

Correlates of Egg-Size Variation in Polygynously Breeding Northern Lapwings

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Most Northern Lapwing (*Vanellus vanellus*) nests have four eggs (Glutz von Blotzheim et al. 1975, Cramp and Simmons 1983), as is typical of most shorebirds. Consequently, variation in clutch investment should be reflected in egg volume, with a fitness premium on laying large eggs (Redmond 1986; Galbraith 1988a, c; Grant 1991). Large eggs yield larger and heavier chicks that have higher growth and survival rates than chicks hatched from smaller eggs (Galbraith 1988a, c; Grant 1991). The lapwing clutch normally amounts to 40 to 50% of female body mass, and egg size shows a high degree (60–70%) of between-clutch variation (e.g. Galbraith 1988c, Blomquist and Johansson 1995), as is also common for other shorebirds (e.g. Väisänen et al. 1972, Redmond 1986, Thompson and Hale 1991). Individual egg investment depends on maternal condition (Drent and Daan 1980, Högstedt 1981, Olsen et al. 1994, McNamara and Houston 1996), and in lapwings maternal mass and condition are positively correlated with egg volume (Galbraith 1988c, Blomquist and Johansson 1995, T. Lislevand pers. comm.). Maternal condition depends on extrinsic factors at the breeding site (e.g. availability of food, the opportunity to forage effectively, and weather) and on intrinsic factors related to genetic predisposition, or acquired previously (Drent and Daan 1980, Högstedt 1980, Schluter and Gustafsson 1993).

In this study, I investigated whether females of different mating status in a population of polygynously breeding (23 to 41% over four seasons) Northern Lapwings differed in their clutch investment. I measured and analyzed egg size of individual females while controlling for clutch size, replacement laying, laying phenology, and year of breeding. I also explored the relationship between food density and egg size.

Methods.—Egg measurements were obtained during four breeding seasons (1991 to 1994) at Haukås outside Bergen in western Norway (60°19' N, 5°29' E). The study site is drained marshland with a homogeneous appearance. Fields are mainly used for hay production, except parts that are grazed by sheep and horses. Additional details on the study area, general observations, procedures, and lapwing mating system are given by Byrkjedal et al. (1997).

Territory borders and mating status were deter-

mined each season using spotting scopes and binoculars. Birds were identified by individual plumage differences in the face, breast, and wing coverts (Byrkjedal et al. 1997). Female mating status was divided into three categories: (1) monogamous, (2) primary polygamous, and (3) secondary polygamous. One tertiary female was included in the "secondary polygamous" group. The criterion for distinguishing between primary and secondary status was laying date of the first clutch. Some nests were found after completion of laying. For these nests I calculated laying date of the first egg by back-dating 30 days from the hatching date, which is the normal incubation period at Haukås (Grønstøl 1996). If an undetected clutch of a primary female was depredated and her replacement clutch was laid after the secondary female's first clutch, then female status would be incorrectly assigned. Incubating females were easily recognized during observation bouts, but unfinished clutches were not as easily discovered because females do not incubate much before clutch completion. One of 34 nests that was discovered before completion was depredated during laying, which, using the Mayfield (1961, 1975) method, yields a probability of nest survival throughout the laying period of 94%. Thus, it is unlikely that status was erroneously assigned in more than perhaps one territory.

Egg breadth and length of 288 eggs from 72 clutches were measured to the nearest 0.05 mm using calipers. Only clutches with four eggs were used to be certain that average egg volume indicated clutch investment. Egg volume estimates from length (*L*) and breadth (*B*) data were calculated using an empirical formula calibrated to Northern Lapwing eggs by Galbraith (1988c):

$$\text{egg volume} = 0.457 LB^2. \quad (1)$$

Earthworms commonly constitute the main food resource for adult lapwings during the nesting season (Klomp 1954, Högstedt 1974, Baines 1990). In order to estimate food density, earthworms were sampled in early September 1992 on six squares in each of 21 territories using formalin extraction (Raw 1959). Sampling squares of 0.25 m² were randomly selected within each territory on which a solution of 0.24% formalin was poured, 3 L at intervals of 10 min. Emerging earthworms were collected and their volume measured. Earthworm volume is easily determined in the field by water displacement, and this measurement is tightly correlated with dry biomass

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TABLE 1. Egg-size differences ($\bar{x} \pm SD$) between first clutches and replacement clutches of the same female in Northern Lapwings. Average clutch values from clutches with four eggs.

