Ornis Fennica 78:23–29. 2001

Male incubation in Northern Lapwings: effects on egg temperature and potential benefits to females

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Received 29 June 1999, accepted 22 May 2000

The Northern Lapwing *Vanellus vanellus* is a polygynous shorebird where both parents incubate. However, males show great individual variation with respect to incubation constancy, possibly resulting in variable degrees of incubation costs in females. Here, the influence of male incubation on egg temperature at the end of female recesses is examined by using a theoretical model of egg cooling combined with observations of incubation rhythm and ambient temperature. Estimated egg temperatures were higher after male incubation than when the nests were left uncovered, and consequently eggs were warmer on average in nests with higher male attentiveness. I suggest that this results in higher costs of egg re-warming in females that are less helped by their males in incubation. Moreover, ambient temperatures in the period of observations never exceeded 20°C. Still, egg temperatures were significantly higher than the presumed physiological zero temperature (25°C) with male intermittent incubation. However, there was no difference when males were absent during recesses. These results could potentially indicate fitness benefits to female Northern Lapwings, male care influencing length of incubation periods and embryo survival. Such trends could not be detected in this study, though.

1. Introduction

The period of nest attendance exposes birds to energetic stress (Yom-Tov & Hilborn 1981, Vleck 1981), and incubating birds have to trade-off their own energetic and nutritional needs against the requirements of the embryos. The costs of caring per individual should therefore be negatively correlated with the degree of bi-parental care. The need for paternal care has traditionally been regarded as a main factor in maintaining monogamy in many bird species, and males may be particularly important for reproductive success when they take part in incubation (Bart & Tornes 1989).

Re-warming a clutch after absence imposes an energetic cost on incubating Zebra Finches *Poephila guttata* (Vleck 1981) and European Starlings *Sturnus vulgaris* (Biebach 1986), increasing with longer recesses and lower ambient temperature. Moreover, Tøien et al. (1986) reported that incubation on four eggs colder than 15°C stimulated a maximum heat production in Bantam Hens *Gallus domesticus*, resulting in an oxygen consumption corresponding to that expected at an ambient temperature of –65°C.

The temperature below which embryonic development stops may be important in deciding recess duration in some species (Løfaldli 1985, Haftorn 1988, Mehlum 1991). In most birds this limit is expected to lie at 25–27°C, and is termed the physiological zero temperature (Drent 1973, White & Kinney 1974, Drent 1975). Cooling might be detrimental to embryos being exposed to low temperatures for longer periods, although eggs of some species have hatched even after cooling to about 0°C (Webb 1987). However, this ability seems to vary among species and is reduced as the embryos grow older.

The Northern Lapwing *Vanellus vanellus* is a polygynous shorebird in which 20%–50% of males mate with two to four females (Berg 1993, Byrkjedal et al. 1997, Parish et al. 1997, Hafsmo et al. 2001). Males normally incubate less than females in this species; their average incubation constancy typically being about 20%–35% (Hegyi & Sasvari 1998, Parish & Coulson 1998, Liker & Székely 1999, this paper). Analyses of incubation rhythms in Northern Lapwings (Lislevand, in prep.) have demonstrated that 1) males show extensive individual variation in parental care during incubation, 2) male incubation is positively correlated with total nest attentiveness which can allow females to take longer recesses, 3) female incubation bouts last longer as the season progress, and 4) females prolong their recesses in warmer weather and stay for longer periods on the nest after long recesses. Further, females mated with polygynous males receive less help from their partners in incubation compared with those mated with monogamous males (G. Grønstøl, pers. comm.). In contrast to females being helped by their mates, females incubating alone are reported to lose weight during the incubation period and suffer from higher predation rates (Hegyi & Sasvari 1998). Consequently, female lapwings might face variable costs of incubation, as well as showing differences in reproductive success, related to the amount of care provided by their mates.

