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Author(s): Fred Cooke, C. Scott Findlay, Robert F. Rockwell
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RECRUITMENT AND THE TIMING OF REPRODUCTION IN LESSER SNOW GEESE (*CHEN CAERULESCENS CAERULESCENS*)

FRED COOKE,[1] C. SCOTT FINDLAY,[1] AND ROBERT F. ROCKWELL[2]
[1]*Department of Biology, Queen's University, Kingston, Ontario K7L 3N6 Canada, and*
[2]*Department of Biology, City College of New York, New York, New York 10031 USA*

ABSTRACT.—Recruitment of offspring into a breeding population of Lesser Snow Geese (*Chen caerulescens caerulescens*) at La Perouse Bay, Manitoba was used as a measure of reproductive success to assess the relative fitness of females who hatched their clutches early, middle, and late in the breeding season. In three of seven seasons investigated, goslings from early-hatching clutches showed significantly greater recruitment rates than their middle- or late-hatching counterparts. No significant differences in recruitment rates were detected in the other four seasons, although early-hatching clutches showed numerically higher recruitment rates in three of these seasons. There is, therefore, some indication of directional selection for early breeding. This conclusion contrasts with that drawn by Cooke and Findlay (1982), who, using fledging success as a measure of reproductive fitness, showed that females whose clutches hatched in the middle period had the highest fitness and concluded that the population was being exposed to stabilizing selection for synchronization. The discrepancy between these results and those presented in this paper indicates that conclusions concerning the action of selection in natural populations depend heavily upon the stage of the life cycle during which reproductive success is estimated. As such, evolutionary biologists must be cautious of relying too heavily on measures taken too early in the life of the organism.
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MEASURES of the reproductive fitness accrued to different segments of a population often provide insight into the action of natural selection. Ever since the writings of Darwin on sexual selection, biologists have been interested in interindividual variability in the timing of breeding within a season. Darwin (1871) argued that birds breeding early in the season had an advantage over later breeding ones in that more offspring of higher quality could be raised. Various measures of reproductive fitness have been used to assess the validity of Darwin's generalization. A seasonal decline of clutch size with hatch date has been demonstrated for several avian species (see Klomp 1970 for review), but it is by no means the only pattern. Blackbirds (*Turdus merula;* Snow 1958) and Robins (*Erithacus rubecula;* Lack 1946) have smaller clutch sizes at both the beginning and end of the breeding season. A seasonal decline in reproductive fitness has also been shown (though less frequently) when fledging success is used as the measure of fitness. O'Donald (1972) and O'Donald et al. (1974), for example, showed a decline in the relative fledging success of Parasitic Jaegers (*Stercorarius parasiticus*) as the breeding season progressed. A similar pattern has been documented in Common Oystercatchers (*Haematopus ostralegus;* Harris 1969), Black-legged Kittiwakes (*Rissa tridactyla;* Cullen, in Perrins 1970), and Razorbills (*Alca torda;* Lloyd 1979) among others. In other species, fledging success and clutch size have different intraseasonal patterns. For example, Findlay and Cooke (1982b) demonstrated larger brood sizes at fledging for those females whose clutches hatched near the population mean, i.e. during the middle hatch period.

Clearly, mean brood size at fledging is a valid measure of reproductive success only if survival to breeding age is similar among all segments of the fledgling population. This assumption is often made, but rarely justified. While offspring recruitment into the breeding population is the best available measure of annual reproductive success, sample sizes are usually too small to make meaningful comparisons. Perrins (1965) used survival to at least 3 months of age as an alternative measure to recruitment. His conclusions were based on the percentage of banded fledglings retrapped or recovered at least 3 months after fledging and included both individuals captured during the winter and those trapped as breeding birds on the study area. Using this measure, he showed the greatest survival among the earliest hatching young. Lack (1966) using a similar measure in his analysis of Pied Flycatcher (*Ficedula hypoleuca*) data collected by Campbell, showed highest recapture rates for birds hatched early in the season. Because most fledglings recaptured as adults were breeders in the study area, this measure approximates true recruitment rates, although it must be recognized that recruits from a particular age cohort will not necessarily all enter the breeding population at the same age. To our knowledge, however, pure recruitment has been used to assess the influence of the timing of reproduction on fitness only by van Noordwijk et al. (1980) in their study of Dutch populations of the Great Tit (*Parus major*). Unfortunately, their conclusions were somewhat limited by small sample sizes despite having 16 yr of useable data.

