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Obligate and facultative partial migration in the Blackbird *(Turdus merula)* and the Greenfinch *(Carduelis chloris)*: uses and limitations of ringing data

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Abstract: MAIN, I. G. (2000): Obligate and facultative partial migration in the Blackbird *(Turdus merula)* and the Greenfinch *(Carduelis chloris):* uses and limitations of ringing data. Vogelwarte 2000: 286–291.

The feasibility of using ring recovery data to distinguish obligate and facultative partial migration is examined. Possible approaches involve (1) the observation of temporal change in the proportion of migrant individuals, and (2) the identification, from ringing and recovery dates, of individuals which migrate from their breeding areas in some winters only. The first approach is illustrated by the progressive decrease during the twentieth century of the proportion of British Blackbirds *(Turdus merula)* recovered overseas; in that case only a model-dependent interpretation is possible. The second approach reveals that the seasonal movements of Norwegian Blackbirds to Britain and Ireland are essentially obligate, whereas those of Norwegian Greenfinches *(Carduelis chloris)* both to Britain and to Denmark are most probably facultative.

Key words: partial migration, obligate, facultative, Blackbird *(Turdus merula),* Greenfinch *(Carduelis chloris).*

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1. Introduction

A useful primary classification of partially migratory behaviour distinguishes obligate partial migration, in which some individuals of a population migrate every year, from facultative partial migration, in which individuals may or may not migrate in any given year (TERRILL & ABLE 1988). To a certain degree the distinction reflects a real biological difference, in that the control mechanisms in obligate partial migration are likely to be innate, whereas facultative partial migration is a response to variable environmental factors such as weather, population density and the availability of food.

This paper investigates the feasibility of using ring recovery data to deduce the part played by the two processes in a given partially migrant population, essentially by revealing the presence of any facultative component. Two possible approaches are considered: (1) the observation of temporal change in the proportion of migrating individuals in a partially migrant population, accompanying temporal change in environmental factors; and (2) the detection, by inspecting the ringing and recovery dates, of individuals which do not migrate every year. The partially migrant species studied were the Blackbird *(Turdus merula)* and the Greenfinch *(Carduelis chloris),* for both of which good numbers of ring recoveries are available. As an example of the first approach, the almost complete transformation during the twentieth century of the British Blackbird from partial migrant to resident is considered. The second approach is applied to recoveries of Norwegian Blackbirds and Greenfinches that migrate to the British Isles, and of Norwegian and Swedish Greenfinches that migrate to Denmark.

2. Methods

One of the many complications to which the study of partial migration is subject (LACK 1943/1944) is that the lengths of the migration journeys are typically shorter than those of wholly migratory species or populations. If the seasonal movements occur entirely within the breeding range, a sample of individuals caught for ringing outside the breeding season may be a confusing mixture of residents, winter visitors and passage birds. An analysis such as the present one, involving birds ringed or recovered in the north of their range, will minimize if not completely avoid that difficulty, but the situation may be further complicated by the migration taking the form of a general southward or westward drift rather than a determined move to a definite wintering ground. In the present study that complication has been tackled by investigating those sectors of the migration journeys which consist of sea crossings, where the birds will not straggle as they might over land.

2.1. Observation of temporal change

Recoveries overseas (in Ireland or continental Europe) were selected for Blackbirds ringed in Britain either as nestlings or as juveniles before the end of August. Such birds may be assumed to be British natives, and confusion by winter visitors from the continent avoided (SNOW 1966).

2.2. Inspection of ringing and recovery dates

As a means of displaying the ringing and recovery dates in a form convenient for inspection, all movements between the ringing and recovery sites in the two areas under study were first classified as either direct, if the ringing and recovery dates fell within the same 12-month period, or indirect, if they fell in different 12-month periods. In the first case the recovered bird can have made only one migration journey in the direction indicated since it was ringed; in the second it may or may not have made two or more such journeys. The 12-month period chosen was June to May when the predominant outward movement from the area in which ringing took place is likely to occur in autumn, and October to September when it is in spring. Frequency distributions of the ringing and recovery dates (numbers of birds ringed or recovered in each calendar month) were then derived for each class of movement in each direction. Additionally, the amount of Greenfinch data has been increased by combining pairs of plots for the movements in the two directions, producing a single pair of frequency distributions of the dates on which individual birds were recorded (ringed or recovered) in the two areas.

