

POTENTIAL INFLUENCE OF EGG LOCATION ON SYNCHRONY OF HATCHING OF PRECOCIAL BIRDS

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Abstract. Although the onset of incubation prior to completion of the clutch leads to developmental asynchrony of the embryos, waterfowl eggs tend to hatch synchronously (within 3–24 hr). The mechanisms waterfowl use to synchronize development of embryos and allow for synchronous hatching are still not well understood. A variety of mechanisms have been proposed, including vocalization by embryos, egg size, egg constituents, and developmental asynchrony at hatching. Empirical evidence for any of these mechanisms, however, is limited for species that lay large clutches (>6 eggs). We hypothesize that the eggs' position within the clutch may synchronize development of embryos of dabbling ducks that lay clutches large enough that central and peripheral eggs may be distinguished. We tested this hypothesis by comparing the developmental stage of central and peripheral eggs and testing for a relationship between the order in which an egg was laid and its position (central or peripheral) within the clutch. We found that eggs laid later were central more often than expected if their distribution were random and that during the first 12 days of incubation central eggs tended to be less developed than peripheral eggs.

Key words: clutch, developmental asynchrony, eggs, embryonic development, hatch synchrony, precocial, waterfowl.

Influencia Potencial de la Localización de los Huevos sobre la Sincronía de Eclosión en Aves Precociales

Resumen. A pesar de que el inicio de la incubación antes de que la puesta esté completa resulta en un desarrollo asincrónico de los embriones, los huevos de aves acuáticas tienden a eclosionar de forma sincrónica (dentro de 3 a 24 h). Los mecanismos que las aves acuáticas usan para sincronizar el desarrollo de los embriones, lo que permite la eclosión sincrónica de los huevos, aún no están bien entendidos. Se han propuesto una variedad de mecanismos, incluyendo vocalizaciones de los embriones, tamaño del huevo, componentes de los huevos y desarrollo asincrónico en el momento de la eclosión. Sin embargo, la evidencia empírica para cualquiera de estos mecanismos es escasa para especies con puestas grandes (>6 huevos). Hipotetizamos que la posición del huevo dentro de la puesta podría sincronizar el desarrollo de los embriones de los patos que tienen puestas suficientemente grandes, de modo que puedan distinguirse los huevos de la periferia y del centro en la puesta. Evaluamos esta hipótesis comparando el estado de desarrollo de los huevos centrales y periféricos, y si existe una relación entre el orden en que un huevo fue puesto y su posición (central o periférica) dentro de la puesta. Encontramos que los huevos puestos más tarde estuvieron más frecuentemente en posiciones centrales de lo esperado que si su distribución fuese al azar, y que durante los primeros 12 días de incubación, los huevos centrales tendieron a desarrollarse menos que los huevos periféricos.

INTRODUCTION

Hatching of young waterfowl (order Anseriformes) is among the most synchronous (young hatch within 24 hr) of all birds (e.g., Leopold 1951). Synchronous hatching had led most biologists to assume incubation does not begin until after the completion of the clutch (Glover 1956). This paradigm was first questioned by Caldwell and Cornwell (1975) when they found that Mallard (*Anas platyrhynchos*) hens started incubating prior to the completion of the clutch. More recent research has

demonstrated that both geese (tribe Anserini) and dabbling ducks (tribe Anatini) begin incubation prior to the completion of the clutch (Caldwell and Cornwell 1975, Afton 1979, Davies and Cooke 1983, Kennamer et al. 1990, Flint et al. 1994, Loos and Rohwer 2004). Incubation prior to the completion of the clutch has likely evolved through pressures of selection for increased viability of eggs in large clutches, decreased time the nest is exposed to predators, and avoidance of egg parasitism (Arnold et al. 1987, Kennamer et al. 1990, Flint et al. 1994, Loos and Rohwer 2004).

Manuscript received 11 February 2010; accepted 29 May 2010.

