

Alien egg retrieval in common pochard: Do females discriminate between conspecific and heterospecific eggs?

David Hořák^{1,2,*} & Petr Klvaňa^{2,3}

¹⁾ Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic (corresponding author's e-mail: horakd@centrum.cz)

²⁾ Department of Zoology, Faculty of Science, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic

³⁾ Bird Ringing Centre, National Museum, Hornoměcholupská 34, CZ-102 00 Praha 10, Czech Republic

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Incorporation of unrelated eggs into a clutch by incubating females (egg retrieval), which has an obvious adaptive value when female retrieves her own egg, seems to be also a part of the reproductive tactics related to brood parasitism. In open nesting waterfowl, the parasitic egg remains frequently outside the nest bowl after the parasitic event. Using time-lapse video recorders, we described experimentally the behavioural reaction of the common pochard (*Aythya ferina*) females towards an egg lying beside the nest. We tested whether the females discriminate between conspecific and heterospecific eggs (brown chicken eggs). All 16 experimental females retrieved both conspecific and heterospecific eggs. We found no apparent differences in female responses towards either egg type. The retrieval of alien eggs can be a result of an imperfect recognition ability of the female, anti-predation defence, or sophisticated tactic related to the brood parasitism. The last explanation seems to be less likely due to imperfect egg recognition abilities in the species.

Introduction

Egg retrieval is defined as incorporation of an unrelated egg into a clutch by an incubating female. It has been observed in several ground nesting waterfowl species (Pevett & Pevett 1973, Duncan 1984, Lank *et al.* 1991). Egg retrieval seems to be, however, also a part of the reproductive tactics related to brood parasitism. In lesser snow geese (*Chen caerulescens caerulescens*), parasites lay their eggs preferentially

to occupied nests where it can be difficult to dislodge the owner female. Then, the parasite female is forced to lay her egg outside the nest bowl and must rely upon the host that will adopt the egg, which frequently happens (Lank *et al.* 1989). The similar situation occurs in open nesting duck species. The parasite and the host meet frequently at the host nest (McKinney 1954, Nudds 1980, Saylor 1996, Sorenson 1997, Hořák & Klvaňa 2008). In such cases, the incubating host remains sitting at the nest and the parasite tries to push the

host female aside the nest. The aggressive interaction of the host is limited to pecking or biting the parasite to the beak or head (McKinney 1954, Sayler 1996, Hořák & Klvaňa 2008) but sometimes no aggression is observed (Nudds 1980). After a short time interval the parasite lays an egg and leaves the nest. Because of fighting and quick movements resulting in changes in nest structure, some of the eggs may drop out of the nest bowl. This could even be an important cost of parasitism in the hosts (Sorenson 1997). The egg of the parasitic female may, however, remain also outside the nest bowl due to her inconvenient laying position (Sayler 1996, Hořák & Klvaňa 2008). In such cases, when the parasite leaves, the host female retrieves occasionally the alien egg among her own eggs (Hořák & Klvaňa 2008). This ensures the appropriate thermal conditions for the developing embryo in the parasitic egg.

The above described behaviour includes an apparent conflict in duck reproductive tactic. On one hand, the host female shows a sort of aggressive reaction towards the intruder, though it is rather slight. On the other hand, the host female retrieves the intruder's egg, if laid outside the nest bowl. Such a response of the host towards the parasite is striking. By definition, the brood parasitism should have an adverse effect on the host fitness, which has been reported in many host-parasite systems (Davies 2000). However, ducks belong to precocial species, which have no demanding parental care after hatching (Afton & Paulus 1992). Therefore, the costs of parasitism are supposed to be relatively low when compared with altricial species (Dugger *et al.* 1999, Dugger & Blums 2001, Roy Nielsen *et al.* 2006a). Low costs of parasitism may serve as an explanation of relatively weak anti-parasite response in ducks. But yet, there seems to be no apparent reason to accept an alien egg laying outside a nest. In fact, such behaviour might be a by-product of a simple instinctive motor pattern (Lorenz & Tinbergen 1938) when the incubating female just protects her own eggs dropped accidentally out of the nest and consequently retrieves the alien egg presumably because she is incapable to recognise it. Indeed, there seems to be no strong selection for evolution of such recognition ability in ducks. However, another possible explanation exists. Recent studies have

proposed that laying eggs into nests of conspecifics can be advantageous for both the parasite and the host. The advent of molecular techniques has suggested the importance of kin selection as the possible process driving the evolution of the conspecific brood parasitism in ducks (Andersson & Åhlund 2000, Andersson 2001). Therefore, if there is a high relatedness between the parasite and the host, the retrieval of an alien egg may increase the inclusive fitness of the host as has been predicted by the theoretical model (Lopez-Sepulcre & Kokko 2002).