Here I use a theoretical model of egg cooling together with data on incubation rhythms and ambient temperature to estimate egg temperatures at the end of recesses in Northern Lapwings. These data are used to investigate how egg temperatures, and thus females' energetic costs of re-warming, are influenced by male intermittent incubation. I also examine if male incubation reduces the risk of egg temperatures falling below the physiological zero temperature, and discuss potential consequences to female fitness resulting from these findings.

2. Material and methods

The field work of this study was conducted in an area of arable land near Bergen, western Norway (60°19′N, 5°29′E). More detailed descriptions of the study area are given by Grønstøl (1996) and Byrkjedal et al. (1997). Pair bonds were tracked in the period preceding incubation by using individual plumage characters to separate individuals (Byrkjedal et al. 1997). When a nest was not found until the clutch was completed, I estimated laying date by counting back 30 days (the normal length of incubation periods in Northern Lapwings [Grønstøl 1996]) from the day of hatching. Nest monitoring was carried out during daylight hours (08:00–21:00) for a total of 18 nests between 24 April and 21 May 1995. Nests were watched through a telescope from elevated ridges close to the fields, 5–26 days after the first egg was laid. Observation bouts lasted on average 243.6 ± 126.3 (SD) minutes, and total observation times for individual nests varied from 923 to 2.919 minutes. I recorded start and end of incubation sessions with an accuracy of one minute for both mates. Males were observed on all nests, but in one case the male was killed by a predator at the onset of incubation, resulting in a very low male incubation constancy. Data on wing length and body mass were collected from 11 females that were trapped on their nests.

Data on air temperatures on the study site are available from 3 May. These were measured in the shade about 15–30 cm above ground every hour during nest monitoring. Temperatures in the preceding period were estimated by using observed temperatures and data from a meteorological station about 25 km from the study site in a linear regression (linear regression: temp. at study site = 1.18 (temp. at meteorological station) – 0.26, $R = 0.92$, $P < 0.001$). I estimated temperatures in the centre of eggs by using cooling curves (per egg) from Olsen (1986) which were measured under standard laboratory conditions in four-egg clutches of Northern Lapwing eggs filled with silicone. Three replicates of these measurements were given for each of three different ambient temperatures (5, 10 and 20°C) at 75% relative ambient humidity. All the variables except the cooling constant k could be found from the curves. Because an egg's cooling rate is constant and in accordance with Newton's law of cooling (Kendeigh 1973), the cooling rate is proportional to the difference between egg-temperature and ambient temperature. Based on this law, the cooling constant could be found from the equation

$$k = -\ln[T(t) - T'] - \frac{\ln[T_0 - T']}{t} \qquad (1)$$

where k = cooling constant, T(t) = temperature in the egg at time t, T′ = ambient temperature, t = exposure time (in minutes) and T_0 = egg-temperature at time 0. This was done by calculating mean values of T(t) from selected points on the three cooling curves at each ambient temperature. From 57 points I then found an average of k = 0.0627 (calculated in 1/min units). Examples of the resulting cooling curves at three different ambient temperatures are shown in Fig. 1. When calculating egg temperatures, I assumed that eggs had reached the maximum incubation temperature if one of the parents had been observed on the nest at least 30 minutes prior to the first recess. This time limit corresponds to the median length of incubation sessions for both sexes (1. quartile = 15, 3. quartile = 50, N = 437), but most of the incubation bouts used for the calculations lasted longer (median = 53 minutes, 1. quartile = 38 minutes, 3. quartile = 73 minutes, N = 107). Maximum temperature was set to be 36°C, as this is close to the nest air temperatures reported in other charadriiform species (Kendeigh 1973, Drent 1975, Webb 1987). I calculated the temperature of the eggs after a given time of re-warming by choosing the ambient temperature to be 36°C and the start temperature to be the one calculated from the preceding period of cooling. The estimated temperature of the re-warmed eggs was then used as start temperature when estimating temperatures after the next period of cooling.