In this paper we investigate the relationship between the timing of reproduction and recruitment rates of female Lesser Snow Goose (*Chen caerulescens caerulescens*) goslings into the breeding segment of the La Perouse Bay colony near Churchill, Manitoba, Canada.

METHODS

The La Perouse Bay Snow Goose Project has been in continuous operation since 1968. It was not until 1973, however, that adequate numbers of goslings were individually marked at hatch to allow for subsequent identification in the breeding population. Each season, up to 2,500 nests are found and visited during the hatching period (usually mid- to late June). Hatching of the eggs within the clutch is highly synchronized (Syroechkovsky 1975, Cargill and Cooke 1981). At the time of hatch, goslings are marked with small individually numbered metal web-tags, which allow for subsequent identification. From 1976 onwards, the web-tag code also indicated the year in which the tag was applied, because it was realized that the legible tags often remained in the web for several years. Approximately 5,000–6,000 goslings are web-tagged each year. Some of these are subsequently rounded up, captured, and banded shortly before fledging (about 6 weeks post hatch). These birds receive individually identifiable colored leg bands so that if they return to the colony, they can be identified at a distance.

Recruitment of goslings into the breeding colony occurs generally between 2 and 5 yr of age (Finney and Cooke 1978). Recruits are identified in one of three ways. They may be sighted at a nest during the incubation or hatching period. They may be sighted with goslings during the post-hatch period from observation towers set at the periphery of the feeding areas. Only leg-banded birds (i.e. birds web-tagged on the day of hatch and subsequently color banded 5–6 weeks later) can be identified by these two methods. The third method involves individuals captured during the annual banding drives. Most nonbreeding geese leave the breeding grounds on a northward molt migration (Abraham 1980), such that virtually all adult geese captured in these drives are breeding birds. Because these individuals are examined in the hand, they can be identified as originating from the La Perouse Bay colony either if they have a web-tag or if they are carrying leg bands, which indicate the bird had a web-tag when originally banded. The tags often remain in the web for several seasons, and it may be several years after hatch before a bird is first found as a recruit. For goslings tagged after 1976, it is possible to identify their natal cohort based upon the tag alone. Unfortunately, goslings tagged before 1976 must have been recaptured and banded (in the same year as they were tagged) in order to be identified as affiliated with a particular natal cohort. Only goslings resighted or recaptured at least 2 yr after their original tagging date are considered to have been recruited into the breeding segment of the population.

Not all recruits that return to the breeding colony are recognized as such. A bird that carries a web-tag but no color band will not be recognized at a nest. Similarly, a bird whose nest fails early in the nesting period will be neither seen nor recaptured. For this reason, we define the term recruitment as the number of recruits detected from a particular cohort (i.e. age class) relative to the number of goslings of that age class that were web-tagged. This value is inevitably considerably smaller than the true frequency of recruits. When goslings are divided into three groups (those from early-, mid-, and late-hatching nests), the detected recruitment rate of each group is measured relative to the number of web-tags applied to that group. There is no reason to believe that the detectability of recruits differs among early-, mid-, and late-nesting birds.

RESULTS

In Snow Geese, strong female natal philopatry combined with a lack of male natal philopatry (Cooke et al. 1975) means that the vast majority of the recruits from the natal cohorts are female. In the following analyses we are therefore concerned only with female recruits. Table 1 shows the detected recruitment rates for each gosling cohort (1973–1979). To ensure sufficient sample sizes, we have restricted our analyses to those cohorts including at least 45

TABLE 1. Detected recruitment into the breeding population of web-tagged female Snow Goose goslings, tagged 1973-1979.

