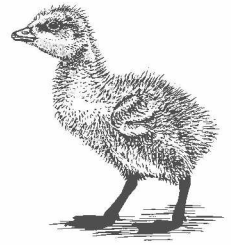


# The adaptive significance of hatching synchrony of waterfowl eggs



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*We estimated the amount of incubation time that first laid Black Brant eggs received before completion of the clutch. First laid eggs received up to 48 hours of incubation before the last egg was laid in Brent clutches. Waterfowl clutches usually hatch within a period of 24 hours, suggesting that some mechanism reduces developmental asynchrony during incubation. The combination of incubation during laying and hatch synchronization mechanisms should be adaptive because these traits reduce nest exposure, maintain egg viability, and result in an earlier hatch date, all of which increase fitness in waterfowl.*

*Keywords: Black Brant, Eggs, Incubation, Hatching*

Incubation in most passerine species begins before completion of the clutch (Slagsvold & Lifjeld 1989), which results in asynchronous hatching within clutches (Magrath 1992). For many altricial species this is thought to be adaptive because it allows for facultative brood reduction (Lack 1947). Several alternative hypotheses explaining the adaptive significance of asynchronous hatching are outlined in Slagsvold & Lifjeld (1989). Conversely, asynchronous hatching is thought to be maladaptive for species with precocial young (Arnold *et al.* 1987, but see Friedl 1993).

Female waterfowl spend more time on their nests as egg-laying progresses (Caldwell & Cornwell 1975, Cooper 1978). Cooper (1978) demonstrated that Canada Geese *Branta canadensis* attend their nests during the latter half of egg laying, but, he thought that this did not result in effective incubation. Yet, Lesser Snow Goose *Anser caerulescens caerulescens* (Syroechkovshy 1975, Cargill 1979) and Mallard *Anas platyrhynchos* (Prince *et al.* 1969) eggs typically hatch in the order in which they are laid, suggesting effective incubation before the clutch is complete. Krechmar & Syroechkovshy (1978) monitored nest attendance and temperature in Snow Geese during laying and found egg temperatures were maintained above ambient following the laying of the first egg and egg temperature gradually increased until the laying of the penultimate egg. Accordingly, nest attendance during laying by Mallards, Northern Shovelers *Anas clypeata* and Wood Ducks *Aix sponsa* resulted in developmental asynchrony at end of laying (Caldwell &

Cornwell 1975, Afton 1979, Kennamer *et al.* 1990).

Our goal in this study was to determine onset of incubation by monitoring egg temperatures during laying by Brent *Branta bernicla nigricans*. We use these data and those from other waterfowl species to discuss the adaptive significance of 1) beginning incubation before egg laying is complete and 2) associated hatch-synchronization mechanisms.

## Methods

This study was conducted during the summer of 1991 on the Brent colony located at the mouth of the Tutakoke River (61°15' N, 165°37' W) on the outer coastal fringe of the Yukon Delta National Wildlife Refuge, Alaska. We located nests early in egg laying by searching areas where females were prospecting for nest sites. We replaced the first laid egg in 6 Brent nests with an epoxy filled egg containing a temperature sensing radio transmitter (Petersen 1991). Pulse rates of transmitters varied as a function of temperature and were received at a central antenna location and translated to a strip chart recorder. The recorder sequentially sampled each nest for 7 minutes every 42 minutes.

## Results and Discussion

Three of the six radio transmitters failed before the clutch was complete, and incomplete data for these three nests were not used. Two of the remaining three fe-

males began effective incubation, as indicated by egg temperature maintained above 28°C, with laying of the second egg. The third female warmed the first egg during the laying of her second egg and began incubation with the laying of the third egg. Each female laid 4 eggs and incubation temperatures varied between 28 and 34 °C after laying was complete. Potential developmental asynchrony at the end of laying was calculated as total hours of incubation that first laid eggs had received when the clutch was completed. Time of laying for the last egg was estimated assuming that one egg was laid every 24 hours, and that the first indication of presence of the female at the nest (i.e. egg warming) was indicative of laying the second egg. Thus, potential developmental asynchrony at end of laying for monitored Brent nests was 24 to 48 hours. We have no data on egg formation time in Brent and actual egg formation time may be greater (Schubert & Cooke 1993, Watson *et al.* 1993, Williams *et al.* 1993), so our estimated developmental asynchrony at end of laying should be considered conservative. Our findings show that Brent, like other species of waterfowl, begin incubation during egg laying.

