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Obligate and facultative migration in birds: ecological aspects

I. Newton

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Abstract This paper is concerned mainly with the differences between obligate and facultative migration in birds. 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 thus characterised by its regularity, consistency and predictability. It 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 the prevailing food supplies or weather conditions. The timing of autumn 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 found in its most extreme form in so-called irruptive migrants. While individual obligate migrants typically return to the same breeding localities year after year, and sometimes also to the same wintering localities, individual irruptive migrants typically breed or winter in widely separated areas in different years, wherever conditions are favourable. It is suggested that these two types of migration are best considered not as distinct, but as lying at opposite ends of a continuum of variation in bird migratory behaviour. 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. Suggestions are made for experimental work on captive irruptive species.

Keywords Breeding dispersal · Facultative migration · Genetic control · Irruption · Obligate migration · Partial migration · Site fidelity

Zusammenfassung

Obligater und fakultativer Vogelzug: ökologische Aspekte

Dieser Artikel befasst sich hauptsächlich mit den Unterschieden zwischen obligatem und fakultativem Vogelzug. Obligater Zug wird als “festverankert” erachtet, da Vögel in diesem Fall ihr Brutgebiet jedes Jahr zu einer bestimmten, offensichtlich vorprogrammierten Zeit verlassen und wiederbesiedeln. Zeitablauf, Zugrichtungen und Zugstrecken sind relativ konstant zwischen verschiedenen Jahren. Diese Art von Zug zeichnet sich demnach aus durch Regelmäßigkeit, Konsistenz und Vorhersagbarkeit und kommt bei Kurzstreckenziehern, vor allem aber bei Langstreckenziehern vor. Im Gegensatz dazu wird fakultativer Vogelzug als optional und als Reaktion auf aktuelle Bedingungen betrachtet. So können Individuen in einigen Jahren ziehen, in anderen aber nicht, je nach Nahrungssituation und Wetter. Der Zeitablauf des Herbstzuges und seine Streckenlänge kann zwischen Individuen und auf Populationsebene von Jahr zu Jahr stark variieren. Fakultativer Zug ist für viele Teilzieher typisch und findet seine extremste Form bei sogenannten irruptiven Arten. Während individuelle obligate Zieher typischerweise alljährlich zu denselben Brutgebieten und manchmal auch zu den selben Wintergebieten zurückkehren, brüten oder

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I. Newton (✉)
Centre for Ecology and Hydrology, Benson Lane,
Crowmarsh Gifford, Wallingford, Oxon OX10 8BB, UK
e-mail: ine@ceh.ac.uk

überwintern individuelle fakultative Zieher in verschiedenen Jahren je nach günstigen Bedingungen häufig in weit voneinander entfernten Gebieten. Jedoch sollten diese beiden Typen von Vogelzug am besten nicht als grundsätzlich verschieden erachtet werden, sondern als Extreme entlang eines Kontinuums von Zugverhalten. Beide Zugtypen sind adaptiv, der eine unter Bedingungen, in denen Ressourcen regelmäßig und vorhersagbar über Raum und Zeit variieren, und der andere unter Bedingungen, in denen Ressourcen unvorhersagbar variieren. Der Artikel schließt mit Vorschlägen zu experimentellen Laborstudien an irruptiven Arten.

Migration in birds is often defined as a regular return movement between breeding and wintering areas. For a long time, ornithologists in Europe have recognised two types of migratory movements (Berthold 2001). Obligate migration is considered “hard-wired”, in that the bird seems pre-programmed to leave its breeding area at a certain time of year, and to return at another time of year. This type of migration is characterised by its regularity, consistency and predictability. It is found in both short-distance and long-distance migrants, but is associated mainly with long-distance complete migrants, including those that migrate between Eurasia and Africa or between North and South America.

In contrast, facultative migration is considered optional, occurring in response to conditions at the time. Individuals migrate in some years but not in others, depending on the prevailing conditions of food or weather. The date of autumn migration and the distance travelled can be highly variable between individuals, and from year to year at the population level. In its extreme form, this type of migration is characterised by its irregularity, inconsistency, and apparent unpredictability. It is typical of many partial migrants, but is seen in most extreme form in so-called irruptive migrants that depend on sporadic tree-seed crops, fluctuating rodent populations, or other inconsistent food sources. Berthold (2001) distinguished two types of partial migration as a “within-population” phenomenon: one in which migration was facultative in all individuals, and another in which migration was obligate in some individuals but not in others (in other words, the tendency to migrate was inherently variable among birds breeding in the same area). The first type would seem to better fit the situation in irruptive migrants, because it would enable individuals to respond immediately to change in food supplies, and adjust their behaviour from year to year according to prevailing conditions.

While considerable understanding has been gained in recent years of the ecological and genetic mechanisms

underlying regular obligate migration in birds (Berthold 2001), much less is known about the ecological and genetic control of irregular facultative migration. In many textbooks on bird migration, irruptions are often dealt with separately from regular obligate migration, as though they were a different phenomenon. My aim in this paper is to compare the essential features of both types of bird movements, and to suggest that they form part of a single spectrum of bird migratory behaviour which is closely linked to the regularity or otherwise of the food supplies on which different species depend. Suggestions are made for further research needs, but for discussion of physiological responses of migrants to environmental cues, see Ramenofsky et al. (2011).