Cohort	Number of detected recruits[a]	Number of goslings web-tagged	Percentage detected recruited
1973	109	3,675	3.0
1974	48	4,471	1.1
1975	124	4,443	2.8
1976	176	5,440	3.2
1977	192	5,306	3.6
1978	104	4,861	2.1
1979	63	5,448	1.2
Total	816	33,644	2.4

[a] The number of detected recruits is based on the total number of individuals affiliated with a particular cohort who were subsequently recaptured or resighted as adults on the colony as of 1982. The number is of course much lower than the absolute number of recruits from the natal cohort in the breeding population.

recruits. Variation among cohorts in detected recruitment rates need not necessarily represent cohort-specific recruitment, inasmuch as (1) birds web-tagged before 1976 could be detected only if they were color banded as goslings; (2) not all color bands are equally legible, leading, for example, to lower counts for the 1974 cohort; and (3) early cohorts have had a greater number of seasons during which they could have been detected (e.g. individuals affiliated with the 1979 cohort could have been observed as breeding birds only in 1981 or 1982).

To assess whether or not there is any relationship between the timing of reproduction and detected recruitment rates, each hatching period (10–12 days in length) was divided into three approximately equal time periods (early-, mid-, and late-hatch). Because hatching is highly synchronized (Findlay and Cooke 1982a), the majority of goslings in any given season hatch in the middle time period. The level of synchrony is similar in all years. Table 2 is a list of the number of goslings tagged and the number recruited within each time period for each gosling cohort (1973–1979). The detected recruitment rates are also illustrated in Fig. 1. For all cohorts except 1979, the numerically highest recruitment rate is associated with the earliest hatching sample, and in 4 of the 7 yr the latest hatching sample showed the lowest recruitment rates. Because a multidimensional contingency analysis of recruitment by time period by cohort indicated a marginally significant three-way interaction, ($P = 0.062$), suggesting that interyear or intercohort differences may occur, each cohort was assessed separately. We detected significant differences in recruitment rates among the three time periods only for the 1973, 1974, and 1978 cohorts. Interestingly, these cohorts originated in late seasons, (i.e. seasons in which the mean hatch date was later than average). The only other late season in the sample is 1979, in which the effect does not occur. We conclude that for some seasons at least, the highest recruitment rates are associated with young from the earliest hatching nests.

Recruitment rates depend both on survival to reproductive age and return to the natal breeding colony. Although natal philopatry is pronounced among female Snow Geese, it is

TABLE 2. Detected recruitment of goslings from early-, mid-, and late-hatching Snow Goose nests, La Perouse Bay, 1973–1979.

		Early			Mid			Late			
Cohort	Mean hatch date	Recruits	Tagged	%	Recruits	Tagged	%	Recruits	Tagged	%	χ^2_2[a]
1973	25 June	24	501	4.8	71	2,668	2.7	14	506	2.8	6.72*
1974	27 June	21	897	2.3	23	2,738	0.8	4	836	0.5	20.8***
1975	21 June	22	619	3.6	72	2,450	2.9	30	1,374	2.2	3.40
1976	18 June	26	540	4.8	104	3,409	3.1	46	1,491	3.1	4.88
1977	15 June	40	950	4.2	135	3,645	3.7	17	711	2.4	4.09
1978	3 July	29	894	3.2	60	3,049	2.0	15	918	1.6	6.76*
1979	27 June	7	943	0.7	45	3,764	1.2	11	741	1.5	2.17

[a] *$P < 0.05$, ***$P < 0.001$.

χ^2 tests the null hypothesis that detected recruitment is independent of time and hatching.