Variable	First clutch	Replacement clutch	% with reduction ^a	df	<i>t</i> ^b	<i>P</i>
Egg volume (ml)	25.59 ± 1.20	22.76 ± 1.32	80	14	2.69	0.018
Egg length (mm)	47.74 ± 1.58	46.66 ± 1.44	80	14	3.23	0.006
Egg breadth (mm)	33.22 ± 0.51	33.01 ± 0.77	60	14	1.56	0.140

^a % of females exhibiting a reduction in trait between first and replacement clutches.

^b Paired *t*-test (two-tailed).

(Nordström and Rundgren 1972). Two bouts of formalin solution were used, because preliminary sampling showed that no earthworms emerged throughout a third treatment. Six territories were resampled in April 1993 (three sampling squares in each territory) to investigate the stability of the earthworm distribution over a period of seven to eight months. Statistical analyses were run on SYSTAT version 5.02 for Windows and SAS/STAT.

Results.—Repeatability of egg sizes was calculated using methods provided in Lessells and Boag (1987) and Becker (1984). Repeatabilities of egg volume, egg length, and egg breadth within clutches for first clutches holding four eggs were $0.582 \pm SE$ of 0.052 ($F = 6.57$, $df = 81$ and 246), 0.525 ± 0.055 ($F = 5.43$, $df = 81$ and 246), and 0.576 ± 0.052 ($F = 6.43$, $df = 81$ and 246), respectively. Repeatabilities of egg volume, egg length, and egg breadth between first and replacement clutches within the same female and season were 0.416 ± 0.048 ($F = 2.60$, $df = 11$ and 15), 0.414 ± 0.048 ($F = 2.58$, $df = 11$ and 15), and 0.657 ± 0.038 ($F = 5.30$, $df = 11$ and 15), respectively (based on results from a two-way nested ANOVA, GLM procedure).

To avoid pseudoreplication when investigating variation among females, I used average egg sizes for each clutch. Average egg volume and egg length were significantly lower in replacement clutches than in first clutches (Table 1), although the decline in egg breadth was not significant. Due to the difference between first and replacement clutches, only first clutches are used in further tests.

Average egg volume differed significantly ($P = 0.029$) among females of different mating status (Table 2). Egg length and egg breadth showed nonsignificant trends of diverging ($P = 0.105$ and $P = 0.078$, respectively). Egg sizes of monogamous and pri-

mary females were similar, whereas eggs of secondary females had a smaller volume (Table 2). The seasonal distribution of laying dates differed among years (median laying date in April was 7.5, 13, 14.5, and 16 from 1991 to 1994, respectively). To standardize the laying phenology among years, laying dates were plotted as the number of days deviating from the median laying date of each season, before testing against average egg volume of first clutches. Egg volume of pooled first clutches declined significantly with laying phenology (Fig. 1A). An ANCOVA with year and status as class variables and laying sequence as a covariate explained significant amounts of variation in egg volume ($F = 1.84$, $df = 17$ and 71, $P = 0.05$). The effect of mating status on egg volume was not significant ($F = 2.31$, $df = 2$ and 71, $P = 0.11$), illustrating that lower egg volumes of secondary females were associated with later laying (Figs. 1B-D). Egg volume did not vary significantly with year ($F = 1.16$, $df = 3$ and 71, $P = 0.33$) or laying sequence ($F = 0.02$, $df = 1$ and 71, $P = 0.90$), but the interaction between year and mating status was significant ($F = 2.26$, $df = 6$ and 71, $P = 0.05$). There were no differences in the slopes of the seasonal decline among females of different mating status ($F = 1.20$, $df = 2$ and 71, $P = 0.31$) or among years ($F = 1.70$, $df = 3$ and 71, $P = 0.18$).