Features of obligate and facultative migrants

Typical features of obligate migrants can be listed 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 being 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 North and South America, or between Eurasia and Africa: swallows, warblers, cuckoos, Arctic-nesting shorebirds, etc.

Typical features of facultative (irruptive) migrants can be listed 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 vary 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) birds 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 *Nyctea scandiaca*, or Eurasian Siskins *Carduelis spinus* and Common Redpolls *Carduelis flammea*. These irruptive species

often show a great spread in terms of timing, directions and distances of outward movements.

Some examples to illustrate these differences

The Lesser Whitethroat *Sylvia curruca* is an example of what would be called an obligate migrant: ring recoveries in Fig. 1 show the migration route of this species from Britain southeast across Europe towards northeast Africa (after which it turns south). Although the maps for autumn and spring show only part of the journey to and from Africa, the important point is that the migration route across Europe is relatively narrow, and there is little directional variation between individuals. This species also migrates within a relatively narrow period after breeding, with 95% of birds leaving Britain within a period of less than eight weeks.

Now contrast this directional pattern with that for an irruptive migrant, the Eurasian Siskin, dependent on sporadic tree-seed crops (Fig. 2). As may be judged from the movements between Britain and continental Europe, Siskins clearly show a much wider spread of directions, routes and distances. They also show much more spread in timing, with migration obvious over at least 12 weeks in autumn, with peak timing varying among years. Figure 3 shows the timing of the migration of Siskins from year to year at Ottenby in south Sweden in relation to the size of birch seed crop (their main autumn food) further north: birds leave several weeks earlier when birch seed is scarce than in years when it is abundant.

Within the directional spread shown by irruptive migrants, there can be marked differences in favoured directions between years. Annual differences can be illustrated by Common Redpolls ringed in Finland in the autumns of two different years (Fig. 4). In 1965, ringed birds moved mainly east-southeast, whereas in 1972 they moved mainly southwest. This difference was explicable, perhaps, if the birds were following seed-crops which differed in location from year to year (being diurnal migrants, they could see masting trees from the air). Another possibility is that, with less firmly fixed directional preferences, these birds were more inclined than most obligate migrants to go with the wind, experiencing mainly easterly winds in one autumn and mainly westerly in another.

Spring movements

Whether a bird is considered a regular or irruptive migrant depends largely on its behaviour in autumn. Regular obligate migrants undertake an outward migration every year,

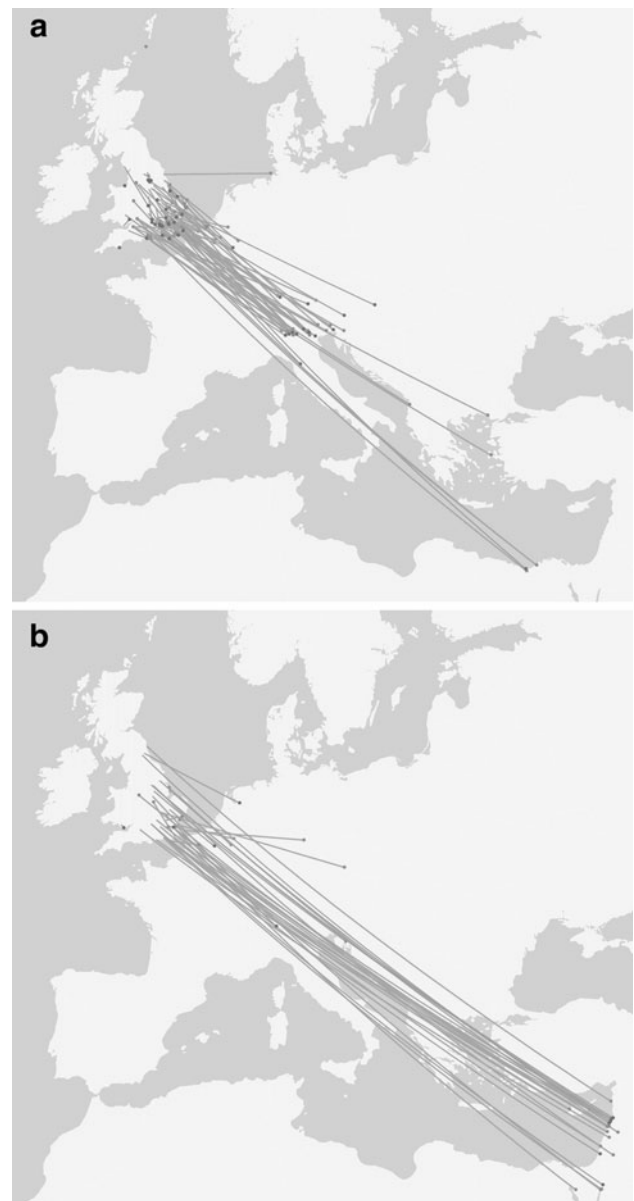


Fig. 1 Migration route of Lesser Whitethroats *Sylvia curruca* between Britain and the eastern Mediterranean region, as indicated by ring recoveries: **a** August–October, **b** March–April. After reaching the eastern Mediterranean region, the birds turn southward to winter in East Africa. Modified from Wernham et al. (2002), with permission from the British Trust for Ornithology

