Leech Lake, Minnesota USA (47°07′N, 94°21′W) (see Reed and Oring [1993] for a more detailed description of the study site). The small size and open habitat of the island allowed us to monitor mating behavior, detect clutch initiation dates, and find nests. Most nests were found early enough in egg-laying that laying sequence was known. Because egg mass decreases during incubation, we corrected egg mass to the initial day of laying as: estimated laying mass = field mass + 0.066 × (number of days since laying) (Lank et al. 1985). Female body mass was measured to the nearest 0.5 g using a Pesola scale. Female mass varied by time in the laying cycle so we adjusted body weights to a common standard of mass on arrival using an analysis of covariance (L. W. Oring, unpubl. data).

Because eggs within a clutch are not statistically independent, we analyzed clutch means (Järvinen and Pryl 1989, Pietiäinen et al. 1986). We compared female mass to the (1) the mean egg mass of all clutches, (2) mean egg mass of first clutch, (3) summed egg mass of all clutches, (4) summed egg mass of first clutch, (5) summed egg mass of last clutch, and (6) number of clutches. We also compared mean egg mass with (7) laying date for first clutches (for females laying in more than one year, mean egg masses and laying dates were averaged across years), (8) clutch number, (9) laying order within a clutch, for all clutches, (10) laying order within first clutches, (11) female identity, and (12) egg length and width. In addition, we compared mean egg masses of females in their first year of laying with their second year using paired comparisons. This was done for (13) all clutches combined, and for (14) first clutches only. Finally, we compared (15) mean egg mass of females to mean egg mass of their daughters.

For analyses 1–7 and 11–15, data were pooled for the same female across clutches and years to ensure statistical independence in the analyses. For analyses 8–12, analyses were weighted by the number of clutches per female. We used analysis of variance for comparisons 1–14; the last analysis was a Spearman rank correlation. Analyses of egg masses included only those eggs that actually were weighed (as opposed to mass estimated from egg dimensions).

RESULTS AND DISCUSSION

Females laid from 1–5 clutches in a season. Egg mass was measured for 343 eggs from 98 clutches of 44 females. Of these, laying sequence was known for 337 eggs. Mean egg mass was 9.5 g (SD = 0.64), length was 3.2 cm (SD = 0.10), and width was 2.4 cm (SD = 0.06) (n = 547 for egg dimensions). None of the independent variables considered was related significantly to egg mass except for egg length and width, and female identity (Table 1). Mean egg mass varied among females, ranging from 8.4–10.4 g, with some females consistently laying heavier eggs than other females. However, egg mass was not related to female mass.

We found no relationship between egg mass or dimensions between mothers and their daughters (Spearman rank correlation, $n = 8$, $r < 0.26$ for egg mass, length, and width; $P > 0.36$ for all), although statistical power was low.

We found no patterns in egg mass within a clutch or across clutches for individual female Spotted Sandpipers. This result is consistent with other studies of shorebirds (Slagsvold et al. 1984, Väisänen et al. 1972). Väisänen et al (1972) studied egg dimensions for five species of shore-

TABLE 1. Results from analyses of variance of different comparisons of egg mass with a variety of independent variables. Degrees of freedom (df) vary with comparison depending on how many clutches were combined to maintain statistical independence. See text for more details of comparisons.

Comparison	df	Type I SS[a]	F	P	r^2
female mass compared to:					
mean egg mass, all clutches	1, 33	0.18	0.66	0.42	0.02
mean egg mass, first clutch	1, 26	0.60	2.15	0.15	0.08
summed egg mass, all clutches	1, 33	60003.2	0.13	0.72	0.00
summed egg mass, first clutch	1, 27	2660.9	0.83	0.37	0.03
summed egg mass, last clutch	1, 49	0.05	0.07	0.79	0.00
number of clutches	1, 33	399.4	0.55	0.46	0.02
mean egg mass compared to:					
laying date, first clutch	1, 30	1.11	0.98	0.33	0.03
clutch number	4, 92	1.16	0.27	0.90	0.01
laying order, within clutch, all clutches	2, 39	0.36	0.09	0.92	0.00
laying order within first clutch	2, 32	0.23	0.11	0.90	0.01
female identity	43, 85	31.9	5.89	<0.0001	0.75
egg length and width	2, 340	101.9	282.6	<0.0001	0.71
mean egg mass, first year of laying compared to second year, by female:					
all clutches combined	1, 44	0.26	0.24	0.62	0.01
first clutch	1, 11	0.80	0.61	0.45	0.05

[a] PROC GLM (SAS 1985)

birds, and two species were found to have interclutch differences in egg volume. However, the difference in both cases was <2.5% of total volume, and the methods indicate eggs were analyzed as independent observations (Pietiänen et al. 1986), which artifically increases sample sizes. It is likely that these species, like Spotted Sandpipers, had no significant pattern in egg size among clutches laid by a female.

Väisänen et al.'s (1972) general conclusion was that interindividual variation accounted for most of the variability in egg size. We also found no patterns in egg size except for individual differences. Mean egg mass among females ranged almost 20%. Female Spotted Sandpipers provide care for eggs and young only when another male is not available for mating (Oring et al. 1994). This, combined with high food availability (Lank et al. 1985), might result in selective pressure to maximize egg size. Although egg size is considered heritable (van Noordwijk et al. 1980), we were unable to detect a significant genetic component in egg mass with our small female-daughter sample. A further indication that females were maximizing egg mass is that egg mass was approximately 19% of female mass. This proportion is larger than that reported for other shorebird species (Jehl 1975).

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