



## Short Communications and Commentaries

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### Intraclutch Egg-Mass Variation in Geese: A Mechanism for Brood Reduction in Precocial Birds?

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Previously, attention has been focused on the biological importance of asynchronous hatching and intraclutch egg-mass variation in altricial birds. Several hypotheses have been presented to explain the adaptive value of asynchronous hatching (for review, see Magrath 1990). One of the most-widely accepted hypotheses, which also makes predictions about the pattern of intraclutch egg-mass variation, is the brood-reduction hypothesis first proposed by Lack (1954).

Lack (1954) suggested that, at the time of egg laying, it will usually be impossible to predict food availability during the rearing period. Therefore, females would produce an "optimistic" number of eggs (i.e. as many eggs as young could be reared under optimal environmental conditions). In times when food was inadequate to raise the entire brood, it would be advantageous to reduce the size of the brood so as to increase the chances of survival and reproduction of the remaining young. Without brood reduction, each nestling would fledge underweight and would have reduced chances of reproductive success. Reduction of brood size under unfavorable conditions would also be advantageous for the parents, since they could save energy that would otherwise be lost through feeding the entire brood. For brood reduction to be effective, a competitive hierarchy among the siblings is necessary. Then the older and larger nestlings could be fed first, according to their greater begging intensity, while the younger and weaker siblings would only get food if the others were satiated. If food was scarce, the smallest nestling would quickly die of hunger, enabling parents to feed those remaining sufficiently. By contrast, if the nestlings are equally competitive, food shortage could result in poor growth of the whole brood. The competitive hierarchy among the young is brought about by asynchronous hatching, which leads to a competitive disadvantage of the younger nestlings due to age (Lack 1954). A decrease of egg mass with the laying order would add to these age-related differences and, therefore, facilitate brood reduction. An increase of egg mass with the laying order is not expected, since this would counteract the competitive disadvantage of the late-hatching young, which is required for an efficient reduction of brood size in years with sudden unfavorable conditions.

Based on the assumption that the pattern of intraclutch egg-mass variation can perhaps indicate pa-

rental strategy, Slagsvold et al. (1984) compared the relative size of the final egg (calculated as percentage deviation from mean egg size of a clutch) in a variety of bird species. They suggested that large birds should tend to adopt the brood-reduction strategy, since such birds are less vulnerable to nest predation than small birds, and predicted a negative relationship between body size of a bird species and relative size of the final egg. Slagsvold et al. (1984) found this to be true both in altricial and in precocial species. This finding supports the idea that the pattern of intraclutch egg-mass variation in a particular species indicates whether the brood-reduction hypothesis is applicable to this species.

All available studies on intraclutch egg-mass variation in geese found that the last egg is usually the lightest one within a clutch (Syroechkovsky 1975, Cooper 1978, Manning 1978, Cargill 1979 [cited in Leblanc 1987b], Ely and Raveling 1984, Leblanc 1987b, Owen and West 1988, J. Lamprecht and T. Friedl unpubl. data). According to the results of Slagsvold et al. (1984) discussed in the previous section, one would expect geese to follow the brood-reduction strategy, since they are large and heavy birds with a small final egg. There is evidence that in geese rapid follicular growth is stimulated just before or at the time of the spring migration (Ankney and MacInnes 1978, Raveling 1978, Wypkema and Ankney 1979). Thus, at the time of egg production, food availability during the following rearing period is highly unpredictable. As mentioned in the introduction, this is another requirement for the brood-reduction strategy to yield a benefit.

However, until now it has been assumed, for two reasons, that feeding of the young by the parents is a prerequisite for a brood-reduction strategy. First, parents could save energy by reducing the size of the brood under unfavorable conditions. Second and most important, brood reduction itself (i.e. death of the late-hatched and, therefore, smaller nestlings) is brought about by the parents, who provide competing nestlings with different amounts of food. Therefore, this strategy has not yet been considered practicable for geese and other precocial birds, which do not feed their young directly.

