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The ecology of bird migration patterns

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Migration in birds can be defined as a regular return movement between geographically separated breeding and wintering ranges. Two types have long been recognized. Obligate migration is considered 'hard-wired', in that the bird seems pre-programmed to leave its breeding area at a certain time each year, and to return at another time. Timing, directions and distances are relatively constant from year to year. This type of migration is found in both short-distance and long-distance migrants, but mainly in the latter. In contrast, facultative migration is considered optional, occurring in response to conditions at the time. Individuals may migrate in some years but not in others, depending on prevailing food supplies or weather conditions. The timing of the outward migration, and the distance travelled, can be highly variable between individuals and, at the population level, between years. Facultative migration is typical of many partial migrants, but is seen in its most extreme form in so-called irruptive migrants. The latter are species which depend on spatially unpredictable food supplies, such as sporadic tree-seed crops (some finches), or cyclically fluctuating rodent populations (some owls and raptors).

Features of obligate and facultative migrants

Typical features of obligate migrants are as follows: (1) consistent scarcity/absence of food in the breeding areas in winter; (2) individuals leave before food supplies collapse – their exodus is anticipatory; (3) timing, directions and distances of outward movements are relatively consistent from year to year; (4) individuals behave in the same way every year, usually returning to the same nesting locality each year and often also to the same wintering locality; (5) many such species migrate long distances, and often travel at night; (6) migration is viewed as under fairly tight genetic control, usually with limited variation between age and sex groups. Examples include the many long-distance migrants that travel each year between Eurasia and Africa, or between North and South America: swallows, warblers, cuckoos, arctic-nesting shorebirds, etc.

Typical features of facultative (irruptive) migrants are as follows: (1) food often remains available in breeding areas throughout the winter, but in amounts that vary greatly from year to year; (2) the proportions of birds that migrate vary from year to year, migration being a flexible response to prevailing conditions; (3) distances and sometimes timing and directions are highly variable from year to year; (4) individuals differ in behaviour from year to year, remaining in some years, migrating short or long distances in others, and often wintering (sometimes also breeding) in widely separated areas in different years; (5) they migrate mainly short distances, depending on year, and often travel by day; (6) migration occurs as a direct response to declining food supplies; (7) migration is under much less rigid genetic control, and there are often marked differences in distances between age and sex groups. Examples include many short-distance partial migrants within Europe or within North America, and especially irruptive species, such as Short-eared Owls *Asio flammeus* and Snowy Owls *Bubo scandiaca*, or Eurasian Siskins *Carduelis spinus* and Common Redpolls *Carduelis flammea*. Marked individuals of these and other irruptive migrants have been found in summer or winter at localities hundreds or thousands of kilometres apart in different years (Newton 2008).

A continuum of behaviour

The two types of migration (obligate and facultative) may be best considered not as distinct but as lying at opposite ends of a continuum of variation in bird migratory behaviour, from rigid and fixed at one end to flexible and variable at the other. Another reason to view the two types as part of a continuum is that some birds apparently switch from obligate to facultative modes during the course of a journey. An example is the White Stork *Ciconia ciconia*, in which the same radio-tracked individuals migrated from Europe only as far as east Africa in some years and on to southern Africa in other years, a journey of 7000–11 000 km in different years, depending on prevailing conditions (Berthold *et al.* 2004). The first part of the journey, covered every year, could be regarded as the obligate stage, and any subsequent part, covered only in certain years, as the facultative stage. Two appropriate modes of behaviour, one following the other, have been detected in the migratory restlessness of captive passerines (Helms 1963).

Genetic control

Three main components of migration are known from the work of Berthold (2001) and others to be under genetic control: (1) timing (or spread of timing in a population), (2) directions (or spread of directions) or (3) distances (or spread of distances) – as reflected in captive birds in the total minutes of migratory restlessness shown per season. (This total is a function of the number of nights with activity and the mean number of minutes of activity per night.) Now imagine adding to these three established components a fourth component – the ratio of obligate to facultative stages in the journey. Imagine that in some species the obligate phase is long-lasting, covering most of the journey, whereas in others it is short/non-existent, covering only a small part of the potential migration, the rest of the variable journey being undertaken on a facultative basis. (Note that facultative migration automatically adds variation in timing and distance, because birds can choose when and how far they go, depending on the conditions they encounter.) If we assume that each of the four components can be varied independently of the others by the action of natural selection – and experimental studies on the first three components would suggest this is the case – then we have a template for explaining all the known variants in northern hemisphere land-bird migration patterns, whether in obligate long-distance or partial and irruptive migrants. Even the most obligatory of migrants can make emergency facultative movements if conditions turn against them, as shown by the unpredicted movements of some Eurasian breeding species in their African wintering areas.

Table 1. Comparison between typical regular and typical irruptive migration. For further details, see Newton (2008).

	Regular (obligate) migrants	Irruptive (facultative) migrants
Habitat-food	Predictable	Unpredictable
Breeding areas	Fixed	Variable
Wintering areas	Fixed	Variable
Individual site fidelity	High	Low
Migration		
Proportion migrating	Constant	Variable
Timing	Consistent	Variable
Distance	Consistent	Variable
Direction	Consistent	Variable
Main presumed ultimate stimulus	Food supply	Food supply
Main presumed proximate stimulus	Daylength	Food supply

Conclusions

Differences between obligate and facultative migrants, as the two extremes of a continuum of migratory behaviour, are summarized in Table 1. The main point is that both systems are adaptive, one to conditions in which resource levels vary regularly and predictably in space and time, and the other to conditions in which resource levels vary unpredictably. Such differences occur not just between species, but also between different geographical populations of the same species (such as Bullfinch *Pyrrhula pyrrhula* and Great Tit *Parus major*), depending on the nature of the food supplies that are regionally available.

References

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