

# Advances in the study of irruptive migration

Ian Newton<sup>1</sup>

Newton I. 2006. Advances in the study of irruptive migration. *Ardea* 94(3): 433–460.

This paper discusses the movement patterns of two groups of birds which are generally regarded as irruptive migrants, namely (a) boreal finches and others that depend on fluctuating tree-fruit crops, and (b) owls and others that depend on cyclically fluctuating rodent populations. Both groups specialise on food supplies which, in particular regions, fluctuate more than 100-fold from year to year. However, seed-crops in widely separated regions may fluctuate independently of one another, as may rodent populations, so that poor food supplies in one region may coincide with good supplies in another. If individuals are to have access to rich food supplies every year, they must often move hundreds or thousands of kilometres from one breeding area to another. In years of widespread food shortage (or high numbers relative to food supplies) extending over many thousands or millions of square kilometres, large numbers of individuals migrate to lower latitudes, as an 'irruptive migration'. For these reasons, the distribution of the population, in both summer and winter, varies greatly from year to year.

In irruptive migrants, in contrast to regular migrants, site fidelity is poor, and few individuals return to the same breeding areas in successive years (apart from owls in the increase phase of the cycle). Moreover, ring recoveries and radio-tracking confirm that the same individuals can breed in different years in areas separated by hundreds or thousands of kilometres. Extreme examples are provided by Common Crossbills *Loxia curvirostra* in which individual adults were found at localities up to 3200 km apart in different breeding seasons, and Snowy Owls *Nyctea scandiaca* at localities up to 2000 km apart. The implication from irruptive migrations, that individuals can winter in widely separated localities in different years, is also supported by ring recoveries, at least in seed-eaters, in which individuals have been found in one winter hundreds or thousands of kilometres from where they were ringed in a previous winter. Most such shifts 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. Extreme examples included a Bohemian Waxwing *Bombycilla garrulus* (6000 km, Ukraine to Siberia), a Eurasian Siskin *Carduelis spinus* (3000 km, Sweden to Iran), a Pine Siskin *C. pinus* (3950 km, Quebec to California), and a Common Redpoll *C. flammea* (8350 km, Belgium to China).

Compared to regular (obligate) migrants, irruptive (facultative) migrants show much greater year to year variations in the proportions of individuals that migrate, and greater individual and year to year variations in the timing, directions and distances of movements. The control systems are flexible in irruptive migrants, enabling individuals to respond to feeding conditions at the time. However, regular and irruptive migrants are probably best regarded, not as distinct categories, but as representing opposite extremes of a continuum of migratory behaviour found among birds, from narrow and consistent at one end to broad and flexible at the other. Both systems are adaptive, the one to conditions in which resource levels are predictable in space and time, and the other to conditions in which resource levels are unpredictable. Depending on the predictability and stability of its food supply, the same



species may behave as a resident or regular migrant in one part of its range, and as an irruptive migrant in another, as exemplified by particular species of both seed-eaters and rodent-eaters.

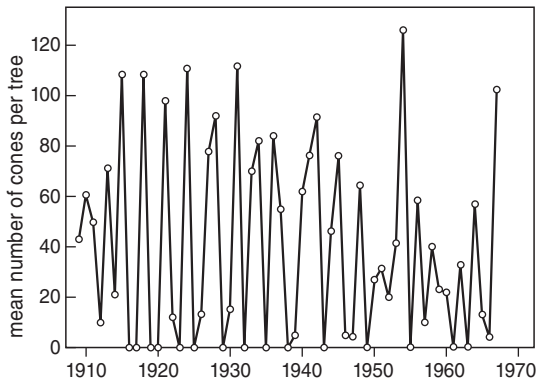
Key words: invasion, irruption, migration, finches, owls

<sup>1</sup>Centre for Ecology and Hydrology, Monks Wood Research Station, Abbots Ripton, Huntingdon, Cambs PE28 2LS, UK; (ine@ceh.ac.uk)

## INTRODUCTION

One of the most striking features of bird migration is its regularity. Most populations of birds migrate at about the same dates, in the same directions, and for similar distances each year, with many individuals returning year after year to the same breeding and wintering localities. This extreme consistency in behaviour is a well-known feature of bird migration. Much research over the past half century has been concerned, one way or another, with the temporal and spatial precision of the journeys, and with the year to year consistency in movement patterns (Berthold 2001). However, consistency in movement patterns has adaptive value only in predictable environments, where birds can be sure of finding suitable conditions year after year in the same breeding or wintering areas. Some bird species exploit habitats or food supplies which are highly variable in distribution and abundance from year to year. In particular localities, habitats or food supplies may be abundant in one year, and practically non-existent the next. Species which most effectively exploit such sporadic resources show much greater flexibility in their movements, concentrating in different areas in different years, wherever resources are plentiful at the time. Such species are often called nomadic or irruptive migrants to distinguish them from regular migrants, which show much more consistent movement patterns from year to year. These two categories of migrants are probably best viewed, not as distinct from one another, but as representing opposite ends of a spectrum of behaviour adapted to the specific conditions that particular populations have to face.

Typical irruptive migrants include: (1) boreal finches and others that depend on fluctuating tree-seed crops; (2) owls and others that depend on cyclically-fluctuating rodent populations; (3) desert birds that depend on sporadic rainfall to create conditions that allow breeding; and (4) water birds that depend on a specific rainfall regime to create appropriate wetland conditions (for examples of which, see Roshier *et al.* 2006). In this paper, I shall consider the first two of these groups, examining the evidence that (1) fluctuations in local numbers are associated with fluctuations in local food supplies, (2) local fluctuations in numbers result largely from movements, and (3) individual birds commonly breed or winter in widely separated localities in different years. A major problem in the study of such species is that they breed mainly in northern regions, where human population density is low, and where the chance of obtaining ring recoveries is extremely small. Moreover, because of their nomadic behaviour, many such species are seldom present in any one area for long enough for detailed study, and the fact that some of the owls are primarily nocturnal adds further difficulties. Hence, much of our understanding of irruptive species is based on scraps of information collected over a long period, and scattered through a wide literature. Previous reviews of this subject area include those of Lack (1954), Svårdson (1957), Ulfstrand (1963), Newton (1972), Bock & Lepthien (1976), and Koenig & Knops (2001). When most of these reviews were written, ringing had provided extremely little evidence to support the major inference from observational evidence, namely that individual birds were irregular in their migration behaviour, breed-



**Figure 1.** Annual fluctuations in the size of Norway Spruce *Picea abies* cone crops in south Sweden, 1909–67. Almost complete fruiting failure occurred in 15 different years out of the 59 years covered. From Hagner (1965) and Götmark (1982).

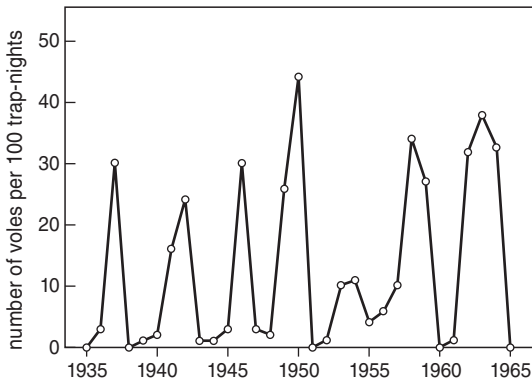
ing or wintering in widely separated localities in different years. Hence, a secondary aim of this paper is to examine some of the evidence from ringing that has emerged in recent years.

## FOOD SUPPLIES

Every naturalist knows that tree-seed crops vary greatly in size from year to year (Fig. 1). In some years trees and shrubs are laden with seeds and fruits of various kinds, but in other years bear almost none. Fruiting depends partly on the natural rhythm of the trees themselves and partly on the weather. Trees of most species require more than one year to accumulate the nutrient reserves necessary to produce a fruit crop. In any one area most of the trees of a species fruit in phase with one another partly because they come under the same weather, and often those of several different species also crop in phase. The result is an enormous profusion of tree fruits in some years, and practically none in others: good crops almost never occur in consecutive years, and nor do poor crops, but each good crop is usually followed by a poor one (Fig. 1; Koenig & Knops 1998, 2000).

Nevertheless, annual seed crops of some tree species fluctuate less than others, with Scots Pine *Pinus sylvestris* producing smaller, but more consistent crops than Norway Spruce *Picea abies*, for example, and Alder *Alnus glutinosa* more consistent crops than Birch *Betula pendula* and *B. pubescens*. Pine and Alder normally produce at least some seed every year, but spruce and birch often fail completely (for annual cropping patterns of different tree species, see Svärdsön 1957, Hagner 1965, Perrins 1966, Götmark 1982, Knox 1992, Thies 1996, Koenig & Knops 1998, 2000; Fig. 1).

The trees in widely separated areas may be on different fruiting regimes, partly because of regional variations in weather, so that good crops in some areas may coincide with poor crops in others. Nevertheless, good crops may occur in many more areas in some years than in others, so the total continental seed production also varies greatly from year to year. An analysis of the fruiting patterns of various boreal conifer species at many localities in North America and Eurasia revealed high synchrony in seed production in localities 500–1000 km apart, depending on tree species. The synchrony declined at greater distances, and by 5000 km no correlation was apparent in the fruiting patterns of particular tree species (Koenig & Knops 1998). These figures give some idea of the range of distances that must separate the successive breeding and wintering areas of some boreal finches if the same individuals are to have access to good tree-seed crops every year of their lives. Some such species eat mainly seeds year-round, but different types of seeds at different seasons (e.g. Common Redpoll *Carduelis flammea*, Eurasian Siskin *C. spinus*), while others eat mainly insects in summer and seeds (or fleshy fruits) in winter (e.g. Bohemian Waxwing *Bombycilla garrulus*, Brambling *Fringilla montifringilla*). The latter tend to concentrate in summer in areas with insect outbreaks (e.g. the Brambling in areas with high densities of the moth *Epirrita autumnata* and the Evening Grosbeak *Hesperiphona vespertina* in areas with Spruce Budworm *Choristoneura fumiferana*, Morris *et al.* 1958, Enemar *et al.* 1984, Lindström *et al.* 2005).



**Figure 2.** Annual fluctuations in the densities of the Red-grey Vole on the Kola Peninsula, northern Russia, 1936–65. From Koshkina (1966).

Similar problems face those species of owls and raptors that specialise on cyclically-fluctuating rodent populations. In temperate, boreal or tundra environments, common species of microtine rodents tend to fluctuate with regular 3–5 year cycles of abundance (Stenseth 1999; Fig. 2). As with tree-seeds, the peaks in rodent numbers are usually synchronised over hundreds or thousands of square kilometres, but out of phase with those in other regions. However, peak populations may occur simultaneously over many more areas in some years than in others, giving a measure of synchrony, for example, to lemming cycles over large parts of northern Canada, with few regional exceptions (Chitty 1950). In addition, the periodicity of vole cycles tends to increase northwards from about three years between peaks in southern boreal regions, increasing to 4–5 years in northern boreal regions. The amplitude of the cycles also increases northwards from barely discernible cycles in some temperate regions to marked fluctuations further north, where peaks may exceed troughs by more than 100-fold (Hansson & Henttonen 1985, Hanski *et al.* 1991, Stenseth 1999). Further north, on the tundra, the periodicity of lemming cycles is in some places even longer (5–7 years between peaks on Wrangel Island, Menyushina 1997), and the amplitude is even

greater, with peaks sometimes exceeding troughs by more than a thousand fold (Shelford 1945). In most places, the increase phase of the cycle usually takes 2–3 years, and the crash phase occurs within one year. In general, specialist rodent-eating birds would have to shift their breeding areas by at least several hundreds of kilometres every few years if individuals were to breed under adequate food conditions every year, and avoid the low years.

### LOCAL FLUCTUATIONS IN DENSITIES

The various species of irruptive migrants, which specialise on tree-seeds (or fleshy fruits) or microtine rodents are listed in Tables 1 & 2 (which include scientific names). Other species also exploit the same foods, but do not depend so heavily on them, so are less affected by their fluctuations. Similarly, some of the species listed in Tables 1 & 2 may be irruptive in some parts of their range but not in others, depending on the breadth of the diet and the level of fluctuation in the entire food supply. Populations that have available to them a wide range of dietary items are less likely to experience a shortage of all types of food in the same year. Examples of species that behave as irruptive migrants in only parts of their range include Eurasian Bullfinch *Pyrrhula pyrrhula*, Wood Nuthatch *Sitta europaea* and various titmice among the seed-eaters, and Tengmalm's Owl *Aegolius funereus*, Common Kestrel *Falco tinnunculus*, Hen Harrier *Circus cyaneus* and Rough-legged Buzzard *Buteo lagopus* among the rodent-eaters. Thus Tengmalm's Owl has been described as a resident generalist predator of small mammals and birds in central Europe, as partially nomadic (with males mainly resident and females moving around) in south and west Finland, and as a highly nomadic microtine specialist in northern Fennoscandia, in areas with pronounced vole cycles and fewer alternative prey (Korpimäki 1986). Such within-species differences in regional behaviour further emphasise the dependence of migratory and other behaviour on the patterns of year to year fluctuation in food supplies.