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Onset of incubation prior to the completion of the clutch leads to as much as 3 days of embryonic developmental asynchrony in geese (average clutch sizes varying from 4 to 6 eggs, Flint et al. 1994) and 5 days of embryonic developmental asynchrony in dabbling ducks (average clutch sizes varying from 6 to 12 eggs, Kennamer et al. 1990, Loos and Rohwer 2004). Although incubation prior to the completion of the clutch leads to developmental asynchrony of the embryos, hatching of the young is synchronous relative to the early developmental asynchrony (Johnson 1974, Munro and Bedard 1977, Afton and Paulus 1992, Flint et al. 1994). Mechanisms proposed to explain how precocial birds synchronize their embryos' development so the chicks hatch simultaneously include vocalization of embryos (Vince 1964, Orcutt 1974, Wolf et al. 1976, Persson and Anderson 1999; but see Nicolai et al. 2004), egg size (Parsons 1972, Flint et al. 1994), egg composition (Hoyt et al. 1979, Vleck et al. 1980, MacCluskie et al. 1997, Nicolai et al. 2004), and developmental asynchrony at hatching (Slattery and Alisauskas 1995). Empirical evidence supporting these proposed mechanisms, especially for species that lay large clutches (>6 eggs), however, is limited.

Vocalization was the first mechanism proposed to synchronize hatching of precocial birds (Vince 1964). Embryos, however, vocalize only 2–3 days prior to hatching, after >90% of their development is complete (Vince 1964, Vleck et al. 1980). This period is likely too short to influence embryonic development substantially, although vocalizations likely synchronize the hatching of young that are already well synchronized developmentally (Nicolai et al. 2004).

Egg constituents (amount of albumen or androgen concentration in the yolk) have also been proposed as a mechanism reducing developmental asynchrony. This mechanism appears more plausible than vocalizations because nutrients provided by the hen during egg formation are used by the embryo early in incubation, when most development occurs (Vleck et al. 1980, Müller et al. 2007, Boonstra et al. 2009). If certain compounds that promote faster growth are found in higher concentrations in eggs laid later, embryos in later eggs would develop faster, synchronizing embryo development and hatching (MacCluskie et al. 1997, Nicolai et al. 2004, but see Boonstra et al. 2009). MacCluskie et al. (1997) tested this hypothesis for ducks by comparing the metabolic rate and incubation length of Mallard eggs held in incubators under constant conditions. They found substantial variation in metabolic rate and incubation length among eggs from different hens and among eggs within a clutch. They also found a positive relationship between metabolic rate and sequence of laying; however, they were not able to detect a relationship between metabolic rate and incubation length. Nicolai et al. (2004) further tested this mechanism for geese with an experiment switching eggs of the Black Brant (*Branta bernicla*). They found a negative linear correlation between sequence of laying and length of embryo development, with first eggs

taking 26.2 days to hatch but fifth eggs taking 22–23 days. Like MacCluskie et al. (1997), however, Nicolai et al. (2004) were unable to detect a relationship between the rate of embryonic development and metabolic rate. Because faster-developing embryos may offset the metabolic costs of faster growth by decreasing the metabolic costs of maintenance, a relationship between developmental rate and metabolic rate may not be expected (Vleck et al. 1980, Konarzewski et al. 2000).

Variation in egg size within a clutch may also play a role in synchronization. Across species, there is a strong relationship between the size of a bird's egg and the length of its incubation (Carey et al. 1980, Zimmermann and Hipfner 2007). Within a species, a similar, albeit much weaker, relationship is apparent (Martin and Arnold 1991, Arnold 1993). Parsons (1972) proposed that birds may use this relationship to influence the developmental synchrony of their embryos. In most waterfowl, egg size increases with each successive egg until the egg associated with the onset of incubation is laid, after which egg size decreases (Cooper 1978, Slagsvold et al. 1984, Leblanc 1987, Robertson and Cooke 1993, Flint et al. 1994, Williams et al. 1993, Boonstra et al. 2009). Although this pattern has also been associated with resource partitioning among young (Boonstra et al. 2009), Flint et al. (1994) proposed a model demonstrating how this pattern of egg-size variation within a clutch should promote synchronization of development.

The results of Nicolai et al. (2004) indicate that variability in egg size and constituents alone allows the eggs laid last to develop approximately 3 days faster than those laid first, so egg size and composition alone could serve as an adequate mechanism for synchronizing development in the Black Brant. Furthermore, through an egg-manipulation experiment, Davies and Cooke (1983) demonstrated that Snow Geese (*Chen caerulescens*) are capable of hatching eggs with asynchronous embryonic development of 2 to 3 days without extending the incubation period but cannot hatch embryos developmentally delayed by 4 days without the incubation period being extended. Therefore, if embryonic development is delayed at a level expected through normal incubation patterns (2–3 days), previously reviewed mechanisms allow all eggs to hatch synchronously within a normal period of incubation. The amplitude of developmental asynchrony, however, increases with clutch size (Kennamer et al. 1990). Dabbling ducks lay clutches of 8–12 eggs, and developmental asynchrony can be >5 days by the completion of the clutch (Huggins 1941, Caldwell and Cornwell 1975, Bellrose 1980, Kennamer et al. 1990, Loos and Rohwer 2004). Although there is currently no way to determine how much egg size and composition may help synchronize the development of dabbling duck embryos, the failure of MacCluskie et al. (1997) to identify a relationship between an egg's position in the sequence of laying and the time its incubation required when held under constant conditions certainly suggests the relationship is weak at best and

unlikely to be adequate to compensate for 5 days of developmental asynchrony.

