

Commentary

# Processes underlying parental care decisions and crèching behaviour: clarification of hypotheses

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*Received 30 March 1999, accepted 7 April 1999*

Pöysä, H. & Milonoff, M. 1999: Processes underlying parental care decisions and crèching behaviour: clarification of hypotheses. — *Ann. Zool. Fennici* 36: 125–128.

Crèching behaviour, or brood amalgamation, resulting in offspring being reared by adults other than their genetic parents, is widespread among animals and several hypotheses have been proposed to account for the behaviour (Eadie *et al.* 1988). In a recent article, Eadie and Lyon (1998) examined the topic by focusing on two important processes involved in brood amalgamation: brood desertion and brood adoption. As concerns the first-mentioned process, they presented a graphic model to determine when it would be profitable for a parent to desert its brood and tested the model experimentally in a field study with Barrow's goldeneyes (*Bucephala islandica*).

We appreciate Eadie and Lyon's (1998) effort to shed light on the long-lived but still unsolved problem (e.g., Eadie *et al.* 1988, Afton & Paulus 1992, Beauchamp 1997). However, we identified potential flaws in their work that need to be addressed. The problems we discuss here relate directly to mechanisms in processes underlying crèching behaviour (*see* also Bustnes & Erikstad 1991, Pöysä 1995). Our commentary has also a more general implication that relates to model building according to the hypothetico-deductive procedure (e.g., Haila 1982, Southwood 1982). In the first part of the critique, we bring up one fundamental problem in Eadie and Lyon's (1998)

experimental design and analyses. In the second part we show how that problem calls the basis of their model into question. Specifically, we clarify differences between two hypotheses that have been proposed to affect parental care decisions, especially in goldeneye ducks (Pöysä *et al.* 1997), i.e. hypotheses that were intermingled by Eadie and Lyon (1998). We consider it important to clarify the hypotheses to avoid confusion in future studies of the topic.

## Problems with experimental design and analyses

Using a graphical model combining the costs and benefits of staying with the present brood, Eadie and Lyon (1998) suggested that there is a threshold brood size below which parents should abandon their current brood in favour of future reproductive opportunities. To test the desertion threshold model, Eadie and Lyon (1998) experimentally manipulated broods of 12 Barrow's goldeneye females by removing ducklings within 24 h after hatching, before the broods left the nest. The 12 experimental broods were reduced to an average size of  $3.5 \pm 0.2$  ducklings; using preliminary observations of natural broods Eadie and Lyon

(1998) suggested that Barrow's goldeneye females were more likely to desert young broods with less than five ducklings. Hatched broods of 14 other females were maintained as controls, brood size at hatching of these broods being  $9.6 \pm 0.8$  ducklings. Hence, the rationale behind the experiment is that brood size at hatching is a reasonable measure of both fitness and the desertion threshold.

The experiment raises several concerns. Here we consider only how the authors analysed and interpreted females' response to brood size, i.e. a problem that directly relates to their desertion threshold model. Eadie and Lyon (1998) knew for sure that four of the manipulated broods were left by the female, whereas four other manipulated broods were not (they did not know for sure the fate of the remaining four broods). Eadie and Lyon (1998) do not give the original sizes of the reduced broods but there must have been variation in their sizes as there was among the control broods (range 5–15 ducklings; cf. Eadie & Lyon: fig. 2). Because the broods were reduced to an average size of 3.5 ducklings, rate of reduction might have differed considerably between the broods. Reduction rate might have been higher in those broods that were deserted than in those that were not. Alternatively, there might have been more mortality after the nest exodus, but before desertion, in those manipulated broods that were deserted than in those that were not.

Similarly, it was surprising and contrary to the proposed brood size threshold model that two control broods of 7 and 8 ducklings were deserted (Eadie & Lyon 1998: fig. 2). One explanation might be that also in these broods there was mortality after the nest exodus but before the broods were deserted. The authors do not mention anything of possible mortality in the manipulated or control broods after nest exodus. However, we would be very surprised if there was no mortality in any of the 10 abandoned broods before desertion or in any of the 16 broods that were not deserted within comparable time. If mortality occurred, then brood sizes the authors give in fig. 2 do not reflect actual brood sizes at the moment of desertion. Furthermore, in the observational study, brood size of deserted broods was  $3.0 \pm 0.3$  ducklings and that of nondeserted broods  $8.0 \pm 0.5$  ducklings. If the 14 broods used as controls in the experiment represent, as they should, average

