# Migration Patterns in West Palaearctic Raptors

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# ABSTRACT

- 1. In the western Palaearctic, as in other parts of the world, a huge latitudinal shift occurs in the distribution of raptors between summer and winter, associated with seasonal changes in food supplies.
- 2. Among Palaearctic breeding species, most species that feed primarily on warm-blooded birds and mammals migrate relatively short distances, remaining within the Palaearctic year round. In contrast, most species that eat mainly cold-blooded prey (reptiles and insects) migrate long distances, mostly into Africa south of the Sahara.
- 3. Within Africa, many more species are found on the east than the west sides of the continent, in savannah or woodland, reflecting west-east trends in species numbers in the Palaearctic. Few species occur in tropical rain forest and in desert.
- 4. As in other Palaearctic-African landbird migrants, a crude correlation is apparent between the sizes of breeding and wintering ranges of different raptor species.

## INTRODUCTION

One obvious feature of birds, compared to many other animals, is their great mobility, as many species can move quickly and economically over long distances, enabling the same individuals to exploit seasonal abundances of food in different regions at different dates. This is the presumed basis of migration (Lack 1954). Of the 42 species of raptors that breed in the western Palaearctic, all migrate in at least some part of their breeding range. Some species move relatively short distances within Europe, while others move longer distances into Africa, south of the Sahara. In this paper, I explore some of the large-scale ecology of raptor migration, examining the relationships between movements and food-supplies and between the geographical extents of breeding and wintering ranges. The

paper is based on information available in the species accounts in Cramp & Simmons (1974) and Brown & Urban (1982). For present purposes, the western Palaearctic is taken as the region covered by Cramp & Simmons (1974).

#### PROCEDURE

From descriptions and maps of breeding and wintering ranges, three sets of figures were calculated: (1) the numbers of west Palaearctic raptor species found breeding or wintering at each 5th degree of latitude from northernmost Europe to southernmost Africa (total span 80°N to 35°S); (2) for certain species the geographical extents of breeding and wintering ranges using maps of equal area projection (Mollweide's homolographic, see Newton 1995); and (3) the number of species wintering in different parts of Africa. Range sizes were calculated only for those species which breed entirely within the Palaearctic and winter entirely within Africa south of the Sahara. Further details of methodology may be found in Newton (1995) and Newton & Dale (1996). For certain analyses, species were classed by diet, according to whether they feed mainly on warm-blooded prey, cold-blooded prey, or on a mixture of both (Table 1).

Table 1. Wintering areas of West	t Palaearctic raptors ir	n relation to di	et.	
Wintering area	Main prey types			
	Warm-blooded	Mixed	Cold-blooded	
North of Sahara	16	0	0	
North and south of Sahara	5	8	2	
South of Sahara	0	4	7	

Significance of variation between categories (examined by Monte Carlo randomisation test):  $\chi_4^2 = 35.9$ , P<0.001.

# SEASONAL CHANGES IN DISTRIBUTION

Figure 1 shows, for raptors breeding in the western Palaearctic, the number of species found at different latitudes, summer and winter. In the breeding season, species numbers are greatest at mediterranean latitudes, with around 30 species, and decline northwards to only two species on the high arctic tundra. In winter, species numbers at different latitudes reflect the general withdrawal of many species from northern regions, and the extension southwards into the southern hemisphere, with some species reaching the southern tip of Africa.

Figure 1. Numbers of raptor species breeding in the west Palaearctic region that are found at different latitudes, summer and winter. The diagram shows the general withdrawal of species from northern regions in winter, and the southward movement into Africa.



#### LATITUDINAL VARIATION

It is common knowledge that migration varies with latitude. Figure 2 shows the proportion of raptor species which breed at different 5° latitudes in Europe and migrate south for the winter. The proportion of species leaving increases with latitude, as the winters become more severe. However, species differ in their migration patterns according to their diets, and the extents to which their foods remain available at high latitudes in winter. If one divides raptors according to whether they feed primarily on warm-blooded prey (birds and mammals, which remain active and available in winter at high latitudes) and cold-blooded prey (reptiles, amphibia and insects, which become inactive and unavailable in winter), differences in migration are apparent (Figure 3).