We propose the physical position of the egg within the nest during incubation as an alternative mechanism that may work alone or in combination with one of the previously described mechanisms to synchronize the development of duck embryos. Clutches of 6 or more eggs tend to form a circle with some eggs being on the periphery of the clutch, the others in the center, surrounded on all sides by the peripheral eggs. This positioning of eggs in the clutch leads to a gradient of temperature, the central eggs being incubated at a temperature as much as 5.6 °C higher than the peripheral eggs (Huggins 1941, Caldwell and Cornwell 1975). Because the relationship between incubation temperature and rate of embryonic development is positive (Prince et al. 1969), we propose the egg's position in the clutch as an alternative mechanism by which waterfowl laying clutches of ≥ 6 eggs synchronize their development. We hypothesize that eggs laid later with less developed embryos are located in the center of the clutch more often than are eggs laid early and so are incubated at a higher temperature, develop faster, and hatch more synchronously. We tested this hypothesis by comparing the developmental stage of central and peripheral eggs and testing for a relationship between an egg's position in the sequence of laying and its position (central or peripheral) within the clutch. We predicted, at least during early incubation when developmental asynchrony should be greatest, that eggs located in the center of the clutch should be less developed than those on the periphery and that eggs laid later should be found in the center of the clutch more often than expected under a random distribution.

METHODS

To test this hypothesis, from April to July 2008 we recorded the sequence and position of the eggs in more than 900 dabbling duck nests on four 9324-ha plots near Bruno, Petersen, Plunkett, and Dixon in the prairie grassland and parkland regions of central Saskatchewan, Canada. We located nests by dragging a modified cable-chain behind two all-terrain vehicles (Klett et al. 1986), driven at a speed of $\geq 8 \text{ km hr}^{-1}$ so as to increase the chance of hens flushing from their nests. To maximize our likelihood of encountering a nest when the hen was present, we searched for nests daily from 07:00 to 14:00 (Klett et al. 1986). Once we located a nest, we marked it with an orange rod directly north of the nest bowl and a numbered wooden post 10 m to the north of the nest. We identified the central eggs and labeled each egg in the nest with a different letter. In the uplands of our study area, duck nests of > 6 eggs have one peripheral ring of eggs and a single or multiple central eggs surrounded on all sides by the peripheral ring. We then candled the eggs to determine their stage of incubation on a modified Weller scale (Weller 1956, see Discussion for details). We revisited the nests every 8 days, labeling any

new eggs, recording which eggs were located in the center of the clutch, and the stage of incubation of the central and one randomly selected peripheral eggs. If there were more than three new eggs, we labeled them with a letter, as we had the previous eggs. If there were three or fewer new eggs, however, we labeled them with a number (to minimize the potential for misclassification) and recorded their incubation stage and placement in the nest on each subsequent visit. We assumed that these numbered eggs were the clutch's last eggs.

LOCATION OF LAST EGGS

Because we visited nests only every 8 days, the number of last eggs we were able to identify in each nest varied from one to three. In other words, in some nests we were able to identify only the final egg, while in others we were able to identify the last two or three. Additionally, because clutch sizes varied from 6 to 12 eggs, the probability of a last laid egg's being central varied with the number of eggs known to be one of the last three and the size of the clutch. Because in most nests the probability of one of the last eggs being located in the center of the clutch on each visit was unique, our options for the statistical analysis were limited to a Cochran–Mantel–Haenszel test (Proc Freq, SAS 9.1) in a $n \times 2 \times 2$ contingency table with order in which the egg was laid (one of the last three vs. all others) as the explanatory variable, location in the clutch (central vs. peripheral) as the response variable, and nest number (n) as the control variable. Because embryonic development may be synchronized prior to the completion of incubation, we analyzed the egg-location data in two ways, one with data from the first 12 days of incubation only, the other with data from the entire incubation period.