In altricial birds, feeding of the young is characterized as a "shared" component of parental effort

(Lazarus and Inglis 1978, 1986). This means that parental costs increase with brood size. In precocial birds, parental care is generally assumed to be "unshared" (Lazarus and Inglis 1978, 1986). Such unshared parental behavior gives an advantage to all young simultaneously and, therefore, is supposed to be independent of brood size. This means that brood reduction could not yield an energy gain for the parents. Yet, recent studies have revealed that even in precocial birds, and especially in geese, shared components of parental behavior exist. Walters (1982) showed that in Southern Lapwings (*Vanellus chilensis*) parents with larger broods spent more time tending and less time foraging than parents with smaller broods. Madsen (1981) found that in Greater White-fronted Geese (*Anser albifrons*) families with a larger number of goslings were more alert compared to smaller families; the same was reported by Sedinger and Raveling (1990) for Cackling Canada Geese (*Bran-ta c. minima*). The study of Lessells (1986) on Atlantic Canada Geese (*B. c. canadensis*) yielded a positive correlation between the mass loss of a female and the number of goslings she reared. In addition, she showed that larger broods were correlated with a delayed laying date of females in the following season. In a study on Bar-headed Geese (*Anser indicus*), Schindler and Lamprecht (1987) found several parental activities to be related to brood size. Vigilance of females, approaching young by both females and males, and attacks of males were positively correlated with brood size, whereas a negative correlation existed between the feeding time of a female and her brood size. These results show that in geese brood reduction could save parental energy and nutrient reserves.

Geese provide their young with food in an indirect way by defending a feeding site and protecting offspring against other geese (e.g. Kear 1970, Lazarus and Inglis 1978, Schindler 1983, Black and Owen 1989, pers. observ.). In years when food is scarce, the defended feeding site may not yield enough food for all young of a family. This would lead to malnutrition and to smaller chances of survival and reproduction for every gosling in the brood. A reduction of brood size would improve the fitness of the remaining goslings and, therefore, increase the reproductive output of the parents.

In contrast to altricial species, geese cannot reduce their brood actively by feeding only the larger young. There are, however, several other mechanisms for brood reduction, some of which are based on the egg-size differences within the clutches. The reduction of brood size can occur during three stages in the breeding cycle, depending on the time when unfavorable environmental conditions exist: (1) before egg laying; (2) during incubation; and (3) after hatching. In each of these phases, different mechanisms will operate.

First, if a female arrives at the breeding grounds in poor condition, resorption of essentially developed follicles is one mechanism to reduce clutch and brood size, since each resorbed ovum stands for the loss of

one egg from her annual reproductive output (Barry 1962, Raveling 1978). Follicular atresia channels the regained energy back into body maintenance (Findlay and Cooke 1982) and, therefore, Hamann et al. (1986) hypothesized that follicular resorption is a mechanism to adjust clutch and brood size to a female's nutrient reserves at the onset of laying.

Second, bad weather and/or food scarcity during incubation may lead to two different mechanisms of brood reduction, which are not mutually exclusive. Cold weather would cause a high energy loss of the incubating female for maintenance of body temperature (Harvey 1971). By extending her incubation pauses for food intake, the female would expose her eggs to an enhanced risk of chilling. Indeed, lighter eggs have a lower hatching probability than heavier eggs (J. Lamprecht and T. Friedl unpubl. data), which among other things could be due to the fact that larger eggs show a greater surface-to-volume relation, making them less vulnerable to cooling. A review of data available for geese revealed that eggs frequently fail to hatch even in successful clutches (i.e. clutches where at least one gosling hatched). Studies of different goose species yielded 43.8% (Kossack 1950), 19.2% (Newton and Kerbes 1974), 23.1% (Inglis 1977), 52.4% (Leblanc 1987a) and 18.5% (Rockwell et al. 1987) of all successful clutches containing at least one unhatched egg. Also, 27.6% (Collias and Jahn 1959) and 17% (Zicus 1981) of all eggs from successful clutches did not hatch in two different populations of Canada Geese. Such hatching failure of single eggs within successful clutches, which may be caused by exposure of the eggs to low temperatures during prolonged nest pauses of the incubating female, would lead to a reduction of brood size at hatching.