Average spring density of earthworms was 55 ml per m² ($\bar{x} \pm SD$ of 88 earthworms, range 224–429) for 21 territories. Average autumn density was 96 ml per m² ($\bar{x} = 478 \pm 94$, range 325–649) for six territories. Dominant species were *Lumbricus rubellus*, *Dendrobaena rubida*, and *Allolobophora* sp., whereas *Dendrobaena octaedra* and *Lumbricus terrestris* were less common. The difference in spring and autumn densities corresponds with data on emergence, activity, and vertical distribution patterns of earthworms

TABLE 2. Egg sizes ($\bar{x} \pm SE$) of female Northern Lapwings of different mating status; $n = 28$ for monogamous females, 23 for primary females, and 21 for secondary females.

Variable	Monogamous	Primary	Secondary	<i>F</i> ^a	<i>P</i>
Egg volume (ml)	23.94 ± 0.22	24.08 ± 0.24	23.20 ± 0.25	3.57	0.029
Egg length (mm)	46.68 ± 0.23	46.93 ± 0.25	46.15 ± 0.26	2.33	0.105
Egg breadth (mm)	33.54 ± 0.12	33.50 ± 0.13	33.15 ± 0.14	2.64	0.078

^a One-way ANOVA.

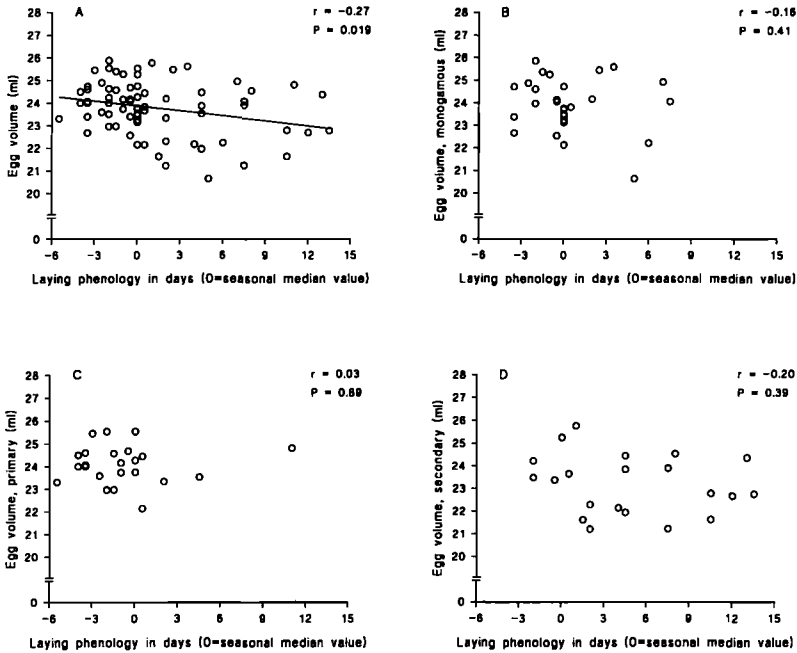


FIG. 1. Average clutch egg volume regressed on laying phenology for all four seasons plotted as number of days discrepancy between laying date of clutches and the median laying date (0) for each season. (A) pooled over all status groups, (B) monogamous females, (C) primary females, and (D) secondary females.