returning each spring, whereas an irruptive migrant might stay in the breeding range or move a short or long distance. If it remains in the breeding range, it may not need to undertake a long spring migration, but it may still move to a different area within the breeding range. However, if it migrates in autumn south of the breeding range, it returns in spring, like a regular migrant, but not necessarily to the same place. At least some irruptive migrants apparently behave in spring as they do in autumn, and break their journey if they encounter areas of abundant food. For



Fig. 2 Movements of Siskins *Carduelis spinus* into and out of Britain and Ireland, as indicated by ring recoveries. Birds ringed or recovered abroad in the breeding season are indicated by a spot. Modified from Wernham et al. (2002), with permission from the British Trust for Ornithology

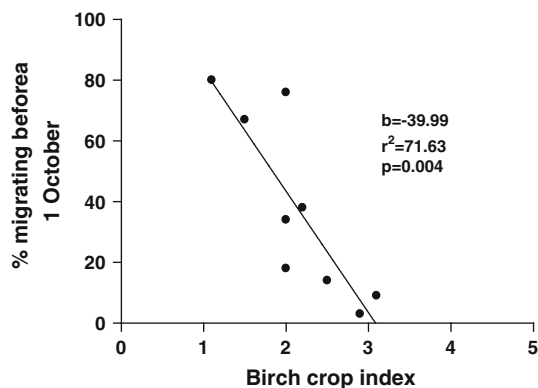


Fig. 3 Numbers and timing of Eurasian Siskins *Carduelis spinus* migrating through Ottenby each year in relation to the size of the birch seed crop further north. Drawn from data in Svårdson (1957)

example, in years of good spruce crops in the southern boreal zone, Redpolls can assemble there in April–May, as the cones open to release their seeds, and can raise an early brood. Once the seeds have fallen, the birds continue to their usual breeding areas in the birch zone further north. To my knowledge, such movements have not been confirmed by ringing, but have been inferred from simultaneous changes in the populations of the two regions and, in particular, from the late arrival in the birch areas in those years of adult Redpolls with recently fledged young (Peiponen 1967; Götmark 1982). The adults then raise another

brood. In most years, with little or no spruce seed, the birds migrate through the boreal zone and raise only the one brood in the north. A similar phenomenon may occur in Siskins (Payevsky 1994; Newton 2008).

Some other irruptive species have been recorded breeding south of their usual breeding range in certain years, giving further evidence of variable spring settling patterns (for examples, see Newton 2008). The implication is that, although irruptive migrants that have travelled south of the breeding range start on a return journey, where they settle is influenced by the food supplies encountered en route, in parallel with the situation in autumn. In both seasons, abundant food can suppress onward migration.

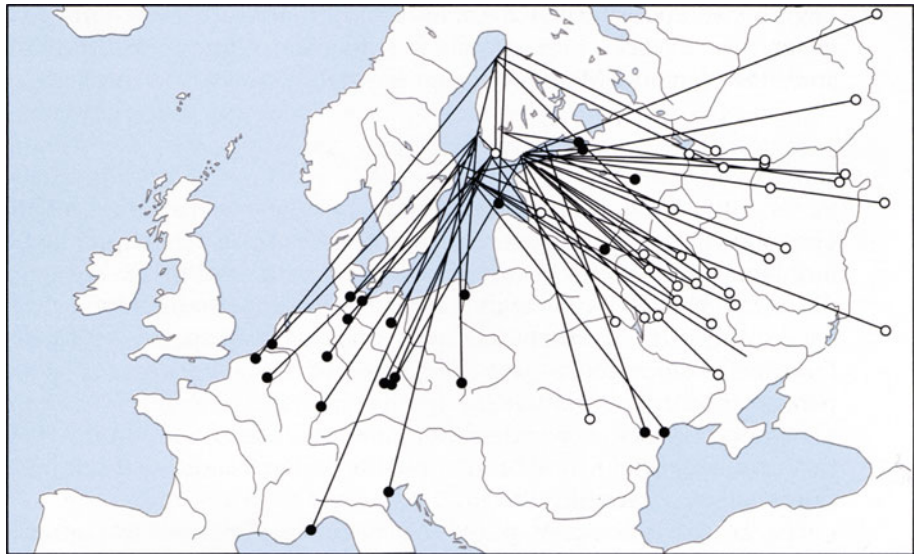
A continuum of behaviour

The two types of migration (obligate and facultative) have been recognised in Europe for a long time; they were formerly called calendar (or instinct) and weather migration. However, it may be more realistic not to distinguish two separate types, but rather to envisage a continuum of variation between extremes, from rigid and fixed at one end to flexible and variable at the other.