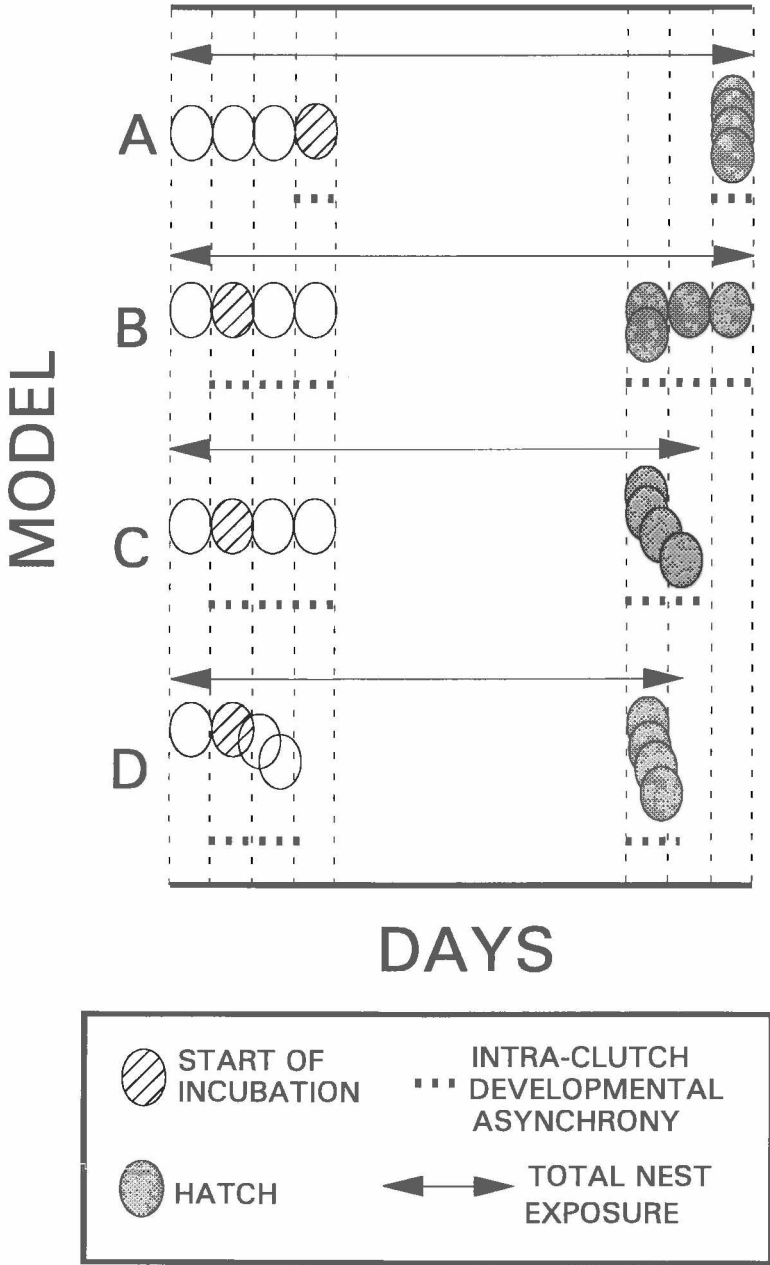
Arnold *et al.* (1987) examined the combination of egg viability and nest predation as a potential factor limiting clutch size in waterfowl. Egg viability (i.e., hatchability) decreases the longer eggs remain in the nest before onset of incubation (Batt & Cornwell 1972, Arnold *et al.* 1987, Arnold 1993). This decrease in egg viability is likely to be greater in arctic nesting waterfowl as sub-freezing temperatures are common during egg laying and exposure to freezing has been shown to reduce viability (Krechmar & Syroechkivsky 1978, Webb 1987). Additionally, incubation time required for hatching increases the longer that onset of incubation is delayed (Arnold 1993). Arnold *et al.* (1987) noted that their egg viability hypothesis favoured females that began incubation during egg laying, and suggested that hatch asynchrony is a cost associated with this strategy (**Figure 1** compare models A and B).