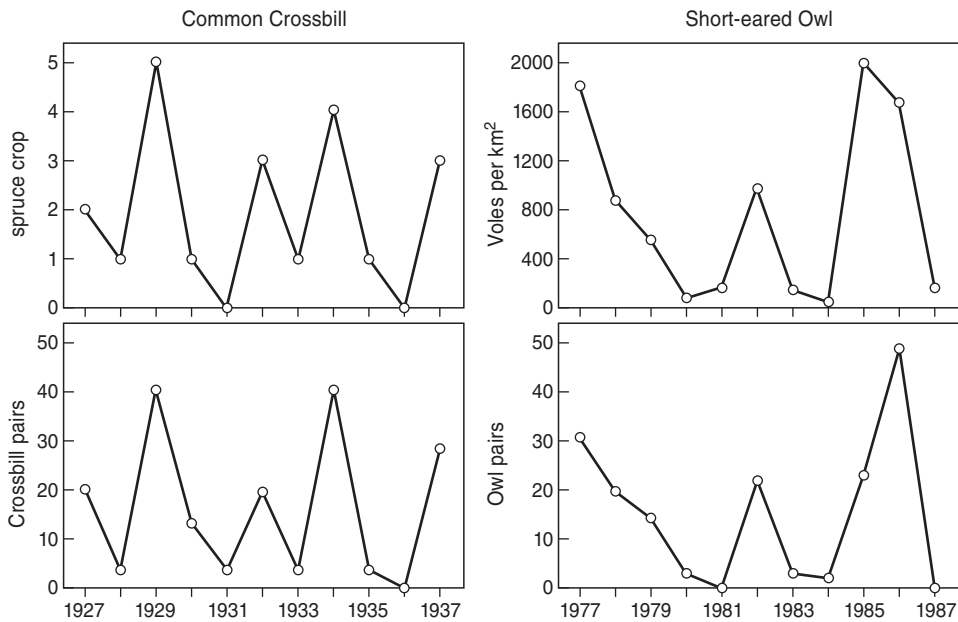
**Table 1.** Established year to year correlations between bird abundance and food supply in seed-eating and fruit-eating birds.

	Summer densities	Winter densities	Autumn emigration	References
Great Spotted Woodpecker <i>Dendrocopos major</i>	•	•	•	Pynnönen 1939, Formosov, 1960, Eriksson 1971
Bohemian Waxwing <i>Bombycilla garrulus</i>			•	Siivonen 1941, Jyrväinen 1975, Bock & Lepthien 1976
Fieldfare <i>Turdus pilaris</i>			•	Jyrväinen 1975
Coal Tit <i>Parus ater</i>			•	Formosov 1965*
Black-capped Chickadee <i>Parus atricapillus</i>			•	Bock & Lepthien 1976
Great Tit <i>Parus major</i>		•	•	Ulfstrand 1962, Perrins 1966, Berndt & Henss 1967
Blue Tit <i>Parus caeruleus</i>		•	•	Ulfstrand 1962, Perrins 1966
Wood Nuthatch <i>Sitta europaea</i>			•	Berndt & Dancker 1960, Enoksson & Nilsson 1983
Red-breasted Nuthatch <i>Sitta canadensis</i>			•	Bock & Lepthien 1976, Widtwehner & Dragula 1984, Davis & Morrison 1987
Brambling <i>Fringilla montifringilla</i>	•	•	•	Silvola 1967, Enemar <i>et al.</i> 1984, Nilsson 1984, Lindström 1987, 2004, Hogstad 2000, Jenni & Neuchulz 1985, Jenni 1987, Eriksson 1970c, Mikkonen 1983
Eurasian Siskin <i>Carduelis spinus</i>	•	•	•	Svärdson 1957, Haapanen 1966, Hogstad 1967, Eriksson 1970b, Petty <i>et al.</i> 1995
Pine Siskin <i>Carduelis pinus</i>	•		•	Bock & Lepthien 1976, Widtwehner & Dragula 1984
Common Redpoll <i>Carduelis flammaea</i>	•		•	Evans 1966, Eriksson 1970a, Enemar <i>et al.</i> 1984
Arctic Redpoll <i>Carduelis flammea</i>	•		•	Bock & Lepthien 1976, Nyström & Nyström 1991
Eurasian Bullfinch <i>Pyrrhula pyrrhula</i>			•	Svärdson 1957
Pine Grosbeak <i>Pinicola enucleator</i>		•	•	Grenquist 1947, Bock & Lepthien 1976
Evening Grosbeak <i>Hesperiphona vespertina</i>			•	Bock & Lepthien 1976
Purple Finch <i>Carpodacus purpureus</i>			•	Bock & Lepthien 1976, Koenig & Knops 2001
Common Crossbill <i>Loxia curvirostra</i>	•	•	•	Reinikainen 1937, Formosov 1960, Newton 1972, Bock & Lepthien 1976, Benkman 1987, Petty <i>et al.</i> 1995
Two-barred Crossbill <i>Loxia leucoptera</i>	•	•	•	Newton 1972, Larson & Tombre 1989, Bock & Lepthien 1976
Parrot Crossbill <i>Loxia pytyopsittacus</i>	•	•	•	Newton 1972
Eurasian Jay <i>Garrulus glandarius</i>			•	Cramp & Perrins 1994
Thick-billed Nuthcracker <i>Nucifraga c. caryocatactes</i>			•	Schütz & Tischler 1941, Mattes & Jenni 1984
Thin-billed Nuthcracker <i>Nucifraga c. macrorhynchos</i>			•	Formosov 1933
Clark's Nuthcracker <i>Nucifraga columbiana</i>			•	Lanner 1996

\*In this species, mass emigration has been more frequently linked with high numbers (which may cause food shortage) or with high spring temperatures which promote high breeding success (Markovets & Sokolov 2002).

**Table 2.** Established year to year correlations between bird abundance and food supply in rodent-eating birds.

	Summer densities	Winter densities	Autumn emigration	References
<b>Diurnal</b>				
Hen (Northern) Harrier <i>Circus cyaneus</i>	●			Hamerström 1969, Hagen 1969
Rough-legged (Hawk) Buzzard <i>Buteo lagopus</i>	●		●	Schüz 1945, Hagen 1969, Court <i>et al.</i> 1988, Potapov 1997
Eurasian (Common) Kestrel <i>Falco tinnunculus</i>	●	●		Cavé 1968, Rockenbauch 1968, Hagen 1969, Korpimäki & Norrdahl 1989
<b>Nocturnal</b>				
Short-eared Owl <i>Asio flammeus</i>	●		●	Korpimäki & Norrdahl 1991, Village 1987
Long-eared Owl <i>Asio otus</i>	●		●	Korpimäki & Norrdahl 1991, Village 1981
Great Grey Owl <i>Strix nebulosa</i>	●		●	Hildén & Helo 1981, Nero <i>et al.</i> 1984, Duncan 1992, 1997, Bull & Duncan 1993
Snowy Owl <i>Nyctea scandiaca</i>	●		●	Shelford 1945, Chitty 1950, Parmelee 1992, Newton 2002
Northern Hawk Owl <i>Surnia ulula</i>	●		●	Korpimäki 1994
Tengmalm's (Boreal) Owl <i>Aegolius funereus</i>	●		-	Korpimäki & Norrdahl 1989



**Figure 3.** Left. Annual fluctuations in the breeding densities of the Common Crossbill in relation to Norway Spruce cone crops in an area of Finland. From Reinikainen (1937). Right. Annual fluctuations in the breeding densities of the Short-eared Owl in relation to Field Vole densities in an area of Finland. From Korpimäki & Norrdahl (1991).

In common with their local food supplies, the breeding densities of many irruptive species, both seed-eaters and rodent-eaters, have been found to fluctuate greatly from year to year (Fig. 3). Response to change in food supply is almost immediate (with no obvious lag), and the increases in numbers from one year to the next are often far greater than could be explained by high survival and reproduction from the previous year, so must also involve immigration. Such observations lead to the inference that year to year changes in local breeding densities are due primarily to movements – immigration or emigration, depending on food conditions at the time.

Among the seed-eaters, local breeding densities can vary from nil or almost nil in poor food years to hundreds or thousands of pairs per 100 km<sup>2</sup> in good food years (for references see Table 1). They contrast with other seed-eaters, whose densities typically vary by less than three-fold from year to year (Newton 1972). Among the rodent eaters, local breeding densities can vary from nil in low rodent years to several tens of pairs per 100 km<sup>2</sup> in intermediate (increasing) or high rodent years. In a 47 km<sup>2</sup> area of western Finland, for example, over an 11 year period, numbers of Short-eared Owls *Asio flammeus* varied between 0 and 49 pairs, numbers of Long-eared Owls *Asio otus* between 0 and 19 pairs, and Common Kestrels between two and 46 pairs, all in accordance with spring densities of *Microtus voles* (Fig. 3, Korpimäki & Norrdahl 1991). All these predators were summer visitors to the area concerned, and settled according to vole densities at the time. Other examples of the range of densities recorded over periods of years for raptors and owls that exploit cyclic prey are given in Newton (2003). In all of them, the year to year increases were so great that they could be explained only by massive immigration. Their fluctuations contrast with findings from other owls and raptors that depend on a wider range of prey species and show much more stable breeding densities from year to year (Newton 1979, 2003). The main points to emerge from these data are that year to year fluctuations in breeding densities are typically very much

greater in irruptive than in regular migrants, that the year to year fluctuations parallel food supplies at the time, and that (by inference) the primary proximate cause of the fluctuations must be movement.

## MOVEMENTS

It is convenient, for present purposes, to distinguish three types of movements: (1) between the breeding localities of different years (natal and breeding dispersal); (2) between breeding and wintering areas (irruptive migration); and (3) between the wintering localities of different years (wintering dispersal). In species of regular migrants, some individuals change their breeding or wintering sites from year to year, but mostly over small distances. In irruptive migrants, such shifts are much more frequent, and can be two or more orders of magnitude greater than in regular migrants. In discussing breeding and wintering dispersal, no implication is intended that birds move directly from one site to another, and in some species, many individuals might migrate between times.

### Turnover rates

One line of evidence suggesting frequent shifts between breeding localities in different years comes from measured rates of turnover in the occupants of particular study areas. In regular migrants, if the birds occupying a particular study area are trapped and ringed in the breeding season, large proportions of the same individuals are usually found breeding in the same area next year. Most are found on the same territories, and those that change territories usually move over relatively small distances, staying within the same area. The proportions of individuals that return to the same area are usually within the range 30–60% for passerines, and 60–90% for non-passerines (Table 3; Newton 2003a). Allowing for expected mortality, such high figures imply that most surviving individuals return to breed in the same limited area year after year. In some such species, the

**Table 3.** Annual return rates of individual birds to same area – regular migrants. For other examples, see Newton (2003a).

	Number ringed	Number (%) recaptured in a later year	Location (years)	Reference
<b>Breeding areas</b>				
Willow Warbler <i>Phylloscopus trochilus</i>	161	50 (31%)	England (6)	Lawn 1982
Chaffinch <i>Fringilla coelebs</i>	173	68 (39%)	Finland (4)	Mikkonen 1983
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	125	70 (56%)	Sweden (7)	Bensch & Hasselquist 1991
Flammulated Owl <i>Otus flammeolus</i>	37	28 (76%)	Colorado (5)	Reynolds & Linkhart 1987
Temminck's Stint <i>Calidris temminckii</i>	173	131 (76%)	Finland (10)	Hildén 1978
Black Kite <i>Milvus migrans</i>	285	247 (87%)	Spain (8)	Forero <i>et al.</i> 1999
<b>Wintering areas</b>				
Great Reed Warbler <i>Acrocephalus arundinaceus</i>	145	62 (43%)	Malaysia (4)	Nisbet & 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 & Sherry 1992
Green Sandpiper <i>Tringa ochropus</i>	115	97 (84%)	England (9)	Smith <i>et al.</i> 1992
White-fronted Goose <i>Anser albifrons flavirostris</i>	531	451 (85%)	Ireland (?)	Wilson <i>et al.</i> 1991
Ruddy Turnstone <i>Arenaria interpres</i>	71	61 (86%)	England (3)	Burton & Evans 1997

same holds for wintering areas, as shown in various passerines, raptors, shorebirds, geese and swans (Table 3; Newton 2003a).

Among irruptive migrants, in contrast, return rates to the same study area are much lower, at least in those species that have been studied (Table 4). For example, among Bramblings, trapped in the breeding season in various areas, individuals were seldom or never caught in the same locality in a later year, so that each year's occupants were different from those the year before (Mikkonen 1983, Lindström 1987, Lindstrom *et al.* 2005, Hogstad 2000). In one such study, only seven (0.6%) of 1238 adults were retrapped in the same study area in a later year, and none of 1806 juveniles, despite a regular annual trapping programme over many years (Lindström *et al.* 2005). Similarly, among Kestrels, of 146 individual breeders trapped and ringed in a 63 km<sup>2</sup> area in Finland over an eleven year period, only 13% of males and 3% of females were found back in the same area in a later year (Korpimäki & Norrdahl 1991). In all the species listed in Table 4, return rates were

extremely low, compared to what would be expected from their annual survival rates. The implication is that a large proportion of breeders changed their nesting localities from year to year.

Interestingly, the return rates of adults to former nesting areas can vary regionally within species, according to the degree of year to year stability in food supply. In comparison with the return rates mentioned above for Kestrels in Finland of 13% males and 3% females, Village (1990) recorded rates of 29% and 18% for males and females in Scotland, and of 43% and 36% in southern England, commenting that the more sedentary nature of the English population was 'due to the greater stability of the food supply both within and between years'. In a study in The Netherlands, as many as 70% of adult Kestrels remained from year to year when vole numbers were on the increase, and as few as 10% when vole numbers crashed (Cavé 1968).