My results depend on the validity of at least three assumptions: 1) the measures of ambient temperature should represent the real temperatures in the nest and be the main factor influencing egg temperature, 2) there should be no differences in incubation ability between the sexes and 3) the heat capacity of a silicone-filled egg should be comparable with that of a natural egg. However, a number of additional factors are known to affect egg temperatures; wind speed and radiation (Bakken et al. 1985), heat loss through the nest floor and differences in nest placements possibly being the most important ones. The estimates of egg temperatures may also be lower than the real egg temperatures, because the ambient temperature is probably higher at the ground than just above it. Further, silicone-filled eggs may have different heat capacities from real eggs (Webb 1987), and as it is not known how representative the laboratory measurements of egg cooling are of actual egg cooling rates this constitutes another potential source of error. Embryos produce their own heat at a certain age (Drent 1973), which may reduce the eggs' cooling rate. The significance of embryonic heat production for the estimated egg temperatures may not be considerable, though, because Drent (1973) found no heat compensation for lowered ambient temperatures in the embryos when incubating Herring Gulls *Larus argentatus* left the nest. As there is no single egg temperature, rather a gradient depending on the distance to the brooding patch (Drent 1973, 1975), cooling of eggs becomes quite complicated (Turner 1997), and may not be easily estimated. Despite these possible errors in my data, the results should provide useful insight into the effect of male incubation in Northern Lapwings, at least when looking at relative differences in incubation temperatures.

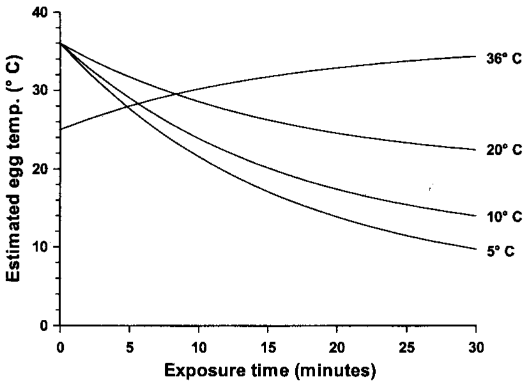

Figure 1. Estimated curve of egg re-warming from 25°C and the cooling curves for Northern Lapwing eggs at three different ambient temperatures (estimated from data in Olsen 1986).

Statistical analyses were performed using SPSS (release 6.0.) and SAS/STAT (version 6.12). Results refer to two-tailed tests with a significance level of alpha = 0.05. To achieve homogeneity of variance, I log-transformed the data on egg temperatures in the two-way nested ANOVA checking for effects of between-female differences and male incubation (Levenes test for homogeneity of variance: $F_{22} = 1.0$, $P = 0.45$). Moreover, nests with less than two observations of temperature levels either with or without male incubation were excluded from this data set.

3. Results

During recesses, female lapwings normally stayed on the territories or on other fields in the vicinity. Therefore, they were probably able to directly observe if their mates were incubating or not in most cases. The median recess duration of females was 11.5 minutes (1. quartile: 5 min., 3. quartile: 28 min., N = 388), and median duration of male incubation sessions was 35 minutes (1. quartile: 12 min., 3. quartile: 56.5 min., N = 135). Excluding the nest where the male was killed by a predator, total male incubation constancies varied from 3.7% to 45.6% (median = 21.9%, 1. quartile = 9.8, 3. quartile = 30.8, N = 17). A two-way nested ANOVA showed that male incubation had a significantly positive influence on egg temperatures at the start of female incubation sessions, while there was no effect of individual females (Table 1). As a consequence, means of egg temperatures per nest at the end of female recesses were positively correlated with male incubation constancies ($r_S = 0.64$, $P < 0.01$, N = 18, Fig. 2), but did not differ between nests of monogamous vs. bigamous males (two sample t-test: $t_{16} = -0.44$, $P = 0.67$, Fig. 2). To check if the differences in male incubation influenced female body condition, I tested for a correlation between the female body mass/wing length ratios (Galbraith 1988) and male incubation constancies, but no relationship could be demonstrated ($r_S = -0.21$, $P = 0.54$, N = 11).

