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## Incubation of Dead Eggs

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Prolonged incubation has been recorded in a number of bird species (Drent 1975). We discuss two types of prolonged incubation: birds that incubate a single clutch for an extended period, and birds that lay several discrete clutches in the same nest and incubate all the clutches together. We provided an example of each type in the Negev Desert, Israel, with particular emphasis on the second type, and we attempted to provide explanations for the occurrence of this behavior.

We observed the first type of prolonged incubation in a pair of Stone Curlews (*Burhinus oedicnemus*), which incubated a clutch of two eggs containing dead embryos (determined by candling) for 75 days (1 June to 14 August 1988) at Sede Boqer (30°52'N, 34°46'E). Incubation was terminated when all the Stone Curlews in the vicinity of Sede Boqer migrated. The second type was observed in a pair of Hoopoes (*Upupa epops*), also at Sede Boqer, from June to August 1988.

On 20 June 1988, the Hoopoes had an inordinately large clutch (23 eggs) in a nest located between the ceiling and roof of an unused building. The nest was enclosed, except for a small hole (ca. 4-cm diameter) through which the adults entered. Over the study period, the Hoopoes laid 32 eggs in the nest. A normal clutch for this species is 4-10 eggs, rarely up to 12 (Cramp and Simmons 1985). In Israel, the usual clutch size is 5-6 eggs (Paz 1987). When we candled these eggs, many contained dead embryos (henceforth called *dead eggs*). We plotted egg mass against egg volume and found four clusters of egg mass. These clusters corresponded with eggshell color; the darker eggs weighed less. The eggshells presumably darken with age as the result of dirt accumulation in the nest. Because eggs lose water continuously with age, with an increased rate of water loss in dead eggs (Rahn and Ar 1974), we assumed that the eggs belonged to four different clutches. This assumption was corrob-

orated in the following manner. The five heaviest eggs (shown by candling to be live eggs) were left in the nest and all the others were removed. When these eggs died, two more clutches (totaling nine eggs) were laid in sequence, each one after the eggs of the preceding clutch had died. A plot of mass against volume for these 14 eggs revealed three clusters that corresponded with the three clutches. Mass decreased with age of clutch. Thus, a total of six clutches were laid in the same nest and none was successful. The eggs of the different clutches were arranged in no obvious pattern in the nest (determined by marking eggs). On three occasions, a broken egg was removed from the nest by the birds and placed some 30 cm away.

To examine the possibility that the retention of eggs with dead embryos in the nest acted as a heat buffer to the other eggs that contained live embryos, we measured temperatures in the nest ( $T_N$ ) and in the surrounding space within the ceiling. We used copper-constantan thermocouples (calibrated against a mercury thermometer approved by the U.S. National Bureau of Standards) with an error of  $\pm 0.1^\circ\text{C}$ . One thermocouple connected to a Campbell model 21X datalogger was placed between the eggs (to record  $T_N$ ) and a second was placed 0.5 m from the nest to record temperature between the ceiling and roof ( $T_C$ ; hereafter known as ceiling temperature). Temperatures were recorded every 5 s and averaged every 15 min. We compared the mean  $T_N$  with all the live and dead eggs ( $n = 23$ ) in place (for two days and nights) to mean  $T_N$  of nests with all dead eggs ( $n = 18$ ) removed (for three days and nights).

Ceiling and nest temperatures approximated sinusoidal curves over time. We divided these data into two groups (for temperatures recorded both before and after dead-egg removal). One group had increasing  $T_N$  and the other decreasing  $T_N$ . We separated the two groups at the crests and troughs of the sinusoidal

TABLE 1. Regression of nest temperature ( $T_N$ ) on ceiling temperature ( $T_C$ ) for heating and cooling curves in a Hoopoe nest before and after dead-egg removal. All coefficients of determination were highly significant ( $P < 0.001$ ).