Asynchronous hatching is thought to be maladaptive in waterfowl because they have precocial young that rely on yolk reserves to meet their energy requirements during the first several days after hatching (Kear 1965, Ankney 1980, Rhymer 1988, Thomas & Brown 1988). Asynchronous

hatching requires that earliest hatched young wait for their later-hatching brood mates before moving to appropriate feeding areas. Thus, asynchronous hatching (**Figure 1**, compare models A and B) should result in depletion of reserves in the first hatching young, potentially reducing their survival. Alternatively, late hatching young may be abandoned in the nest to increase survival of the earliest hatching young in a brood (Cargill 1979, Williams *et al.* 1993).

Kenamer *et al.* (1990) reported that developmental asynchrony at end of laying increased with clutch size, suggesting that females begin incubation with the laying of the same egg regardless of number of eggs remaining to be laid. The developmental asynchrony observed in waterfowl at end of laying (this study; 2.2 days, Kenamer *et al.* 1990; 1-2 days, Caldwell & Cornwell 1975, Afton 1979) is greater than that usually observed during hatching (6-10 hours, Caldwell & Cornwell 1975; 2-8 hours, Afton 1979; <24 hours, Cargill & Cooke 1981). Therefore, if incubation in waterfowl begins during laying, as data suggest, some mechanism must exist to synchronize hatching within clutches (Afton 1979, Davies & Cooke 1983). Davies & Cooke (1983) showed that Lesser Snow Goose embryos in eggs added to nests after onset of incubation can accelerate their development, thereby, at least partially, synchronizing hatch with the remainder of the clutch.

Parsons (1972) suggested that reduced size of the last egg in Herring Gull *Larus argentatus* clutches may be an adaptation to synchronize hatching within clutches, as second laid eggs are smaller and require less incubation than first laid eggs. Egg size is positively related to incubation period among species (Worth 1940, Rahn & Ar 1974). Within species, this pattern, although weak, has been reported for Northern Shovelers (Arnold 1993), Japanese Quail *Coturnix japonica* (Martin & Arnold 1991) and Herring Gulls (Parsons 1972). Studies on Mallards, Blue-winged Teal *Anas discors*, and several passerines, however, have failed to demonstrate a positive relationship between egg size and incubation period (Magrath 1992, Arnold 1993). It is worth noting, however, that none of the above studies controlled for potential genetic or maternal differences in egg development time among females, which could preclude detection of within-clutch relationships.



**Figure 1. Diagrammatic representation of four models of incubation and hatch synchronization.** Intra-clutch developmental asynchrony (IDA) is the difference in development between the most advanced and the most delayed egg in a clutch. Model A, where incubation begins at the end of laying, has low IDA and the longest nest exposure. Model B, where incubation begins with the laying of the second egg, has the same nest exposure and hatch date as model A, and high IDA. Model C, where incubation also begins with the laying of the second egg, incorporates a hatch synchronization mechanism and has lower total nest exposure, an earlier hatch date, and intermediate IDA compared to models A and B. Model D incorporates the decrease in laying interval through laying. This model has the lowest total nest exposure, earliest hatch date, and relatively low developmental asynchrony both at the end of laying and at hatch.

Intraclutch egg size patterns of geese tend to show an overall decrease in egg size with increasing egg number, especially for the last egg (Syroechkovshy 1975, Ankney & Bisset 1976, Manning 1978, Cargill 1979). Where the intraclutch egg size pattern is known in greater detail, egg size initially increases, then declines with position in the laying sequence (Cooper 1978, Leblanc 1987, Owen & West 1988, Flint & Sedinger 1992, Robertson & Cooke 1993, Williams *et al.* 1993). Thus, Brent appear to begin incubation with laying of the largest egg (second in a clutch of 4) in the clutch, and egg size declines linearly until the clutch is complete (Flint & Sedinger 1992). Alisauskas (1986) reported that American Coot *Fulica americana* chicks from smaller eggs hatched with tissues that were less mature (see Ricklefs *et al.* 1980) than young from large eggs, suggesting accelerated development of young from small eggs. Thus, young from small eggs may require less incubation as a result of egg size per se, but they may also hatch less mature. In either case, the pattern of intra-clutch egg size variation observed in waterfowl may be an adaptation to synchronize hatching (Flint & Sedinger 1992, Arnold 1993, Robertson & Cooke 1993).

