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Responses of Snow Geese to Artificially Induced Hatching Asynchrony and Increased Clutch Size

GREGORY J. ROBERTSON[1], MEGAN A. OWEN[2], AND R. F. ROCKWELL[2,3]

[1]*Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada;*
[2]*Department of Biology, City College of New York, 138th Street at Convent Avenue,*
New York, New York 10031, USA; and
[3]*Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street,*
New York, New York 10024, USA

A common feature of precocial birds is the tendency for their clutches to hatch synchronously (Flint et al. 1994). Usually, synchronously hatching clutches have higher numbers of young leaving the nest (Clark and Wilson 1981). In clutches hatching asynchronously, late-hatched young tend to get left behind when the brood leaves the nest.

In theory, clutches can only hatch synchronously if incubation begins with the laying of the last egg, but waterfowl generally begin incubation before the laying of the last egg (Afton and Paulus 1992). In compensation, embryos in later-laid eggs exhibit accelerated hatching to some degree and hatch with the rest of the clutch (Vince 1964, Davies and Cooke 1983). Clutch size can play an important role in hatching synchrony. For example, there is more time during laying of larger clutches to initiate incubation and increase the hatching asynchrony of the clutch (Kennamer et al. 1990). Also, unequal incubation constancy of certain eggs may be more frequent in larger clutches.

Our purposes were to: (1) determine how Snow Geese (*Anser caerulescens caerulescens*) respond to experimentally induced hatching asynchrony; (2) determine if this response differed if the asynchrony was induced by extra eggs (increasing clutch size) or by swapping eggs (maintaining the same clutch size);

and (3) determine if female Snow Geese will abandon their nest if the clutch size is artificially increased.

Methods.—This study was performed in the summer of 1994 at La Pérouse Bay (58°43′N, 93°27′W), 30 km east of Churchill, Manitoba. A colony of Snow Geese have been studied here since 1968. A description of the study area and general field methods are included in Cooke et al. (1995).

The experimental manipulation of the Snow Goose clutches occurred on 4 June, approximately 11 days after the mean nest-initiation date of the colony. All birds in the study area had begun to incubate their clutches. We used 40 four-egg clutches in the experiment, each of which was randomly assigned to one of two manipulations: (1) additions, or (2) swaps. In the "addition nests," two eggs gathered from nearby two- and three-egg nests were added to the four-egg clutch, raising the clutch size to six. This was done to determine whether artificially enlarged clutches could be incubated successfully by Snow Geese, and what the response would be to the resulting hatching asynchrony. In "swap nests," a pair of four-egg nests were chosen, two eggs from each nest were exchanged with each other, leaving the clutch size at four eggs. An effort was made to only swap eggs of similar laying sequences; laying sequences were roughly determined by the degree of staining of the

eggs. The laying sequences to be switched were selected randomly. Data from unmanipulated nests provided a sample of control nests, the data from these nests were collected as part of the long-term nesting study at La Pérouse Bay. In all, 27 unmanipulated four-egg clutches were monitored. All nests were marked with numbered flags, length and maximum breadth of eggs were measured with callipers (± 0.1 mm), and eggs were individually numbered with a felt pen.

Nests were visited daily once hatching began. During each visit nest contents were recorded. After the clutch had hatched, the number of hatch membranes was recorded, and any abandoned eggs and dead goslings were collected. Every egg was designated as missing (unknown source), depredated, abandoned, found dead in nest, rotten, or successfully hatched. Eggs were only designated successful if a hatch membrane could be attributed to each of the goslings leaving the nest. Fortunately, every egg could be accounted for and classified by fate. The length of time the female attended the nest during hatching is given as the number of days between when the first pipped egg was seen and when the parents were no longer present at the nest.

Statistical tests and data manipulations were conducted using the SAS statistical software package (SAS Institute 1990). Means and standard deviations are presented.

Results.—All 40 (20 swap and 20 addition) experimental nests and all 27 control nests reached the hatching stage successfully, with no loss of any eggs during the incubation period. At least one gosling successfully left the nest from all clutches. The distribution of the number of eggs not hatching from control, addition, and swap nests is presented in Figure 1. A higher proportion of the eggs in control nests hatched (103/108 eggs, 95.3%) than those in swap nests (59/80, 73.8%; $G = 18.5$, $P = 0.001$) and in addition nests (69/120, 57.5%; $G = 50.1$, $P = 0.001$) A significantly higher proportion of the eggs hatched in swap nests than those in addition nests ($G = 5.62$, $P = 0.018$).