Another reason to view the two types as opposite ends of a continuum, rather than distinct types, is that some birds seem to have both types, apparently switching from obligate to facultative modes during their migration. For example, White Storks *Ciconia ciconia* leave eastern Europe every year to winter in the warmer climates of Africa, but radio tracking has shown that the same individuals departing from the same nest sites year after year can vary their wintering areas, travelling around 7,000 km to East Africa in some years, and moving further on to southern Africa in other years, resulting in a total journey of around 11,000 km (Berthold et al. 2002, 2004). The first part of the journey—which all individuals undertake—could be regarded as obligatory, and the second part as facultative, allowing great variation in wintering area from year to year, contingent upon rainfall and resulting food supplies. Some years ago, Terrill (1990) suggested that the obligate phase of migration takes the bird over areas where it could not usually survive in winter, and the later facultative phase over areas where, in one place or another, it should find suitable conditions every year. In some years, in response to changing conditions, a bird may move further down the migration route after the main autumn migration season, as in hard weather movements.

One possibility, therefore, is that all bird migrations have both obligate and facultative phases, but with the relative lengths of the two phases varying between populations. In some species, most of the migration may be obligate (or fixed distance); in others it may be mostly or

Fig. 4 Winter recoveries of Common Redpolls *Carduelis flammea* ringed in Finland. Circles winter 1965–1966, dots winter 1972–1973. After Zink and Bairlein (1995)



entirely facultative (or variable distance). I will return to this point later, but I will first discuss some of the consequences of obligate and facultative migrations for site fidelity.

Site fidelity

Table 1 shows examples of obligate migrants in which all (or almost all) individuals returned to the same breeding and wintering areas in successive years, as shown from the repeated trapping or re-sighting of marked individuals. In these birds, return rates to breeding and wintering areas were high, within the range 30–60% for passerines and 60–90% for non-passerines. From what we know of annual survival rates, we can infer that all (or almost all) surviving individuals returned to the same breeding and wintering localities year after year. Return rates were lower for passerines because their annual survival rates are lower than in non-passerines.

Now compare these species with some facultative (irruptive) migrants (Table 2) in which return rates to specific breeding and wintering areas are extremely low (sometimes nil). In Bramblings *Fringilla montifringilla* caught over several summers in Lapland, only seven (0.6%) out of 1,238 adult birds were caught there in more than one year (Lindström et al. 2005). Low return rates to particular localities occur because, as shown by other ring recoveries, individuals can breed in widely separated areas in different years, wherever food supplies are good at the time (Newton 2008). Extreme examples include the Red Crossbill *Loxia curvirostra*, in which ringed individuals were reported from localities up to 3,200 km apart in different breeding seasons (January–April) (Newton 2006b), and the Snowy Owl *Nyctea scandiaca*, in which radio-

tagged individuals were found at localities up to 1,928 km apart in successive breeding seasons (Fuller et al. 2003).

Low site fidelity is also evident from ring recoveries in wintering areas (Table 2). At specific wintering localities, return rates were mostly less than 1% in various seed-eaters (including Bramblings, Newton 2008), and 3% in longer-lived Snowy Owls (Smith 1997), again because birds winter in widely separated areas in different years. Most such shifts recorded by ring recoveries could be regarded as lying at different points on the same migration axis, but some were apparently on different axes, as the birds were recovered in winter far to the east or west of where they were ringed in a previous winter (Newton 2008). Table 3 gives a few examples from hundreds available: in the Common Redpoll, some individuals were reported from places more than 8,000 km apart in different winters. Displacements were mostly within the Eurasian or North American land masses, but one Redpoll was ringed in Michigan in one winter and recovered 10,200 km away in eastern Siberia in another winter. Some of these birds made their move from one winter to the next, presumably having returned to the breeding range in the interim and taken different directions each autumn. Others were recovered two or more years after they were ringed, so could have made this move in two or more annual steps, gradually shifting across a continent. But whether in one or more steps, it is clear that the migrations of some irruptive species are spatially highly variable (for further details see Newton 2006a, 2008).

Genetic control

The arguments above were based on field data, but to understand irruptive migration, we need to explore how such a flexible system could fit with knowledge of the

Table 1 Annual return rates of individual birds to the same area: regular migrants