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3. Results and discussion

3.1. Observation of temporal change

The Blackbird's present status as a largely sedentary species in Britain and Ireland (BERTHOLD 1990) is a recently acquired one. This is strikingly exemplified by the overseas movements of Blackbirds presumed to have been hatched in Britain (Fig. 1). The four indicated blocks of ringing years between 1909 and 1997 yielded a total of approximately 3,000 recoveries each, but in that period the proportion of overseas recoveries fell by more than an order of magnitude (Table). But migration had by no means ceased four decades ago: 15 birds ringed between 1959 and 1961 were recovered overseas.

A simple interpretation of this result is that decreasing environmental pressures have progressively reduced the need for facultative movements within the population. A presumably related tendency for European Blackbirds, formerly restricted to woodland and woodland edge habitats, to move into increasingly hospitable human settlements has been observable for at least 200 years (CRAMP 1988). Moreover, recent decades have seen milder winters, making weather-induced facultative movements less necessary. Such an interpretation depends, however, on a model which assumes that all environmentally-induced movements are facultative. The possibility cannot be excluded that the environmental changes act through natural selection to change the proportion of migrating individuals in an obligate partially migrant population (with or without an admixture of eruptive and other truly facultative processes). An extensive body of experimental work, summarized by BERTHOLD (1999), has shown that most if not all of the physiological characteristics necessary for a migratory lifestyle are genetically controlled. Moreover, some of these characteristics are inherited together as 'migratory syndromes', facilitating micro-evolutionary change in the proportion of migrating individuals in a partially migrant population under the influence of changing environmental conditions. Evidence for facultative movements deduced from model-independent information about the behaviour of individual birds will be more reliable.

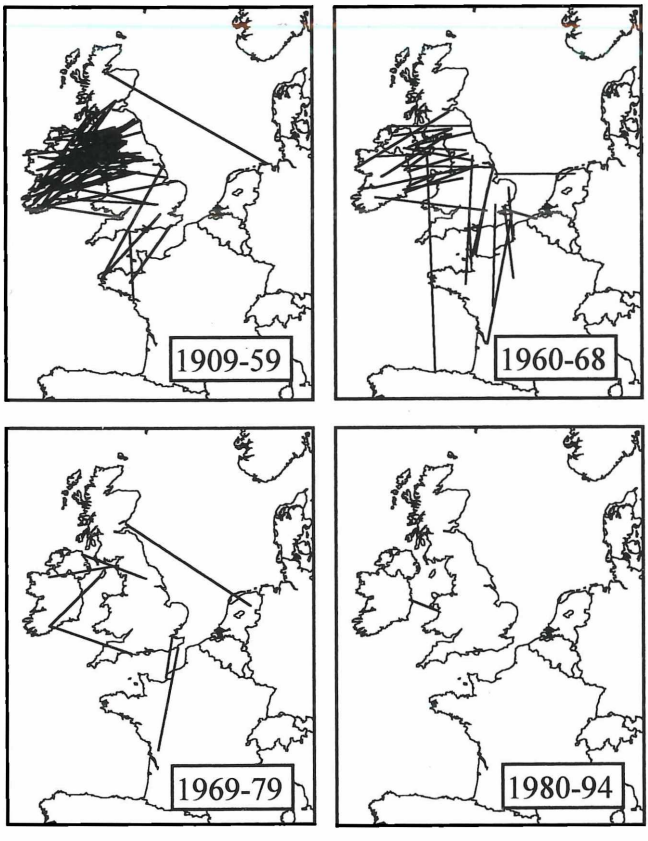

Fig. 1: Overseas movements of Blackbirds ringed in Britain, either as pulli or as juveniles before 1 September, in the periods indicated. Ringing and recovery locations are joined by straight lines, with no implication as to the route taken. See also the Table.