Among the irruptive species studied, return to wintering sites was even lower than return to breeding sites. Despite some very large numbers



**Table 4.** Annual return of the individual birds to the same area – irruptive migrants.

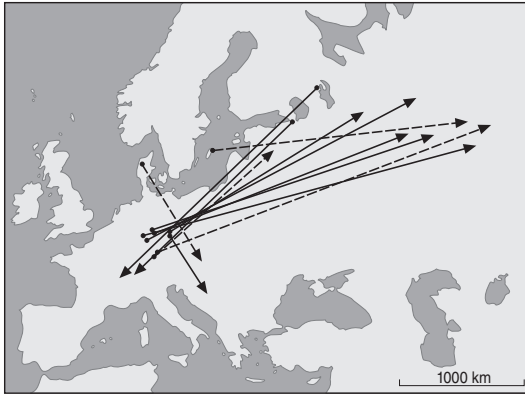
	Number ringed	Number (%) recaptured in a later year in the same place	Location (years)	Reference
<b>Breeding areas</b>				
Brambling <i>Fringilla montifringilla</i>	1238	7 (0.6%)	Sweden (19)	Lindström et al.2005
Eurasian Siskin <i>Carduelis spinus</i>	391	30 (7.7%)	Scotland (6)	Shaw 1990
Pine Siskin <i>Carduelis pinus</i>	1322	4 (0.003%)	Oklahoma (?)	Baumgartner & Baumgartner 1992
Common Redpoll <i>Carduelis flammea</i>	?	? (<1%)	Alaska (?)	Troy 1983
Cedar Waxwing <i>Bombcilla cedrorum</i>	54	2 (3.7%)	Ohio (6)	Putnam 1949
Kestrel <i>Falco tinnunculus</i>	217	17 (7.8%)	Finland (5)	Korpimäki 1988
Saw-whet Owl <i>Aegolius acadicus</i>	52	1 (1.9%)	Idaho (14)	Marks & Doremus 2000
<b>Wintering areas</b>				
Evening Grosbeak <i>Hesperiphona vespertina</i>	2637	0 (0)	New York (18)	Yunick 1983
	>1700	48 (0.003%)	Pennsylvania (14)	Speirs, in Newton 1972
Pine Siskin <i>Carduelis pinus</i>	3810	0 (0)	New York (18)	Yunick 1983
	4045	0 (0)	New York (2)	Yunick 1997
	1322	4 (0.3%)	Oklahoma (4)	Baumgartner & Baumgartner 1992
Common Redpoll <i>Carduelis flammea</i>	7946	0 (0)	New York (18)	Yunick 1983
	1800	0 (0)	New Hampshire (?)	Troy 1983
	5200	16 (0.3%)	Alaska (?)	Troy 1983
Purple Finch <i>Carpodacus purpureus</i>	2822	13 (0.5%)	New York (18)	Yunick 1983
	1015	51 (5.0%)	North Carolina (5)	Blake 1997
Brambling <i>Fringilla montifringilla</i>	2330	16 (0.5%)	England (7)	Browne & Mead 2003
Snowy Owl <i>Nyctea scandiaca</i>	227	7 (3.1%)	Maryland (15)	Smith 1997

ringed, return rates of seed-eaters were mostly nil or less than 1% (but with Purple Finch *Carpodacus purpureus* at 5% in one area), and in the Snowy Owl *Nyctea scandiaca* only about 3% (Table 4). Evidently, extremely few individuals of such species returned to the same areas in subsequent years. They showed little or no site fidelity, summer or winter, compared with regular migrants.

#### Distances between breeding localities of different years

For some species, ring recoveries give some idea of the distances that separate the breeding sites of the same individuals in different years, or the wintering sites of the same individuals in different years. The main breeding season of spruce-feeding

Common Crossbills *Loxia curvirostra* in Europe is in January–April, when the cones begin to open (Newton 1972). Eight adults trapped and ringed in this period one year were recovered in the same period in a later year. Apart from one bird which had moved only 28 km, the rest had moved distances of 790–3170 km, with none at lesser distances (Fig. 4). Similarly, four Crossbills ringed as chicks or recently-fledged juveniles were recovered in later breeding seasons at distances of 1100–2950 km away, with none at lesser distances (Fig. 4; see also Newton 1972, 2006, Zink & Bairlein 1995). In spruce areas, I have found not a single record of a Crossbill in the same place in successive years. This contrasts sharply with the situation in an area of northern Spain where Crossbills fed on



**Figure 4.** Ringing and recovery sites of Common Crossbills that were both ringed and recovered in different breeding seasons (taken as January–April in areas of Norway Spruce). Continuous lines – ringed as adults (representing breeding dispersal); dashed lines – ringed as juveniles (representing natal dispersal). Compiled mainly from information in Schloss (1984); also from Danish Ringing Report (1965), Swiss ring recoveries provided by Dr. L. Jenni, and Russian ring recoveries provided by Dr. K. Litvin.

**Table 5.** Examples of irruptive species in widely separated localities in different breeding seasons (breeding dispersal). For Common Crossbills see Fig. 4.

	Distances (km)
<b>Finches</b>	
Brambling <i>Fringilla montifringilla</i>	280, 420, 580
Common Redpoll <i>Carduelis flammea</i>	280, 550
Eurasian Siskin <i>Carduelis spinus</i>	120
Pine Siskin <i>Carduelis pinus</i>	347, 1138
Evening Grosbeak <i>Hesperiphona vespertina</i>	322–946 ( $n = 4$ )
Parrot Crossbill <i>Loxia pytyopsittacus</i>	340
<b>Owls</b>	
Short-eared Owl <i>Asio flammeus</i>	420, 500, 1300, 1400
Long-eared Owl <i>Asio otus</i>	>450 ( $n = 3$ )
Great Grey Owl <i>Strix nebulosa</i>	41–684 ( $n = 27$ )

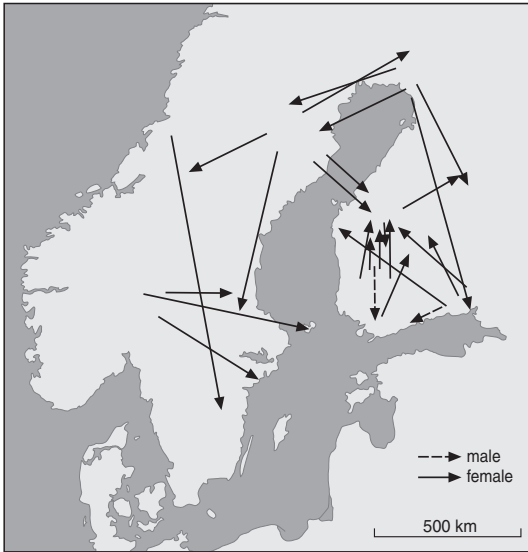
Sources: finches: Newton 1972, Brewer *et al.* 2000; owls: see references in text.

The Swedish Ringing reports provide a record of natal dispersal distances for Bullfinch of 424 km, for Short-eared Owl of 575 km, and for Northern Hawk Owls of 242, 208 and 104 km. The Finnish Ringing reports provide two records of natal dispersal distances of Short-eared Owls at 1300 and 1600 km.

Pyrenean Pine *Pinus unicincta*, which produces a consistent cone crop from year to year. In this area, many individual Crossbills were found by repeated trapping to be resident in the same area year after year (Senar *et al.* 1993). The same presumably holds in other pine areas in Europe, most of which hold local races of large-billed crossbills (see Marquiss & Rae 2002 for *Loxia scotica*). In North America, Brewer *et al.* (2000) gave two records of Red Crossbills at places 1288 km apart (November 1969 – October 1971) and 1409 km apart (May 1991 – May 1992); these dates could have fallen within the autumn and spring breeding periods. Although relevant ring recoveries are few, other irruptive finches have also been found in different breeding seasons at localities up to several hundred kilometres apart (Table 5).

Turning now to owls, extensive data are available only for Tengmalm's Owl, which nests readily in boxes and has been studied at many localities in northern Europe. In this species, the males are mainly resident and the females highly dispersive. Both sexes tend to stay in the same localities if vole densities remain high, moving no more than about 5 km between nest boxes used in successive years, but if vole densities crash, females move much longer distances, with many having moved 100–600 km between nest sites in different years (Fig. 5). In contrast, fewer long movements were recorded from males, with only two at more than 100 km. The greater residency of males was attributed to their need to guard cavity nest sites which are scarce in their conifer forest nesting habitat, while their smaller size makes them better able than females to catch birds, and hence survive (without breeding) through low vole conditions (Korpimäki *et al.* 1987).

Far fewer records are available for other nomadic owl species, because the chances of recording marked individuals at places far apart are low. However, in a study of Short-eared Owls in south Scotland, 21 breeders were tagged in 1976. Vole numbers then crashed, and only one of the tagged birds remained to breed in the area in 1977. Two others were reported in spring 1977 in nesting habitat 420 km and 500 km to the north-



**Figure 5.** Ringing and recovery sites of adult Tengmalm's Owls that were ringed and recovered in different breeding seasons. Continuous lines – females; dashed lines – males. Only movements greater than 100 km are shown. From Newton (2003), compiled from information in Löfgren *et al.* (1986), Korpimäki *et al.* (1987) and Sonerud *et al.* (1988).

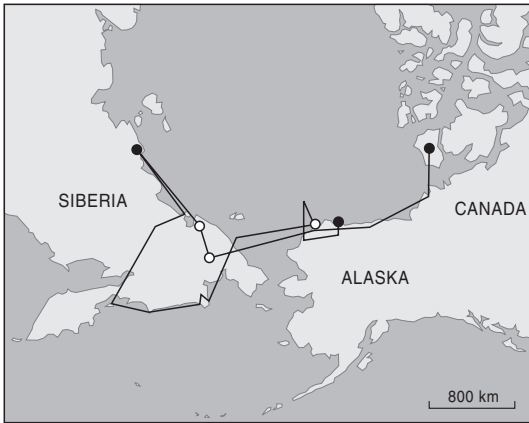
west, and the latter, at least, was proved to breed there (Village 1987). In contrast, of seven breeders tagged in 1977, when vole numbers began to increase, three bred again in the same area in 1978. Hence, as in Tengmalm's Owl, individuals seemed more likely to remain to breed in successive years when voles were increasing than when they were declining.

Recoveries of Northern Hawk Owls *Surnia ulula* and Great Grey Owls *Strix nebulosa* ringed as breeding adults include examples of both males and females residing in an area from one nesting season to the next when microtine abundance remained high, and of both sexes leaving when microtine populations declined (Sonerud 1997, Duncan 1992). Adult radio-marked Great Grey Owls in Manitoba and northern Minnesota dispersed 41–684 km (mean 329, SD 185,  $n = 27$ ) between breeding sites in response to prey popula-

tion crashes. Eleven marked birds that did not disperse died (Duncan 1992, 1997). Two ringed adult Great Grey Owls in northern Europe were found at localities 300 km and 430 km apart in different breeding seasons (Hildén & Solonen 1987). The only other ringing-based records known to me involve three adult Long-eared Owls in North America, which were found at localities more than 450 km apart in different breeding seasons (Marks *et al.* 1994).

Four adult Snowy Owls were radio-tagged while nesting near Point Barrow in Alaska, and tracked by satellite over the next 1–2 years (Fuller *et al.* 2003). These birds mostly stayed in the Arctic but dispersed widely in different directions from Point Barrow, reaching west as far as 147°E and east as far as 116°W, a geographical spread encompassing nearly one third of the species Holarctic breeding range. Two birds that bred at Point Barrow in 1999 were present during the next breeding season in northern Siberia (147°E and 157°E respectively), up to 1928 km east of Point Barrow, and then in the following breeding seasons they were on Victoria Island (116°W) and Banks Island (122°W) respectively in northern Canada (Table 6; Fig. 6). The two birds that bred at Point Barrow in 2000 were present on Victoria and Banks Islands in the breeding season of 2001. The successive summering areas of these four birds were thus separated by distances of 628–1928 km. From the dates they were present, some could have bred successfully, while others were unlikely to have done so, having arrived too late or left too early. None returned to the same breeding or wintering site used in a previous year, but three passed through Point Barrow in 2001.

These various irruptive owls and raptors thus contrast greatly with more sedentary populations, which exploit more stable food supplies. In such species, adults usually remain in their territories year after year, with only small proportions moving to other territories, usually nearby (for Tawny Owl *Strix aluco*, Ural Owl *S. uralensis* and Barn Owl *Tyto alba* see Saurola 1989, 2002, Petty 1992, Taylor 1994). One consequence of such site fidelity is strong mate fidelity, as partners remain



**Figure 6.** Movements of a radio-tagged female Snowy Owl tracked by satellite between the summers of 1999 and 2001. Filled circles show known likely breeding sites in three consecutive years (see Table 6), and open circles show other sites where the bird spent more than four weeks at a time. Constructed from information in Fuller *et al.* (2003).

**Table 6.** Locations of four adult female Snowy Owls in successive breeding seasons. All were radio-tagged at Point Barrow, Alaska in 1999 (numbers 54 and 57) or 2000 (numbers 80 and 81), and tracked by the Argos satellite system. From Fuller *et al.* (2003).

Owl number	Breeding seasons		
	1999	2000	2001
54	Alaska <sup>1</sup> 71°N, 156°W	Siberia <sup>3</sup> 70°N, 157°E	Victoria Island <sup>3</sup> 73°N, 108°W
57	Alaska <sup>1</sup> 71°N, 156°W	Siberia <sup>2</sup> 71°N, 147°E	Banks Island <sup>2</sup> 73°N, 121°W
80		Alaska <sup>1</sup> 71°N, 156°W	Victoria Island <sup>3</sup> 73°N, 115°W
81		Alaska <sup>1</sup> 71°N, 156°W	Banks island <sup>2</sup> 73°N, 122°W

<sup>1</sup>Known to have bred. <sup>2</sup>Probably bred. <sup>3</sup>Unlikely to have bred successfully.

Great circle distances between places where successful breeding was known or probable were 628 km between Point Barrow and Banks Island (bird 81) 1548 km between Siberia and Banks island (bird 57) and 1928 km between Point Barrow and Siberia (bird 57).

together year after year, so long as neither dies nor changes territory.