	Number ringed	Number (%) recaptured in a later year	Location (years)	Reference
Breeding areas				
Willow Warbler <i>Phylloscopus trochilus</i>	161	50 (31%)	England (6)	Lawn (1982)
Chaffinch <i>Fringilla coelebs</i>	173	68 (39%)	Finland (7)	Mikkonen (1983)
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	125	70 (56%)	Sweden (7)	Bensch and Hasselquist (1991)
Flammulated Owl <i>Otus flammeolus</i>	37	28 (76%)	Colorado (5)	Reynolds and Linkhart (1987)
Temminck's Stint <i>Calidris temminckii</i>	173	131 (76%)	Finland (10)	Hildén (1979)
Black Kite <i>Milvus migrans</i>	285	247 (87%)	Spain (8)	Forero et al. (1999)
Wintering areas				
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	145	62 (43%)	Malaysia (4)	Nisbet and Medway (1972)
Northern Parula (Warbler) <i>Parula americana</i>	65	32 (48%)	Puerto Rico (5)	Staicer (1992)
American Redstart <i>Setophaga ruticilla</i>	111	56 (57%)	Jamaica (3)	Holmes and Sherry (1992)
Green Sandpiper <i>Tringa ochropus</i>	115	97 (84%)	England (9)	Smith et al. (1992)
White-fronted Goose <i>Anser albifrons</i>	531	451 (85%)	Scotland (22)	Wilson et al. (1991)
Ruddy Turnstone <i>Arenaria interpres</i>	71	61 (86%)	England (3)	Burton and Evans (1997)

For other examples, see Newton (2008)

Table 2 Annual return rates of individual birds to the same area: irruptive migrants

	Number ringed	Number (%) recaptured in a later year	Location (years)	Reference
Breeding areas				
Brambling <i>Fringilla montifringilla</i>	1,238	7 (0.6%)	Sweden (19)	Lindström et al. (2005)
Eurasian Siskin <i>Carduelis spinus</i>	391	30 (7.7%)	Scotland (6)	Shaw (1990)
Pine Siskin <i>Carduelis pinus</i>	1,322	4 (0.3%)	Oklahoma (?)	Baumgartner and Baumgartner (1992)
Cedar Waxwing <i>Bombicilla cedrorum</i>	54	2 (3.7%)	Ohio (6)	Putnam (1949)
Wintering areas				
Evening Grosbeak <i>Hesperiphona vespertina</i>	2,637	0 (0%)	New York (18)	Yunick (1983)
Pine Siskin <i>Carduelis pinus</i>	3,819	0 (0%)	New York (18)	Yunick (1983)
Common Redpoll <i>Carduelis flammea</i>	7,946	0 (0%)	New York (18)	Yunick (1983)
Common Redpoll <i>Carduelis flammea</i>	5,200	16 (0.3%)	Alaska (?)	Troy (1983)
Purple Finch <i>Carpodacus purpureus</i>	2,822	13 (0.5%)	New York (18)	Yunick (1983)
Brambling <i>Fringilla montifringilla</i>	2,330	16 (0.5%)	England (7)	Browne and Mead (2003)

For other examples, see Newton (2008)

genetic control of migration, gained almost entirely from studies of captive birds. 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 minutes¹ of migratory

restlessness shown per season (Berthold and Helbig 1992; Pulido and Berthold 2003). Now imagine adding to these three aspects a fourth component—the ratio of obligate to facultative stages in the journey. In some species, the obligate phase is long-lasting, covering most of the journey; in others it is short/nonexistent, covering only a small part of the potential migration, with the rest of the variable journey being undertaken on a facultative basis. If we assume that each of the four components can be varied independently of the others by the action of natural selection—and the experimental studies on the first three

¹ The total minutes of migratory restlessness is a function of the number of nights with activity and the mean number of minutes per night.

Table 3 Examples of irruptive species in widely separated localities in different winters (December–March)

	Ringed	Recovered	Distance (km)
Bohemian Waxwing <i>Bombycilla garrulus</i>	Sweden	Siberia	3,060
	Sweden	Siberia	4,070
	Poland	Siberia	4,500
	Ukraine	Siberia	6,000
	British Columbia	South Dakota	1,360
	Sweden	Russia	2,980
	Sweden	Russia	2,280
	Sweden	Russia	2,910
Cedar Waxwing <i>Bombycilla cedrorum</i>	California	Alabama	3,000
Brambling <i>Fringilla montifringilla</i>	Belgium	Turkey	3,000
	Britain	Greece	2,500
Eurasian Siskin <i>Carduelis spinus</i>	Belgium	Lebanon	3,000
	Sweden	Iran	3,000
Pine Siskin <i>Carduelis pinus</i>	Ontario	California	3,537
	Quebec	California	3,950
	New York	British Columbia	3,470
	Tennessee	British Columbia	3,780
	Pennsylvania	Washington	2,800
Common Redpoll <i>Carduelis flammea</i>	Sweden	Russia	1,800
	Hungary	Siberia	3,300
	Belgium	China	8,350 ^a
	Alaska	New Brunswick	5,200
	Quebec	Alaska	4,850
	New Jersey	Alberta	3,250
	Saskatchewan	Vermont	2,550
	New Jersey	Alberta	3,250
	New Jersey	Manitoba	2,100
	Alaska	Saskatchewan	2,730
Evening Grosbeak <i>Hesperiphona vespertina</i>	Michigan East	Siberia	10,200
	Maryland	Alberta	3,400
	Virginia	Newfoundland	2,200
	Quebec	Georgia	1,750
Eurasian Bullfinch <i>Pyrrhula pyrrhula</i>	Finland	Siberia	1,900
	Finland	Siberia	2,350