Abb. 1: Als Nestling oder Jungvogel vor dem 1. September in Großbritannien beringte Amseln, die innerhalb der angegebenen Zeiträume jeweils aus Übersee zurückgemeldet wurden. Beringungs- und Wiederfundsorte wurden mit einem Strich verbunden, was jedoch ohne Relevanz für den tatsächlich geflogenen Zugweg ist. Vgl. auch die Tabelle.

Table : Blackbirds ringed in Britain, either as pulli or as juveniles before 1 September, in the periods indicated: total numbers of recoveries, and numbers of overseas recoveries. See also Fig. 1.

Tab.: In Großbritannien als Nestling oder Jungvogel vor dem 1. September beringte Amseln in vier Zeitabschnitten: jeweils Gesamtzahl der Wiederfunde und Wiederfunde in Übersee (letztere absolut und in Prozent). Vgl. auch Abb. 1.

Years ringed	Total recoveries	Overseas recoveries	Per cent overseas
1909–1959	2,892	65	2.2
1960–1968	2,965	28	0.94
1969–1979	3,001	7	0.2
1980–1994	2,842	1	0.04

3.2. Inspection of ringing and recovery dates

Facultative partial migration may be inferred if individuals are captured in their breeding and (occasional) wintering areas in different winters. Such occurrences have been sought in presence date distributions such as those shown in Fig. 2 for the Norwegian Blackbird and Greenfinch populations that migrate to the British Isles. It can be seen that very few of the migrant Blackbirds are ever found in Norway between December and February (Fig. 2a), suggesting obligate partial migration, whereas appreciable numbers of the migrant Greenfinches can be in Norway in these

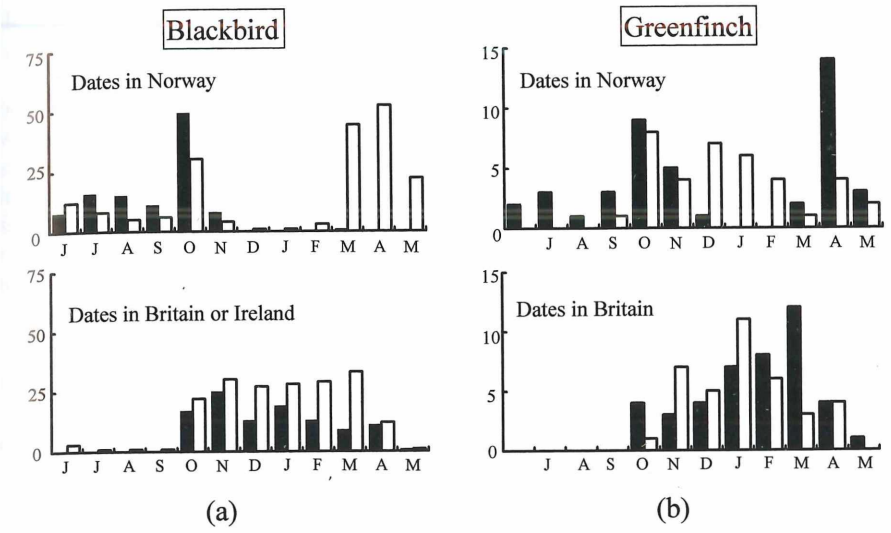

Fig. 2: Frequency distributions of ringing and recovery dates. Filled and unfilled bars respectively show the numbers of records in each calendar month, for 'direct' and 'indirect' movements as defined in the text. In the case of indirect movements, distributions for all 12-month periods later than that in which ringing occurred are combined. (a) Blackbird movements from Norway to Britain and Ireland (n = 296). Upper: ringing dates in Norway for birds recovered in Britain or Ireland. Lower: recovery dates in Britain or Ireland for birds ringed in Norway. (b) Greenfinch movements between Norway and Britain (n = 80): adapted from Main (1999). Upper: ringing or recovery dates in Norway for birds recovered or ringed in Britain. Lower: recovery or ringing dates in Britain for birds ringed or recovered in Norway.

