EGG LAYING OF A GOLDEN PLOVER *PLUVIALIS APRICARIA*

On 17 June 1966, 07.00 hours, a female landed approximately 50 m. from a nest, which I later found 1 km. north of Rössebo, Dalsland, Sweden. She stood still with neck upstretched, then ran a few metres, stopped and looked, ran again—and so on. When flushed, she flew low for about 100 m. and then stood erect giving alarm calls. I was unable to find the nest. Had there been an egg I feel certain that I would have found it. When I left the area and hid at 07.30, the female flew to within 30 m. of the nest and then slowly returned to it. Half an hour later I flushed her and found a single cool egg. The nest involved a considerable structure built up about 25 cm. above ground on top of a small clump of moss and grass. The female did not go to the nest again that day.

At 06.00 hours, 18 June, two plovers circled the marsh and flew away. When about 400 m. from the nest, the female left her mate and returned to the marsh. She landed some distance from the nest and then ran to it in spurts. There she sat until 07.30 when she called and flew off. At 07.50 she returned, landed about 100 m. from the nest and began feeding. I flushed her at 09.00 and she flew toward the nest and sat there calling as I approached. There were two cool eggs in the nest.

At 15.00 hours, 19 June, the female was sitting on three warm eggs. I did not take egg temperatures but the eggs did not feel as warm as when under full incubation. The nest at this time did not differ noticeably from when I first found it. I was unable to follow further the progress of this nest.

Nethersole-Thompson (*in* Bannerman 1961, ' The Birds of the British Isles ', Vol. 10) stated that the male sometimes waits for a female while she is laying or brooding an early egg. In this case he did not. My observations coincide with those of Nethersole-Thompson regarding the start of incubation for he stated that although intermittent brooding sometimes occurs after the laying of the first egg, true incubation does not begin until after the third, or more often, the fourth egg is laid. Brooding started after the third egg was laid but I do not believe incubation began then. Nethersole-Thompson found the interval between laying of many eggs to be 48–60 hours (exceptionally 120). He did not mention intervals shorter than 48 hours. Jourdain (*in* Witherby *et al.* 1940, ' Handbook of British Birds', Vol. 4.) stated that the normal interval between the laying of eggs was 48 hours. In the case of the nest here described, I believe the second egg was laid 22·5–24 hours after the first; and that the third was laid no more than 31·5 hours after the second. The latter interval is accurate even if an egg had been laid before I first saw the female go to the nest. Just why the laying interval was so much shorter than previously reported I do not know. Perhaps it can be accounted for by individual variation; perhaps there is some relationship to the fact that the eggs were laid so late in the year.

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NOTES ON THE CLICKING OF AVIAN EGG-YOUNG, WITH COMMENTS ON ITS MECHANISM AND FUNCTION

In a recent paper suggesting the synchronization of hatching by stimuli emanating from eggs, Vince (1966, ' Anim. Behav. ' 14: 34–40) briefly reviewed the published comments on the possible origin of the clicking sound which is produced by the young of nidifugous birds while in the egg. She notes that this sound has been considered by some to be due to contact between bill and shell, and that others, including myself, have connected it with respiratory movements. This would seem to be a fair survey of the

basic comments published on this particular behaviour. It is not entirely true, however, to say that " The mechanism underlying the clicks and also their function remain obscure ". This does less than justice to my own brief note on the subject which reported numerous clicking observations, and one purpose of this communication is to plead for the continued recognition of the value of " simple " descriptive science. We perhaps should remember the comments of Bernard (1865, ' An Introduction to the Study of Experimental Medicine ') that " experimental reasoning is absolutely the same, whether in sciences of observation or in experimental sciences, " and that " a naturalist observing animals in all the conditions necessary to their existence, and deducing from these observations consequences verified and controlled by other observations—such a naturalist uses the experimental method even though he performs no experiments, properly speaking ".