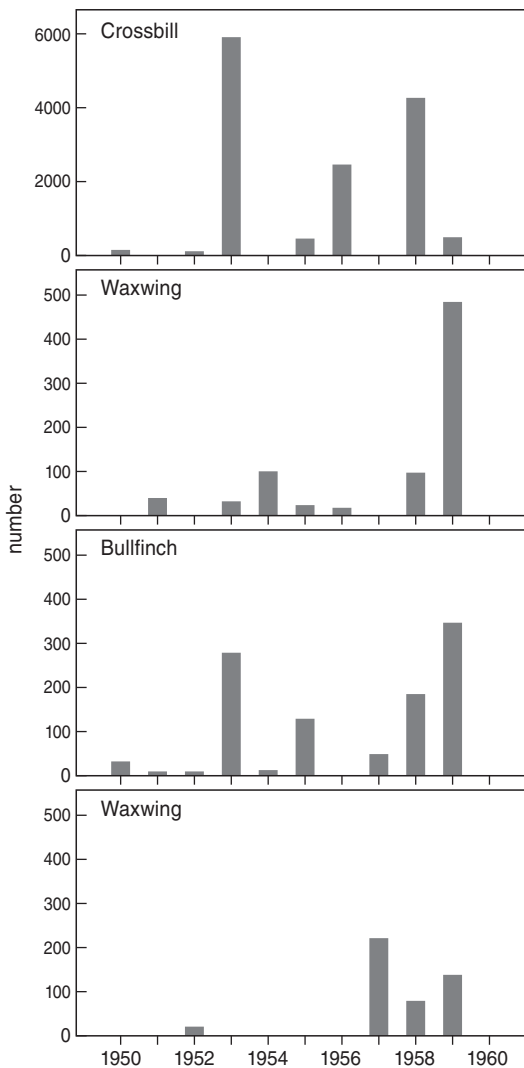
Regarding natal dispersal, movements exceeding 1000 km have been documented from ringing for Short-eared Owl (up to about 4000 km), Long-eared Owl (up to about 2300 km) and Northern Hawk Owl (up to 2700 km) (Table 5; Saurola 1983, 1997, 2002, Cramp 1985). In Tengmalm's Owl, natal dispersal distances tend to be longer in females than in males (as in many other birds), and longer in poor food years than in good ones (Sonerud *et al.* 1988). These movements contrast with those of resident owl species between natal site and breeding site, which are mostly less than 20 km, with few exceeding 100 km (Saurola 2002, Taylor 1994, Petty 1992).

Among diurnal raptors, Galushin (1974) summarised data from Russian ring recoveries showing that irruptive (mostly vole eating) species had much longer dispersal distances than non-irruptive ones. The mean natal dispersal distance of the Rough-legged Buzzard was given as 1955 km (but with no mention of sample size). He also pointed out that, within species, the populations in some parts of the range were more irruptive, and dispersed over wider distances, than those in other parts, depending on their food supplies, citing the Common Kestrel and Common Buzzard *Buteo buteo* as examples.

Summarising, there is ample evidence from the year to year population changes, and from the turnover in the occupants of particular breeding areas, that individual breeders of irruptive species commonly change their nesting areas from year to year, and ring recoveries have confirmed that such movements can occur over distances of hundreds or thousands of kilometres. This fits the expectation from geographical patterns in tree cropping and vole cycles.

**Irruptive migrations**

While some irruptive species seem to remain within the breeding range every year, but change breeding localities, others also winter at lower latitudes, at least in certain years. Typically, the numbers of birds undertaking migration, and the distances involved, vary greatly from year to year, so



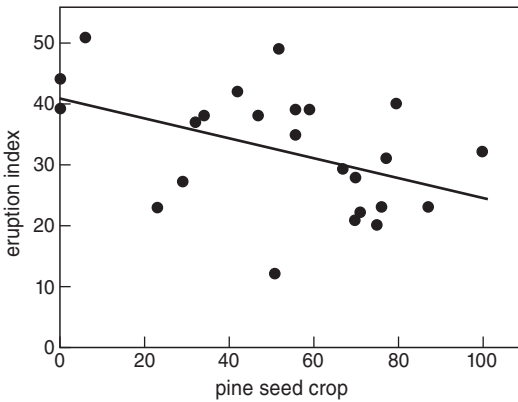
**Figure 7.** Annual variations in the numbers of four irruptive species counted while migrating over Falsterbo in southern Sweden, 1950–1960. From Ulfstrand *et al.* (1974).

that the birds reach the more distant parts of their wintering range only in certain years, hence the term irruptive migration. Huge annual variations in the numbers of migrants are evident at migration watch sites, such as Falsterbo and Ottenby in Sweden, in which the numbers of some irruptive species can vary from nil in some years to many

thousands of individuals in other years (Fig. 7). For example, over an 11-year period (1950–60), the Eurasian Jay *Garrulus glandarius* count in seven years at Falsterbo was nil, but in 1955 it reached more than ten thousand. Over the same period, Eurasian Siskins varied from 4220 to 35 904, Common Redpolls from nil to 489, Eurasian Bullfinches from nil to 360, Great Tits *Parus major* from 2 to 7438, Blue Tits *Parus caeruleus* from 7 to 3595 and Coal Tits *Parus ater* from nil to 18 785 (Ulfstrand *et al.* 1974). These annual fluctuations are far greater than those recorded in more regular long-distance migrants (counts of which typically vary by up to 3–4 fold, occasionally up to ten-fold, between years, Edelstam 1972, Ulfstrand *et al.* 1974, Roos 1991).

For many species, clear evidence has emerged that major emigrations follow periodic crop failures (seed eaters) or crashes in prey populations (raptors). Irruptive migrations therefore occur in response to annual, as well as seasonal, reductions in local food supplies. The effect of food shortage is often accentuated because the birds themselves tend to be numerous at such times, as a result of good survival and breeding in the previous years, when food was plentiful (Lack 1954, Berndt & Dancker 1960, Berndt & Henss 1967, Newton 1972, Koenig & Knops 2001). It is not, therefore, merely poor food supplies that stimulate large-scale emigration, but poor supplies relative to the numbers of birds present. Sometimes poor food supplies are associated with low bird numbers and little emigration occurs, while at other times moderate food supplies are associated with exceptionally high bird numbers and large-scale emigration (for Bohemian Waxwing see Siivonen 1941, Cornwallis & Townsend 1968, for Great Tit see Ulfstrand 1962, Perrins 1966; for Purple Finch see Koenig & Knops 2001). It is the ratio of birds to food that seems to count: the greater the imbalance, the greater the proportion of birds that leaves, presumably as a result of competition (see below).

The extent of autumn emigration has been related to food supplies in almost all seed-eating and fruit-eating species discussed here (Table 1,



**Figure 8.** Irruptions of Red-breasted Nuthatches in relation to pine cone production in western North America. On Spearman Rank correlation,  $P < 0.05$ . The pine seed index was calculated as the proportion of sites surveyed each year that had greater than average seed crops. The irruption index was calculated from the Christmas Bird Counts, as the proportion of sites south of  $50^{\circ}\text{N}$  at which greater than expected numbers of Red-breasted Nuthatches were recorded. Expected numbers for each year were calculated from a regression of the annual totals on year for the whole 21-year count period, 1968–88. Based on data in Koenig & Knops 2001, in which the relationship was given as significant ( $P < 0.05$ ) on a Spearman Rank Correlation test.

Fig. 8). Moreover, the various species that depend heavily on the same seed or fruit crops tend to irrupt in the same years: examples include Blue Tits and Great Tits which both feed heavily on Beech-mast, and Common Crossbills and Great Spotted Woodpeckers *Dendrocopos major*, which both feed heavily on spruce seeds. The autumn of 2004 in Denmark, at the time of this workshop, was marked by irruptions from the northeast of Eurasian Bullfinches, Pine Grosbeaks *Pinicola enucleator*, Fieldfares *Turdus pilaris* and Bohemian Waxwings, all of which depend in autumn on Rowan fruits. Where different tree species fruit in phase with one another, the numbers of participating species is increased further. Over much of the boreal region of North America, conifer and other seed crops tend to fluctuate biennially, and in alternate years of poor crops several species that

depend on them migrate to lower latitudes. For much of the 20<sup>th</sup> century, at least eight species of boreal seed eaters tended to irrupt together, in response to a widespread, synchronised pattern of seed crop fluctuations (namely Common Redpoll, Pine Siskin *Carduelis pinus*, Purple Finch, Evening Grosbeak, Red Crossbill, White-winged Crossbill *Loxia leucoptera*, Red-breasted Nuthatch *Sitta canadensis* and Black-capped Chickadee *Parus atricapilla*). These species vary in the proportions of conifer and broad-leaved tree seeds in their diets (Bock & Lepthien 1976, Kennard 1976, Koenig & Knops 2001). Over periods of years, different species of trees in the same area can drift in and out of synchrony with one another, affecting the movements of birds. During the period 1921–50, the biennial pattern and synchrony between the various North American seed eaters was less marked than before or after this period (Larson & Bock 1986).

The role of food shortage (relative to numbers) in stimulating autumn emigration is shown in another way, namely that some species which take food from garden-feeders have become less irruptive over the past 40 years, as increasing amounts of food have been provided. Such winter feeding was held responsible for turning a previously migratory population of Great Tits in the city of Oulu in northern Finland into a resident one (Orell & Ojanen 1979), and reduced movements by various tit species, attributed to the same cause, have been recorded in other parts of western Europe over the same period (Wernham *et al.* 2002).

Among rodent-eating species, irruptions of Snowy Owls from the tundra to the boreal and temperate regions of North America have been documented since about 1880. Throughout this 120-year period, irruptions have occurred every 3–5 years, at a mean interval of 3.9 (SE 0.13) years (Newton 2002). Moreover, in periods when information on lemmings was available from the breeding areas, mass southward movements of owls coincided with widespread crashes in lemming numbers (Shelford 1945, Chitty 1950). In western North America, irruptions of Snowy Owls were not well synchronised with those in the east, presumably reflecting asynchrony in lemming

cycles between breeding regions. The irruptions were also less regular and less pronounced in the west than in the east, with some birds appearing on the northern prairies every year, and some of the same marked individuals appearing on the same territories in different (not necessarily consecutive) winters (Kerlinger *et al.* 1985).

In eastern North America, two other vole eaters, the Rough-legged Buzzard and Northern Shrike *Lanius excubitor*, have irrupted at similar 3–5 year intervals, mostly (but not always) in the same years as Snowy Owls (Davis 1937, 1949, Speirs 1939, Shelford 1945, Lack 1954). Perfect synchrony between the three species would perhaps not be expected, because their breeding ranges only partly overlap. The buzzard and the shrike breed mainly in the transition zone between forest and tundra, while the owl breeds on the open tundra, but part of the owl population winters in the transition zone. Nevertheless, with most invasions of each species coinciding with those of the other species, the level of synchrony is striking.

In North America, Northern Hawk Owl irruptions tend to occur at 3–5 year intervals (modified by snow cover, and in different years in different regions; Duncan & Duncan 1998). Great Grey Owl irruptions are also occasionally recorded south and east of the usual breeding range, with big flights noted in eastern regions in 1978, 1983, 1991 and 1995 (Nero *et al.* 1984, Davis & Morrison 1987, Bull & Duncan 1993, National Audubon Field Notes for later years), while Saw-whet Owl *Aegolius acadicus* migrations are also much more marked in some years than in others (National Audubon Field Notes). In Europe, the Great Grey, Long-eared and Short-eared Owls seem to migrate on regular 3–4 year patterns (Harvey & Riddiford 1996, Schmidt & Vauk 1981, Hildén & Helo 1981). This would be expected from the 3–4 year crashes in microtone rodent populations.

#### **Distances between wintering areas of different years**

Not surprisingly, individuals of irruptive species are often recorded in widely separated localities in different winters, sometimes on opposite sides of a

continent (Table 7). Extreme examples include a Pine Siskin ringed in Quebec in one winter and recovered in California in a later winter, an Evening Grosbeak ringed in Maryland in one winter and recovered in Alberta in a later one, and a Redpoll ringed in Belgium in one winter and recovered in China in a later one. All these birds are likely to have returned to the breeding range in the interim, and taken a markedly different migration direction in the second year. A Common Redpoll was recorded in North America in one winter and Eurasia in a later one, having been ringed in Michigan and recovered near Okhotsk in Siberia, some 10 200 km to the northeast (Troy 1983).

The extent to which irruptive finches wander for food is well shown by the Evening Grosbeak, which breeds in conifer forests and moves south or southeast in autumn. This species feeds mainly on large, hard tree-fruits, but also visits garden feeding trays, a habit which makes it easy to catch. Over 14 winters, 17 000 individuals were ringed at a site in Pennsylvania. Of these, only 48 (0.003%) were recovered in the same place in subsequent winters, yet 451 others were scattered among 17 American States and four Canadian Provinces. Another 348 birds that had been ringed elsewhere were caught at this same locality, and these had come from 14 different States and four Provinces (D.H. Speirs, in Newton 1972). These recoveries show how widely individual Grosbeaks range, and how weak is their tendency to return to the same place in later years.

As far as I am aware, few ring recoveries from different winters are yet available for any species of irruptive owl, which have been trapped in much smaller numbers. However, the satellite-tagged Snowy Owls mentioned above were present in widely separated localities in different winters, and often moved long distances within a winter (Fuller *et al.* 2003). Another Snowy Owl was ringed near Edmonton in January 1955 and recovered 330 km to the southeast in Saskatchewan in January 1957 (Oeming 1957). There is also an intriguing record of a Long-eared Owl ringed in California in April and recovered in Ontario in October of the same year (Marks *et al.* 1994).

**Table 7.** Examples of irruptive species in widely separated localities in different winters (December–March). 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, being recovered in winter far to the east or west of where they were ringed in a previous winter.