Abb. 2: Häufigkeitsverteilung für die Zeitpunkte der Beringungen und Wiederfunde. Ausgefüllte bzw. nicht ausgefüllte Säulen stehen für die Häufigkeit im entsprechenden Monat von „direktem" und „indirektem" Zug (nähere Erläuterungen dazu s. Text). Bei „indirektem" Zug wurden alle 12-Monatsperioden nach der Periode, in der die Beringung erfolgte, zusammengefaßt. a) Amselzug von Norwegen nach Großbritannien und Irland (n = 296); oben: Beringungsmonat in Norwegen von Vögeln, die in Großbritannien bzw. Irland zurückgemeldet wurden; unten: Wiederfundsmonat von in Norwegen beringten Grünlinge in Großbritannien und Irland. b) Grünlingszug zwischen Norwegen und Großbritannien (n = 80), verändert nach Main 1999; oben: Monat der Beringung bzw. des Wiederfunds in Norwegen von Vögeln, die in Großbritannien wiedergefunden bzw. beringt wurden; unten: Monat des Wiederfunds bzw. der Beringung in Großbritannien von Grünlingen, die in Norwegen beringt bzw. wiedergefunden wurden.

months (Fig. 2b). The latter are all birds involved in indirect movements (unfilled bars): they have all been ringed or recovered in Britain between autumn and spring, but they have also been found in Norway in an earlier or later winter. Thus these individuals migrate in some years only, i.e. they are contributing to facultative partial migration in their population[1]. The fact that Norwegian Greenfinches never reach Ireland (in fact are rarely found far from the east coast of Britain) also suggests an occasional, environmentally-induced sea crossing rather than an annual migration.

[1] It has been suggested (Main 1999) that the movements of the Greenfinches reaching northern Britain actually constitute the facultative phase of an obligate partial migration (Terrill & Able 1988) by the majority population of Norwegian Greenfinches to the south and west coasts of Norway.

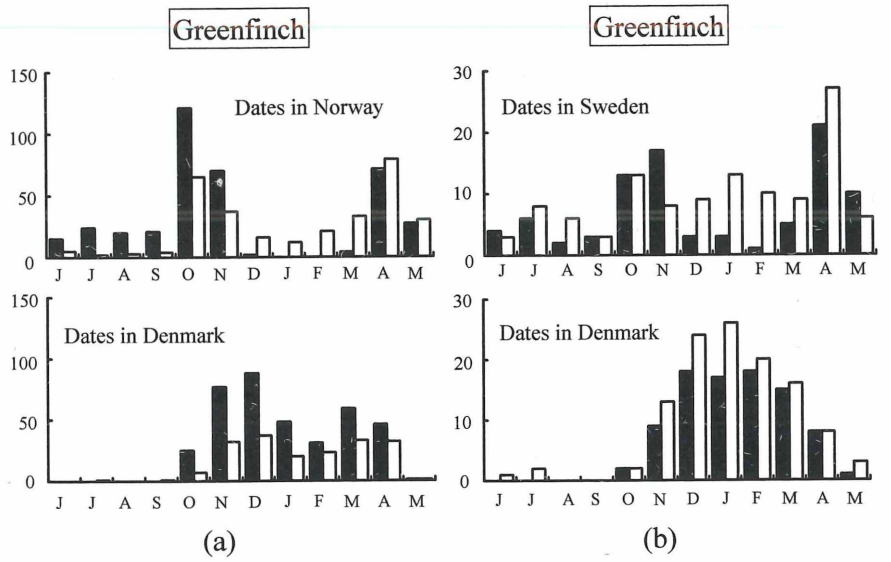

Fig. 3: Frequency distributions of ringing and recovery dates: details as for Fig. 2. (a) Greenfinch movements between Norway and Denmark (n = 677). Upper: ringing or recovery dates in Norway for birds recovered or ringed in Denmark. Lower: recovery or ringing dates in Denmark for birds ringed or recovered in Norway. (b) Greenfinch movements between Sweden and Denmark (n = 203). Upper: ringing or recovery dates in Sweden for birds recovered or ringed in Denmark. Lower: recovery or ringing dates in Denmark for birds ringed or recovered in Sweden.