Overall, proportionately more eggs hatched in the swap nests than in addition nests. However, there is a problem with this comparison. If the introduced eggs hatched before the goose's own eggs, it would be expected that all of the unhatched eggs in the nest would be affected. This would result in two eggs being affected in the swap nests and four eggs in the addition nests. A test was made to determine if the number of nests in which none, versus some, of the goose's own eggs hatched was different between the two treatments. In 15 of the 20 addition nests, at least one of the goose's own eggs hatched; in 18 of 20 of the swap nests at least one of the goose's own eggs hatched. This difference was not significant (Fisher's exact test, $P = 0.204$).
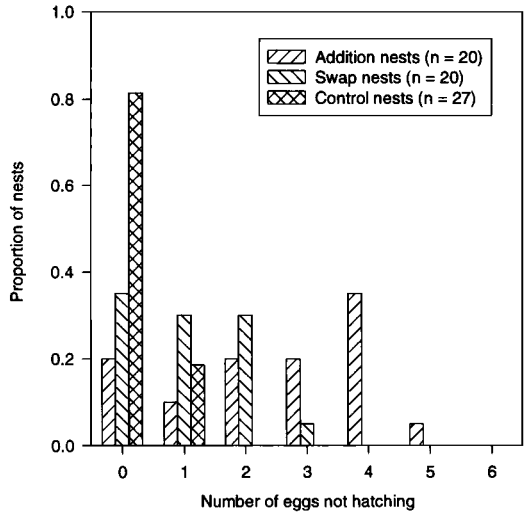

Fig. 1. Total number of Snow Goose eggs failing in control, swap, and addition nests at La Pérouse Bay, Manitoba.

There was no difference in the length of time female geese remained at the nest after hatching had begun between the two treatments (addition nests, $\bar{x} = 1.45 \pm 0.60$ days; swap nests, $\bar{x} = 1.48 \pm 0.72$ days; t-test, $t = 0.11$, $P = 0.90$). Based on our experimental design it was not possible to pre-assign certain levels of asynchrony to the experimental nests. However, it was possible to determine the time of hatching in the swap nests for the two groups, this provides a minimum estimate of the level of asynchrony introduced to each nest. In eight pairs of swap nests, hatching began one day earlier in one nest than in the other; in the other two pairs of nests, hatching began at least three and four days earlier in one of the nests.

In the control nests, four of the eggs that failed were rotten and one disappeared during the hatching period. In the swap nests, 17 of 21 unsuccessful eggs were found abandoned in the nest after the parents had left, three of the eggs disappeared during the hatching period, and one was rotten. In addition nests, 47 of 51 unsuccessful eggs were abandoned in the nest, 3 eggs disappeared, and 1 was rotten.

Discussion.—Snow Geese do not respond to an artificial clutch-size increase by abandoning their nests. If Snow Geese are partitioning all of their nutrient reserves into eggs, incubation, and brood rearing, and at each of these stages more offspring result in higher energy expenditure, it might be expected that Snow Geese may abandon their nest when faced with an increased clutch size. This is not the case, however. Although Lesser Snow Geese use considerable nutrient reserves for breeding (egg laying and incubation; Ankney and MacInnes 1978), there is good evidence

that food is available for the geese, right after snow melt (at least at the southerly colony of La Pérouse Bay; Ganter 1994; see also Gauthier and Tardif 1991). Faced with an increased number of eggs to incubate, a female goose has the option to forage longer during incubation brakes, if indeed increased clutch sizes result in high energy demands during incubation (Haftorn and Reinersten 1985). Regardless, female Snow Geese are able to successfully bring eggs to the hatching stage with clutches larger than they lay. Barnacle Geese (*Branta bernicula*) can successfully incubate clutches in which the length of the incubation period was artificially elongated (I. Tombre and K. E. Erikstad pers. comm.). Other studies of waterfowl have shown that females can successfully incubate clutches over twice the size of a regular clutch (Rohwer 1992 and references therein).