These recoveries, which are selected as extreme examples from among many, refer mainly to birds that seemed to be on a different migration axis in different winters, as they were recovered in winter far to the east or west of where they were ringed in a previous winter

Sources of records are given in Newton (2008). Yunick (1997) gives additional information on Pine Siskins, while Brewer et al. (2000) list 12 Redpolls that were trapped in different winters at places 1,345–4,836 km apart in North America

^a This movement is matched by at least three others almost as long: from Norway to eastern China, Finland to eastern China, and eastern China to Sweden, respectively

components would suggest this—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, or some North

American breeding species in their Central-South American wintering areas (Terrill and Ohmart 1984). In captivity, individual Garden Warblers *Sylvia borin* developed migratory restlessness when deprived of food in winter, well outside the usual migration period (Gwinner et al. 1988).

Some early experimental work on the migratory restlessness of captive birds lends support to the idea of a

two-phase migration. In White-throated Sparrows *Zonotrichia albicollis*, Helms (1963) identified two subdivisions of migratory behaviour in both spring and autumn. The first phase (which he called the “motivational subdivision”) was characterised by intense and continuous night-time activity, while the second phase (the “adaptational subdivision”) was less intense, with numerous interruptions and greater variability. Helms (1963) aligned these two phases with the behaviour of free-living birds during spring migration, as they switched from an intense, highly directed phase to a more casual “wandering phase” during which they searched for suitable habitat and took advantage of local opportunities. In addition, observations of the directional preferences of caged migrants revealed an increasing variance in headings towards the end of the migratory period (Wiltschko and Wiltschko 2003), which is again consistent with a terminal more facultative phase in behaviour.

Clearly we need more research on captive irruptive species. Existing studies on a small number of obligate migrant species could be usefully extended to irruptive species to examine in captivity: (1) the spread of directional preferences among birds from the same population; (2) the spread in onset and duration of migratory restlessness within a population, its relationship with nutritional condition, and whether the pattern of migratory restlessness suggests obligate and facultative stages; and (3) the effects of reduced food supply and other external influences on migratory restlessness at different dates through autumn and winter. The important requirement is to integrate the testing of “environmental influences” into future experiments on the migratory behaviour in birds (most of which have so far been conducted under standard conditions on young birds in their first migration season).

One way in which migratory behaviour could be fixed or flexible yet based on the same underlying genetic control system is through flexible reaction norms that are subject to both genetic and environmental influences. Imagine a genetically influenced “migratory threshold” (above which migration is stimulated), but in which the threshold is also responsive to environmental conditions, such as feeding opportunities or weather. Among obligate migrants, the threshold (under genetic influence) would be set low, so that migration was readily induced under a wide range of environmental conditions. Among facultative migrants, the threshold would be set higher, depending to a greater extent on environmental conditions, especially food supplies, which could influence bird behaviour at each stage of the journey and thereby result in longer movements in some individuals or years than in others. If the genetic component also caused a change in threshold level during the migration season, this would be one way in which the bird could shift from obligate to facultative modes during a

single journey. A seasonal change in the threshold level would in any case seem necessary to bring migration to an end. This takes us outside the scope of this paper, but for further discussion of such potential control mechanisms involving polygenic control of a continuously varying trait, reaction norms and environmentally sensitive thresholds, see Roff (1996), Chan (2005) and van Noordwijk et al. (2006).

The food situation for an individual depends not only on the amount of food in the local environment, but also on its dominance status with respect to other individuals. In many facultative migrants, the subordinate sex and age groups typically migrate in greater proportions, at earlier dates, or extend further from the breeding areas than dominant adults (Gauthreaux 1982; Newton 2008). Thus, in many passerines, females migrate in greater proportion than males, juveniles in greater proportion than adults, and late-hatched juveniles in greater proportion than early-hatched ones (e.g. Smith and Nilsson 1987). Such sex and age differences have led to the notion that competition for food (or its effect on body condition) is involved as a proximate mechanism stimulating migration in those individuals least able to survive in the current conditions (Gauthreaux 1982). In years poor in food, this effect is likely to extend further up the social hierarchy, affecting a greater proportion of the overall population. That the effects of food supply can be mediated by social dominance was shown in experiments on captive Dark-eyed Juncos *Junco hyemalis*, in which subordinate individuals which suffered the greatest deprivation were most likely to accumulate fat and show migratory restlessness (Terrill 1987). Another aspect of social behaviour which could help to stimulate migration in some situations is the level of “excitement” evident in some migrants before departure (Lack 1954), and which was found to transfer between individuals in captivity, affecting their migratory restlessness (Chan 2005).