Figure 2. Proportion of raptor species breeding at different 5° latitudes in the west Palaearctic which migrate south for the winter. Only species which move out completely from a given latitude were classed as migratory there.



Within each group, the proportion of migrant species increases with latitude, following the general trend in Figure 2, and in birds as a whole (Newton & Dale 1996). But at any one latitude, a larger proportion of cold-blooded than warm-blooded feeders leaves for the winter, while species with mixed diets are intermediate (Figure 3A). Furthermore, the cold-blooded feeders from any one latitude generally move longer distances than the warm-blooded feeders (Figure 3B). The reasons for this difference are fairly obvious, in that species that feed on cold-blooded prey and breed at high latitudes must winter in the tropics or the southern hemisphere, if they are to have access to the same types of prey year-round.

#### WINTER DISTRIBUTION

Of the 21 species of west Palaearctic raptors that eat mainly warm-blooded prey, 16 winter entirely within Eurasia and the other five partly in Eurasia and partly in Africa (Table 1). Of the 9 species that eat mainly cold-blooded prey, none winter entirely in the Palaearctic and most winter entirely in Africa. Moreover, all six insectivorous species winter not merely south of the Sahara, but also south of the equator, where the seasons are reversed. So these species live in almost perpetual summer, conditions in which their insect food supplies remain plentiful. The 12 species with mixed diets show intermediate patterns. Such patterns again underline the link between Figure 3. Migration in relation to diet in west Palaearctic raptors. A. Proportion of breeding species which migrate from different 5° latitudes. B. Distances moved, as measured by the latitudinal shift between the latitudinal centres of breeding and wintering ranges. Lines calculated by regression analysis.



migration and the seasonal changes in specific food sources (Newton 1979).

How within Africa are the various species distributed during the northern winter (October-March)? Figure 4 shows the number of Palaearctic raptor species which winter in different parts of the continent. No species is known to winter regularly in the Sahara. In the region south of the Sahara, fewest species occur in the rain forest of the west equatorial region, in the desert areas of the southwest and northeast, and in Madagascar. All these regions hold less than five regular Palaearctic species in the northern winter. Larger numbers occur over the rest of the continent in savannah or woodland habitats. The largest numbers occur down the eastern half of the continent, where different regions support 13-16 species. One reason for the west-east pattern is that fewer species enter Africa from the west than from the east Palaearctic, reflecting species numbers in the Palaearctic which also increase from west to east. Only twelve raptor species cross in numbers at Gibraltar into western Africa (Bernis 1975, Porter & Beaman 1985), compared with more than twice that number moving through Israel into eastern Africa (Christersen et al. 1986, Shirihai & Christie 1992, Frumkin et al. 1995, Leshem & Yom-Tov 1996)

#### MIGRATION AND GEOGRAPHICAL RANGE

Among birds as a whole (not just raptors) about 57 landbird species breed entirely in the Palaearctic and winter entirely in Africa, so that their breeding and wintering ranges are completely separated geographically (Newton 1995). I marked their breeding and wintering ranges on maps of equal area projection, measured the geographical extent of these ranges, and then plotted one against the other (Figure 6). Comparing species, the sizes of breeding and wintering ranges are correlated. Despite much scatter, the general trend is for species that have large breeding ranges also to have large wintering ranges, and vice versa (Figure 5A). Why should this be? Much might depend on the ecology of the species concerned, in that species able to tolerate a wide range of ecological or climatic conditions in their summer range might also be able to tolerate a similar wide range of conditions in their winter range. But the relationship might also simply reflect the abundance levels of

Figure 4. Numbers of Palaearctic raptor species which are found in the northern winter (October-March) in different parts of Africa, south of the Sahara. Numbers are shown on a grid basis in which the sides of each grid square are equivalent to 2° of latitude.



the different species concerned, in that those species that have the largest populations (for whatever reason) spread over the largest areas summer and winter. These two explanations are not mutually exclusive. Despite the general correlation between sizes of breeding and wintering ranges, the relationship is not one to one. The regression slope in Figure 5A is 0.7. On average, then, wintering ranges are only about two-thirds as large as breeding ranges. Perhaps wintering areas have greater carrying capacity than breeding areas, as expected of tropical regions.