	Ringed	Recovered	Distance (km)
Bohemian Waxwing <i>Bombycilla garrulus</i>	Sweden	Siberia	3060
	Sweden	Siberia	4070
	Poland	Siberia	4500
	Ukraine	Siberia	6000
	British Columbia	South Dakota	1360
	Sweden	Russia	2980
	Sweden	Russia	2280
	Sweden	Russia	2910
Cedar Waxwing <i>Bombycilla cedrorum</i>	California	Alabama	3000
Brambling <i>Fringilla montifringilla</i>	Belgium	Turkey	3000
	Britain	Greece	2500
Eurasian Siskin <i>Carduelis spinus</i>	Belgium	Lebanon	3000
	Sweden	Iran	3000
Pine Siskin <i>Carduelis pinus</i>	Ontario	California	3537
	Quebec	California	3950
	New York	British Columbia	3470
	Tennessee	British Columbia	3780
	Pennsylvania	Washington	2800
Common Redpoll <i>Carduelis flammea</i>	Sweden	Russia	1800
	Hungary	Siberia	3300
	Belgium	China	8350 <sup>a</sup>
	Alaska	New Brunswick	5200
	Quebec	Alaska	4850
	New Jersey	Alberta	3250
	Saskatchewan	Vermont	2550
	New Jersey	Alberta	3250
	New Jersey	Manitoba	2100
	Alaska	Saskatchewan	2730
Michigan	East Siberia	10200	
Evening Grosbeak <i>Hesperiphona vespertina</i>	Maryland	Alberta	3400
	Virginia	Newfoundland	2200
	Quebec	Georgia	1750
Eurasian Bullfinch <i>Pyrrhula pyrrhula</i>	Finland	Siberia	1900
	Finland	Siberia	2350

<sup>a</sup>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.

Sources: Rydzewski 1939, Cornwallis & Townsend 1968, Newton 1972, Eriksson 1970a, Zink 1981, Troy 1983, Baumgartner & Baumgartner 1992, Cramp & Perrins 1994, Zink & Bairlein 1995, Glutz von Blotzheim *et al.* 1997, Yunick 1997, Brewer *et al.* 2000; plus records from Olaf Runde from the Norwegian Ringing Scheme and Thord Fransson from the Swedish Ringing Scheme. Yunick (1997) gives additional information on Pine Siskin, while Brewer *et al.* (2000) list 12 Redpolls that were trapped in different winters at places 1345–4836 km apart in North America.



### Timing of autumn emigration

In at least some irruptive migrants, the timing of autumn emigration appears much more variable than among regular migrants, being markedly earlier in peak years. Thus the peak dates for the passage of Siskins through Falsterbo during 1949–88 varied from 15 August (in 1988) to 17 November (in 1958), the last date the station was manned that year (Roos 1991), and elsewhere heavy southward movements have been seen as late as December–January. Over a 9-year period, Svärdsön (1957) attempted to relate the numbers of Siskins passing through Ottenby Bird Observatory in south Sweden to the size of the birch crop further north. The birds tended to pass in largest numbers, and at the earliest dates, in years when the birch crop was poor. The tendency for birds to linger longer in the north in years of good tree-seed crops has been noted in many other irruptive seed-eaters, as has their tendency to arrive earlier in more southern wintering areas in invasion years (e.g. for Great Spotted Woodpecker see Eriksson 1971, for Bohemian Waxwing see Cornwallis & Townsend 1968, for Fieldfare see Tyrväinen 1975, for Brambling see Eriksson 1970c). Earlier autumn arrival in invasion than other years has also been noted among Northern Hawk Owls in North America (Duncan & Duncan 1998).

### Directional spread

A greater spread in migration directions in irruptive compared to typical migrants is apparent both from observations and from ring recoveries. For example, at the Courland Spit in the southeast Baltic, ring recoveries of various non-irruptive species obtained in autumn–winter lay within an arc of up to 100° from the ringing site, but in irruptive species the spread was much greater: in the Eurasian Jay 198°, in the Bohemian Waxwing 237°, in the Brambling 188° and in the Eurasian Siskin 298° (Payevsky 1998). Similar differences in directional spread between regular and irruptive migrants have been noted at many other ringing sites. They contrast with non-irruptive species, which typically show a much narrower directional spread, the ring recoveries of many species from

particular areas appearing to lie within narrow corridors (for examples see Newton 1972, Bairlein 2001).

It is not yet clear, however, to what extent the wider directional spread in irruptive migrants occurs within years, or results from different main directions in different years. However, in the Common Redpoll, the migration direction from Fennoscandia seems to have varied markedly between years. Whereas in 1965 most ring recoveries came from directions E–SE (mostly in Russia), in the later invasions of 1972 and 1986 they came from directions to the SW (mostly in western Europe) (Zink & Bairlein 1995, Lensink *et al.* 1986, Thies 1991). This could be explained if the birds were tracking seed-crops, which took them in different directions from their breeding areas in different years, but this explanation remains untested. No equivalent data known to me are available for owls, but three young from a brood of Snowy Owls ringed on Southampton Island took different directions on their first migration, with one recovered in winter on Sakhalin Island (roughly to the west), and the others at two widely separated localities in Ontario (roughly to the south) (Parmelee 1992).

### Movements within a winter

Whether finches or owls, irruptive migrants do not necessarily remain in the same localities throughout a winter, as evident from both observations and trapping-and-ringing, which has revealed much within-winter turnover in the individuals present at particular sites, or the occurrence of the same individuals at widely separated sites within the same winter (for Brambling see Browne & Mead 2003, for Eurasian Siskin see Senar *et al.* 1992, for Bohemian Waxwing see Wernham *et al.* 2002, for Cedar Waxwing *Bombycilla cedrorum* see Witner *et al.* 1997, for Great Grey Owl see Nero *et al.* 1984, for Snowy Owl see Smith 1997, Fuller *et al.* 2003). The implication is that, in the non-breeding period, individuals move around, but generally further along the same migration route, perhaps in continual search for good feeding areas. In effect, many of the seed eaters travel progressively further from their breeding areas during the

non-breeding period, stripping food crops as they go (for Pine Grosbeak see Grenquist 1947, for Common Redpoll, Bohemian Waxwing and Fieldfare see Haila *et al.* 1986).

## BREEDING IN WINTERING AND MIGRATION AREAS

It is not only in autumn that migration may be halted by a good food supply. How far irruptive finches move northwards in spring, and where they settle, depends partly on how much food they meet on the way. The Common Redpoll provides a striking example, for this species curtails its migration by up to several hundred kilometres to breed in southern Fennoscandia in some of the years when the spruce crop there is good. Once the seeds have fallen, the birds in some years move further north to their usual birch-scrub breeding habitat, where they raise another brood. Such movements have not been proved by ringing, but have been inferred from the simultaneous changes in the populations of the two regions and, in particular, from the late arrival in these years of birds in the birch areas with free-flying young. Such events have been documented in at least seven different years (Peiponen 1967, Hildén 1969, Götmark 1982, Antikainen *et al.* 1980). In most other years, with no early nesting, only the later single brood was raised. A similar split migration may sometimes occur in the Siskin: in at least four different years at the Courland Spit in the eastern Baltic, adults and recently fledged juveniles were seen migrating north-eastwards in June; some of the adults were clearly in pairs and many trapped females had a well-developed brood patch, showing that they had already nested (Payevsky 1971). In June 1959, a juvenile Siskin was caught 25 days after having been banded in Germany, 750 km to the southwest. The adult Siskins involved in these movements would have had time to nest again in the same year. Some other irruptive species have also been recorded breeding well to the south of their usual breeding range in certain years, even in wintering areas where food remained abundant,

giving further evidence for variable settling patterns. This habit is usual in crossbills (e.g. Lack 1954, Newton 1972), and has been recorded occasionally in various other species, including Great Spotted Woodpecker (Eriksson 1971), Bohemian Waxwing (Cornwallis & Townsend 1968), Cedar Waxwing (Kaufman 1984), Coal Tit (Wernham *et al.* 2002), Brambling (Otterlind 1954, Eriksson 1970c), Lesser Redpoll *Carduelis f. cabaret* (Newton 1972), Eurasian Siskin (Svårdson 1957), Pine Siskin (Yunick 1997), and Northern Bullfinch (Svårdson 1957).

Various species of owls have also been recorded nesting well outside their regular range in years of abundant food, often following invasions (Duncan & Duncan 1998). For example, several hundred pairs of Snowy Owls bred on the tundra of Swedish Lapland in 1978, where they had been rare to non-existent in many previous years (Andersson 1980). Snowy Owls bred in Finnish Lapland in 1974, 1987, and 1988, but before these dates, none was seen for several decades (Sauola 1997). Similarly, Northern Hawk Owls bred in an area in Norway in the peak years of only four out of seven observed vole cycles (Sonerud 1997). This lack of response may arise because in many years the entire owl population can be absorbed in certain parts of the range with abundant prey, without needing to search out other parts. In Fennoscandia, the numbers of Snowy and Hawk Owls at any time seems to be influenced not only by the occurrence of a rodent peak, but by the arrival of large numbers of immigrants from further east (Sonerud 1997). In more central parts of the range, the owls may exploit a much greater proportion of the rodent peaks. When voles were plentiful, Hawk Owls have also bred in invasion areas, well south of their usual breeding range in North America (Duncan & Duncan 1998). Among diurnal raptors, numbers of Rough-legged Buzzards, Kestrels and Pallid Harriers *Circus macrourus* were found breeding outside the regular range in localities where voles were plentiful (Galushin 1974).

The salient point to emerge from these various findings concerns the flexibility in the behaviour of irruptive species, and their tendency to stop at

almost any stage in their journeys if they reach an area of abundant food. This response may lead at least some individuals of some species to breed in their wintering areas or to break a spring migration, and breed well outside their regular nesting range.

### **COPING WITH A BOOM-AND-BUST ECONOMY**

By changing breeding and wintering areas between years, both seed-eaters and rodent-eaters lessen the effects of the massive food shortages to which they would be exposed if they used the same areas every year. Some specialist seed-eaters would be unlikely to survive more than 1–2 years in the same areas because good tree-fruit crops are nearly always followed by almost total failures. Their movements soften the impact of crop failures, but they may still be exposed to a hugely fluctuating food supply, as reflected in their reproductive rates. For irruptive seed-eaters, most of the available information on reproduction is based on the duration of breeding or on juvenile-to-adult ratios in different years. In an area of northern Sweden, Bramblings bred every year over a 19-year period, but in greatly varying numbers, depending on food supply (Lindstrom *et al.* 2005). Post-breeding juvenile-to-adult ratios varied more than ten-fold over this period, reaching up to 3.54 in good food years and sinking as low as 0.33 in poor ones. The Redpolls and Siskins mentioned above can breed for more than twice as long in good spruce years than in other years (giving time for 2–3 broods instead of 1–2), and could thereby more than double their production of young. Among Common Crossbills, the annual variations may be even greater, for in mixed conifer areas in which different tree species release their seeds in widely different months, individual Crossbills could in theory breed for more than nine months each year, raising brood after brood (Newton 1972). But in areas containing only Norway Spruce individuals breed for no more than half this time or, in poor cone years, not at all.

The fact that juveniles often predominate among irruptive species caught on migration has been taken as evidence that irruptions follow good breeding seasons (Lack 1954). Care is needed, however, because in such partial migrants juveniles often leave the breeding area in greater proportion and earlier than adults. Nevertheless, when most of the migrants in particular years are adults, this probably gives a reliable indication of a poor breeding season. This situation was recorded, for example, among Common Crossbills in 1963, when young formed only 6, 8, 31 and 37% of the birds caught at four localities in western Europe (Newton 1972). This compares with up to 88% recorded in other irruption years.

Specialist rodent-eaters are known for raising large families (up to eight or more young per brood in some species) in years when prey are plentiful, but few or none in years when prey are scarce throughout, or crash from abundance to scarcity during summer (Cramp 1985, Newton 2002). Juveniles formed 85% of 80 Northern Hawk Owls obtained on irruption in northern Europe in 1950, 100% of 52 obtained in 1976, and 88% of 150 museum skins collected over several years (Cramp 1985). Not all owl invasions follow good breeding years, however, and after a known poor year, only four out of 126 Great Grey Owls trapped in Manitoba in 1995 were juveniles (Nero & Copland 1997). In Snowy Owls, juveniles predominated in invasion years, but in other years when few owls appeared, the majority were adults and many were underweight (Smith 1997). Such observations reveal that, while irruptive finches and owls move away from areas poor in food, they do not altogether avoid the effects of fluctuating supply. The birds are likely also to suffer poorer survival in low food years, but I know of no relevant studies.

### **DISCUSSION**

Given all this information, how do irruptive migrants differ from regular migrants (Table 8)? In the first place, their numbers at particular locali-

**Table 8.** Comparison between typical regular and typical irruptive migration.

	Regular (obligate) migrants	Irruptive (facultative) migrants
<b>Habitat food</b>	Predictable	Unpredictable
<b>Breeding areas</b>	Fixed	Variable
<b>Wintering areas</b>	Fixed	Variable
<b>Site fidelity</b>	High	Low
<b>Migration</b>		
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

ties seem to fluctuate much more from year to year than do those of regular migrants, and in most species, these fluctuations have been clearly linked to fluctuations in local food supplies. The fact that these birds can go from absence or near absence to abundance in less than one year strongly suggests the role of movements in influencing local densities, giving greatly varying patterns of distribution across the range from year to year. Movement has been confirmed by the high turnover rates in the occupants of particular areas, and by the long breeding dispersal distances found for a small number of individuals from ring recoveries. It is now clear that irruptive seed-eaters and rodent-eaters can travel hundreds or thousands of kilometres between the breeding areas used in different years. They can also spend the winter in widely separated areas in different years, up to several thousand kilometres apart. Many individuals of irruptive seed-eaters have been recorded at different points on the same migration axis in different winters, but some have been recorded on different axes, recovered thousands of kilometres to the east or west of where they were ringed in a

previous winter. This is strikingly different behaviour from that of regular migrants, which usually return to the same breeding localities year after year, and also often to the same wintering localities, migrating more or less directly between the two.