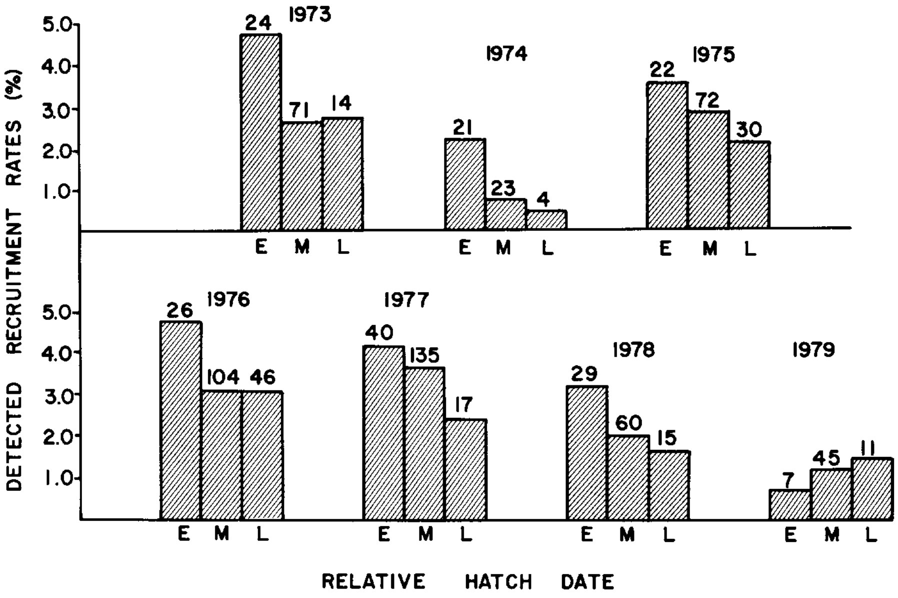

Fig. 1. Detected recruitment rates of early- (E), mid- (M), and late- (L) hatching goslings (1973–1979).

possible that the observed variation in recruitment as a function of the timing of reproduction simply reflects differences in philopatry. Conceivably, early-hatching goslings are more philopatric than their late-hatching counterparts because of the greater length of time spent in the brood-rearing area, an important factor in the development of philopatry (see Cooke and Abraham 1980). Alternatively, differential recruitment may reflect true differences in prereproductive survivorship.

The hypothesis that differential recruitment reflects differential survival (rather than differential philopatry) was tested using band-recovery data. A large number of marked individuals are shot each year and reported to the U.S. Fish and Wildlife Service. Most Snow Geese die before reaching reproductive age, but a few geese banded as goslings are shot after the age of 3 yr (considered the average age of first breeding). As indicated in Table 3, recovery rates are highest among goslings from the early-hatching nests (0.48%) and lowest among the goslings from late-hatching nests (0.22%). These differences are not significantly different at the 5% level ($\chi^2_2 = 5.11$, $P < 0.1$) but have the same trend as the recruited sample. Assuming, as do most demographers (e.g. Tanner 1978), that recoveries represent a sample of the living population, these results suggest that the higher recruitment of goslings from early-hatching nests is due to the enhanced probability of survival of these goslings to reproductive age.

Because of this variability in the age of first breeding, one question of particular importance to the dynamics of the population is whether or not there is any relationship between the timing of reproduction and age of first breeding. That is, do goslings hatched from early nests tend to enter the breeding population at a different age from their late-hatching counterparts? To assess this question, we define $N(x, t)$ as the number of female goslings hatched

Table 3. Recoveries of web-tagged female goslings shot at least 3 yr after original banding.

	Early	Mid	Late
Year			
1973	6	20	3
1974	6	7	2
1975	2	18	4
1976	1	12	4
1977	6	13	0
1978	0	1	0
Total	21	71	13
Number of goslings tagged, 1973–1978	4,401	17,959	5,836
Percentage recovered	0.48	0.40	0.22

TABLE 4. Recruits from early-, mid-, and late-hatching goslings in relation to age at first capture as breeding birds.

Age at first capture	Relative hatch date			Total
	Early	Mid	Late	
2	17	55	16	88
3	9	56	16	81
4	14	32	13	59
Total	40	143	45	228

$\chi^2_2 = 4.83$ N.S.

in time period t who were first recaptured as breeding adults age x, $2 \leq x \leq 4$. To ensure sufficient sample sizes, recruits are pooled over cohorts 1976–1978. If it is assumed that the probability of capturing a female on the colony (provided that she is in fact present) is independent of the time at which she hatched as a gosling, differences in the age of maturation should be manifested in differing distributions of age of first capture as a function of hatch date. As indicated in Table 4, there is no evidence of such a phenomemon. We conclude that there is no evidence that the timing of parental reproduction affects age of offspring maturation.