broods in their study area (i.e., average size 9.6 ducklings), then there must have been on average 69% mortality before abandonment in the deserted broods and 17% mortality in the nondeserted broods of comparable age in the observational study. In fact, the authors reveal (p. 400) that there was brood mortality in the observational study and, therefore, they used the number of young censused immediately prior to desertion rather than the number of young at hatch. So, in the experimental study (Eadie & Lyon 1998: fig. 2) the authors used brood sizes at hatching without mortality (except the one caused by manipulation in the 12 broods; but see above for the possibility of additional mortality in the experimental broods) whereas in the observational study (Eadie & Lyon 1998: fig. 3) the authors used brood sizes after mortality that had occurred after nest exodus. We consider the comparison between their experimental and observational results rather problematic.

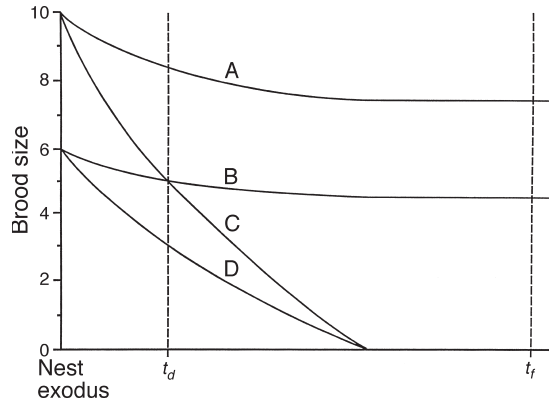
Summarising, there must have been brood mortality both in the experimental study and in the observational study prior to desertion, i.e. information that is necessary for correct interpretation of the experiment and analyses (*see* also below). However, the authors fail to consider this mortality. This is surprising, because they were aware of an earlier study in which it was shown that congeneric common goldeneye (*B. clangula*) females based their decision of desertion on previous brood success, or brood mortality, and not on brood size (Pöysä *et al.* 1997). We have good reason to suspect that the finding with common goldeneyes applies as well to Barrow's goldeneye females, and should be considered. Because the mortality rate probably varied considerably between the broods in Eadie and Lyon's (1998) study, and this variation was not controlled for in the analyses, one cannot be sure that brood size *per se* affected brood desertion.

### **Desertion threshold: brood size or brood success?**

The fundamental assumption in the Eadie and Lyon's (1998) desertion threshold model is that brood size *per se* affects desertion; neither in the definition of the desertion threshold nor in the tests

of the model do the authors mention anything about the role of brood mortality prior to desertion. Specifically, judging from their experiment, Eadie and Lyon (1998) assume that brood size at hatching is a reasonable measure of the desertion threshold. However, as we have indicated above, the authors confound brood size and brood mortality prior to desertion. There are two distinguishable hypotheses for parental effort or, as in this case, for brood desertion: the 'brood size' hypothesis and the 'brood success' hypothesis, both of which are based on parental investment theory (see Pöysä *et al.* 1997; see also Carlisle 1982). The reproductive value of the current brood depends on both the number of young and the survival prospects of each of them. Thus, parents may provide more care to larger broods either because of the direct effect of brood size *per se* on reproductive value (the brood size hypothesis), or because past mortality as reflected by current brood size, predicts future mortality of the brood, and hence, its reproductive value (the brood success hypothesis). Thus, according to the brood size hypothesis, brood size *per se* is a reasonable cue for desertion whereas, according to the brood success hypothesis, brood mortality rate prior to the decision is a correct cue for desertion. Because there was an alternative and more plausible hypothesis available, we find Eadie and Lyon's (1998) model building a bit odd in the light of the hypothetico-deductive procedure (e.g., Haila 1982, Southwood 1982). Considering what was found earlier with the two hypotheses, Eadie and Lyon (1998) should have falsified the brood success hypothesis before basing their model on the brood size hypothesis. Instead, they build their model on a hypothesis that had been falsified in an earlier study.

To make the difference between the hypotheses as clear as possible we consider a simple hypothetical but biologically reasonable example. Let's assume a sample of four broods in which brood mortality rate is independent of brood size (Fig. 1), as it appears to be in goldeneye broods (Milonoff *et al.* 1995, Eadie & Lyon 1998). The decision whether to desert or not is made by the females at a reasonable point of time  $t_d$  after nest exodus; fledging takes place at  $t_f$ . Broods A and C are of equal size at hatching as are broods B and D. Broods A and B both experience 17% mortality prior to  $t_d$  and 10% mortality between  $t_d$  and  $t_f$ .