To judge from the variable extent and timing of their migrations, many irruptive species – while genetically equipped to migrate – must presumably respond directly to food conditions at the time. Only in this way could they show the level of flexibility in movement patterns recorded. Food shortage apparently acts not only as the ultimate causal factor to which migration is supposedly adapted (Lack 1954), but also as the main proximate factor delaying or promoting departure from particular localities. The influence of any endogenous rhythm or daylength change in triggering movement seems less in irruptive than in more regular migrants. Nevertheless, irruptive migrants tend to leave their wintering areas at fairly consistent dates each spring, although as explained above, where they stop to breed is highly variable, depending on the food encountered en route.

In irruptive species, both seed-eaters and rodent eaters, local densities are related to food supplies from year to year within the regular range, but not necessarily in more distant peripheral wintering areas, which are visited only when food is scarce further north. In peripheral areas, there may be many years when food is abundant, but few if any migrants turn up to exploit it, having settled in good feeding areas already encountered. Conversely, irruptive migrants may turn up in remote areas in some years only to find their favoured foods are lacking (as shown, for example, by the large numbers of Jays which irrupted into western Europe in 1983, a year almost devoid of acorns, John & Roskell 1985).

The ease with which particular individuals could gain food is likely to depend, not only on food abundance, but on the density of other birds, which could reduce feeding rates through depletion and interference competition. In this way, the likelihood of an individual migrating is a function of population density as well as of food density

(Lack 1954, Newton 1972, Berndt & Henss 1967, Koenig & Knops 2001). Tyrväinen (1975) noted that emigration of Fieldfares from southern Finland occurred when their main food crop (Rowan berries) had been reduced to an average of about two fruits per inflorescence. The date at which this occurred depended on both the initial crop size and the number of consumers. The role of competitive interactions in reducing feeding rates of individuals is well known from field studies of wild birds (e.g. Goss-Custard *et al.* 1984, Sutherland 1996), and the role of competitive interactions in the development of migratory condition was demonstrated experimentally in captive birds by Terrill (1990). In both situations, the effects of competition fell most strongly on the subordinate (usually younger) individuals.

Experiments on captive birds have also confirmed that individuals can develop migratory restlessness in response to food deprivation in winter, well outside the normal migration period (Biebach 1985, Gwinner *et al.* 1985). For example, the Garden Warbler *Sylvia borin* shows spontaneous nocturnal restlessness during the autumn migration period (September–December) on unlimited food. In winter, these warblers are generally not active at night. However, they become so if deprived of food at a time when they would normally have settled in winter quarters (Gwinner *et al.* 1985). That deprived birds can put on fat may seem surprising, but they seem to do so through changes in physiology and behaviour, feeding for much longer each day than normal. After late January, migratory activity could not be reactivated when birds were subjected to restricted food treatment.

Although variations in autumn movements among seed-eating birds are most marked in those species that depend on the seeds of trees, they are also apparent to some extent in those that eat the seeds of herbaceous plants. In arid regions, the local production of such seeds can vary greatly from year to year, according to rainfall patterns, and in other regions their availability on the ground is affected by patterns of agriculture or snowfall. Many such species concentrate at differ-

ent points on the migration route in different years, depending on seed supply (Pulliam & Parker 1979, Dunning & Brown 1982), and ringed individuals have occurred at widely separated points on that route in different winters (Newton 1972, Ketterson & Nolan 1982), or have moved further along the route at varying dates during the course of winter (Haila *et al.* 1986, Terrill & Ohmart 1984). This is what many would call irruptive behaviour in less extreme form, with more directional consistency.

In considering the proximate control of migration, a distinction has been drawn between obligate migration (formerly called 'instinct' or 'calendar' migration) and facultative migration (formerly called 'weather' migration). In obligate migration, all main aspects are viewed as under firmer endogenous (genetic) control, mediated by daylength changes (Berthold 2001). This internal control gives a high degree of year to year consistency in the timing, directions and distances of movements. For the most part, each individual behaves in the same way year after year, being much less influenced by prevailing conditions. In response to endogenous stimuli and daylength change, obligate migrants often leave their breeding areas each year well before food supplies collapse, and while they still have ample opportunity to accumulate body reserves for the journey.

In contrast, facultative migration is viewed as a direct response to prevailing conditions, especially food supplies, and the same individual may migrate in some years, but not in others. Within a population, the proportions of individuals that leave the breeding range, the dates they leave and the distances they travel, can vary greatly from year to year, as can the rate of progress on migration, all depending on conditions at the time (see above, also Svårdson 1957, Newton 1972, Terrill 1990, Moore *et al.* 2003). In consequence, facultative migrants have been seen on migration at almost any date in the non-breeding season, at least into January, and their winter distributions vary greatly from year to year. Although in such facultative migrants, the timing and distance of movements may vary with individual circumstances, other

aspects must presumably be under firmer genetic control, notably the directional preferences and the tendency to return at appropriate dates in spring.

In general, it seems that obligate migration occurs in populations that breed in areas where food is predictably absent in winter, whereas facultative migration occurs in populations that breed in areas where food is plentiful in some winters and scarce or lacking in others. The distinction between obligate and facultative migrants is important because it reflects the degree to which individual behaviour is sensitive to prevailing external conditions, and hence varies from year to year. The advantage of strong endogenous control, as in obligate migrants, is that it can permit anticipatory behaviour, allowing birds to prepare for an event, such as migration, before it becomes essential for survival, and facilitating fat deposition before food becomes scarce. But such a fixed control system is likely to be beneficial only in predictable circumstances, in which food supplies change in a consistent manner, and at about the same dates, from year to year. It is not suited to populations which have to cope with a large degree of spatial and temporal unpredictability in their food supplies. It is these aspects of food supply which probably result in irruptive migrants showing greater variations in autumn timing, directions and distances, selection having imposed less precision on these aspects than in regular migrants. Both regular and irregular systems are adaptive, but to different types of food supplies. Nevertheless, obligate and facultative migrants are best regarded, not as distinct categories, but as opposite ends of a continuum, with predominantly endogenous control (= rigidity) at one end and predominantly external control (= flexibility) at the other. Irruptive migrants, with their facultative behaviour, belong in the latter category.

Another reason for not drawing a sharp distinction between the two categories is that many birds seem to change from obligate to facultative mode during the course of their journeys, as the endogenous drive to migrate wanes with time and distance, and the stimulus to continue becomes more directly dependent on local conditions (Terrill

& Ohmart 1984, Gwinner *et al.* 1985, Terrill 1990). Theoretically, the initial obligate phase of any journey might take the migrant across regions where the probability of overwinter survival is practically zero: where any individuals that attempted to winter there in the past were eliminated by natural selection. As migration continues into more benign areas, and survival probability increases, the bird switches to a facultative mode, in which it benefits by responding to local conditions, stopping where food is abundant. Such a two-phase migration, with obligate and facultative stages, would also ensure that, in any particular year, the bird migrated no further than necessary. In some species only the tail end of the migration may be facultative, in others the entire journey (as in many irruptive species). Viewed in this way, it is easier to see how regional variation in the obligate/facultative balance might evolve within species, as food supplies across the breeding range change from the more predictable to the less predictable, partly in association with the diversity of food types available, and with the degree of their year to year fluctuation. This is little different in principle from the transition from resident to migratory found in many bird species from low to high latitudes. It accounts for why some species, such as Great Tit or Common Kestrel, are essentially resident in some parts of their geographical range, irruptive in other parts, and perhaps regular migrants in yet other parts (Cramp & Simmons 1980, Cramp & Perrins 1993). Each mode of behaviour is adapted to the stability and predictability of food supplies in the region concerned.

## ACKNOWLEDGEMENTS

I am grateful to Thord Fransson, Lukas Jenni, Constantin Litvin, Olaf Runde, and Kasper Thorup for providing details of interesting ring recoveries, and to Rudi Drent and Kasper Thorup for the many thoughtful comments on this paper they provided in their capacity as referees.

## REFERENCES

- Andersson M. 1980. Nomadism and site tenacity as alternative reproductive tactics in birds. *J. Anim. Ecol.* 49: 175–184.
- Antikainen E., Skarén U., Toivanen J. & Ukkonen M. 1980. The nomadic breeding of the Redpoll *Acanthis flammea* in 1979 in North Savo, Finland. *Orn. Fenn.* 57: 124–131.
- Bairlein F. 2001. Results of bird ringing in the study of migration routes. *Ardea* 89: 7–19.
- Baumgartner F.M. & Baumgartner A.M. 1992. Oklahoma bird life. University Press, Norman, Oklahoma.
- Benkman C.W. 1987. Food profitability and the foraging ecology of crossbills. *Ecol. Monogr.* 57: 251–267.
- 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.
- Berndt R. & Dancker P. 1960. Der Kleiber, *Sitta europaea*, als Invasionsvogel. *Vogelwarte* 20: 193–198.
- Berndt R. & Henss M. 1967. Die Kohlmeise, *Parus major*, als Invasionsvogel. *Vogelwarte* 24: 17–37.
- Berthold P. 2001. Bird migration: a general survey (2nd edition). Oxford University Press, Oxford.
- Biebach H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experimentia* 41: 695–697.
- Blake C.H. 1967. Purple Finches at Hillsborough, N.C., 1961–65. *Bird-banding* 38: 1–17.
- Bock C.E. & Lepthien L.W. 1976. Synchronous eruptions of boreal seed-eating birds. *Amer. Nat.* 110: 559–571.
- Brewer D., Diamond A., Woodsworth E.J., Collins B.T. & Dunn E.H. 2000. Canadian Atlas of Bird Banding, Vol. 1. Canadian Wildlife Service, Ottawa.
- Browne S.J. & Mead C.J. 2003. Age and sex composition, biometrics, site fidelity and origin of Brambling *Fringilla montifringilla* wintering in Norfolk, England. *Ring. Migrat.* 21: 145–153.
- Bull E.L. & Duncan J.R. 1993. Great Grey Owl. *The Birds of North America* 41: 1–15.
- Burton N.H.K. & Evans P.R. 1997. Survival and winter site fidelity of Turnstones *Arenaria interpres* and Purple Sandpipers *Calidris maritima* in northeast England. *Bird Study* 44: 35–44.
- Cavé A.J. 1968. The breeding of the Kestrel, *Falco tinnunculus* L., in the reclaimed area Oostelijk Flevoland. *Netherlands J. Zool.* 18: 313–407.
- Chitty H. 1950. Canadian arctic wildlife enquiry, 1943–49, with a summary of results since 1933. *J. Anim. Ecol.* 19: 180–193.
- Cornwallis R.K. & Townsend A.D. 1968. Waxwings in Britain and Europe during 1965/66. *Brit. Birds* 61: 97–118.
- Court G.S., Bradley D.M., Gates C.C. & Boag D.A. 1988. The population biology of Peregrine Falcons in the Keewater District of the Northwest Territories, Canada. In: Cade T.J., Enderson J.H., Thelander G.J. & White C.M. (eds) *Peregrine Falcon populations. Their management and recovery: 729–739*. The Peregrine Fund, Boise.
- Cramp S. 1985. *Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 4*. Oxford University Press, Oxford.
- Cramp S. & Simmons K.E.L. 1980. *Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 2*. Oxford University Press, Oxford.
- Cramp S. & Perrins C.M. 1993. *Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 7*. Oxford University Press, Oxford.
- Cramp S. & Perrins C.M. 1994. *Handbook of the Birds of Europe, the Middle East and North Africa, Vol. 9*. Oxford University Press, Oxford.
- Davis D.E. 1937. A cycle in Northern Shrike emigrations. *Auk* 54: 43–49.
- Davis D.E. 1949. Recent emigrations of Northern Shrikes. *Auk* 66: 293.
- Davis D.E. & Morrison M.L. 1987. Changes in cyclic patterns of abundance in four avian species. *Am. Birds* 41: 1341–1347.
- Duncan J.R. 1992. Influence of prey abundance and snow cover on Great Grey Owl breeding dispersal. Unpubl. PhD thesis. University of Manitoba, Winnipeg.
- Duncan J.R. 1997. Great Grey Owls (*Strix nebulosa nebulosa*) and forest management in North America: a review and recommendations. *J. Raptor Res.* 31: 160–166.
- Duncan J.R. & Duncan P.A. 1998. Northern Hawk Owl. In: Poole A. & Gill F.B. (eds) *The Birds of North America*, No. 356: 1–28. Academy of Natural Sciences, Philadelphia & AOU, Washington.
- Dunning J.B. & Brown J.H. 1982. Summer rainfall and winter sparrow densities – a test of the food limitation hypothesis. *Auk* 99: 123–129.
- Edelstam C. (ed) 1972. *The visible migration of birds at Ottenby, Sweden*. Suppl. 7 to *Vår Fågelvärld*.
- Enemar A., Nilsson L. & Sjöstrand B. 1984. The composition and dynamics of the passerine bird community in a subalpine birch forest, Swedish Lapland. A 20-year study. *Ann. Zool. Fenn.* 21: 321–338.
- Enoksson B. & Nilsson S.G. 1983. Territory size and population density in relation to food supply in the Nuthatch *Sitta europaea* (Aves). *J. Anim. Ecol.* 52: 927–935.
- Eriksson K. 1970a. Ecology of the irruption and wintering of Fennoscandian Redpolls (*Carduelis flammea* coll.). *Ann. Zool. Fenn.* 7: 273–282.