Artificially induced asynchrony reduced the hatching success of clutches by causing the abandonment of late-hatching eggs. In naturally large clutches, there is a higher percentage of the last-laid egg being abandoned by the female goose (Williams et al. 1993a). In clutches increased by intraspecific nest parasitism, parasitically laid eggs have a lower hatching success than other eggs since they are usually laid late in the laying cycle or during early incubation and, subsequently, are abandoned (Lank et al. 1990). In nests in which we increased the clutch size, the hatching success was lower than in those nests in which we simply switched eggs. This is probably due to the added eggs hatching first; four eggs (or 66%) were left behind in the addition nests, but only two (50%) eggs in the swap nests. If entire nests are examined, however, there was no difference in the proportion of nests in which the geese hatched some of their own eggs in the swap and addition nests. It appears that the increase in clutch size does not result in reduction of the hatching success of the nest.

Female Snow Geese abandoned up to five eggs in our study; there is little flexibility in this behavior. Eggs not hatching within a day or two of hatching of the first egg were left behind. Davies and Cooke (1983) showed that female Snow Geese will wait, on average, two days for unhatched eggs. A similar result was seen in Burmese Junglefowl (*Gallus gallus spadiceus*). In nests where the entire clutch hatched, the hatching period took 20.8 h; if there were unhatched eggs in the nest the female would wait on average 36.8 h before leaving the nest (Meijer and Siemers 1993). The fitness disadvantage to leaving eggs behind is clear, abandoned eggs will invariably perish, even if there is a viable embryo in the egg.

The question then is: Why do Snow Geese prefer to abandon eggs as opposed to wait for them to hatch? If the late-hatching eggs are nonviable—either the embryo has died or the egg is infertile—then the reason for leaving it behind is obvious. However, even if the embryo is simply late in developing (e.g. it is the last-laid egg; Cargill and Cooke 1981), there

still could be a selective advantage for the female to take her brood away to the brood-rearing grounds.

Snow Goose goslings can survive for no more than four days on their initial yolk reserves (Ankney 1980), so there is pressure to begin feeding quickly. Additionally, goslings need a few days of practice before they become efficient foragers (Manseau and Gauthier 1993). Hence, they use their yolk reserves to gather the necessary foraging experience. If goslings that have hatched have to wait for brood mates they will use up their yolk reserves without gaining foraging experience. It may be in the parents' best interest to abandon the late-hatching egg and lead the rest of the brood to the foraging grounds as soon as possible (see also Flint et al. 1994).

This particular situation is further exacerbated at La Pérouse Bay. Goslings that feed on high-quality salt-marsh graminoids display a higher growth rate and attain a larger size than those feeding on relatively lower-quality vegetation (Gadallah and Jefferies 1995a, b). The phenologies of the plants at La Pérouse Bay are such that only those families reaching the coastal feeding flats early in the hatching and brood-rearing periods obtain high-quality forage (Williams et al. 1993b, see also Lindholm et al. 1994). Late-hatching families have to make do with the overgrazed salt-marsh swards and/or inland swards of higher fiber, lower-quality plants. Therefore, a female goose may be faced with the choice of leaving the nest immediately and losing one gosling, but having access to good-quality food for her remaining brood, or waiting for that one gosling to hatch and subjecting her entire brood to poorer feeding conditions. If the availability of food is declining quickly, it may be a higher reproductive pay-off for the female to lead her brood immediately away, and abandon the late-hatching young. This choice is analogous to the cost-of-delay hypothesis put forth by Drent and Daan (1980) regulating clutch size and the timing of breeding.

Finally, as mentioned, many eggs are laid parasitically after the host has begun incubation (Lank et al. 1990). Even if the parasite cannot lay the egg right in the nest of the host, the attendant female will try to roll the egg into her nest because nests that have eggs left outside of them tend to attract predators (Lank et al. 1991). By abandoning a late egg, a parasitized female pays the small cost of incubating the egg, and then simply leaves the unrelated young behind. Females that abandon late-hatching eggs generally will not have to raise unrelated young, especially when the parasitism rate is high. Although having extra unrelated young in the brood is probably not a detriment to the fitness of the parents (Williams et al. 1994), waiting for these late-hatching young to hatch may be deleterious.