Table 1. Variance table for estimated egg temperatures at the start of female incubation sessions in Northern Lapwings, with or without male intermittent incubation. Results from a two-way nested ANOVA, GLM procedure, treating each female as a random factor nested within male participation category (incubates or not).

Source	DF	SS	MS	F	P
Male participation	1	0.83	0.83	19.56	< 0.001
Individual female	24	0.98	0.04	0.96	0.52

Of the 18 nests included in this study, the incubation periods are exactly known for only six clutches, all lasting 29 or 30 days. All eggs in these nests hatched, and it was therefore not possible to detect any differences in breeding success among the females related to variation in incubation rhythm and egg temperatures.

During observations of incubation rhythms, ambient temperatures never exceeded 19.8°C in the study area (minimum = 1.5°C, mean = 11.0°C ± 4.2°C (SD), N = 81). There was therefore always a risk that temperatures in the lapwing eggs would drop below the physiological zero temperature (25°C) if the eggs were left exposed long enough. However, egg temperatures at the end of female recesses were significantly higher than this limit in cases with intermittent male incubation (mean = 29.7 ± 4.8 (SD); one-sample t-test: t = 10.2, $P < 0.001$, N = 95). In contrast, when males did not incubate, egg temperatures did not differ from 25°C (mean = 25.4 ± 5.1 (SD); one-sample t-test: t = 0.87, P = 0.39, N = 172). To examine the possibility that females responded to lowered cold tolerance as the embryos grew older, I correlated egg temperatures at the start of female incubation sessions with number of days since egg laying. No such relationship could be detected, however ($r_S = -0.02$, $P = 0.78$, N = 214).

4. Discussion

In Northern Lapwings, male incubation has a positive effect on egg temperatures at the beginning of female incubation bouts. Moreover, the data presented here indicate that females manage to keep the egg temperature above the presumed physiological zero temperature when males are incubating, but this pattern is less evident when males are absent during a recess.

The finding that females are exposed to lower egg temperatures when returning to the nest after male absence might imply that the energetic costs of rewarming decrease with increasing levels of male participation in incubation. In a relatively cold environment like the lapwing fields, birds have to increase their metabolism to keep the eggs warm (Tøien et al. 1986, Tøien 1989), and Biebach (1986) calculated that re-warming increased the energy consumption by 18% during day-light incubation in the White-crowned Sparrow *Zonotrichia leucophrys*. Thus, female Northern Lapwings could receive considerable energetic benefits from being helped by their mates. Together with increased time to spend foraging resulting from male care (Lislevand, in prep.), this could potentially have a positive effect on body condition, but there was no such trend in my data. However, the weight measurements were not standardised regarding time of day and season when they were collected, making comparisons questionable.

The estimates of egg temperatures were on average not lower than the presumed physiological zero temperature (25°C), but were significantly higher after male intermittent incubation. Because female recess duration is positively correlated with temperature and weather, as well as being shorter in periods of rain (Lislevand, in prep.), this result fits the pattern that should be predicted if birds adjusted their incubation rhythm in order to maintain continuous embryo development. It was not possible to detect any differences in embryo development and embryo survival that could be linked to variable levels of paternal care in the present work. However, as the data are sparse this issue should be subject to further studies.

The observations indicating that females adjusted their time off the nest in order to avoid egg cooling below 25°C coincide with observations in 14 passerines (Haftorn 1988) and four species of shorebirds; the Great Snipe *Gallinago media*, the Eurasian Dotterel *Charadrius morinellus*, the Temminck's Stint *Calidris temminckii* (Løfaldli 1985), and the Grey Phalarope *Phalaropus fulicarius* (Mehlum 1991). Only the present study has been carried out on a species where both mates incubate. Some uncertainties exist in the conclusions of all these studies. Only Haftorn (1988) and Mehlum (1991) measured egg temperatures directly, while the results from the remaining four species are based on estimates. Further, according to Webb (1987) the "physiological zero" is not constant among species or even between different ages within a species. I am not aware of any studies that have compared direct measurements of egg temperatures with exact knowledge of a species' physiological zero temperature in order to examine how important this temperature limit is to decide recess patterns in birds. Hence, future research on this issue is highly recommended.