in southern Sweden, which show increasing earthworm activity and abundance from April to September (Nordström 1975, Rundgren 1977). Because earthworm abundance among corresponding sample squares was highly correlated between September 1992 and April 1993 ($r = 0.85$, $n = 18$, $P < 0.001$), I used sampling results from September 1992 as food-density estimates for both the 1992 and 1993 breeding seasons. Earthworm density (ml per m^2) measured in 1992 was not correlated with average egg volume of first clutches in that year ($r = -0.05$, $P = 0.95$, $n = 18$) or with egg volume when clutches were pooled over 1992 and 1993 ($r = -0.13$, $P = 0.54$, $n = 25$; Fig. 2A; mean values used in cases of more than one clutch on the same territory). Earthworm availability for each female (ml per m^2 multiplied by territory size in m^2 and divided by number of females) also was not correlated with egg volume in 1992 ($r = -0.10$, $P = 0.68$, $n = 18$) or with egg volume when clutches were pooled over 1992 and 1993 ($r = -0.01$, $P = 0.16$, $n = 25$; Fig. 2B).

Discussion.—Egg volume differed between females of primary and secondary status, but this effect disappeared when I controlled for seasonal effects. These results indicate that later-nesting females, which (by definition) are biased toward secondary females, have smaller egg volumes. Some important costs of early breeding are low temperature, high risk of snow (Beintema and Visser 1989), and low in-

vertebrate activity owing to low soil temperature (Nordström 1975), balanced by benefits from having the opportunity to choose among several vacant males and/or territories and prospects of early hatching. Such costs may be better endured by females in good physical condition (Andersson and Gustafsson 1995). Aside from being of intrinsic higher quality, these individuals choose a mate/territory first, lay earlier, and become primary (or monogamous) females, all of which may allow larger eggs. Time of arrival at breeding site is age dependent in many birds (e.g. Perrins 1970, Forslund and Pärt 1995), and food supplementation experiments have shown that laying date and clutch size depend on body condition (Drent and Daan 1980, and references therein), which again may be determined by age, breeding experience, and physiological condition.

Differences in maternal condition among females may be reinforced by social interactions. Lapwings experience at least some costs of sharing male/territory, because aggressive interactions between polygynous females nesting on the same territory is regularly observed at Haukås (pers. obs.). Secondary females might have higher interference costs of intruding on and sharing a territory than do primary females (Maynard Smith and Parker 1976, Forslund and Pärt 1995), which subsequently might affect their egg size adversely. If females experience differ-

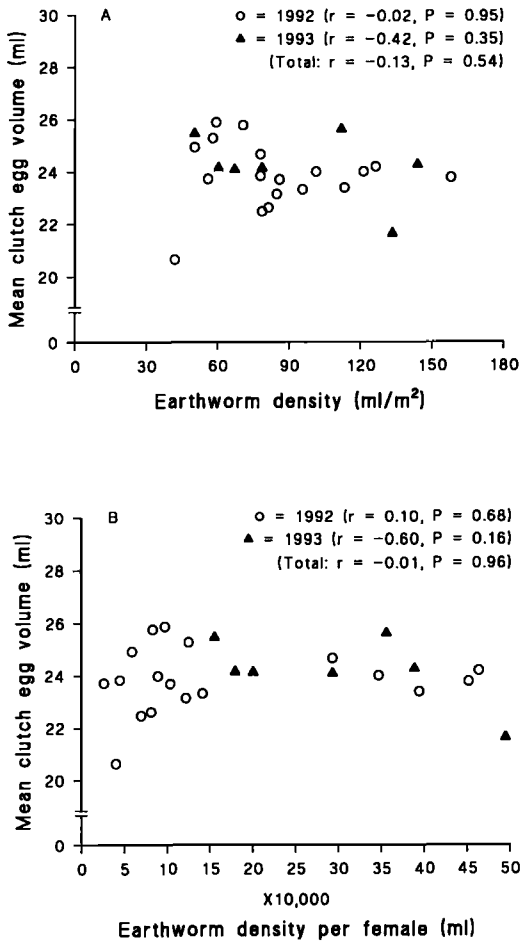


FIG. 2. Average clutch egg volume of first clutches containing four eggs on each territory plotted against (A) average earthworm density on the territories (volume of earthworms per m²), and (B) estimated total earthworm abundance per female (territory size in m multiplied with volume of earthworms in ml per m² and divided by number of females on territory).