VARIATION IN EMBRYO DEVELOPMENT

We used an analysis of variance (ANOVA, Proc GLM, SAS 9.1) to compare the stages of embryo development in central and peripheral eggs on each visit to a nest. If more than one egg was central, we averaged those eggs' developmental stage. As in the analysis of egg distribution, we analyzed the embryo-development data twice, once using data from the first 12 days of incubation only and once using data from the entire incubation period.

RESULTS

LOCATION OF LAST EGGS

Of the nests we located, 45% were of the Blue-winged Teal (*Anas discors*), 22% of the Gadwall (*A. strepera*), 18% of the Northern Shoveler (*A. clypeata*), 11% of the Mallard, and 1% each of the American Wigeon (*A. americana*), Green-winged Teal (*A. crecca*), Northern Pintail (*A. acuta*), and Lesser Scaup (*Aythya affinis*). We found strong evidence that an egg's location in the nest was dependent on the order in which it was laid. The last three eggs were found in a central position more

often than expected both when we considered data from the first 12 days of incubation only (136 nests visited 139 times; $\chi^2 = 5.47$, $P = 0.019$) and when we considered data for the entire incubation period (136 nests observed 225 times; $\chi^2 = 6.90$, $P = 0.009$).

VARIATION IN EMBRYONIC DEVELOPMENT

We located 976 nests in which the clutch was complete but within the first 12 days of incubation, as determined by egg candling. Results of the ANOVA indicate a marginally significant difference in developmental stage between embryos in central eggs (mean = 6.3 days of incubation) and those in peripheral eggs (mean = 6.6 days of incubation; $F_{974} = 2.74$, $P = 0.098$). But the analysis of data from the entire incubation period suggested no difference in the stage of embryonic development between central and peripheral eggs ($F_{1,1962} = 0.65$, $P = 0.421$).

DISCUSSION

In a detailed study of incubation behavior of the Mallard, Caldwell and Cornwell (1975) found evidence that late in incubation eggs are not randomly distributed in the clutch, some being central more often than would be expected under a random distribution. They speculated that heavier eggs may gravitate toward the center of the clutch because of the rounded shape of the bottom of the nest bowl, but they provided no indication that an egg's position in the clutch may be related to the order in which it was laid. We found strong evidence of a relationship between an egg's position in the clutch and its position in the sequence of laying with later eggs being found in the central position more often than expected, supporting our hypothesis. Embryos in Mallard eggs maintained at 39.4 °C developed 165 hr (6.8 days) faster than those in eggs maintained at 35.6 °C (Prince et al. 1969). Therefore, although egg size and composition may also play a role in the synchronization of embryonic development, the temperature gradient of 5.6 °C between the central and peripheral eggs observed by Huggins (1941) and Caldwell and Cornwell (1975) indicates that egg positioning alone could be adequate to overcome the 5 days of developmental asynchrony observed in dabbling ducks. Positioning of eggs with less developed embryos in the center of the nest could be achieved actively by the hen or passively through the size and density of eggs and shape of the nest bowl.

As embryos develop, they use water and nutrients for maintenance and growth and release carbon dioxide along with other waste gasses, leading to a decrease in the egg's density (Rahn and Ar 1974, Carey et al. 1980). Therefore, because of their greater density, eggs with the least developed embryos should gravitate toward the center of the clutch. We found a discernable difference between the development of central and peripheral eggs during the first 12 days of incubation only, while eggs laid later were more likely to be in the center of the clutch throughout incubation. This difference

suggests that variation in egg density due to developmental asynchrony may not play a large role in egg position. Alternatively, as a duck lays a clutch, the size of its eggs appears to decrease progressively (Slagsvold et al. 1984). If the last eggs are smaller, even if their density is similar to that of earlier eggs, they should gravitate toward the center of the clutch. Therefore egg size may explain the pattern in egg distribution we observed.

It is also possible that hens are able to assess embryo development and actively place eggs with less developed embryos in the center of the clutch. Hens appear to be very good at assessing the condition of the eggs and embryos, maintaining temperature and humidity precisely enough to outperform humans with incubators. Hens reposition eggs numerous times a day to ensure hatchability (Caldwell and Cornwell 1975). There is no information available regarding the ability of hens to assess the health and development of the embryos, but if hens are able to determine embryonic development, they certainly have the opportunity to actively maintain the least developed eggs in a central position.