In the present study, we endeavour to describe experimentally the egg retrieval in an open nesting duck species. We performed a simple egg addition experiment in the common pochard (*Aythya ferina*) — a representative of *Aythiini* tribe in which conspecific brood parasitism occurs frequently (Rohwer & Freeman 1989, Yom-Tov 2001). At our study sites, the species is a semi-colonial breeder which is frequently parasitized by conspecifics as well as other duck species particularly by tufted duck (*Aythya fuligula*) (D. Hořák unpubl. data). The aims of this paper are (i) to describe the reaction of an incubating female towards an experimentally added alien egg, and (ii) test whether the female's behaviour differs towards the conspecific and heterospecific egg.

Material and methods

The field data were collected in 2006 (six nests) and 2008 (ten nests) within the Třeboň Basin Biosphere Reserve (49°08'N, 14°44'E) and Poodří Landscape Protected Area (49°45'N, 18°09'E) in the Czech Republic. The two localities did not differ in overall environmental characteristics and all monitored nests were situated in the similar type of vegetation. Nest searching was realised on islands within artificial fishponds from mid-May to mid-June from 10:00 to 17:00 (CET). We located nests by observing the swimming females and systematic searching the vegetation in surroundings of potential nest locations. In found nests, we recorded the clutch size and estimated the phase of incubation using candling (Weller 1956). Only clutches of average size (8 ± 0.5 , $N = 16$) and at the beginning of incuba-

tion (1–7 day of incubation) were included into the experiment. Nests were visited only once before the recording started. We recorded vegetation density using a cover box (Rivers *et al.* 2003), type and maximum height of vegetation at each nest. Then, we performed experiments on nests with similar vegetation cover characteristics to rule out the effect of vegetation cover. For the nest recording we had three independent video systems. Each set consisted of a miniature black-and-white camera with high resolution, a time-lapse video recorder (VCR; Mitsubishi HS-1096E). The camera was set up approximately 30–50 cm from a nest, and ca. 30 cm above the ground. We aimed it down at the nest to monitor the nest bowl and the closest environs. All nests were recorded for three days when we used 96-hr mode (2 frames s^{-1}) and standard 4-hour VHS videotapes.

Experiment

We simulated a parasitic event by introducing a heterospecific egg (non-mimetic brown chicken egg which is similar to pochard's egg in size and shape but differs in colour) and conspecific egg (fresh pochard egg collected from non-experimental nest within the study area). As a control treatment we made a visit during which no egg was added. The order of treatments we set random. We placed the egg outside the nest ca. 10 cm off the nest rim and recorded the nest continuously without disturbing for 24 hours. During the next visit we replaced the egg by another egg type or no egg was added (control treatment). We viewed all videotapes from start to finish on fast-forward mode to detect whether the female had not later removed the parasitic egg from the nest. We analysed the female's behaviour after her arrival at the nest. We recorded the time from arrival to discovering of the parasitic egg, her reaction to the parasitic egg, and time from the egg discovery to egg retrieval. We determined the discovering of the parasitic egg as the bill contact with the egg.

Values are presented as means \pm 1SE. In statistical analyses, treatments within each nest were treated as dependent samples. We used Mann-Whitney *U*-test, Wilcoxon matched pair

test, and Freidman ANOVA for data analyses. Statistical analyses were performed in Statistica 6.0 (StatSoft Inc. 2004).