ent costs of competition due to differing quality, they can be expected to settle on territories in an ideal despotic pattern (Fretwell 1972, Galbraith 1988d) rather than an ideal free, as assumed by the Polygyny Threshold Model (Verner 1964, Verner and Willson 1966, Orians 1969). The significant interaction between year and mating status indicated that although primary females had a higher average egg volume in all years, the difference varied over the seasons (average differences were 1.13 ml, 1.14 ml, 0.35 ml, and 0.25 ml from 1991 to 1994, respectively). The density of females on polygynous territories was higher in 1991 (2.4 per territory) and 1992 (2.5 per

territory) than in 1993 (2.0 per territory) and 1994 (2.0 per territory; Byrkjedal et al. 1997). This could tentatively suggest that secondary females had higher interference costs in the two former years, resulting in a relatively lower egg volume.

Density of earthworms did not covary with egg size, which was somewhat unexpected because other studies have identified earthworm density as an important proximate factor in determining egg volume (Galbraith 1988c, Baines 1990). The lack of a relationship between earthworm numbers and lapwing egg size at Haukås could be because earthworm densities at Haukås were so high that other factors had a comparably larger effect on determining individual differences in egg size. Mean earthworm densities on lapwing territories at Haukås were similar to densities reported as "rich" by others (e.g. Baines 1990). If earthworm density was the most important predictor of egg size, then late nesters would be expected to lay larger eggs, because earthworm density increases seasonally (Nordström 1975, Rundgren 1977, this study).

Eggs of replacement clutches were markedly smaller than eggs of first clutches. A reduction in egg size would be expected if egg production exhausts endogenous resources that are difficult to replenish (e.g. calcium or protein; Jones 1976, Jones and Ward 1976). Late-hatched lapwing chicks have a lower survival and growth rate than early hatched chicks, which probably is related to vegetation height and availability of surface invertebrates (Galbraith 1988a, b). If larger eggs take longer to form, and if the seasonal decline in chick survival more than offsets chick-survival benefits of large eggs, then late nesters would be expected to lay smaller eggs than early nesters, even if maternal condition is equal (Winkler and Allen 1996). The higher capacity for heat retention of larger eggs during incubation recesses also would predict a preponderance of large eggs early in the season when temperatures are lower (P. Hendricks pers. comm.).

Repeatability tests of egg dimensions showed that within-female variation in egg size resulted from variation in egg length, whereas mean differences in egg breadth contributed more to differences in egg volume among females of different mating status than did egg length (Table 2). Lapwing egg breadth has a lower coefficient of variation (as in a range of bird species; e.g. Olsen et al. 1994) and seems more individually specific than egg length (also found in other birds; e.g. Preston 1958, Myrberget 1977, and references therein). This might be caused by anatomical constraints, like in commercial turkeys, where vent diameter, oviduct diameter, and the internal distance between the pubic bones show high between-female variation and are positively correlated with egg size (Hocking 1993).

A certain proportion of the individual variation in egg size is heritable (Väisänen et al. 1972, Ojanen et

al. 1979, Josef and Beser 1988, Galbraith 1988c), but it is also possible that egg size increases with age and becomes phenotypically fixed in older birds. Several studies have found age-related effects on egg breadth and/or volume (Preston 1958, Coulson 1963, Coulson et al. 1969, Myrberget 1977, Gratto et al. 1983, Thompson and Hale 1991, Robertson et al. 1994). Indeed, in Northern Lapwings egg breadth and egg volume were significantly lower in yearlings than in older birds in each of four age classes (i.e. 2, 3, 4, ≥ 5 years). The overall difference between yearlings and older birds was 7.8% in breadth and 5% in volume (D.M.B. Parish et al. pers. comm.). My results suggest that the condition of secondary female lapwings is lower than that of primary females, perhaps because these females are younger and less experienced than primary females.

