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SHORT NOTE

Accidental or intentional eggshell breakage? A report of intriguing observations in dunnocks (*Prunella modularis*)

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The avian eggshell is an important protective structure that supports embryonic development (Deeming 2002). Eggshells must withstand the pressure of the incubating parent, but also allow successful hatching (Birchard & Deeming 2009). These 2 opposing evolutionary forces result in a highly specialised structure that predominately remains undamaged during incubation. Eggshell breakage in the nest, therefore, is atypical even if eggs are unfertilised or embryos are not viable. Here we detail 3 events of unusual eggshell breakages immediately after which the females abandoned their nests. We discuss possible explanations for these abnormal incidents of breakage, including physical failure and intentional egg pecking behaviour.

We studied the reproductive biology of a population of dunnocks (*Prunella modularis*) in the Dunedin Botanic Garden (45° 51′ S, 170° 31′ E) from September 2014 to January 2015. We intensively searched for nests, and then followed the egg laying order, the duration of incubation, and brooding of young. We placed data loggers (Hobo Pro U23-003, Onsetcomp Inc, USA) in 12 dunnock nests to compare the temperature within the nest to that of ambient temperature (note that only 1 of 3 nests discussed in this note was subject to temperature monitoring - Nest B). We found a total of 79 nests with an average clutch size of 3.1 eggs (range = 2-4, SD = 0.6), and the average duration of incubation was 11.8 days (SD = 0.9). After incubation, we observed combinations of hatchlings, eggs with non-visible embryos (which were likely unfertilised), and eggs with developed but non-viable embryos. We observed that eggshells of those unhatched eggs (55.6% with non-visible embryos, n = 35, and 44.4% of non-viable embryos, n = 28) remained in an undamaged condition. Nonetheless, we observed unusual breakages of the eggshell (Fig. 1) in 3 nests (6 eggs in total) that were in the final days of incubation.

Nest A was found on 9 November 2014. From 16 November, 4 eggs were incubated for 12 days (female with the band ID: A183475, New Zealand

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Fig. 1. Eggshell breakages observed in Nest A. Damaged eggs (bottom, left and top) were all fertilised, whilst the undamaged egg (right) did not contain a visible embryo.

National Bird Banding Scheme). On the 13th day, the eggs were found cold and the nest deserted. Of the 4 eggs, 3 were cracked on 1 side, through the eggshell but without damage to either the outer and inner membranes (Fig. 1). The cracks extended from the middle of the shell to the tip and after further examination, a rotting embryo was found within each. The remaining egg was undamaged and did not contain a visible embryo.

Nest B was found on 25 November 2014. Incubation of 3 eggs (female band ID: A185111) started on 1 December and continued for 13 days. On the 14th day, 2 of the eggs were found with the same cracking patterns observed in the eggs of Nest A. The eggshells had been cracked, but without the outer and inner membrane being punctured. The cracks extended from the middle of the shell to the tip, and within both eggs a rotting embryo was found. As found with Nest A, the remaining egg was undamaged and did not contain a visible embryo.

Nest C was found on 4 January 2015. It contained 3 eggs, which were already in the process of being incubated (female band ID: A183566). Upon finding the nest, an egg was already found cracked on 1 side but the crack differed in both shape and size to the egg cracks in the previously described nests. The clutch was incubated for a further 2 days before a chick hatched from 1 of the undamaged eggs. Upon further examination, another crack had appeared on the already damaged egg. This crack was located on the opposite side of the egg and exhibited similar cracking patterns to the eggs of Nests A and B, with the outer and inner membranes intact. Inside the cracked egg, a dead embryo was found whilst the undamaged egg did not contain a visible embryo.