Regression of $T_N$ on $T_C$	$r^2$	Slope	Intercept	df	ANCOVA
Heating curve					
Nest with dead eggs	0.99	0.65	12.51	164	$F = 214.22^*$
Nest without dead eggs	0.98	0.81	8.00	336	
Cooling curve					
Nest with dead eggs	0.96	0.60	15.28	211	$F = 150.63^*$
Nest without dead eggs	0.95	0.75	9.85	527	

\*  $P < 0.001$ .

curves. We plotted a linear regression for  $T_N$  against  $T_C$  for each of the two groups for each experimental procedure. In this way, we compared heating and cooling rates of the nest when the nest contained all eggs and when it contained only live eggs. The slopes of the regression lines (Table 1) were significantly steeper after removal of dead eggs from the nest for both heating and cooling curves (ANCOVA,  $P < 0.001$ ).

In addition to differences in heating and cooling rates, we examined the mean  $\pm$  SE absolute difference between  $T_N$  and  $T_C$ . The mean  $\pm$  SE absolute difference was significantly greater ( $P < 0.05$ ,  $t$ -test) in the nest with both live and dead eggs ( $3.65 \pm 0.14^\circ\text{C}$ ) than in the nest with only live eggs ( $2.50 \pm 0.08^\circ\text{C}$ ).

We compared the proportion of time that  $T_N$  was above  $40^\circ\text{C}$  relative to the total time that  $T_C$  was above  $40^\circ\text{C}$  for both experimental procedures. The deep-body temperatures of birds are ca.  $40^\circ\text{C}$  (Whittow 1986). As a result, we chose  $40^\circ\text{C}$  as the temperature above which it was likely to be difficult for Hoopoes to control egg temperature, particularly because the birds were unable to use convective cooling in this enclosed nest. When the nest contained dead and live eggs,  $T_N$  was above  $40^\circ\text{C}$  for 81% of the time (11.25 h) that  $T_C$  exceeded  $40^\circ\text{C}$ . When the nest contained only live eggs,  $T_N$  was above  $40^\circ\text{C}$  for 100% of the time (20.66 h) that  $T_C$  exceeded  $40^\circ\text{C}$ .

The incubation of a single clutch for an extended period, as recorded in the Stone Curlew, also occurs in other bird species (e.g. *Oceanites oceanicus* [Beck and Brown 1972], *Pachyptila desolata* [Tickell 1962], *Charradius vociferus* [Powers 1978]). Drent (1975) suggested that prolonged incubation was a functional response caused by the inherent variability in incubation period. Holcomb (1970) reviewed some of the records of prolonged incubation and suggested that birds prolonged incubation by 50–100% in excess of the normal period (75% on average) to provide a safety margin in case of slow embryo growth. The incubation period of the Stone Curlews in this study (75 days) was 288% longer than the normal period (26 days; Paz 1987). It is unlikely that this was to provide a safety margin to embryo growth. We suggest that prolonged incubation in this species is due to the absence of a be-

havioral releaser to terminate incubation. Incubation was only terminated when the birds migrated, the stimulus to migrate apparently being stronger than that to continue incubating.

The second type of prolonged incubation has rarely been reported. Livne (1972) reported a European Goldfinch (*Carduelis carduelis*) that incubated three clutches simultaneously, of which only the eggs of the last-laid clutch hatched. The total incubation period for this goldfinch female was 110 days, the normal incubation period for this species is 13 days (Paz 1987).

One advantage to retaining dead eggs in the nest lies in the heat-buffering capacity of dead eggs. Both cases of birds that retained dead eggs in the nest which also contained live eggs occurred in the summer in the Negev Desert. In the Hoopoe nest, dead eggs appeared to act as a heat buffer. Dead eggs reduced heating and cooling rates of the nest, and increased the absolute difference between  $T_N$  and  $T_C$ . Moreover, when dead eggs were in the nest, the percentage of time that  $T_N$  remained above what we consider to be the limit of the birds' ability to control nest temperature ( $40^\circ\text{C}$ ) was reduced considerably. Retention of dead eggs in the nest appears to improve heat-buffering capacity.

