Tectofugal and thalamofugal: A proposal for longitudinal studies in goose behaviour

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The value of the comparative method in ethology was established at the intra- and intergeneric level about 60 years ago. Here I suggest that intraspecific comparisons of behaviour at long intervals may also be instructive (though in less dramatic ways) and discuss some of the difficulties in promoting and carrying out intergenerational research projects, using studies of geese as examples.

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The comparative study of the motor patterns of the Anatinae by Konrad Lorenz (1941, 1971) is one of the classics of ethology (*ie* heard of but now rarely read). As he pointed out, and as those of us who have looked at geese know well, motor patterns are extremely stable. My purpose here is to suggest that it may be instructive to see whether those basic patterns are used in different packages within the wide range of social activities of geese, as those activities change over time in response to changes in the numbers, distribution and lifestyles of geese.

I was delighted to learn, from a recent paper on the presentation of visual stimuli to birds (Dawkins & Woodington 1997), that they effectively have two visual systems which are both anatomically and functionally distinct. The thalamofugal pathway (OPT complex or visual wulst) receives input largely from the monocular lateral field while the tectofugal pathway (nucleus rotundus) receives largely from the frontal field (Shimuzu & Karten 1993), which may have a considerable degree of binocular overlap. The monocular lateral field is specialised for the detection of distant moving objects whereas the frontal field appears to be more concerned with the resolution of static near objects (Hodos 1993).

That distinction suggests some interesting questions in the study of goose behaviour. For example, is only the tectofugal pathway used when geese are identifying what bits of what plants they should take? Does the lateral field play any part in a goose's identification of other individuals (*eg* by putting them in the context of a family or other social group)? Does the lateral field play a dominant role in decision-making at large geographical scales? And so on.

But here I use the distinction between the tectofugal and thalamofugal pathways as an analogy for two approaches to the study of goose behaviour. Now, as in the past, most research projects are short, to fit the needs and interests of academics and their graduate students. These researchers are mostly tectofugal specialists, aiming to resolve static close-up problems.

Given the reluctance of funding agencies – whether governments, foundations or research councils – to make long-term commitments that restrict their flexibility, brief encounters with the world of geese are likely to remain the norm. Yet, as the La Perouse Bay study of Snow Geese has shown (Cooke, Rockwell & Lank 1995), lengthy projects enable us to ask and answer many questions that short ones cannot. What I propose here is that we should also explore the possibilities of thalamofugal studies on distant moving objects, by which I mean not only comparative studies of different species or of a single species in different places but also studying changes in goose behaviour over time ('longitudinal' rather than 'lateral').

Because of practical difficulties of working continuously on a project over a quarter-century and more, I propose that some researchers try working in such a way that others can repeat the central elements of their studies at intervals of 10-100 years.

Long-term monitoring of animal populations and habitats is a familiar idea. Looking carefully at changes over time in the behaviour of animals is less familiar; though a minute's thought will remind us that some kinds of change are commonplace, such as shifting from feeding on salt marshes to improved grasslands and cereal crops (Owen 1982). These must involve an adjustment of 'search images' by the geese, on both micro- and meso-scales.

White-fronted Geese

Forty-six years ago I published a paper about the agonistic behaviour of White-fronted Geese *Anser albifrons* wintering at Slimbridge, England in 1949-1952 (Boyd 1953). Twenty years later, Myrfyn Owen looked very successfully at the feeding behaviour of later generations of these geese at Slimbridge (Owen 1971, 1972a,b). Given the range-wide changes that have occurred in their numbers, distribution and feeding choices over the last fifty years, it should be instructive to look again at the winter behaviour of White-fronted Geese, not only at Slimbridge and elsewhere in western Europe, but also here in North America.

Many winter flocks that used to consist of tens or hundreds of geese have now enlarged to thousands or tens of thousands. Has the recent great concentration of White-fronted and other geese in The Netherlands in winter made it necessary for them to modify their social relationships? If so, how, and to what effect? Do the mechanisms ensuring 'peace, order and good government' among geese that seemed to be effective in the 1950s still work well in the 1990s? If not, how have they changed?

In small groups of geese, it was possible for all the members to know each other. Now that seems less likely, though White-fronted Geese still know many of their immediate neighbours, which is made easier by the common occurrence close to a mated pair (with or without young of the year) of most of their progeny of earlier years. That was first proved by Tony Fox and his collaborators, studying Greenland White-fronted Geese *Anser albifrons flavirostris* (Warren *et al.* 1993), a relatively small independent population of less than 25,000 birds. But, though I didn't prove it in 1953, these 'prolonged families' are also evident in Siberian and North American *A. albifrons*, each numbering more than half a million birds. This may mean that even large flocks of White-fronted Geese are rather more 'structured' than those of some other geese.