- Eriksson K. 1970b. The autumn migration and wintering ecology of the Siskin *Carduelis spinus*. *Ornis Fenn.* 47: 52–68.
- Eriksson K. 1970c. Wintering and autumn migration ecology of the Brambling *Fringilla montifringilla*. *Sterna* 9: 77–90.
- Eriksson K. 1971. Irruption and wintering ecology of the Great-spotted Woodpecker *Dendrocopos major*. *Ornis Fenn.* 48: 69–76.
- Evans P.R. 1966. Autumn movements, moult and measurements of the Lesser Redpoll *Carduelis flammea cabaret*. *Ibis* 108: 183–216.
- Forero M.G., Donázur J.A., Blas J. & Hiraldo F. 1999. Causes and consequences of territory change and breeding dispersal distance in the Black Kite. *Ecology* 80: 1298–1310.
- Formosov A.N. 1933. The crop of cedar nuts, invasions into Europe of the Siberian Nutcracker (*Nucifraga caryocatactes macrorhynchos* Brehm) and fluctuations in the numbers of the Squirrel (*Sciurus vulgaris* L.). *J. Anim. Ecol.* 2: 70–81.
- Formosov A.N. 1960. La production de graines dans les forêts de conifères de la taiga de l'USSR et l'envahissement de l'Europe occidentale par certaines espèces d'oiseaux. *Proc. Int. Orn Congr.* 12: 216–229.
- Formosov N.N. 1965. Irregularities in the mass autumn migration of the Coal Titmouse. *Comm. Baltic Commission Study Bird Migr.* 3: 89–90. (In Russian, with English summary)
- 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*: 359–366. Springer Verlag, Berlin.
- Galushin V.M. 1974. Synchronous fluctuations in populations of some raptors and their prey. *Ibis* 116: 127–134.
- Glutz von Blotzheim U.N. 1997. *Handbuch der Vögel Mitteleuropas*, Band 14/II Passeriformes (5, Teil). Wiesbaden, Aula Verlag.
- Goss-Custard J.D., Clarke R.T. & Durell S.E.A. 1984. Rates of food intake and aggression of Oystercatchers *Haematopus ostralegus* on the most and least preferred mussel *Mytilus edulis* beds of the Exe Estuary. *J. Anim. Ecol.* 53: 233–245.
- Götmark F. 1982. Irruption breeding of the Redpoll, *Carduelis flammea*, in south Sweden in 1975. *Vår Fågelvärld* 41: 315–322.
- Grenquist P. 1947. Über die Biologie des Hakengimpels. *Orn. Fenn.* 24: 1–10.
- Gwinner E., Biebach H. & Kries I.V. 1985. Food availability affects migratory restlessness in caged Garden Warblers (*Sylvia borin*). *Naturwissenschaften* 72: 51–52.
- Haapanen A. 1966. Bird fauna of Finnish forests in relation to forest succession. *Ann. Zool. Fenn.* 3: 176–200.
- Hagen Y. 1969. Norwegian studies on the reproduction of birds of prey and owls in relation to micro-rodent population fluctuations. *Fauna* 22: 73–126.
- Hagner S. 1965. Cone crop fluctuations in Scots Pine and Norway Spruce. *Studia Forestalia Svecica* No 33.
- Haila Y., Tiainen J. & Vepsäläinen K. 1986. Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland. *Ornis Fenn.* 63: 1–9.
- Hamerström F. 1969. A harrier population study. In: Hickey J.J. (ed) *Peregrine Falcon populations: their biology and decline*: 367–383. University of Wisconsin Press, Madison.
- Hanski I., Hansson L. & Henttonen H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60: 353–367.
- Hansson L. & Henttonen H. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67: 394–402.
- Harvey P.V. & Riddiford N. 1996. An uneven sex ratio of migrant Long-eared Owls. *Ring. Migrat.* 11: 132–135.
- Hildén O. 1969. Über Vorkommen und Brutbiologie des Birkenzeisigs (*Carduelis flammea*) in Finnisch-Lapland in Sommer 1968. *Orn. Fenn.* 46: 93–112.
- Hildén O. 1978. Population dynamics in Temminck's Stint *Calidris temminckii*. *Oikos* 30: 17–28.
- Hildén O. & Helo P. 1981. The Great Grey Owl *Strix nebulosa* – a bird of the northern taiga. *Ornis Fenn.* 58: 159–166.
- Hildén O. & Solonen T. 1987. Status of the Great Grey Owl in Finland. In: Nero R.W., Clark R.J., Knapton R.J. & Hamre R.H. (eds) *Biology and conservation of northern forest owls*: 116–120. Fort Collins, USDA For. Serv. Gen. Tech. Rep. RM-142. Co., USA.
- Hogstad O. 1967. Density fluctuations of *Carduelis spinus* in relation to the cone crops of Norway Spruce. *Sterna* 7: 255–259.
- Hogstad O. 2000. Fluctuation of a breeding population of Brambling *Fringilla montifringilla* during 33 years in a subalpine birch forest. *Ornis Fenn.* 77: 97–103.
- Holmes R.T. & Sherry T.W. 1992. Site fidelity of migratory warblers in temperate breeding and neotropical wintering areas: applications for population dynamics, habitat selection, and conservation. In: Hagan III J.M. & Johnston D.W. (eds) *Ecology and conservation of neotropical migrant landbirds*: 563–575. Smithsonian Institution Press, Washington.
- Jenni L. 1987. Mass concentrations of Bramblings *Fringilla montifringilla* in Europe 1900–1983: their dependence upon beech mast and the effect of snow cover. *Ornis Scand.* 18: 84–94.
- John A.W.G. & Roskell J. 1985. Jay movements in autumn 1983. *Brit. Birds* 78: 611–637.



- Kaufman K. 1984. The changing seasons. *Am. Birds* 38: 992–996.
- Kennard J.H. 1976. A biennial pattern in the winter distribution of the Common Redpoll. *Bird-Banding* 47: 232–237.
- Kerlinger P., Lein M.R. & Sevick B.J. 1985. Distribution and population fluctuations of wintering Snowy Owls (*Nyctea scandiaca*) in North America. *Ecology* 63: 1829–1834.
- Ketterson E.D. & Nolan V. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. *Auk* 99: 243–259.
- Knox A.G. 1992. Species and pseudospecies: the structure of crossbill populations. *Biol. J. Linn. Soc.* 47: 325–335.
- Koenig W.D. & Knops J.M.H. 1998. Scale of mast seeding and tree-ring growth. *Nature* 396: 225–226.
- Koenig W.D. & Knops J.M.H. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *Amer. Nat.* 155: 59–69.
- Koenig W.D. & Knops J.M.H. 2001. Seed crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.* 70: 609–620.
- Korpimäki E. 1986. Gradients in population fluctuations of Tengmalm's Owl *Aegolius funereus* in Europe. *Oecologia* 69: 195–201.
- Korpimäki E. 1994. Rapid or delayed tracking of multi-annual vole cycles by avian predators? *J. Anim. Ecol.* 63: 619–628.
- Korpimäki E., Lagerström M. & Saurola P. 1987. Field evidence for nomadism in Tengmalm's Owl *Aegolius funereus*. *Ornis Scand.* 18: 1–4.
- Korpimäki E. & Norrdahl K. 1989. Predation of Tengmalm's Owls: numerical responses, functional responses and dampening impact on population fluctuations of voles. *Oikos* 54: 154–164.
- Korpimäki E. & Norrdahl K. 1991. Numerical and functional responses of Kestrels, Short-eared Owls and Long-eared Owls to vole densities. *Ecology* 72: 814–825.
- Koshkina T.V. (1966). On the periodic changes in the numbers of voles (as exemplified by the Kola peninsula) (in Russian). *Bull. Moscow Soc. Naturalists, Biol. Section* 71: 14–26.
- Lack D. 1954. *The natural regulation of animal numbers*. Oxford University Press, Oxford.
- Lanner R.M. 1996. *Made for each other. A symbiosis of birds and pines*. Oxford University Press, Oxford.
- Larson D.L. & Bock C.E. 1986. Eruptions of some North American boreal seed-eating birds, 1901–1980. *Ibis* 128: 137–140.
- Larson T. & Tombre I. 1989. Cyclic irruptions of Two-barred Crossbills in Scandinavia. *Fauna Norv. Ser. C, Cinclus* 12: 3–10.
- Lawn M.R. 1982. Pairing systems and site tenacity of the Willow Warbler *Phylloscopus trochilus* in southern England. *Ornis Scand.* 13: 193–199.
- Lensink R., van der Bijtel H.J.V. & Schols R.M. 1986. Invasion of Redpolls *Carduelis flammea* in the Netherlands in 1986. *Limosa* 62: 1–10.
- Lindström Å. 1987. Breeding nomadism and site tenacity in the Brambling *Fringilla montifringilla*. *Ornis Fenn.* 64: 50–56.
- Lindström Å., Enemar A., Andersson G., von Proschwitz T. & Nyholm N.E.I. 2005. Density-independent reproductive output in relation to a drastically varying food supply: getting the density measure right. *Oikos* 110: 155–163.
- Löfgren O., Hörnfeldt B. & Carlsson B.-G. 1986. Site tenacity and nomadism in Tengmalm's Owl (*Aegolius funereus* (L.)) in relation to cyclic food production. *Oecologia* 69: 321–326.
- Markovets M.Y. & Sokolov L.V. (2002). Spring ambient temperature and movements of Coal Tits. *Avian Ecol. Behav.* 9: 55–62.
- Marks J.S., Evans D.L. & Holt D.W. 1994. Long-eared Owl. In Poole A., Stettenheim P. & Gill F. (eds) *The Birds of North America* No. 133 Academy of Natural Sciences, Philadelphia & AOU, Washington.
- Marks J.S. & Doremus J.H. 2000. Are northern Saw-whet Owls nomadic? *J. Raptor Res.* 34: 299–304.
- Marquiss M. & Rae R. 2002. Ecological differentiation in relation to bill size amongst sympatric, genetically undifferentiated crossbills (*Loxia* spp.). *Ibis* 144: 494–508.
- Mattes H. & Jenni L. 1984. Ortstreue und Zugbewegungen des Tannenhähers *Nucifraga caryocatactes* im Alpenraum und am Rande der Maar/Schwäbische Alb. *Orn. Beob.* 81: 303–315.
- Menyushina I.E. 1997. Snowy Owl (*Nyctea scandiaca*) reproduction in relation to lemming population cycles on Wrangel Island. In: Duncan J.R., Johnson D.H. & Nicholls T.H. (eds) *Biology and Conservation of Owls of the Northern Hemisphere*: 572–582. Second Int. Symp., Feb. 5–9, 1997. Winnipeg, Manitoba, Canada: United States Dep. Agric.
- Mikkonen A.V. 1983. Breeding site tenacity of the Chaffinch *Fringilla coelebs* and the Brambling *F. montifringilla* in northern Finland. *Ornis Scand.* 14: 36–47.
- Moore F., Mabey S. & Woodrey M.S. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries. In: Berthold P., Gwinner E. & Sonnenschein E. (eds) *Avian migration*: 281–292. Springer Verlag, Berlin.
- Morris R.F., Cheshire W.F., Miller C.A. & Mott D.G. 1958. The numerical response of avian and mammalian predators during a gradation of the spruce budworm. *Ecology* 39: 487–494.

- Nero R.W., Copland H.W.R. & Mezibroski J. 1984. The Great Grey Owl in Manitoba, 1968–83. *Blue Jay* 42: 129–190.
- Nero R.W. & Copland H.W.R. 1997. Sex and age composition of Great Grey Owls (*Strix nebulosa*) winter 1995/1996. In Duncan J.R., Johnson D.H. & Nicholls T.H. (eds) *Biology and Conservation of Owls of the Northern Hemisphere*: 587–590. Second Int. Symp., Feb. 5–9, 1997. Winnipeg, Manitoba, Canada: United States Dep. Agric.
- Newton I. 1972. *Finches*. Collins, London.
- Newton I. 1979. Population ecology of raptors. Poyser, Berkhamsted, Herts.
- Newton I. 2002. Population limitation in Holarctic owls. In: Newton I., Kavanagh R., Olson J. & Taylor I.R. (eds) *Ecology and conservation of owls*: 3–29. CSIRO Publishing, Collingwood, Victoria, Australia.
- Newton I. 2003. The role of natural factors in the limitation of bird of prey numbers: a brief review of the evidence. In Thompson D.B.A., Redpath S.M., Fielding A.H., Marquiss M. & Galbraith C.A. (eds) *Birds of prey in a changing environment*: 5–23. The Stationary Office, Edinburgh.
- Newton I. 2003a. The speciation and biogeography of birds. Academic Press, London.
- Newton I. 2006. Movement patterns of Common Crossbills *Loxia curvirostra* in Europe. *Ibis* 148: 782–788.
- Nilsson S.G. 1984. The relation between the beech mast crop and the wintering of Brambling, *Fringilla montifringilla*, and Wood Pigeon, *Columba palumbus*, in south Sweden. *Vår Fågelvärld* 43: 135–136.
- Nisbet I.C.T. & Medway L. 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. *Ibis* 114: 451–494.
- Nyström B. & Nyström H. 1991. Effects of bad weather on the breeding of the Redpoll *Carduelis flammea* in a year with a poor birch seed crop in southern Lapland. *Ornis Svecica* 1: 65–68.
- Oeming A.F. 1957. Notes on the Barred Owl and the Snowy Owl in Alberta. *Blue Jay* 15: 153–156.
- Orell M. & Ojanen M. 1979. Mortality rates of the Great Tit *Parus major* in a northern population. *Ardea* 67: 130–139.
- Otterlind G. 1954. Migration and distribution. A study of the recent immigration and dispersal of the Scandinavian avifauna. *Vår Fågelvärld* 13: 1–99.
- Parmelee D.F. 1992. Snowy Owl. In Poole A., Stettenheim P. & Gill F. (eds) *The Birds of North America* 19: 1–20. Academy of Natural Sciences, Philadelphia & AOU, Washington.
- Payevsky V.A. 1971. Atlas of bird migrations according to banding data at the Courland Spit. In: Bykhovskii B.E. (ed) *Bird Migrations. Ecological and physiological factors*: 1–124. Leningrad.
- Payevsky V.A. 1998. Bird trapping and ringing as an inexhaustible source of most valuable data for demographic investigators (with special reference to the work of the Biological Station Rybachy). *Avian Ecol. & Behav.* 1: 76–86.
- Peiponen V.A. 1967. Südliche Fortpflanzung und Zug von *Carduelis flammea* (L.) in Jahre 1965. *Ann. Zool. Fenn.* 4: 547–549.
- Perrins C.M. 1966. The effect of beech crops on Great Tit populations and movements. *Brit. Birds* 59: 419–432
- Petty S.J. 1992. Ecology of the Tawny Owl *Strix aluco* in the spruce forests of Northumberland and Argyll. PhD thesis, Open University, Milton Keynes.
- Petty S.J., Patterson I.J., Anderson D.I.K., Little B. & Davison M. 1995. Numbers, breeding performance, and diet of the Sparrowhawk *Accipiter nisus* and Merlin *Falco columbarius* in relation to cone crops and seed-eating finches. *For. Ecol. & Manage.* 79: 133–146.
- Potapov E.R. 1997. What determines the population density and reproductive success of Rough-legged Buzzards, *Buteo lagopus*, in the Siberian tundra? *Oikos* 78: 362–376.
- Pulliam H.R. & Parker T.A. 1979. Population regulation of sparrows. *Fortschritte der Zoologie* 25: 137–147.
- Putnam L.S. 1949. The life history of the Cedar Waxwing. *Wilson Bull.* 61:141–182.
- Pynnönen A. 1939. Beiträge zur Kenntnis der Biologie finnischer Spechte. *Ann. Soc. Zool. –Bot. Fenn. Vanamo* 7: 1–166.
- Reinikainen A. 1937. The irregular migrations of the Crossbill, *Loxia c. curvirostra*, and their relation to the cone-crop of the conifers. *Ornis Fenn.* 14: 55–64.
- Reynolds R.T. & Linkhart B.D. 1987. Fidelity to territory and mate in Flammulated Owls. In: Nero R.W., Clark R.J., Knapton R.J. & Hamre R.H. (eds) *Biology and conservation of northern forest owls*: 234–238. U.S. Dept. Agric., Forest Service, Rocky Mountain Forest & Range Experimental Station, Fort Collins, Colorado.
- Rockenbauch D. 1968. Zur Brutbiologie des Turmfalken (*Falco tinnunculus* L.). *Anz. orn. Ges. Bayern* 8: 267–76.
- Roos G. 1991. Visible bird migration at Falsterbo in autumn 1989, with a summary of the occurrence of six *Carduelis* species in 1973–90. *Anser* 30: 229–253.
- Roshier D.A., Klomp N.I. & Asmus M. 2006. Movements of a nomadic waterfowl, Grey Teal *Anas gracilis*, across inland Australia – results from satellite telemetry spanning fifteen months. *Ardea* 94: 461–475.
- Rydzewski W. 1939. Compte rendu de l'activité de la Station pour l'étude de migrations des oiseaux pour l'année 1937. *Act. Orn. Mus. Zool. Pol.* 2: 431–527.