Given the preponderance of evidence that hens begin incubating before completing the clutch, we were surprised that the evidence for less development of the central eggs was not stronger. We believe the weakness of this relationship is most likely due to the inherent subjectivity and imprecision in the technique we used to estimate embryonic development. Weller (1956) categorized development of duck eggs into seven stages (fresh, 4, 8, 12, 16, 20, and 22 days) and described embryonic development at each of the stages. To increase precision, we attempted to identify developmental stages intermediate between those categories when it appeared appropriate. For example, if an embryo's developmental stage appeared to be somewhere between 4 and 8 days, but closer to 8 than to 4, we recorded it at 7 days of development. Even with the considerable error likely associated with egg candling we found weak evidence for a difference in development between central and peripheral eggs only during the first half of incubation, while the last eggs were more likely to be in the center of the clutch throughout the entire incubation period. Thus some if not all of the developmental asynchrony was corrected by mid incubation, supporting the assertion of Nicolai et al. (2004) that while vocalization may help synchronize hatching, it has little influence on overall development. Chicks vocalize only 2–3 days prior to hatching after >90 % of their embryonic development is complete and after most asynchrony appears to have been compensated for (Vince 1964, Vleck et al. 1980). An alternative interpretation of our results is that variance associated with measurement error increases as embryos develop, though we found no evidence to indicate this was the case.

In conclusion, numerous mechanisms may be acting to promote synchrony in development and hatching within clutches of precocial birds. Although it is unclear whether the mechanism influencing placement of eggs in the clutch is active or passive, our results indicate this placement is one of

potentially many mechanisms by which birds laying large clutches ensure developmental synchrony of their embryos.

ACKNOWLEDGMENTS

We thank Delta Waterfowl Foundation and Southern Illinois University, Carbondale (SIUC), for funding and support of this study. We are grateful to the landowners of Bruno, Petersen, Plunkett, and Dixon, Saskatchewan, for allowing us to search for nests on their property. Thank you to J. Dassow, M. Moore, A. Dath, J. McMahonill and E. Bulla for providing assistance in the field. Activities during this study were approved by the SIUC Institute of Animal Care Use Committee protocol 05-057.