Jacques Van Impe took up the study of the flock composition and behaviour of White-fronted Geese in 1964 (and of Bean Geese, *A. fabalis* in 1969) in southern Zeeland (Van Impe 1978, 1988, 1996). At first, many of his findings seemed to differ from and contradict mine. Some of the apparent differences turned out to be procedural – how to sample within flocks, recognising that geese on the periphery tend to include more and larger families than those at the core (where families often seem less coherent), and so on. One important difference was that amongst the geese in Zeeland many families appeared to break up, or hold together very loosely, in midwinter (Van Impe 1978), unlike those in the relatively small wintering group in England. Loosening of family ties in midwinter has since been seen in other geese, including *Brant leucopsis, B. bernicla* and *B. canadensis.* But in many cases the family units seem to come together again shortly before spring migration and they are very obvious among flocks in staging areas (personal observations). Van Impe and I are in close agreement on what observations in England and The Netherlands have shown about changes over time in family-sizes and the age-composition of Russian White-fronted Geese wintering in north-west Europe, and on the likely causes of those changes. But neither of us has been able to spend sufficient effort in the last twenty years to determine whether changes in flock composition may have affected, or perhaps been affected by, the agonistic behaviour of the geese.

Fifty years is an extremely short period for fundamental changes in the behavioural repertoire of a species that may have been around for more than a million years. We would not expect the basic elements of behaviour to have changed; but the intensity and frequency of agonistic encounters, and methods of choosing feeding areas and food plants, might well have done so.

When I considered repeating my early work, but by looking at the masses of geese in The Netherlands, rather than the remnant at Slimbridge, I ran into an odd assortment of practical problems. Could I still read my original pencilled field-notes, nearly 50 years after they had been written? What had become of the analyses I had carried out that were not included in the published account? What comparisons would be appropriate, given the differences in locality and goose abundance, as well as in time, and my inability to recreate the mind-set behind the notations I had used originally?

These kinds of question will have to be dealt with in making behavioural comparisons over time. Pencil notes have largely been replaced by records in some computer language on a diskette. The immediate gain in legibility is considerable. Yet it is far from certain that investigators 50 years from now will be assured of access to today's data. Their technology and software are sure to be very different.

Keeping past records accessible is being badly neglected in developing and maintaining databases of many kinds. In recent years, staff engaged in maintaining routine records have been among the earliest and most numerous casualties of 'down-sizing'. For most managers, in most enterprises, trying to keep up with the latest computer fashions does more for their job security and chances of promotion than ensuring that old records are not lost or deliberately destroyed. This is increasingly damaging to the culture and traditions of organisations, as well as resulting in major losses of scientific information. It seems unlikely that this kind of wastage can be ended, at least until a government has suffered a major computer disaster, such as the loss of all its tax records.

Not all blame can be put on administrators. Biologists themselves tend to suppose that old records, especially those made by other people, are not worth keeping, certainly not worth spending time on indexing and filing.

How observations should be made and recorded also presents long-term problems. For effective comparison of behaviour over time, it is necessary that the most recent data should be obtained in the same ways as the earliest. This runs at once into a substantial difficulty. One of the ways in which young scientists have traditionally sought to differentiate themselves from older ones (and the dead) is by adopting 'new and improved' technology and statistical methods. It seems not to be difficult to persuade amateur field observers to continue using methods that were devised 20 years ago. But no self-respecting young professional wants to be laughed at for using obsolete techniques; and many of them derive much of their scientific satisfaction from making procedural improvements. The solution presumably lies in adopting an incremental approach, in which the original methods of gathering, recording and analysing data are maintained, while being supplemented by new procedures, so that the reliability of each periodic set of records increases over time, rather than falling away, as happens in censuses and surveys when methods are fixed while the geese being studied are changing their numbers, whereabouts and ways.

The involvement over time of different teams of observers, whether 'amateurs' or 'professionals', in repeated studies of behaviour could only be useful if it were possible both to codify exactly what had to be looked for and recorded and to provide training programmes that would bring people with inter-generation differences in education and background to closely similar levels of proficiency. I know of no cases where this has been done, in our own or in other fields. It has proved possible to achieve consistency between observers with very different backgrounds in assessing abdominal profiles (Madsen *et al.* 1997), a matter of judgement, not measurement, as many records of behaviour are likely to be. Some experiments in standardising recording of behaviour should be made.