Findlay and Cooke (1982b) showed that early-hatching nests had a lower effective brood size at fledging than mid-hatching nests. This was attributed to increased gull predation on early-hatching families, who are particularly vulnerable in the brood-rearing area. As more families hatch, predator swamping serves to reduce the incidence of brood loss. Among the early-hatching nests, complete brood loss is high, whereas those families in which at least one gosling survives to fledging have a higher than average brood size. Thus, disappearance of complete broods was cited as the explanation for the lower effective brood size at fledging of early-hatching nests.

Findlay and Cooke (1982b) point out that there is another potential explanation for the relatively high complete brood loss from the earlier-hatching nests. Only a relatively small sample of families is caught in the banding drives, and, if earlier-hatching families have a tendency to wander farther from the brood-rearing area, they will have a lower probability of being caught. The higher apparent disappearance of early-hatching families might then arise from greater dispersal rather than higher mortality. Higher mortality was inferred, because a smaller proportion of the goslings web-tagged from the earlier-hatching nests appeared in the banding drives. The recruitment data in this paper present a somewhat different picture, however. Here, the goslings from the earliest-hatching nests tended to show the highest recruitment rates, implying higher survivorship. These two apparently contrasting conclusions may, in part, reflect a violation of the assumption that the probability of a particular family being recaptured in our banding sample was (assuming it survived) independent of its hatch date.

Conceivably then, some of the early-hatching families considered to have suffered complete brood loss did, in fact, survive but dispersed out of the area in which banding drives were conducted. This hypothesis can be evaluated by considering two different recruitment groups. As mentioned previously, for seasons 1976–1979 we have two identifiable types of recruits: (1) those caught and color banded in their gosling year and subsequently recaptured or resighted as breeding adults, and (2) those web-tagged as goslings, not captured in their gosling year, but later caught as breeding adults and recognized by the web-tag, which they were still carrying. If early-hatching families do have a lower probability of being recaptured in our banding sample, sample 1 should contain a smaller proportion of early-hatched recruits than sample 2. Data in Table 5 indicate that for all four years (1976–1979), no differences were detected between the two samples. This suggests that goslings from early-hatching nests do not leave the area more frequently than those from later nests and thus strengthens the conclusions of Findlay and Cooke (1982b) that mortality due to predators, rather than dispersal, accounts for the low fledging success of the early-hatching nests in their study.

DISCUSSION

Our results suggest that goslings hatched from early nests tend to have the highest recruitment rates into the breeding segment of the La Perouse Bay colony. This enhanced recruitment probably reflects lower mortality among early-fledging goslings during the prereproductive stages of the life cycle. Greater recruitment among early-hatched young is most

Table 5. Comparison of two recruitment samples of Snow Geese to check for sampling bias.

Year	Sample[a]	Early	Mid	Late	Total	χ^2_2
1976	1	15	49	18	82	2.53
	2	11	55	28	94	
1977	1	22	87	11	120	1.20
	2	18	48	6	72	
1978	1	3	15	3	21	2.53
	2	26	46	12	84	
1979	1	4	23	3	30	2.28
	2	3	22	8	33	
Total	1	44	174	35	253	4.34
	2	58	171	54	283	

[a] Sample 1: webtagged as goslings, recaptured and banded in gosling year, caught or sighted as breeding adults. Sample 2: webtagged as goslings, not recaptured in gosling year, caught or sighted as breeding adult.

marked in late seasons, that is, in seasons where late snow disappearance leads to a delay in reproductive activities. Abraham (1980) showed that mean laying date was closely correlated with date of snow disappearance at the La Perouse Bay colony. These findings lend credence to the views of Barry (1962) and Cooch (1961) that nesting success in arctic-breeding waterfowl is strongly influenced by the short breeding season and that natural selection should favor mechanisms that result in (1) nesting as early as possible within a breeding season and (2) finely tuned responses to the immediate environmental conditions on the breeding grounds. In general, the earliest-laying birds hatch first and the latest-laying last, but hatching is more synchronized than laying (Findlay and Cooke 1982a). Findlay and Cooke (1982b) showed that the earliest-laying and hatching birds had the largest clutch sizes and largest number of goslings leaving the nest. Despite this, the earliest-hatching nests did not have the highest overall fledging success: females whose clutches hatched during the peak hatch period had the greatest effective brood size (Findlay and Cooke 1982b)