Results

Description of female behaviour

In total, we recorded the behaviour of 16 breeding females. We found no differences between two study years (localities) in any of tested variables (Mann-Whitney *U*-test: all $P > 0.14$), thus we pooled the data for further calculations. In two cases, the monitoring systems failed and we obtained only information whether the experimental eggs were retrieved or not. It follows that we gathered video data about behaviour of 14 females in total. When coming to nest, the majority of females (12) behaved in a similar way. Following time values represent the within female means calculated from all relevant treatments. Having approached to the nest, females looked to the nest for 50.8 ± 5.7 ($N = 12$) seconds on average. Then, they sat down on the eggs and started preening behaviour, repairing nest rims and vegetation cover in the vicinity of the nest. During the nest reparation females found the experimental egg (except from control treatment). The interval between sitting on the nest and touching the experimental egg was 73.0 ± 27.3 ($N = 12$) In 49.7 ± 29.2 ($N = 12$) seconds on average after locating the experimental egg, females retrieved it and continue in comfort behaviour and nest reparation. When females stopped repairing the nests rims and changing their sitting position, we considered the process of coming to the nest finished. On average, it was after 189.4 ± 23.7 ($N = 12$) seconds from sitting down on the nest. There were some slight differences in reactions of two experimental females which are therefore not included in the descriptive computations above. The first one reacted differently on the conspecific egg. This female put the egg inside the nest immediately after approaching the nest i.e. before sitting on the nest (after 8 seconds from coming to the nest). The second one discovered and retrieved the conspecific egg after a longer period (after 87 minutes and 31 seconds, and 88 minutes and 1 second, respectively) when she was already

calmly sitting on the nest. Those females, however, showed no differences in behaviour during other treatments, if compared with the rest of the sample.

Differences among experimental treatments

In all 16 cases females retrieved both the conspecific as well as heterospecific experimental eggs. In 14 females in which behavioural recordings were available, we tested between-treatment differences in duration of particular phases of “coming to the nest” behaviour (a period between sitting on the nest and finishing the comfort behaviour and nest reparation). We did not find any differences in total time spent by “coming to the nest” behaviour between experimental treatments — addition of conspecific egg, chicken egg, and control (Friedman ANOVA: $\chi^2 = 3.167$, $N = 12$, $df = 2$, $P = 0.205$). Similarly, we found no between-treatment differences in the time interval between sitting on the nest and experimental egg location (Wilcoxon matched pair test: $Z = 0.314$, $N = 12$, $P = 0.754$), nor in the interval between locating and retrieving the experimental egg (Wilcoxon matched pair test: $Z = 1.490$, $N = 13$, $P = 0.136$). Two females mentioned above were excluded from two former analyses due to differences in behavioural pattern. One of them could be used for the latter analysis because we were able to identify the period between egg location and its retrieval. But after all, the limited information provided by statistical analyses should be noted because of low statistical power of the tests (no higher than 28% in all behavioural analyses).

Discussion

In the present study, we endeavoured to describe experimentally the reaction of the common pochard females towards alien eggs placed close to their nests. The results of our manipulative experiment show no basic differences between the female reactions towards the conspecific and heterospecific egg. The experimental females

accepted all eggs placed nearby their nests independently to which treatment group they belonged. Typically, the females retrieved the egg after sitting down on the clutch. One of the females, however, retrieved the egg immediately after arriving to the nest before sitting down and another one after longer period. We explain those excesses by difference in time of the egg discovery. Females usually discover the egg during nest reparation at the beginning of the incubation bout. The odd females presumably discovered the egg immediately after arrival to the nest or much more later when changing incubating position. Such differences are rather caused by randomness or variation in relative egg location than differences in perception abilities of individual females.

The acceptance of eggs located in the vicinity of the nests is a common behaviour in ground nesting waterfowl (Prevett & Prevett 1973, Lank *et al.* 1989, Lank *et al.* 1991) even the retrieval of heterospecific eggs has been reported for waterfowl species (Duncan 1984). Why to retrieve an alien egg which did not drop from the nest but was rather laid by another female? Several hypotheses have been proposed (Lank *et al.* 1991). First, it may be caused by low recognition ability of an individual. The female may retrieve an alien egg because is not able to recognize it from her own eggs. It has been previously shown in birds that females can discriminate their own eggs from foreign eggs (Lahti & Lahti 2002, Lyon 2007). However, it does not need to hold true in all species even if they are closely related (Saino & Fasola 1993). Moreover, the alien egg recognition ability is probably low in common pochard (and waterfowl in general) because its eggs have no shell patterning which is the important clue for egg recognition (Lahti & Lahti 2002). In any case, our results support “the low recognition ability hypothesis” because all females retrieved a heterospecific egg which differed markedly in colour. The second possible explanation for alien egg retrieval comprises the protection of the nest against potential predators (Lank *et al.* 1989) as any single egg laying close to the nest is a conspicuous object within the surrounding environment. According to this hypothesis the female should retrieve all eggs laying