Unfavorable weather during incubation may also force females to leave the nest before hatching is completed. Hatching in geese and other precocial species is generally called synchronous, yet it extends over about 24 h (Kossack 1950, Collias and Jahn 1959, Brakhage 1965, Newton and Kerbes 1974). The goslings usually remain in the nest for another 24 h, which is assumed to be important for imprinting to the parents and the development of their motor abilities (Collias and Jahn 1959, Brakhage 1965, Newton and Kerbes 1974, Inglis 1977, Cooper 1978). If the female leaves the nest soon after hatching of the last young because she is on the verge of starvation, the last-hatched gosling may be less-well imprinted and less able to follow the family. Indeed, last-hatched Lesser Snow Goose (*Anser caerulescens caerulescens*) goslings are more often abandoned in the nest than earlier-hatched siblings (Cargill 1979, cited in Leblanc 1987b). Syroechkovsky (1975) found that in Snow Geese last-hatched goslings have the highest mortality of all young. Cooch (1961) stated that in the blue morph of Snow Geese the probability of survival is poor for last-hatched goslings. Apparently, if brood reduction occurs, it is the last-hatched young that is most likely to die. Since in geese the eggs hatch in

the same sequence as they have been laid (Syroechkovsky 1975, Cargill and Cooke 1981), most nutrients can be saved by making the last egg the lightest.

Third, if low temperatures and food scarcity set in after hatching but during the rearing period, brood reduction may be brought about by the size differences between the goslings. Hatchling mass is highly correlated with egg mass both in altricial and in precocial birds (Parsons 1970, Schifferli 1973, Howe 1976, Batt and Prince 1979, O'Connor 1979, Ankney 1980, Williams 1980, Moss et al. 1981, Bancroft 1984, Rofstad and Sandvik 1985, Thomas and Peach Brown 1988, Veiga 1990). It has been shown that in precocial species heavier young have a higher probability of survival (Ankney 1980, Moss et al. 1981) and, therefore, the last gosling hatching from the lightest egg may have a higher probability of dying first. About 13% of all goslings die before fledging in Greylag Geese (*Anser anser*; Newton and Kerbes 1974). For Canada Geese, Collias and Jahn (1959) reported an overall gosling mortality of 7%. Partial losses occurred in 19% of all broods. Other studies on Canada Geese revealed 32% (Brakhage 1965) and about 35% (Zicus 1981) gosling mortality. Over a study period of 11 years, Rockwell et al. (1987) found in Lesser Snow Geese that 64.7% of the families suffered partial brood losses. These results suggest that partial brood loss and, thus, brood reduction is common in geese. In addition, gosling mortality occurs mainly during the first two weeks after hatching (Brakhage 1965, Zicus 1981, Schindler 1983), thereby minimizing the energy investment lost through the death of young.

I have pointed out some factors that argue for the adaptive value of intraclutch egg-mass variation in geese. Data on the breeding biology of these birds support the idea that the brood-reduction hypothesis, which was previously discussed only in connection with altricial birds, can be applied to geese and other precocial species. How can this hypothesis be tested? One possibility would be to compare populations of one goose species breeding under different ecological conditions. The sudden occurrence of low temperatures and food shortage should cause a high rate of brood reduction. Therefore, in populations living under environmental conditions with large and unpredictable fluctuations, a lower egg mass of the last egg compared with the mean egg mass of a clutch would be expected than in populations living in a more constant environment. A comparison of the growth of young in natural broods and artificially reduced broods in years when food is scarce could reveal data on the extent of competition among siblings. One would expect it to be greater in larger broods. Lack of substantial egg-mass differences within clutches should lead to a delayed death of the young in seasons when brood reduction is necessary. This would result in a higher energy loss both for the parents (due to enhanced parental activities) and for the remaining siblings (due to prolonged competition). Therefore, within a population, clutches with a larger variation

in egg masses should be more successful under sudden unfavorable conditions than clutches with eggs of similar masses.

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