Migration of geese to Iceland

Let me turn to a very different example of a change in behaviour over time. When I was in Iceland in May 1997, I was able to extract records of the arrival dates of geese from an unpublished collection of bird arrival dates reported by a national network of observers organised by Finnur Gudmundsson, chiefly in the period 1935-1970. I had already assembled published and unpublished dates of departures from Scotland, and of arrivals noted at some Icelandic weather stations. Five species of geese are involved. Greylag Geese and Pink-footed Geese breed extensively in Iceland. White-fronted and Barnacle Geese breeding in Greenland, and Brent Geese breeding in the Queen Elizabeth Islands, also spend two to five weeks in Iceland en route from the British Isles to their breeding areas. There are not enough records of those staging geese to give any clear impression of changes in their times of migration and the Pink-footed Geese do not seem to have altered the timing of their spring migration from Scotland in any consistent way. Most of them leave Scotland and arrive in Iceland between 25 April and 5 May, and have done so at least since 1933.

Yet the time of migration of Greylag Geese *has* changed. In the earliest years for which I have found records (1909-1914) they did not reach Iceland until 23-28 April. By 1940, the mean date of arrival had advanced to 12-15 April; and in recent years the first arrival has been in late March or the first week of April and nearly all have arrived by mid-April, seemingly irrespective of the occurrence of periods when the wind directions and speeds were favourable or unfavourable. Why Greylag Geese have migrated earlier while Pink-footed Geese have not is puzzling, given that they spend the winter, and assemble in staging areas in northern Scotland in early spring, in overlapping areas and eat mostly similar foods. It may be because Greylag Geese, nesting in the lowlands, are able to begin nesting before the end of April, while Pink-footed Geese, breeding until very recently only in the higher interior of Iceland and in east Greenland, are prevented from doing so by the general persistence of snow cover there well into May. It is probably impracticable, simply by recording departures and arrivals, to separate possible causes and effects. In the present context, the point is that, for whatever reasons Greylag Geese are choosing to leave Scotland several weeks earlier now than they did 80 years ago.

Recent developments in radio- and satellite-telemetry are making it possible to look at the performance of migrating individuals in new ways. Much more is to come, if the costs of the devices and of access to data recorded at satellite tracking stations continue to fall. One of the immediate results has been to increase our awareness and understanding of how hazardous migratory flights can be, even for large and powerful birds.

In the spring of 1997 we resumed a study of the behaviour of Greenland White-fronted Geese at a staging area in west Iceland where observations had also been made in 1990 (Fox *et al.* 1997). Geese newly arrived from Ireland or Scotland, having used much of their energy reserves in flying 900-1,500 km, had relatively flat abdominal profiles. By the time they moved on, some within a few days, the majority 3-4 weeks later, most of the geese had obviously replaced and increased their reserves. Yet repeated recording of the abdominal profiles of marked individuals showed that some of them had increased their profiles much less than expected from the median values for their age- and sex-classes at different dates and that a few left with lower profiles than they had had earlier in their stay. It was also obvious that many of the geese resumed their migration with lower profiles than those of geese seen on the same dates in 1990. The effects of these variations on survival and breeding success, especially of the marked birds with known histories, will emerge in the next few years. Here they exemplify the need to ensure that studies on condition and feeding behaviour at intervals of many years take full account of the scale and nature of short-term variability.

I have had an embarrassing example of this need in another field. In 1995 I repeated a nest census of Rooks *Corvus frugilegus* on the Mendip Hills in England that I had first made in 1945. There had been a large decrease, supported by counts by other people in a few of the intervening years. So I claimed that conditions for Rooks had been better at the end of the Second World War than in recent years. In 1996 I repeated the census and found more nests than in 1945.

Conclusion

The kinds of studies I am proposing offer small prospects of early pay-off, with no proven examples that they can be carried out successfully. They would require substantial alterations in the ways in which researchers on goose behaviour carry on their business. Yet I suggest that it may be worth a serious attempt to explore how longitudinal studies could be organised so as to give them a reasonable chance of success. No group at a single university or research institution is likely to want to carry the risk. The International Goose Research Groups might be able to do so, as one of their co-ordinating functions. They have already tackled, with considerable success, many of the problems of setting up and maintaining databases. A lot more 'development work' will be needed to produce effective protocols for long-term studies of behaviour. I am fading from the scene, so that the enterprise needs to be led by someone else. Are there any volunteers who share this murky vision of starting to write history now?

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