Abb. 3: Häufigkeitsverteilung für die Zeitpunkte von Beringungen und Wiederfunden (Details wie Abb. 2). a) Grünlingszug zwischen Norwegen und Dänemark (n = 667); oben: Monat der Beringung bzw. des Wiederfunds in Norwegen von Vögeln, die in Dänemark wiedergefunden bzw. beringt wurden; unten: Monat des Wiederfunds bzw. der Beringung in Dänemark von Vögeln, die in Norwegen beringt bzw. wiedergefunden wurden. b) Grünlingszug zwischen Schweden und Dänemark (n = 203); oben: Monat der Beringung bzw. des Wiederfunds in Schweden von Vögeln, die in Dänemark wiedergefunden bzw. beringt wurden; unten: Monat des Wiederfunds bzw. der Beringung in Dänemark von Vögeln, die in Schweden beringt bzw. wiedergefunden wurden.

In Fig. 3 are compared Greenfinch movements between Norway and Denmark, with those between Sweden and Denmark. It is known (MAIN 2000) that most Geenfinches moving between Norway and Denmark cross the Skagerrak separating Norway from the Danish mainland (Jutland). Like the migrants to Britain, these birds may be found in their native Norway in all months of the year (Fig. 3a), but nearly all those there during the winter (December to March) are involved in indirect movements. These individuals must spend at least one winter of their lives in Norway, and at least one south of the Skagerrak, since nearly all direct movements to Denmark (filled bars) are accomplished before the end of November.

The corresponding data for Swedish birds (Fig. 3b) do not support such a clear-cut interpretation. Greenfinch movements between Sweden and Denmark predominantly involve the Danish islands (MAIN 2000). The migrants may be found in Sweden in any month, but now significant numbers of those there in winter are ones involved in direct movements. In fact, because Denmark can be reached from Sweden by means of relatively leisurely movements involving only short sea crossings, with none of the urgency of a major crossing to be completed before the onset of winter, the distinction between direct and indirect movements is not such a useful one in this case. This

illustrates the simplification which can be achieved by restricting the analysis to regions separated by substantial water bodies.

In conclusion, it appears practicable to test for the operation of facultative partial migration, between well-separated areas, by seeking individuals marked and recovered in different winters within the two areas in question. Even in cases lacking the quantities of data available for the species discussed here, a small number of recoveries fulfilling the criteria might provide a useful indication. The alternative approach, looking for changes in the proportion of migrant individuals simultaneous with changes in environmental factors, may be useful if data can be taken over a sufficient period, but any deduction must ultimately depend on a particular model of partial migration.

Zusammenfassung

Obligater und fakultativer Teilzug bei Amseln *(Turdus merula)* und Grünlingen *(Carduelis chloris)*: Möglichkeiten und Grenzen des Beringungsexperimentes.

Es wird untersucht, inwieweit Ring-Wiederfunde für eine Unterscheidung zwischen obligatem und fakultativem Teilzug verwendet werden können. Mögliche Vorgehensweisen sind 1) die Erfassung zeitlicher Unterschiede im Ausmaß ziehender Individuen und 2) die Identifizierung von Individuen anhand von Beringungs- und Wiederfunddaten, die nur in einigen Wintern aus ihren Brutgebieten abwandern. Mit dem ersten Ansatz wird aufgezeigt, daß bei britischen Amseln *(Turdus merula)* im Verauf des 20. Jahrhunderts der Prozentsatz von Wiederfunden aus Übersee progressive abnahm. Eine Interpretation ist in diesem Fall allerdings nur im Rahmen eines Modells möglich. Der zweite Ansatz zeigt, daß die Abwanderung norwegischer Amseln nach Großbritannien und Irland im wesentlichen obligat ist, während die Abwanderung norwegischer Grünlinge *(Carduelis chloris)* sowohl nach Großbritannien als auch nach Dänemark sehr wahrscheinlich fakultativ sein dürfte.

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