In my note of 1965 (' Nature, Lond. ' 206: 315) I pointed out that the suggestions that the clicking was the result of bill-shell contact could hardly be tenable as the shell membranes, against which the bill is pressed, are soft and moist, and that the bill with its egg-tooth are enclosed in the mucous-like layer which at this time covers the whole of the young bird. It is clearly impossible for such an apparatus to produce a sharp—sometimes even metallic—clicking. Further, the upward nodding movements of the head which result in the pipping of the shell are, for the most part, slow and deliberate (Driver 1960, ' Behaviour Studies in Sea Ducklings '). The sounds produced by the bill-shell pressure are complex creaking and breaking sounds, and these, with the rapid " swallowing " sounds produced by hyoid movements, are quite distinct from those of clicking (Driver & Gunn 1961, ' B.B.C. disk no. 25101 '; Driver 1962, ' Anim. Behav. ' 10: 388–389).

Vince (1966, ' Anim. Behav. ' 14: 34–40) quotes Breed (1911, ' Behav. Monogr. ' 1:(1)) who reports that in chick embryos observed through holes in the shell " the clicking sounds seemed to accompany the rhythmical heavings of the animal which I took to be breathing ". I have noted (Driver 1965, ' Nature, Lond. ' 206:315) that the simple technique of cutting a hole in the shell makes it possible to observe movements and sounds directly and simultaneously, and that my observations, on many species, indicate that clicking always accompanies respiratory movements and continues for some hours after hatching. Vince, however, comments that clicking " has not been investigated in any detail ".

As there seems to be some doubt on these points this may be an opportune moment to present the observational data more clearly, particularly as they may have relevance to the problems of the mechanism and function of clicking.

TECHNIQUES AND OBSERVATIONS

I have observed clicking, and its temporal connexion with respiratory movements, in numbers of individuals varying from a few to over a hundred, in thirteen species of Anseriformes, four species of Galliformes, two species of Gruiformes, and five species of Charadriiformes (for detailed list, see Driver 1967, ' Quail Q. ' 4: 5–11).

Observations have been made on eggs of a variety of species hatching under natural conditions, and on selected eggs placed in an incubator. Eggs hatching naturally have been studied at the time when the end of the shell is almost broken off, and the young bird may be seen relatively clearly. Observations have also been made on newly-hatched young.

In incubator-hatched eggs an observation hole has been cut through the shell and outer shell membrane into the air space at the blunt end of the egg. The holes were positioned asymmetrically so that the shell was not weakened and normal hatching behaviour was not interfered with. The air space is at its maximum volume shortly before hatching, and the bird's head, or at least its bill, can be clearly seen, having

broken through the inner shell membrane into the air space. The observation holes were kept covered with adhesive plaster when observations were not being made. There was no apparent interference with hatching as a result of these operations.

For up to three days prior to the bird emerging from the egg—the period varying with the species and other circumstances—clicking and vocalizations can be heard from the egg. In my studies this period has begun with the rupture of the inner shell membrane by the bill of the young, the bill thus entering the air space, connecting the animal's respiratory system with a gaseous medium for the first time. There has only been one exception to this, which was a young Pied-billed Grebe *Podilymbus podiceps* in a well-incubated egg. This animal vocalized with the inner shell membrane intact. No clicking was observed in any egg-young with the inner shell membrane intact.

Observations made in the simple manner here described show that the clicking sounds always accompany the respiratory movements of ventilation. They are irregular in that an inspiratory or expiratory movement does not always result in audible clicking. Also, clicking may be coincident with inspiration and/or expiration, and this may vary in an individual bird over time. Further, the clicking not infrequently has a creaking quality, making the sound quite distinct from " normal " clicking. Any change in ventilation rate is partnered by a change in rate of clicking. When the bird vocalizes each note is frequently accompanied by a click. The clicking has persisted for some hours after hatching in all young birds observed in this study, and it can then be clearly observed that the clicking sounds are temporally connected with movements of inspiration and/or expiration (Driver & Gunn 1961, ' B.B.C. Disk no. 25101 '; Driver 1962, ' Anim. Behav. ' 10: 388–389). These observations on the connection between clicking and respiration confirm and amplify those of Breed (1911, ' Behav. Monagr. ' 1: (1)), and of Goethe (1955, ' Z. Tierpsychol. ' 12: 402–433) for the Herring Gull *Larus argentatus*, and Lind (1961) for the Black-tailed Godwit *Limosa limosa*. Vince (1966, ' Anim. Behav. ' 14: 34–40) also notes that clicking " may be heard in the early stages of lung ventilation soon after the sound of breathing becomes audible as a very faint click in time with the breathing. After this clicking may sometimes be intermittent (there may be gaps when breathing may be heard without any sound of clicking) but it becomes louder and louder and finally regular loud clicking begins, which over-rides the sound of breathing ".