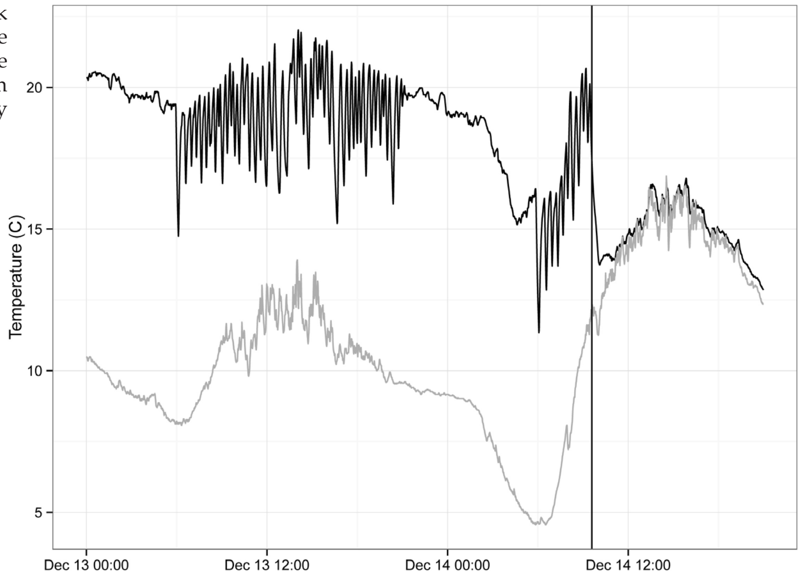
In all 3 cases (nests A, B and C) in which we observed egg breakage, the damaged eggs had visible embryos, but we suggest that those embryos did not cause the breakage in a hatching attempt. First, the egg breakage extended from the middle to the top of the egg, and the inner membrane was not broken (Fig. 1). In a normal hatching sequence, the inner membranes are punctured and the shell cracked along the equator of the egg. Second, the embryos were found in an early stage of development and thus too young to have initiated hatching. The egg breakage, therefore, rather than caused by the embryos, might be a result of failure in the physical condition of the eggshell. Other potential causes of the egg breakage might be adult pecking behaviour. We evaluate and discuss both possibilities below.

Two physical processes may have weakened the eggshell, causing the breakage described. On the one hand, pore formation is a process essential for maintaining a suitable environment for embryonic development (Kutchai & Steen 1971; Burton & Tullett 1985), allowing the developing embryo to respire (Soliman *et al.* 1994). Whilst such a process is a necessity, the pore system could potentially make the eggshells more brittle, threatening their integrity (Ar *et al.* 1979). On the other hand, external environmental conditions, for example, pollutants in the form of air-borne heavy metals and soil acidification may limit calcium availability for embryos to extract during development. Such a limitation ultimately produces a thinner shell, which compromises the integrity of the egg (Nybø *et al.* 1995; Graveland & Drent 1997; Eeva & Lehikoinen 2004). There is, consequently, the possibility that during incubation the female inadvertently crushed the eggs that potentially exhibited weakened shells. Yet, it is intriguing why the breakage only happened in only 6 of *ca.* 250 eggs.

Breakages in dunnock eggshells directly by adult birds have been previously reported as a consequence of male-male competition (Davies 1985). Davies suggested that if the beta males in a socially polyandrous group were unable to copulate with the female to the point of guaranteed paternity they may, albeit uncommonly, destroy the eggs in an attempt to recover opportunities for copulation. We, however, found that eggshell breakage happened just before or at the onset of hatching, which limits the likelihood of a male-male competition behaviour causing these breakage incidents.

Interestingly, in the 3 nests discussed, the females were incubating beyond the average length of the incubation period (> 11.8 days). Therefore, at that point, females had to 'decide' to either continue their incubation or desert the nest. Such a critical 'decision' might have lead females to inspect the

Fig. 2. Nest B temperature (black line) and environment temperature (grey line). Note that the female deserted the nest around 09:30 am on 14 December 2014 (indicated by the vertical black line).



egg viability before departure (note that females abandoned their nests just after the eggs cracked, see Fig. 2 for nest B as an example). However, this idea is questionable as the eggshell breakages observed show extensive breakage in the calcareous shell layer whilst the membranes remained intact. Alternatively, we would expect a pattern such as localised puncture marks if the female inspecting behaviour were responsible for the damage.

In conclusion, it remains unclear whether these unusual incidents of eggshell breakage were caused by a physical failure of the egg or induced by parental behaviour. Although we propose that the former is more likely, further research is necessary to support this idea. We suggest studying these types of incidents in-depth because they may provide insights into the factors that could have caused the physical failure of these eggshells. Additionally, because events of egg failure are not common, long-term studies are of great value in this regard. Recent advances in field ornithological techniques, including video recording and detailed measurements of the eggshell characteristics, such as shell thickness and pore structure would potentially help provide answers to the questions raised in this short note. Future research should focus on elucidating whether shell thickness and pore structure varies across females, whether this is related to these breakage events, and if it is, what may be causing the variability in eggshell structure.

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