LITERATURE CITED

- AFTON, A. D. 1979. Incubation temperatures of Northern Shoveler. *Canadian Journal of Zoology* 57:1052–1056.
- AFTON, A. D., AND S. L. PAULUS. 1992. Incubation and brood care, p. 62–108. *In* B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [EDS.], *Ecology and management of breeding waterfowl*. University of Minnesota Press, Minneapolis, MN.
- ARNOLD, T. W. 1993. Factors affecting egg viability and incubation time in prairie ducks. *Canadian Journal of Zoology* 71: 1146–1152.
- ARNOLD, T. W., F. C. ROHWER, AND T. ARMSTRONG. 1987. Egg viability, nest predation, and the adaptive significance of clutch size in prairie ducks. *American Naturalist* 130:643–653.
- BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. Stackpole, Harrisburg, PA.
- BOONSTRA, T. A., M. E. CLARK, AND W. L. REED. 2009. Maternal resource variation across the laying sequence of Canada Geese *Branta canadensis maxima*. *Journal of Avian Biology* 40:520–528.
- CALDWELL, P. J., AND G. W. CORNWELL. 1975. Incubation behavior and temperatures of the Mallard duck. *Auk* 92:706–731.
- CAREY, C., H. RAHN, AND P. PARISI. 1980. Calories, water, lipid, and yolk in avian eggs. *Condor* 82:335–343.
- COOPER, J. A. 1978. The history and breeding biology of the Canada Geese of Marshy Point, Manitoba. *Wildlife Monographs* 61.
- DAVIES, J. C., AND F. COOKE. 1983. Intracut hatch synchronization in the Lesser Snow Goose. *Canadian Journal of Zoology* 61:1398–1401.
- FLINT, P. L., M. S. LINDBERG, M. C. MACCLUSKIE, AND J. S. SEDINGER. 1994. The adaptive significance of hatching synchrony of waterfowl eggs. *Wildfowl* 45:248–254.
- GLOVER, F. A. 1956. Nesting and production of the Blue-winged Teal (*Anas discors* Linnaeus) in northwest Iowa. *Journal of Wildlife Management* 20:28–46.
- HOYT, D. F., R. G. BOARD, H. RAHN, AND C. V. PAGNELLI. 1979. The eggs of Anatidae: conductance, pore structure, and metabolism. *Physiological Zoology* 52:438–450.
- HUGGINS, R. A. 1941. Egg temperatures of wild birds under natural conditions. *Ecology* 22:148–157.
- JOHNSON, T. W. 1974. A study of Mottled Duck broods in the Merritt Island National Wildlife Refuge. *Wilson Bulletin* 86:68–70.
- KENNER, R. A., W. F. HARVEY IV, AND G. R. HEPP. 1990. Embryonic development and nest attentiveness of Wood Ducks during egg laying. *Condor* 92:587–592.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish and Wildlife Service Resource Publication 158.
- KONARZEWSKI, M., A. GARVIN, R. McDEVITT, AND I. R. WALLIS. 2000. Metabolic and organ mass responses to selection of high growth rates in domestic chickens *Gallus domesticus*. *Physiological and Biochemical Zoology* 73:237–248.
- LEBLANC, Y. 1987. Egg mass, position in the laying sequence, and brood size in relation to Canada Goose reproductive success. *Wilson Bulletin* 99:663–672.
- LEOPOLD, F. 1951. A study of nesting wood ducks in Iowa. *Condor* 53:209–220.
- LOOS, E. R., AND F. C. ROHWER. 2004. Laying-stage nest attendance and onset of incubation in prairie nesting ducks. *Auk* 121:587–599.
- MACCLUSKIE, M. C., P. L. FLINT, AND J. S. SEDINGER. 1997. Variation in incubation periods and egg metabolism in Mallards: intrinsic mechanisms to promote hatch synchrony. *Condor* 99:224–228.
- MARTIN, P. A., AND T. W. ARNOLD. 1991. Relationships among fresh mass, incubation time, and water loss in Japanese Quail. *Condor* 93:28–37.
- MUNRO, J., AND J. BÉDARD. 1977. Crèche formation in the Common Eider. *Auk* 94:759–771.
- MÜLLER, W., M. LESSELS, P. KORSTEN, AND N. VON ENGELHARDT. 2007. Manipulative signals in family conflict? On the function of maternal yolk hormones in birds. *American Naturalist* 169:E84–E86.
- NICOLAI, C. A., J. S. SEDINGER, AND M. L. WEGE. 2004. Regulation of development time and hatch synchronization in Black Brant (*Branta bernicla nigricans*). *Functional Ecology* 18:475–482.
- PARSONS, J. 1972. Egg size, incubation date, and incubation period in the Herring Gull. *Ibis* 114:536–541.
- PERSSON, I., AND G. ANDERSSON. 1999. Intracut hatch synchronization in pheasants and Mallard ducks. *Ethology* 105:1087–1096.
- PRINCE, H. H., P. B. SIEGEL, AND G. W. CORNWELL. 1969. Incubation environment and the development of Mallard embryos. *Journal of Wildlife Management* 33:589–595.
- ORCUTT, A. B. 1974. Sound produced by hatching Japanese Quail as potential aids to synchronous hatching. *Behavior* 50:173–184.
- RAHN, H., AND A. AR. 1974. The avian egg: incubation time and water loss. *Condor* 76:147–152.
- ROBERTSON, G. J., AND F. COOKE. 1993. Intracut egg size variation and hatching success in the Common Eider. *Canadian Journal of Zoology* 71:541–549.
- SLAGSVOLD, T., J. SANDVIK, G. ROFSTAD, O. LORENTSEN, AND M. HUSBY. 1984. On the adaptive value of intracut egg-size variation in birds. *Auk* 101: 685–697.
- SLATTERY, S. M., AND R. T. ALISAUSKAS. 1995. Egg characteristics and body reserves of neonate Ross' and Lesser Snow Geese. *Condor* 97:970–984.
- VINCE, M. A. 1964. Social facility of hatching in Bobwhite quail. *Animal Behaviour* 12:531–534.
- VLECK, C. M., D. VLECK, AND D. F. HOYT. 1980. Patterns of metabolism and growth in avian embryos. *American Zoologist* 20:405–416.
- WELLER, M. W. 1956. A simple field candler for waterfowl eggs. *Journal of Wildlife Management* 20:111–113.
- WILLIAMS, T. D., D. B. LANK, AND F. COOKE. 1993. Is intracut egg-size variation adaptive in the Lesser Snow Goose? *Oikos* 67:250–256.
- WOOLF, N. K., J. L. VIXLY, AND R. R. CAPRANICA. 1976. Prenatal experience and avian development: brief auditory stimulation accelerates the hatching of Japanese Quail. *Science* 194:959–960.
- ZIMMERMANN, K., AND J. M. HIPFNER. 2007. Egg size, egg shell porosity, and incubation period in the marine bird family Alcidae. *Auk* 124:307–315.