Conclusions

Table 4 summarises differences between obligate and facultative migrants, the two extremes of a continuum. The nature of migration apparently varies with the types of food supplies to which different bird species are exposed. Regular (obligate) migration is associated with food supplies that are predictable in time and space, and is consistent in timing, direction and distance from year to year, whereas irregular (facultative) migration is associated with food supplies that—to varying degrees—are unpredictable in time and space, and is variable in timing, direction and distance from year to year. In its most extreme form, facultative migration is manifested as irruptions, and individual participants show little or no site fidelity from year

Table 4 Comparison between typical regular and typical irruptive migration

	Regular (obligate) migrants	Irruptive (facultative) migrants
Habitat/food	Predictable	Unpredictable
Breeding areas	Fixed	Variable
Wintering areas	Fixed	Variable
Site fidelity	High	Low
Autumn 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	Probably day length ^a	Food supply

^a The timing of autumn migration is highly modified by other factors, such as the completion of previous events in the annual cycle (whether breeding or moult), which can delay departure. In both regular and irruptive migrants, flights are also dependent on appropriate weather conditions

to year. 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 change unpredictably.

The advantage of strong endogenous control, as found in obligate migrants, is that it can permit anticipatory behaviour, allowing birds to prepare for migration before it becomes essential for survival, facilitating fat deposition before food becomes scarce. Such a fixed control system is likely to be beneficial only in predictable circumstances, in which food supplies change in a consistent and timely manner, and at about the same dates, and it is essential where information on environmental conditions ahead is not available (that is, in wintering long-distance migrants). It is not suited to populations which have to cope with a large degree of spatial and temporal unpredictability in their food supplies. Migratory behaviour in such populations, while under genetic influence, seems much more sensitive to prevailing conditions, and hence varies from place to place and year to year. Both regular and irregular systems are adaptive, but to different types of variation in food supplies. Nevertheless, to reiterate, obligate and facultative migrants are probably best regarded not as distinct types but as opposite ends of a continuum of migratory behaviour, with predominantly hard-wired (internal) control at one end and predominantly external control (= flexibility) at the other. Although the timing and distance of movements of facultative migrants may vary with

individual circumstances, other aspects must presumably be under more rigid genetic control, notably the directional preferences and timing in spring when birds return to the breeding range.

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References

- Baumgartner FM, Baumgartner AM (1992) Oklahoma bird life. Oklahoma University Press, Norman
- Bensch S, Hasselquist D (1991) Territory infidelity in the polygynous great reed warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *J Anim Ecol* 60:857–871
- Berthold P (2001) Bird migration: a general survey, 2nd edn. Oxford, Oxford University Press
- Berthold P, Helbig AJ (1992) The genetics of bird migration: stimulus, timing and direction. *Ibis* 134:35–40
- Berthold P, Bosch W, van den Jakubiec Z, Kaatz C, Kaatz M, Querner U (2002) Long-term satellite tracking sheds light on variable migration strategies of White Storks (*Ciconia ciconia*). *J Ornithol* 143:489–495
- Berthold P, Kaatz M, Querner U (2004) Long-term satellite tracking of white stork (*Ciconia ciconia*) migration: constancy versus variability. *J Orn* 145:356–359
- Brewer D, Diamond A, Woodsworth EJ, Collins BT, Dunn EH (2000) Canadian atlas of bird banding, vol 1. Ottawa, Canadian Wildlife Service
- Browne SJ, Mead CJ (2003) Age and sex composition, biometrics, site fidelity and origin of Brambling *Fringilla montifringilla* wintering in Norfolk, England. *Ringing Migr* 21:145–153
- Burton NHK, Evans PR (1997) Survival and winter site fidelity of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in northeast England. *Bird Study* 44:35–44
- Chan K (2005) Partial migration in the silvereye (*Aves Zosateropidae*): pattern, synthesis and theories. *Ethol Ecol Evol* 17:349–363
- Forero MG, Donazar JA, Blas J, Hiraldo F (1999) Causes and consequences of territory change and breeding dispersal distance in the black kite. *Ecology* 80:1298–1310
- Fuller M, Holt D, Schueck L (2003) Snowy owl movements: variation on a migration theme. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 359–366
- Gauthreaux SA (1982) The ecology and evolution of avian migration systems. In: Farner DS, King JR (eds) Avian biology, vol 6. Academic, New York, pp 93–167
- Götmark F (1982) Irruptive breeding of the redpoll, *Carduelis flammea*, in South Sweden in 1975. *Vår Fågelvärld* 41:315–322
- Gwinner E, Schwabl H, Schwabl-Benzinger I (1988) Effects of food-deprivation on migratory restlessness and diurnal activity in the garden warbler *Sylvia borin*. *Oecologia* 77:321–326
- Helms CW (1963) The annual cycle and *Zugunruhe* in birds. *Proc Int Orn Cong* 13:925–939
- Hildén O (1979) Territoriality and site tenacity of Temminck's Stint *Calidris temminckii*. *Ornis Fenn* 56:56–74
- Holmes RT, Sherry TW (1992) Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: applications for population dynamics, habitat selection, and conservation. In: Hagan JM, Johnston DW III (eds) Ecology, conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC, pp 563–575