Yolk and albumen content of eggs varies within and among clutches (Alisauskas 1986, Hepp *et al.* 1987, Owen & West 1988). Alisauskas (1986) reported that egg composition varied with position in the laying sequence in American Coots. Owen & West (1988), however, found no relationship between egg sequence and egg composition in Barnacle Geese *Branta leucopsis*. Among-egg variation in lipid metabolism suggests variation in development rate for both American Coots and Wood Ducks (Alisauskas 1986, Hepp *et al.* 1987). Based on these relationships, we hypothesize that the intraclutch pattern in egg composition also may be an adaptation to synchronize hatching within clutches of waterfowl.

Incubation during laying, combined with mechanisms to reduce incubation time for eggs laid after the start of incubation, will reduce the overall exposure period of the nest (Figure 1, compare models B and C), thereby reducing probability of predation, while reducing intraclutch asynchrony at hatching. Accelerated development of last laid eggs has the effect that as additional eggs are added after onset of incubation, total exposure period of the nest is in-

creased by less than the laying interval for each additional egg. Furthermore, laying interval between eggs may vary with egg sequence number (Eisenhauer & Kirkpatrick 1977, Cooper 1978, Schubert & Cooke 1993, Watson *et al.* 1993). Several studies suggest that egg laying interval declines with increasing egg sequence number (Eisenhauer & Kirkpatrick 1977, Cooper 1978, but see Watson *et al.* 1993). Schubert & Cooke (1993) demonstrated a similar pattern with the exception of a long interval between the penultimate and ultimate egg. The reduction in time necessary to form later eggs may be related to their progressively smaller size and reduced total nutrient demands for egg formation. This pattern would reduce intraclutch developmental asynchrony at end of laying, shorten nest exposure period, and advance hatch date (Figure 1, compare models C and D). Additionally, egg laying interval declines with increasing clutch size (Schubert & Cooke 1993, Watson *et al.* 1993), thus intraclutch developmental asynchrony, nest exposure period, and hatch date should not increase uniformly with clutch size.

Initiation of incubation during laying, combined with acceleration of development of eggs laid after the start of incubation, results in an earlier hatch date for a given initiation date and clutch size (Figure 1, compare models B, C, and D). Young hatching at a later date suffer higher mortality during brood rearing (Dow & Fredga 1984, Flint 1993) and fewer are recruited into the breeding population irrespective of survival to fledging (Cooke *et al.* 1984, Gauthier 1989). Additionally, forage quality and availability for arctic nesting geese begins declining during the hatching period, and late hatching young are at a nutritional disadvantage (Sedinger & Raveling 1986). Later hatching Lesser Snow Geese and Black Brent grow more slowly (Cooch *et al.* 1991, Sedinger & Flint 1991), and are smaller as adults (Cooch *et al.* 1991, Sedinger, Flint & Lindberg unpubl.). Thus, the combination of incubation during laying and hatch synchronization mechanisms could be an adaptation to take advantage of declining food resources (hurry-up hypothesis of Clark & Wilson 1981). The fitness advantage of early hatch date should be incorporated into the model of Arnold *et al.* (1987).

Any reduction in the overall incubation period would shorten the nest exposure

period and increase nesting success. Several studies have shown that eggs can be stimulated to hatch in a shorter than normal period (Vince 1966, Orcutt & Orcutt 1976, Davies & Cooke 1983). If a mechanism exists to accelerate development rate, selection should favour all eggs developing at this faster rate. There may, however, be a cost associated with this increased development rate; more rapidly developing

young may be less mature at hatch and less able to thermoregulate. These costs of accelerated development rate may be the cause of reduced juvenile survival to fledging for young from eggs laid later in the clutch sequence (Flint 1993, Williams *et al.* 1993). The adaptive significance and physiology of hatch synchronization mechanisms in waterfowl deserves further study.

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