Returning to raptors, although 11 Eurasian species winter entirely in Africa, we can be sure of the winter ranges of only 8; for the others there is the possibility of confusion between migrant and resident species (or races) within Africa, making the exact determination of the ranges of migrants difficult. But in so far as any conclusions can be drawn from 8 points, the raptors seem to fit the trend for landbirds as a whole, giving a general correlation between the sizes of breeding and wintering ranges but with much scatter (Figure 5B). Our understanding of such relationships may well improve as more information from Africa becomes available.

#### DISCUSSION

Lack (1954) suggested that migration could evolve in any bird population in which individuals survived better by moving out for the winter than by staying in their breeding areas year-round. The usual reason that breeding areas become unsuitable during part of the year is shortage of food. The foods of some raptor species at high latitudes (notably cold-blooded prey) become completely unavailable in winter, while the foods of other species (warm-blooded prey) become much reduced (as some mammal-prey hibernate and some bird-prey migrate south). The advantages of southward migration in autumn are therefore obvious.

It is less obvious why any birds migrate north again in spring, especially since some wintering areas seem able to support the birds year-round. Indeed, many migratory populations of raptors and other birds share wintering areas with other populations of their species or with populations of related species which do in fact breed in the wintering areas concerned. But if no birds moved north in spring, this would leave vast areas and summer food supplies at high latitudes greatly under-used. Under these conditions, any birds which moved north to breed in spring, with added benefit of long days, might well raise more young than if they stayed in their wintering areas and competed with the residents and summer migrants breeding there. Hence, individual species at each latitude are likely, through natural selection, to develop migration if they survive best by moving south in autumn and if they breed best by moving north in spring. For migration to evolve, an overall advantage must accrue Figure 5. Relationship between sizes of breeding and wintering ranges of 57 landbird species (including raptors, A) and of eight raptor species (B) which breed entirely in the Palaearctic and winter entirely in Africa south of the Sahara.



from the outward southern movement and the return northward movement, the two together giving a net benefit over residency. Conversely, the resident habit is likely to occur in those populations in which, on the average, migration involves greater losses than staying put. The greater prevalence of migration at higher latitudes, evident in raptors as well as in other birds, has been explained in terms of the greater amplitude there of seasonal changes in temperature and hence in food-supplies (Herrera 1978, Terborgh 1989). For most bird species, at whatever latitude, food is more plentiful in summer than in winter. Thus most species are likely to face a winter bottleneck during which their numbers are reduced by food-shortage, if not by other factors. Some are able to reduce the effects of this bottleneck by moving south, where food remains more plentiful. After the winter, the reduced numbers of resident birds are unable to exploit completely the summer flush of food, leaving a surplus which is available for summer visitors. The higher the latitude and the colder the winters, the greater the difference between summer and winter supplies is likely to be, and hence the greater the scope for summer migrants. The degree of this seasonal difference in food-supplies could therefore be the main factor leading to a progressively bigger proportion of the avifauna (including raptors) being migratory at higher latitudes.

For some raptor species, migration is not a simple two-season movement between fixed breeding and wintering areas. Some species, it seems, spend much of the time between breeding seasons on the move, pausing a few weeks here and a few weeks there, before moving on. Examples include Black Kite *Milvus migrans* and Lesser Spotted Eagle *Aquila pomarina*, which are well known to concentrate in areas of temporary food abundance (Newton 1979). Their populations form a huge continually shifting biomass, which moves first south then north over the earth's surface in regular seasonal patterns. They have an itinerant lifestyle which enables them to exploit short-term food-supplies at different places, at different times as they occur. In a sense, such species ride the crest of a wave, which ebbs and flows over a wide range of latitude, with the changing seasons.

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