- Saurola P. 1983. Movements of Short-eared Owl (*Asio flammeus*) and Long-eared Owl (*A. otus*) according to Finnish ring recoveries. *Lintumies* 18: 67–71.
- Saurola P. 1989. Ural Owl. In: Newton I. (eds) *Lifetime reproduction in birds*: 327–345. Academic Press, London.
- Saurola P. 1997. Monitoring Finnish owls 1982–1996: methods and results. In: Duncan J.R., Johnson D.H. & Nicholls T.H. (eds) *Biology and Conservation of Owls of the Northern Hemisphere*: 363–380. Second Int. Symp., Feb. 5–9, 1997. Winnipeg, Manitoba, Canada: United States Dep. Agric.
- Saurola P. 2002. Natal dispersal distances of Finnish owls: results from ringing. In: Newton I., Kavanagh R., Olsen J. & Taylor I. (eds) *Ecology and conservation of owls*: 42–55. CSIRO Publishing, Collingwood, Victoria, Australia.
- Schloss W. 1984. Ringfunde des Fichtenkreuzschnabels (*Loxia curvirostra*). *Auspicium* 7: 257–284.
- Schmidt R.C. & Vauk G. 1981. Zug Ringfunde auf Helgoland durch ziehender Waldohreulen und Sumpfohreulen (*Asio otus* and *A. flammeus*). *Vogelwelt* 102: 180–189.
- Schüz E. 1945. Der europäischer Rauhfussbuzard, *Buteo l. lagopus* (Brünn.), als Invasionsvogel. *Jahr. Vereins Vaterländische Naturkunde Württemberg* 97–101: 125–150.
- Schüz E. & Tischler F. 1941. Invasion von Dickschnabel-Tannenhähern (*Nucifraga caryocatactes*) in Nordost-Deutschland, Herbst 1940. *Vogelzug* 12: 25–26.
- Senar J.C., Burton P.J.K. & Metcalfe N.B. 1992. Variation in the nomadic tendency of a wintering finch *Carduelis spinus* and its relationship with body condition. *Ornis Scand.* 23: 63–72.
- Senar J.C., Borrás A., Cabrera T. & Cabrera J. 1993. Testing for the relationship between coniferous crop stability and Common Crossbill residence. *J. Field Orn.* 64: 464–469.
- Shaw G. 1990. Timing and fidelity of breeding for Siskins *Carduelis spinus* in Scottish conifer plantations. *Bird Study* 37: 30–35.
- Shelford V.E. 1945. The relation of Snowy Owl migration to the abundance of the Collared Lemming. *Auk* 62: 592–596.
- Siivonen L. 1941. Über die Kausatzusammenhänge der Wanderungen beim Seidenschwanz *Bombycilla g. garrulus* (L.). *Ann. Soc. Zool. – Bot. Fenn. Vanamo* 8: 1–38.
- Silvola T. 1967. Changes in the bird populations in Utsjoki, Finnish Lapland in 1964–1966, caused by the mass-occurrence of the caterpillar *Oporinia autumnata*. *Ornis Fenn.* 44: 65–67.
- Smith K.W., Reed J.M. & Trevis B.E. 1992. Habitat use and site fidelity of Green Sandpipers *Tringa ochropus* wintering in southern England. *Bird Study* 39: 155–164.
- Smith N. 1997. Observations of wintering Snowy Owls (*Nyctea scandiaca*) at Logan Airport, East Boston, Massachusetts from 1981–1997. In: Duncan J.R., Johnson D.H. & Nicholls T.H. (eds) *Biology and Conservation of Owls of the Northern Hemisphere*: 591–597. Second Int. Symp., Feb. 5–9, 1997. Winnipeg, Manitoba, Canada: United States Dep. Agric.
- Sonerud G. 1997. Hawk Owls in Fennoscandia: population fluctuations, effects of modern forestry, and recommendations on improving foraging habitats. *J. Raptor Res.* 31: 167–174.
- Sonerud G.A., Solheim R. & Prestrud K. 1988. Dispersal of Tengmalm's Owl *Aegolius funereus* in relation to prey availability and nesting success. *Ornis Scand.* 19: 175–181.
- Speirs J.M. 1939. Fluctuations in numbers of birds in the Toronto Region. *Auk* 56: 411–419.
- Staicer C.A. 1992. Social behaviour of the Northern Parula, Cape May Warbler, and Prairie Warbler wintering in second-growth forest in southwestern Puerto Rico. In: Hagan J.M. & Johnston D.W. (eds) *Ecology and conservation of neotropical migrant landbirds*: 308–320. Smithsonian Inst. Press, Washington, D.C.
- Stenseth N.C. 1999. Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87: 427–461.
- Sutherland W.J. 1996. From individual behaviour to population ecology. Oxford University Press, Oxford.
- Svärdson G. 1957. The 'invasion' type of bird migration. *Brit. Birds* 50: 314–343.
- Taylor I. 1994. Barn Owls. Predator-prey relationships and conservation. University Press, Cambridge.
- Terrill S.B. 1990. Ecophysiological aspects of movements by migrants in the wintering quarters. In: Gwinner E. (eds) *Bird migration. Physiology and ecophysiology*: 130–143. Springer Verlag, Berlin.
- Terrill S.B. & Ohmart R.D. 1984. Facultative extension of fall migration by Yellow-rumped Warblers (*Dendroica coronata*). *Auk* 101: 427–438.
- Thies H. 1991. Invasionen des Birkenzeisigs (*Carduelis flammea flammea*) nach Norddeutschland und ihre Ursachen – eine Literaturstudie. *Corax* 14: 73–86.
- Thies H. 1996. Zum Vorkommen des Fichtenkreuzschnabels (*Loxia curvirostra*) und anderer *Loxia*-Arten im Segeberger Forst 1970–1995 mit besonderer Erörterung der Zugphänologie. *Corax* 16: 305–334.
- Troy D.M. 1983. Recaptures of Redpolls: movements of an irruptive species. *J. Field Ornithol.* 54: 146–151.
- Tyrväinen H. 1975. The winter irruption of the Fieldfare *Turdus pilaris* and the supply of rowan-berries. *Ornis Fenn.* 52: 23–31.

- Ulfstrand S. 1962. On the non-breeding ecology and migratory movements of the Great Tit (*Parus major*) and the Blue Tit (*Parus caeruleus*) in southern Sweden. Suppl 3 to Vår Fågelvärld.
- Ulfstrand S. 1963. Ecological aspects of irruptive bird migration in northwestern Europe. Proc. Int. Orn. Congr. 13: 780–794.
- Ulfstrand S., Roos G., Alerstam T. & Osterdahl L. 1974. Visible bird migration at Falsterbo, Sweden. Suppl. 8 to Vår Fågelvärld.
- Village A. 1981. The diet and breeding of Long-eared Owls in relation to vole abundance. Bird Study 28: 129–138.
- Village A. 1987. Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. Ornis Scand. 18: 198–204.
- Village A. 1990. The Kestrel. T. & A.D. Poyser, London.
- Wernham C.V., Toms M.P., Marchant J.H., Clark J.A., Siriwardena G.M. & Baillie S.R. 2002. The migration atlas: movements of the birds of Britain and Ireland. T & A.D. Poyser, London.
- Widrechner M.P. & Dragula S.K. 1984. Relation of cone crop size to irruptions of four seed-eating birds in California. Amer. Birds 38: 840–846.
- Wilson H.J., Norriss D.W., Walsh A., Fox A.D. & Stroud D.A. 1991. Winter site fidelity in Greenland White-fronted Geese *Anser albifrons flavirostris*, implications for conservation and management. Ardea 79: 287–294.
- Witner M.C., Mountjoy D.J. & Elliot L. 1997. Cedar Waxwing. In A. Poole, Stettenheim P. & Gill F. (eds) The Birds of North America No. 309: Academy of Natural Sciences, Philadelphia & AOU, Washington.
- Yunick R.P. 1983. Winter site fidelity of some northern finches (Fringillidae). J. Field Ornithol. 54: 254–258.
- Yunick R.P. 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. 1981. Der Zug europäischer Singvögel. Herausgegeben von der Vogelwarte Radolfzell am Max-Planck-Institut für Verhaltensphysiologie, Vogelzug Verlag Möggingen.
- Zink G. & Bairlein F. 1995. Der Zug Europäischer Singvögel. Aula Verlag, Wiesbaden.

## SAMENVATTING

Dit artikel bespreekt de trekpatronen bij twee groepen vogels die bekend staan om hun invasies: (1) vinkachtigen en vogels die afhankelijk zijn van bomen waarvan de vruchtdracht tussen jaren sterk fluctueert en (2) uilen en andere vogels die afhankelijk zijn van cyclisch fluctuerende knaagdierpopulaties. Beide groepen specialiseren zich op voedsel dat van het ene jaar op het andere een factor 100 talrijker of schaarser kan zijn. Over grote gebieden bekeken, lopen fluctuaties in zaadproductie en aantallen knaagdieren niet synchroon, en een laag voedselaanbod in het ene gebied kan samengaan met hoog aanbod in een ander gebied. Om te broeden in een gebied met voldoende voedsel, moeten individuen daarom vaak honderden of duizenden kilometers trekken. In jaren dat er een voedseltekort is op een schaal van duizenden of miljoenen vierkante kilometers trekken grote aantallen vogels naar zuidelijker streken, wat daar als een 'invasie' ervaren wordt. De verdeling van vogelpopulaties kan dus zowel in de zomer als in de winter sterk variëren tussen de jaren. In het broedgebied blijken de aantallen 'invasievogels' sterk in dichtheid te fluctueren. Deze grote fluctuaties kunnen alleen door grootschalige verplaatsingen verklaard worden en niet door variaties in voortplantingssucces of sterfte. 'Invasievogels' vertonen amper plaatstrouw, in tegenstelling tot gewone trekvogels. Ze kunnen in opeenvolgende jaren broeden op plekken die honderden of duizenden kilometers uit elkaar liggen (3200 km bij een Kruisbek *Loxia curvirostra*). Een zelfde patroon geldt voor de winter: vogels kunnen op duizenden kilometers afstand van de plek waar ze de vorige winter waren geringd, overwinteren. Een extreem geval is een Barmsijs *Carduelis flammae* die in China werd gevangen na in België te zijn geringd op 8350 km afstand. Vergeleken met gewone trekvogels laten 'invasievogels' een veel grotere variatie zien in het aandeel trekkende vogels. Individuen laten tussen jaren een grote spreiding zien in tijdstip, richting en afstand van bewegingen/trek, waarbij ze kennelijk adequaat kunnen reageren op veranderingen in het voedselaanbod. 'Echte trekvogels' en 'invasievogels' kunnen het beste beschouwd worden als extremen op een *continue* schaal van trekgedrag, van scherp afgebakend en consistent aan de ene kant en breed en flexibel aan de andere kant. Beide typen zijn adaptief, de ene aan voorspelbare omstandigheden, de andere aan onvoorspelbare. Afhankelijk van de voorspelbaarheid van voedselomstandigheden kan een zelfde soort zich gedragen als standvogel of gewone trekvogel in het ene deel van zijn verspreidingsgebied, en als invasievogel in een ander deel.

Received 18 December 2004; accepted 26 March 2006