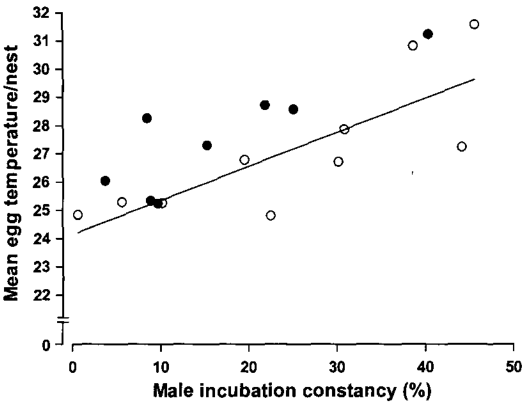

Figure 2. The relationship between mean egg temperatures at the beginning of female incubation bouts and male incubation constancies on nests of monogamous (open dots) and polygynous (filled dots) males in Northern Lapwings.

Egg temperatures were not related to age of embryos in this study, as should have been expected if females exploit the higher cold tolerance in young embryos (Drent 1975, Webb 1987) to stay longer off the nest. My data do not include the periods of egg laying (stable incubation does not occur before the clutch is completed in Northern Lapwings [own obs.]) or the last few days of incubation. It is therefore possible that egg temperatures were kept higher just prior to hatching. Nevertheless, changes in embryonic cold tolerance do not seem to be an important factor in controlling incubation rhythm of Northern Lapwings.

Acknowledgements: I am grateful to Ingvar Byrkjedal for excellent help both in the field and when writing this paper. Thanks also to Arild Breistøl who provided very useful statistical advice, and to Brage Førland who solved the mathematical puzzles of the egg-cooling model. Scott H. Stoleson and an anonymous referee are acknowledged for providing comments that considerably improved the manuscript, as are Gaute Bø Grønstøl, Göran Högstedt and Odd W. Jacobsen for fruitful discussions on different aspects of the study. I am also indebted to Euan Dunn for kindly correcting the English, and Göran Högstedt for the

Swedish translation of the abstract. The work was financially supported by the Norwegian Directorate for Nature Management and my parents Alfhild and Reinert Lislevand.

Sammanfattning: **Ruvning av tofsvipehanen: Effekten på äggtemperaturen och tänkbara fördelar för honan.**

Båda könen ruvar hos den polygyna tofsvipan *Vanellus vanellus*. Hanarna uppvisar stor individuell variation i ruvningskonstans, vilket möjligen åsakar honarna en motsvarande variation i ruvningskostnader. I detta arbete undersöktes betydelsen av hanens ruvning för eggtemperaturen vid slutet av honans recess. Med hjelp av en modell för äggavkylning i kombination med uppgifter om ruvningsrytm och lufttemperatur kunde äggtemperaturen beräknas. Dessa teoretiska värden var högre när hanen ruvade än när äggen inte ruvades och generellt var äggen varmare med ökande grad av hanruvning. Jag föreslår därför att kostnaden att återuppvärma äggen är omvendt proportionell mot den hjälp i ruvningen hanen bistår med. Trots att yttertemperaturen aldrig översteg 20 grador C var äggen signifikant varmare än 25 grador (äggens termoneutrala temperatur) efter at hanen ruvade. Sådana skillnader observerades inte efter recessar utan ruvningshjelp av hanen. Det är därför närliggande att anta att hanens ruvning kan påvärka ruvningspäriodens lengd och embryoöverlevnaden, men sådanna effekter kunde inte spåras i denna studie.

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