- Lack D (1954) The natural regulation of animal numbers. Oxford, University Press
- Lawn MR (1982) Pairing systems and site tenacity of the willow warbler *Phylloscopus trochilus* in Southern England. *Ornis Scand* 13:193–199
- Lindström Å, Enemar A, Andersson G, von Proschwitz T, Nyholm NEI (2005) Density-independent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos* 110:155–163
- Mikkonen AV (1983) Breeding site tenacity of the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in northern Finland. *Ornis Scand* 14:36–47
- Newton I (2006a) Advances in the study of irruptive migration. *Ardea* 94:432–460
- Newton I (2006b) Movement patterns of common crossbills *Loxia curvirostra* in Europe. *Ibis* 148:782–788
- Newton I (2008) The ecology of bird migration. Academic, London
- Nisbet ICT, Medway L (1972) Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114:451–494
- Payevsky VA (1994) Age and sex structure, mortality and spatial winter distribution of Siskins (*Carduelis spinus*) migrating through eastern Baltic area. *Die Vogelwarte* 37:190–198
- Peiponen VA (1967) Südliche Fortpflanzung und Zug von *Carduelis flammea* (L.) in Jahre 1965. *Ann Zool Fenn* 4:547–549
- Pulido F (2012) Evolutionary genetics of partial migration in birds—the threshold model of migration revisited. *Oikos* (in press)
- Pulido F, Berthold P (2003) Quantitative genetic analyses of migratory behaviour. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 53–77
- Putnam LS (1949) The life history of the cedar waxwing. *Wilson Bull* 61:141–182
- Ramenofsky M, Cornelius J, Helm B (2011) Physiological and behavioural responses of migrants to environmental cues. *J Orn* (in press)
- Reynolds RT, Linkhart BD (1987) Fidelity to territory and mate in Flammulated Owls. In: Nero RW, Clark RJ, Knapton RJ, Hamre RH (eds) Biology, conservation of northern forest owls. Rocky Mountain Forest & Range Experimental Station, Fort Collins, pp 234–238
- Roff DA (1996) The evolution of threshold traits in animals. *Q Rev Biol* 71:3–35
- Shaw G (1990) Timing and fidelity of breeding for Siskins *Carduelis spinus* in Scottish conifer plantations. *Bird Study* 37:30–35
- Smith N (1997) Observations of wintering Snowy Owls (*Nyctea scandiaca*) at Logan Airport, East Boston, Massachusetts from 1981 to 1997. In: Duncan JR, Johnson DH, Nicholls TH (eds) Biology and Conservation of Owls of the Northern Hemisphere: 2nd Int Symp, Winnipeg, Manitoba, Canada, 5–9 Feb 1997, pp 591–597
- Smith HG, Nilsson J-Å (1987) Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): an evaluation of different hypotheses. *Auk* 104:109–115
- Smith KW, Reed JM, Trevis BE (1992) Habitat use and site fidelity of green sandpipers *Tringa ochropus* wintering in southern England. *Bird Study* 39:155–164
- Staicer CA (1992) Social behaviour of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico. In: Hagan JM, Johnston DW (eds) Ecology, conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington, DC, pp 308–320
- Svårdson G (1957) The “invasion” type of bird migration. *B Birds* 50:314–343
- Terrill SB (1987) Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). *Behav Ecol Sociobiol* 21:1–11
- Terrill SB (1990) Ecophysiological aspects of movements by migrants in the wintering quarters. In: Gwinner E (ed) Bird migration. Physiology, ecophysiology. Springer, Berlin, pp 130–143
- Terrill SB, Ohmart RD (1984) Facultative extension of fall migration by yellow-rumped warblers (*Dendroica coronata*). *Auk* 101:427–438
- Troy DM (1983) Recaptures of redpolls: movements of an irruptive species. *J Field Ornithol* 54:146–151
- van Noordwijk AJ, Pulido F, Helm B, Coppack T, Delingat J, Dingle H, Hedenström A, van der Jeugd H, Marchetti C, Nilsson A, Pérez-Tris J (2006) A framework for the study of genetic variation in migratory behaviour. *J Ornithol* 147:221–233
- Wernham CV, Toms MP, Marchant JH, Clark JA, Siriwardena GM, Baillie SR (2002) The migration atlas: movements of the birds of Britain and Ireland. T & AD Poyser, London
- Wilson HJ, Norriss DW, Walsh A, Fox AD, Stroud DA (1991) Winter site fidelity in Greenland white-fronted geese *Anser albifrons flavirostris*: implications for conservation and management. *Ardea* 79:287–294
- Wiltschko W, Wiltschko R (2003) Mechanisms of orientation and navigation in migratory birds. In: Berthold P, Gwinner E, Sonnenschein E (eds) Avian migration. Springer, Berlin, pp 433–456
- Yunick RP (1983) Winter site fidelity of some northern finches (Fringillidae). *J Field Ornithol* 54:254–258
- Yunick RP (1997) Geographical distribution of re-encountered Pine Siskins captured in upstate, eastern New York during the 1989–90 irruption. *N Amer Bird Bander* 22:10–15
- Zink G, Bairlein F (1995) Der Zug Europäischer Singvögel. AULA-Verlag, Wiesbaden