Although, at first, it may seem counter-productive for Snow Geese to abandon readily late-hatching eggs, there are a number of reasons why a goose abandoning late-hatching young will increase her reproduc-

tive output. In an experimental situation, Snow Geese will abandon up to five eggs in their own nests. It appears that there is little flexibility for Snow Geese to continue incubation very long after some of the brood has hatched. However, this inflexibility is probably adaptive. In a natural situation, Snow Geese will tend to abandon nonrelated (parasitic), inviable, and infertile eggs. Even if the last eggs in the nest are viable, it may be a higher reproductive pay-off for the goose to lead her partial brood immediately to the brood-rearing grounds.

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Status and Habitat Area Requirements of the Veery in Illinois

JAMES R. HERKERT

Illinois Endangered Species Protection Board, 524 South Second Street, Springfield, Illinois 62701, USA

The Veery (*Catharus fuscescens*) is an occasional summer resident in northern and parts of central Illinois (Bohlen 1989), where it is known to breed in mature bottomlands, mesic upland forests, and sandy hillocks interspersed with bogs and other low-lying wet areas (Graber et al. 1971, Graber and Graber 1973; Illinois Department of Conservation, Natural Heritage Database unpubl. data). Historically, Veeries also occasionally bred in urban residential habitat in Illinois (Pratt 1890). Apparently, this species has always been relatively rare in Illinois (Nelson 1876, Ford 1956) and, as recently as 1971, their nesting distribution in the state was considered to be "poorly known" (Graber et al. 1971). The Veery is presently listed as a threatened species in Illinois (Herkert 1992).

Research in Wisconsin and the mid-Atlantic states has shown that Veeries are sensitive to reductions in the sizes of forest tracts, and avoid relatively small forest patches (Robbins 1980, Temple 1986, Robbins et al. 1989). However, because Freemark and Collins (1992) have shown that the landscape context of forest fragments significantly affects the distribution of forest bird species, comparisons of habitat area requirements between regions where forest habitat is moderately abundant with the extensively fragmented regions of the Midwest should be made with caution. For example, in the mid-Atlantic states, where Robbins et al. (1989) studied habitat area requirements of forest birds, 30 to 75% of the landscape was forested. In contrast, only 4 to 7% of northern Illinois' landscape is forested (O'Neill et al. 1988).

Previous studies of midwestern forest bird habitat-area associations have been based on the likelihood of encountering birds in woodlots of various sizes (e.g. Temple 1986, Blake and Karr 1987). However, because a significant proportion of area-sensitive forest bird species in small, isolated forest patches may be unmated (Gibbs and Faaborg 1990, Villard et al. 1993), estimates of habitat area requirements based only on presence/absence data may not accurately reflect the true breeding requirements of these species. The purpose of my study was to examine the habitat-area requirements of the Veery in Illinois using data from known nesting areas.

Methods.—Since 1982, Veeries are known to have bred at 22 sites in Illinois (Fig. 1). The criteria used to identify breeding sites included in this study were: (1) observation of nests with eggs or young ($n = 12$); (2) behavioral observations that suggested nesting (e.g. adult birds seen carrying food during nesting season; $n = 3$); (3) observations of recently fledged young ($n = 3$); (4) observations of nine or more territorial males in a particular woodlot in a single year ($n = 4$); and (5) repeated observations of Veeries from the same woodlot in multiple years ($n = 2$). Breeding-bird records were compiled from the Illinois Department of Conservation's Natural Heritage Database (1982–1992), the Illinois Breeding Bird Atlas project (1986–1991), and Illinois' field notes for the breeding season published in the *Illinois Audubon Bulletin* (1982–1983) and *Illinois Birds and Birding* (1984–1990). Only records from 1982 through 1992 are included in this analysis.

Forest-habitat area and configuration for sites with known Veery breeding were obtained from 1:40000 aerial photographs taken in 1988 (Markhurd Corporation, Minneapolis, Minnesota). Forest cover for Veery breeding sites was estimated by dividing the aerial photographs into 1-mm² cells. Each grid cell represented 40 m² of habitat (0.16 ha). Grid cells were classified into three categories: forested interior (grid cells containing only forest habitat), forested edge (grid cells containing forest and forest-edge habitat), and nonforested. Forest boundaries were determined by delineating breaks in the forest canopy that were at least 40 m in width. Forest cover in disturbed areas (e.g. housing subdivisions and other developments) adjacent to breeding sites were not included in the habitat-area calculations.

Four habitat-area variables were calculated for Veery breeding sites: (1) The total area of contiguous forested habitat at each breeding site was estimated. (2) The core area or amount forest habitat at least 80