Examination of color-banded birds should reveal whether female mating status and egg size are influenced by age. In addition, monitoring of settlement patterns, competitive behavior, and body condition of polygynous individuals will provide a clearer insight into the mechanisms by which mating status is established among female Northern Lapwings.

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LITERATURE CITED

- ANDERSSON, M. S., AND L. GUSTAFSSON. 1995. Glycosylated haemoglobin: A new measure of condition in birds. *Proceedings of the Royal Society of London Series B* 260:299–303.
- BAINES, D. 1990. The roles of predation, food, and agricultural practice in determining the breeding success of the Lapwing (*Vanellus vanellus*) on upland grasslands. *Journal of Animal Ecology* 59:915–929.
- BECKER, W. A. 1984. *Manual of quantitative genetics*. Academic Enterprises, Pullman, Washington.
- BEINTEMA, A. J., AND G. H. VISSER. 1989. The effect of weather on time budgets and development of chicks of meadow birds. *Ardea* 77:181–192.
- BLOMQUIST, D., AND O. C. JOHANSSON. 1995. Trade-offs in nest site selection in coastal populations of Lapwings *Vanellus vanellus*. *Ibis* 137:550–558.
- BYRKJEDAL, I., G. B. GRØNSTØL, T. LISLEVAND, K. M. PEDERSEN, H. SANDVIK, AND S. STALHEIM. 1997. Mating systems and territory in Lapwings *Vanellus vanellus*. *Ibis* 139:129–137.
- COULSON, J. C. 1963. Egg size and shape in the Kittiwake and their use in estimating age composition of populations. *Proceedings of the Zoological Society of London* 140:211–227.
- COULSON, J. C., G. R. POTTS, AND J. HOROBIN. 1969. Variation in the eggs of the Shag (*Phalacrocorax aristotelis*). *Auk* 86:232–245.
- CRAMP, S., AND K. E. L. SIMMONS (Eds). 1983. *Birds of the western Palearctic*, vol. 3. Oxford University Press, Oxford.
- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68:225–252.
- FORSLUND, P., AND T. PÄRT. 1995. Age and reproduction in birds—Hypotheses and tests. *Trends in Ecology and Evolution* 10:374–378.
- FRETWELL, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey.
- GALBRAITH, H. 1988a. Adaptation and constraint in the growth pattern of Lapwing *Vanellus vanellus* chicks. *Journal of Zoology (London)* 215:537–548.
- GALBRAITH, H. 1988b. Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. *Journal of Applied Ecology* 25:487–503.
- GALBRAITH, H. 1988c. Effects of egg size and composition on the size, quality and survival of Lapwing *Vanellus vanellus* chicks. *Journal of Zoology (London)* 214:383–398.
- GALBRAITH, H. 1988d. The effects of territorial behaviour on Lapwing populations. *Ornis Scandinavica* 19:134–138.
- GLUTZ VON BLOTZHEIM, U. N., K. M. BAUER, AND E. BEZZEL. 1975. *Handbuch der Vögel Mitteleuropas*, Band 6. Akademische Verlagsgesellschaft, Wiesbaden, Germany.
- GRANT, M. C. 1991. Relationships between egg size, chick size at hatching and chick survival in the Whimbrel *Numenius phaeopus*. *Ibis* 133:127–133.
- GRATTO, C. L., AND F. COOKE. 1983. Nesting success of yearling and older breeders in the Semipalmated Sandpiper *Calidris pusilla*. *Canadian Journal of Zoology* 61:1133–1137.
- GRØNSTØL, G. B. 1996. Aerobic components in the songflight display of male Lapwings as cues in female choice. *Ardea* 84:45–55.
- HOCKING, P. M. 1993. Relationship between egg size, body weight and pelvic dimensions in turkeys. *Animal Production* 56:145–150.
- HÖGSTEDT, G. 1974. Length of the pre-laying period in the Lapwing *Vanellus vanellus* in relation to its food resources. *Ornis Scandinavica* 5:1–4.
- HÖGSTEDT, G. 1980. Evolution of clutch-size in birds: adaptive variation in relation to territorial quality. *Science* 210:1148–1150.
- HÖGSTEDT, G. 1981. Should there be a positive or a negative correlation between survival of adults in a bird population and their clutch size? *American Naturalist* 118:568–571.