In light of the findings of Findlay and Cooke (1982b), the enhanced recruitment from early-hatching nests documented here is somewhat paradoxical. Despite fewer goslings per nest at fledging, more survive to be recruited into the breeding population. This suggests that those early goslings that do survive the rigors of the early post-hatch period (when predation appears to be heaviest) enjoy greater subsequent survival than their later-hatching counterparts. Early-hatching goslings are heavier when caught at banding and have longer flight feathers (as measured by growth of 9th primary) than mid- and late-hatching goslings. Early-hatching goslings caught on 30 July in 1978 weighed 1,385.9 ± 19.2 g, mid-hatching goslings 1,259 ± 15.7 g, and late-hatching goslings 1,082.5 ± 39.2 g. Early-hatching goslings had a 9th primary of 111.9 ± 2.3 mm, mid-hatching goslings measured 84.2 ± 1.8 mm, and late-hatching goslings measured 58.4 ± 5.2 mm. Because banding is carried out as close to fledging as possible, it seems reasonable to assume that these morphological differences reflect the older age of the earliest-hatching goslings and that in general the earliest goslings to hatch are the earliest goslings to fledge. Thus, early-hatching goslings undoubtedly have more time to achieve optimal condition before the fall migration. Cooch et al. (1960) showed interseasonally that mean weights of immature geese in the fall staging areas at James Bay in early October were highest in seasons with earliest mean hatch dates. They suggested that lower weights at this time would increase the vulnerability of geese to mortality during the fall migration. If the same argument can be applied intraseasonally, the higher recruitment of early-hatching goslings could be understood.

An alternative (but not mutually exclusive) explanation for the higher recruitment of early-hatching goslings relates to parental condition. Ankney and MacInnes (1978) showed a correlation between clutch size and the nutrient-reserve status of arriving females. There is also a negative correlation between clutch size and laying date (Findlay and Cooke 1982a). Thus, earliest-laying females appear to be those with the largest nutrient reserves. Although the genetic and environmental determinants of nutrient-reserve status are unknown, a large nutrient reserve may confer a considerable reproductive advantage, not only in allowing for the production of more eggs but also allowing for more effective post-fledging care. If larger nutrient reserves are indicative of general quality and/or condition, then perhaps it is only high-quality birds that can nest earliest, more effectively care for their young, and ultimately produce more offspring that survive to breeding age. If "quality" is, like most other quantitative traits, approximately normally distributed in the population, then one would expect only a small proportion of high-quality birds in any one breeding season. As such, it is not surprising that a relatively small proportion of females hatch their clutches during the early period. Previously, Findlay and Cooke (1982a, 1983) demonstrated high repeatability and heritability for both hatch date and clutch size, and Hamann (1983) has recently shown a high repeatability for laying date. These findings suggest that at least part of the variation in timing of nesting can be ascribed to additive genetic variation among females.

Findlay and Cooke (1982b) demonstrated that the highest reproductive success in terms of average number of goslings fledged was associated with those females whose clutches hatched during the middle period. This led Cooke and Findlay (1982) to suggest that hatch date was a trait under stabilizing selection, the optimum being an intermediate date. The results described in this paper, where recruitment is used as the measure of reproductive success, suggest that there may be directional selection for early nesting.

It is important to remember that annual fledging success and annual recruitment into the breeding population are both components of reproductive fitness related to different stages of the life history. We are not able at present to measure all the components. We do not know if timing of breeding is correlated with adult survival rates. The high repeatability of laying date and clutch size reported earlier does suggest, however, that annual measures of fecundity (fledging success and recruitment) are reasonable measures of life-time fecundity, unless, of course, these are inversely correlated with longevity.

In conclusion, it is salutary to recognize that the deductions we make concerning the action of natural selection are highly dependent upon the measure of fitness that we choose. In the example given in this paper, our data suggest that directional selection for early hatching is occurring at the La Perouse Bay colony. We feel that recruitment into the breeding colony is a better measure of annual reproductive fitness than fledging success and suggest that selective pressures influencing time of nesting are more complex than we previously envisaged.

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