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## Himalayan Birds Face Uphill While Singing

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Animal vocalizations are not omnidirectional. A few species such as bats are able to beam their transmissions (Schnitzler and Grinnell 1977); in many species there is an acoustic shadow behind and beside the animal (Archibald 1974, Gerhardt 1975, Witkin 1977), probably produced by sound wave interference patterns (Hunter et al. 1986). Laboratory experiments in which various sounds were broadcast from the mouth of a European Starling's (*Sturnus vulgaris*) body and rerecorded in three planes determined that the acoustic shadow effect was strongest behind and below the bird, i.e. in the direction of the tail (Hunter et al. 1986). I observed the orientations of birds singing on steep slopes which imply that their choice of direction may be affected by the directionality of their vocalizations.

In March and April 1980, four colleagues and I observed 40 different birds that sang on steep slopes in the Kulu and Ravi valleys of the Western Himalayas, India (see Gaston et al. 1983 for a description of the study area). We recorded the orientation to slope (upslope, downslope, or parallel), beak level with respect to a horizontal plane (the bisector of the angle formed by the mandibles was within 15° of level, or up, or down), bird species, time, tree height, perch height, and tree height relative to forest canopy. In March 1988, I made eight similar observations in the Langtang area of central Nepal. The observations were made on 21 species of passerine (sample sizes >1 are indicated in parentheses): *Dicrurus leucophaeus*, *Hypsipetes madagascariensis*, *Pomatorhinus erythrogenys*, *Garrulax lineatus*, *Culicicapa ceylonensis*, *Seicercus xanthoschistos*, *Erithacus cyanurus*, *Phoenicurus frontalis* (3), *Saxicola ferrea* (4), *Monticola cinclorhynchus*, *Turdus boulboul*, *T. viscivorus*, *Parus monticolus* (4), *P. melanolophus* (8), *P. rubidiventris* (2), *P. dichrous*, *Sitta leucopsis* (3), *Anthus hodgsoni*, *Coccothraustes icteroides* (8), *C. affinis* (3), and *Pyrrhula erythrocephala*. (Taxonomy follows Ali and Ripley 1983.) Only initial observations were recorded, not subsequent changes,

and thus each observation represented a different individual.

Of the 48 observations, 37 were upslope, 9 parallel to the slope, and 2 were downslope. If birds were oriented without respect to slope, the distribution would presumably be 25% upslope, 50% parallel, and 25% downslope. The observed distribution differs significantly from the expected ( $\chi^2 = 69.79$ ,  $P \ll 0.005$ ). Even with a very conservative interpretation in which 50% of the observations were expected to be upslope and 50% parallel or downslope, the observed and expected still differ ( $\chi^2 = 13.04$ ,  $P \ll 0.005$ ). Steepness of slope (range 35-70%), tree height (2-38 m), and perch height (2-38 m) had no detectable relationship with orientation. However, most of the perch heights recorded were quite high ( $\bar{x} = 92\%$  of tree height); we probably undersampled birds that sang from low, inconspicuous perches, and these birds may have had a different orientation.

The directionality of sounds emitted by birds will differ depending on whether they face upslope or downslope (Fig. 1). Sounds produced by birds that face upslope will carry relatively far in that direction because sound emission in front of a bird and above horizontal is relatively strong. For the same reason, the sounds produced by birds that face downslope will carry best up into the air and not be readily heard near the ground. Unless there is a need to communicate with birds flying overhead, this may explain our observation that birds almost never sing facing downhill. It is probably not possible for birds to correct for this effect by changing the orientation of their beak because the beak has virtually no effect on directionality (Hunter et al. 1986). Other anatomical constraints may inhibit birds from leaning forward or lowering their beaks to sing. We recorded 28 cases in which the beak was held above the horizontal, 9 in which it was level, and none in which it was pointed down.

There are some alternative explanations for the ob-