- JONES, P. J. 1976. The utilization of calcareous grit by laying *Quelea quelea*. *Ibis* 118:575-576.
- JONES, P. J., AND P. WARD. 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed *Quelea quelea quelea*. *Ibis* 118:547-574.
- JOSEF, H., AND M. BESER. 1988. Eimasse des Kiebitz (*Vanellus vanellus*). *Charadrius* 24:225-235.
- KLOMP, H. 1954. De terreinkaus van de Kievit, *Vanellus vanellus* (L.). *Ardea* 42:1-39.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116-121.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. *Wilson Bulletin* 73:255-261.
- MAYFIELD, H. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- MAYNARD SMITH, J., AND G. PARKER. 1976. The logic of asymmetric contests. *Animal Behaviour* 24:159-175.
- MCNAMARA, J. M., AND A. I. HOUSTON. 1996. State dependent life histories. *Nature* 380:215-221.
- MYRBERGET, S. 1977. Size and shape of eggs of Willow Grouse *Lagopus lagopus*. *Ornis Scandinavica* 8:39-46.
- NORDSTRÖM, S. 1975. Seasonal activity of lumbricids in southern Sweden. *Oikos* 26:30-315.
- NORDSTRÖM, S., AND S. RUNDGREN. 1972. Volumetric estimation of body size in lumbricids. *Oikos* 23:278-280.
- OJANEN, M., M. ORELL, AND R. A. VÄISÄNEN. 1979. Role of heredity in egg size variation in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scandinavica* 10:22-28.
- OLSEN, P. D., R. B. CUNNINGHAM, AND C. F. DONNELLY. 1994. Avian egg morphometrics: Allometric models of egg volume, clutch volume and shape. *Australian Journal of Zoology* 42:307-321.
- ORIANI, G. H. 1969. On the evolution of mating systems in birds and mammals. *American Naturalist* 103:589-603.
- PERRINS, C. M. 1970. The timing of birds' breeding seasons. *Ibis* 112:242-255.
- PRESTON, F. W. 1958. Variation of egg size with age of parent. *Auk* 75:476-477.
- RAW, F. 1959. Estimating earth-worm population by using formalin. *Nature* 184:1661-1662.
- REDMOND, R. L. 1986. Egg size and laying date of Long-billed Curlews *Numenius americanus*: Implications for female reproductive tactics. *Oikos* 46:330-338.
- ROBERTSON, G. J., E. G. COOCH, D. B. LANK, R. F. ROCKWELL, AND F. COOKE. 1994. Female age and egg size in the Lesser Snow Goose. *Journal of Avian Biology* 25:149-155.
- RUNDGREN, S. 1977. Seasonality of emergence in lumbricids in southern Sweden. *Oikos* 28:49-55.
- SCHLUTER, D., AND L. GUSTAFSSON. 1993. Maternal inheritance of condition and clutch size in the Collared Flycatcher. *Evolution* 47:658-667.
- THOMPSON, P. S., AND W. G. HALE. 1991. Age-related reproductive variation in the Redshank *Tringa totanus*. *Ornis Scandinavica* 22:353-359.
- VÄISÄNEN, R. A., O. HILDÉN, M. SOIKKELI, AND S. VUOLANTO. 1972. Egg dimension variation in five wader species: The role of heredity. *Ornis Fennica* 49:25-44.
- VERNER, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. *Evolution* 18:252-261.
- VERNER, J., AND M. F. WILLSON. 1966. The influence of habitats on mating systems of North American passerine birds. *Ecology* 47:143-147.
- WINKLER, D. W., AND P. E. ALLEN. 1996. The seasonal decline in Tree Swallow clutch size: Physiological constraint or seasonal adjustment? *Ecology* 77:922-932.

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