Population biology

Three-year cycles of lemmings and Arctic geese explained

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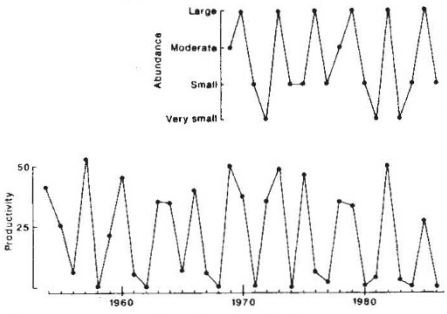
EVERYONE knows that many populations of lemmings vary enormously in size and that these variations follow fairly regular cycles. Arctic biologists are equally aware that these variations have profound effects on the predators of lemmings such as Arctic foxes: when lemming populations crash, the predators produce few, if any, young, despite turning to alternative forms of prey. Reproductive output is also variable in geese that breed in the Arctic, especially the dark-bellied brent goose *Branta b. bernicla*, in which the proportion of first-year birds in wintering populations is usually either less than 10 or greater than 30 per cent (see figure). Yet it was not until 1979 that Roselaar suggested[1] that the variations in the reproductive success of geese are linked to those in the populations of lemmings, through predators of lemmings turning to the eggs and young of ground-nesting birds in years when lemmings were not available. This suggestion seems to have been largely ignored until it was repeated recently by Ron Summers[2]. The possibility is of more than academic interest: populations of brent geese have increased greatly in recent years and are causing agricultural damage, so they need to be managed — and successful management depends on understanding the population processes of the species.

The breeding productivity of the geese seems to show cycles with a periodicity of three years. Unfortunately, as Myrfyn Owen points out[3], cycles of this periodicity are the most difficult to distinguish from purely random fluctuations using the usual statistical tests. Indeed, the number of turning points (the criterion of one standard test) expected in a random series is identical with the number that occur in a strict three-year cycle! Summers and Underhill[4] have now subjected the brent goose data to more powerful tests, in which the lengths of runs of 'good' or 'poor' years, not just the number of runs, are taken into account: there is no doubt that the breeding output of the geese does, indeed, follow a three-year cycle, though with sufficient variation that it is difficult to predict output in advance.

Owen[3] also points out that the original data presented by Summers are insufficient to show a formally significant correlation between reproductive output of brent geese and numbers of lemmings, but a slightly more extensive set of data shows a significant correlation[4]. Further, André Dhondt[5] argues that the correlation to be expected is not just a simple one of high output in good lemming years and poor output in lemming crashes. This is partly because the cycles are three years in length, not two, and partly because weather is likely also to affect the breeding output of the geese, as it affects that of many birds breeding in the Arctic. Dhondt suggests that the only definite prediction that can be made is that output of geese will be poor in years immediately after lemming peaks, as predators will then be common but will have no lemmings to feed on: the facts are that production was poor in 9 out of 10 such years. In peak years, when predator numbers may still be increasing (as they lag behind those of lemmings) and when there will be plenty of food to go round, geese would be expected to reproduce well, unless weather conditions were against them: production was, in fact, good in 6 out of 10 peak years, the four failures presumably being in years of poor weather. The situation in years preceding peaks will depend on how far the predator populations lag behind those of lemmings. If the lag is considerable then the increasing lemming populations will be more than enough for the still small populations of predators, and good reproduction of geese in those years would be expected unless the weather was poor: in fact, production was good in 9 out of 11 such years.



Variation in abundance of lemmings (top) and productivity of dark-bellied brent geese (bottom) breeding in the Taimyr peninsula. Productivity is measured as the percentage of first-year birds in the succeeding winter population (data from ref. 4).

Weather has generally been considered to be an important cause of variation in the reproductive success of geese that breed in the Arctic. Summers and Underhill[4] show that, although summer temperatures seem to have some effect on the productivity of dark-bellied brent geese, the effect is small compared with the apparent effect of lemming numbers. But the most important meteorological information, the timing and distribution of snow cover in the early part of the breeding season, is not available and other measures, such as mean temperature and precipitation, have to be used as surrogates. Furthermore, Hugh Boyd[6] points out that the correlations between the breeding production of Siberian brent geese and weather variables have themselves altered with time, as mean weather conditions, variability of weather and goose numbers have changed.

Boyd[6] also notes that brent geese do not breed until they are three years old, so that a three-year cycle of breeding output is likely to persist for some time after a particularly good or particularly poor year. Thus, although weather does not itself vary on a three-year cycle, it could be responsible for triggering three-year cycles in goose productivity. But there is a final piece of evidence that implicates lemming predators: three species of wading birds that breed in the same areas as the brent geese also show marked fluctations in reproductive output, which are correlated with those of the brent geese and with the lemming cycle. Because they mature more rapidly than the geese, the three-year cycles in the productivity of the wading birds cannot merely be intrinsic ones triggered by weather conditions. Also, their wintering areas, migration patterns and foods are different from those of the geese, so feeding conditions before the breeding season (which are known to be important in determining reproductive success in many Arctic birds) cannot be responsible for the three-year cycle.

A valuable test of the importance of lemming predators to the cycles of productivity of brent geese would be data for the goose population breeding on Svalbard (Spitzbergen), where there are no lemmings. Unfortunately, there are also no data. Indeed, the whole analysis of the population biology of brent geese is bedevilled by the lack of sufficiently detailed and sufficiently extensive data: the data-gathering has simply not kept pace with the growth of the population. Great advances could also be made if there was more collaboration between western European wildfowl biologists working on the birds in the winter, and those in the Soviet Union, who are able to study them on their breeding grounds. Until such collaboration occurs, the fascinating interplay of geese, predators, lemmings and weather cannot be fully understood. □

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3. Owen, M. *Bird Study* **34**, 147-149 (1987).
4. Summers, R.W. & Underhill, L.G. *Bird Study* **34**, 161-171 (1987).
5. Dhondt, A.A. *Bird Study* **34**, 151-154 (1987).
6. Boyd, H. *Bird Study* **34**, 155-159 (1987).

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