around her nest independently of their origin. Accumulation of alien eggs in the nest should be, of course, physically constrained by the nest size or incubation ability of the female. Indeed, not all eggs laid beside nests are accepted by nesting females (Lank *et al.* 1989). Within our study areas, one or more eggs laid outside the nest are found near approximately 10% of all nests located (D. Hořák & P. Klvaňa unpubl. data). Based on our results we cannot reject the “anti-predation defence hypothesis”. At the first step, the comparison of egg retrieval rates among different environments would be more informative. The third, and the most sophisticated explanation, which harbours an inclusive fitness advantage should be considered. The female may retrieve an alien egg because it was laid by a close relative. By adopting the egg, the host female provides adequate thermal conditions for development of the egg of the parasite and if it survives the host female gains inclusive fitness benefits (*sensu* Andersson & Åhlund 2000). The results of Roy Nielsen *et al.* (2006b) have recently implied that the retrieval of an alien egg might be a part of a sophisticated tactic. They showed that parasites choose hosts randomly but the hosts presumably more likely accept the eggs of close relatives. Presumptions of the evolution of such sophisticated behaviour are either the existence of kin recognition among females or a high probability that the parasite coming to the nest is a close relative of the host. The latter case may be facilitated for instance by philopatry of females breeding at a locality (*see* Andersson & Waldeck 2007 for discussion). Our data did not support the existence of kin recognition based on egg appearance in the common pochard, because females did not discriminate even between conspecific and heterospecific eggs. However, we excluded the effect of the physical contact between the host and the parasite. Perhaps, nesting females can better discriminate between kin and non-kin duck than between kin and non-kin egg. Clearly, such scenario seems to be more likely. Kin discrimination in a conspecific parasitic system is reported in goldeneyes (*Bucephala clangula*) (Andersson & Åhlund 2000; but note that the role of kin selection in evolution of conspecific brood parasitism is questioned in the species, *see* Pöysä 2003,

2004) and possibly other duck species (Semel & Sherman 2001). The probability of an egg to be retrieved might be then influenced by information obtained during female-female interaction. However, to be successful, parasites should preferably lay eggs when the host female is in the laying stage. Otherwise, the parasitic eggs would have an incubation delay and do not hatch on time. During egg laying phase the females are not continuously at the nest which lowers the probability that the parasite and the host meet each other. Consequently, it plays down the individual based kin recognition in evolution of egg retrieval behaviour. Despite, the time spent by the duck females on the nests is reported to increase during laying sequence (Sorenson 1997, Åhlund 2005) and, moreover, host females may be present at their nest during majority of parasitic events (Sorenson 1997). Unfortunately, we do not have information about proportion of time spent by the females common pochards at their nest during early stages of breeding not even about the frequency of host-parasite interactions at the nests. In our experiment, no female under any treatment got into contact with any other conspecifics as well as representatives of other duck species. Although, we only had a view of the close vicinity of the nest, not of a wider area around it, we believe that acceptance of an alien egg lying close to the nest was not influenced by the presence of other individuals around the nest.

In conclusion, a parasitic egg occasionally drops out of the nest during the parasitic event in ground nesting ducks (Saylor 1996, Hořák & Klvaňa 2008). We described experimentally the reaction of the incubating female of common pochard towards such an egg. Moreover, our results show that the female does not discriminate between conspecific and heterospecific eggs when retrieving them. We highlight the conflict in the reproductive tactics which results from adoption of an alien egg. It can be explained by imperfect recognition abilities of the females, anti-predation defence, or sophisticated tactic related to brood parasitism. The last explanation seems to be, however, less likely due to lack of sufficient egg recognition abilities and lower probability of meeting the parasite during early egg laying period.

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