DISCUSSION

The observations outlined above strongly suggest that the mechanism of clicking is connected with that of the respiratory movements. It is difficult to understand Vince's comment that " it may be possible to link the occurrence of clicking with developmental stages in the embryo such as the sealing off of the allantoic circulation and drawing in of the yolk sac, which may be observed through windows in the shell ". If clicking is so clearly connected with respiratory movements the most profitable line of investigation must be to seek its origin within the respiratory system itself. The nature of the sound is such that we would expect a vibrating surface and resonating chamber to be involved, as in so many animal acoustic signals. The alternative possibility of a stridulating mechanism is an unlikely one. It is also unlikely that any of the other internal organs could work in such a way as to produce a clicking sound.

As clicking is apparently restricted to the general hatching period, beginning and ending up to roughly 24 hours from the time of emergence, we may suspect that an organ system that begins to function during that time is involved. Taken with the other evidence this suggests that clicking is a result of the operation of the newly-functioning respiratory system (Driver 1965, ' Nature, Lond. ' 206: 315). Clicking could thus be due to movements of the cartilages of trachea, bronchi, or syrinx, the sounds gradually ceasing as use consolidates the tissues and controls of the respiratory system.

If clicking be an accidental consequence of the respiratory system's early operation, we would not necessarily assume clicking to be functional—in the usual sense of the term. That there is no apparent difference between the clicking of species which do, and do not, synchronize their hatching (Vince 1966, ' Anim. Behav. ' 14: 34–40) is to be expected.

Experiments are now being developed to investigate the operational connection between clicking and the movements of respiration. If clicking is accidental in origin, and if it is operational in the synchronization of hatching, it will provide an interesting example of fortuitous behaviour being turned to an animal's advantage.

ACKNOWLEDGMENTS

This work was begun while I held a Carnegie Arctic Research Scholarship and field grants from the Arctic Institute of North America, with Mr. C. W. Nicol as assistant. I am also greatly indebted to Professor J. Stanley of McGill University, Professor N. Tinbergen, F.R.S. of the University of Oxford, Dr. A. H. Hochbaum of The Delta Waterfowl Research Station, Manitoba, and Professor J. R. Platt of the University of Michigan. All have provided advice, encouragement and facilities. For permission to work in the Ravenglass gullery, Cumberland, I thank Major G. Pennington and the Cumberland County Council. I also acknowledge the support of grant MH 07147 from the National Institute of Mental Health, U.S. Public Health Service.

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17 February 1967.

MIGRANT WADERS IN THE INDIAN OCEAN

While working on the R.R.S. " Discovery " during the International Indian Ocean Expedition in 1963 and 1964, I observed small numbers of waders at sea in the Indian Ocean. Details of the ship's itinerary can be found in reports published by the Royal Society (1963, 1964, 1965, ' International Indian Ocean Expedition, R.R.S. " Discovery " Cruise Reports ' 1–3), but a brief summary of our cruises during the recognised seasons of migration is given here to indicate the extent of our coverage. In the autumn of 1963, the " Discovery " was working primarily in the central Arabian Sea and in the seas between the Seychelles Is. and East Africa; in spring 1964, the ship was working primarily in mid-ocean; while in autumn 1964, the ship undertook a survey of the eastern Somali coast. My observations of land-birds other than waders have been published elsewhere (Bailey 1966, ' Ibis ' 108: 421–422).

Several species of waders are, clearly, regular and abundant non-breeding migrants to the islands of the western Indian Ocean. Earlier published records (mostly summarized by Watson, Zusi & Storer 1963, ' Preliminary Field Guide to the Birds of the Indian Ocean '. Smithsonian Inst.) show that eight species are particularly widespread, namely the Turnstone *Arenaria interpres*, the Grey Plover *S. squatarola*, the Greater Sand-plover *Charadrius leschenaultii*, the Whimbrel *Numenius phaeopus*, the Curlew *N. arquata*, the Greenshank *Tringa nebularia*, the Common Sandpiper *Actitis hypoleucos*, the Sanderling *Crocethia alba*, and the Curlew Sandpiper *Erolia testacea*. Of these, the Turnstone is probably the most abundant. For all these species the islands of the Indian Ocean are clearly an important wintering area.