**Fig. 1.** A hypothetical example illustrating differences in the predictions of brood desertion between the brood size and brood success hypotheses. The decision whether to desert or not a brood is made at the moment of  $t_d$  after nest exodus;  $t_f$  indicates the moment of fledging (time scale irrelevant). Broods A and B experience a 17% mortality prior  $t_d$  and a 10% mortality between  $t_d$  and  $t_f$  whereas broods C and D experience a 50% mortality prior  $t_d$  and, independently of the decision, completely vanish before  $t_f$ . Brood size at nest exodus or at  $t_d$  (the brood size hypothesis) does not provide a correct cue for the decision about desertion whereas brood mortality rate prior  $t_d$  (the brood success hypothesis) does.

Broods C and D both experience 50% mortality prior to  $t_d$  and completely vanish before  $t_f$ . As we have shown with actual data for common goldeneyes (Pöysä *et al.* 1997), early brood mortality (prior to  $t_d$  in our model example) correctly predicts later brood mortality, an important assumption of the brood success hypothesis. Also, the timing of brood mortality in the example resembles reality, because brood mortality in goldeneyes usually is highest soon after nest exodus (e.g., Savard *et al.* 1991, Milonoff *et al.* 1995, Pöysä *et al.* 1997). Clearly, brood size at hatching is not a reliable cue for desertion, because it does not correctly predict the number of fledged young.

In accordance with this, but in contradiction to Eadie and Lyon's (1998) brood size threshold model, we found that brood desertion was not at all associated with brood size at nest exodus (or at hatching) despite the fact that some broods were well below the proposed desertion threshold (range of brood sizes 2–13 at hatching; cf. Pöysä *et al.* 1997: table 2). Our example further reveals that brood size at the moment of decision also does not appear to be the most reliable cue for desertion but

that the decision when to desert is based primarily on the prior mortality rate of the brood. A comparison between broods B and C makes the difference between the brood size and brood success hypotheses most clear. At  $t_d$  broods B and C are of equal size. Thus, the prediction of the brood size hypothesis would be the same for both females; yet the decisions are likely to be different. In contrast, the brood success hypothesis correctly predicts that brood C should be deserted (high mortality prior  $t_d$  predicting high future mortality) but brood B should not be deserted (low mortality prior  $t_d$  predicting high survival prospects).

We used data from 25 common goldeneye broods that were followed from hatching until the age of 40 days (from Pöysä *et al.* 1997: p. 104; see the original article for methodological details) to confirm that, indeed, early mortality rate of the brood rather than brood size at hatching is a reliable predictor of the number of fledged young. Brood size at the age of 40 days (range of brood size 0–7) was not associated with brood size at hatching (range 3–11) (Kendall's rank correlation,  $\tau = 0.114$ ,  $p > 0.30$ ,  $n = 25$ ) but it was strongly associated with the daily mortality rate during the first week (range of mortality rate 0–0.889) ( $\tau = -0.597$ ,  $p < 0.0001$ ,  $n = 25$ ) and even with the daily mortality rate during the first half of the first week (range 0–0.857) ( $\tau = -0.515$ ,  $p < 0.0001$ ,  $n = 25$ ). Also in an experimental study in which clutch size and, thus, brood size at hatching was manipulated for common goldeneyes, mean chick production was found not to differ between treatment groups (Milonoff & Paananen 1993).

Threshold mortality rate for desertion is not precisely predicted by the brood success hypothesis, however Eadie and Lyon (1998) also could not predict precisely the brood size at which desertion should occur (p. 399). We emphasize that our example simply demonstrates the difference between the two hypotheses, and is not a model with quantitative predictions. In any case, considering the biological realism of brood mortality patterns and parental care decisions in goldeneye females and the results of analyses in which both brood size and brood mortality rate have been considered simultaneously, we conclude that the brood success hypothesis provides a more reasonable basis than the brood size hypothesis to study desertion thresholds in goldeneye ducks. We suggest that the brood success hypothesis should be

considered in other studies addressing parental care decisions in general.

*Acknowledgements:* We thank J. McA. Eadie, B. E. Lyon and R. Pierotti for useful comments on the manuscript and the Evo duck research group, especially P. Nummi, P. Runko, V. Ruusila and V.-M. Väänänen for stimulating discussions about philosophical issues in doing science.

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