Ecological causes and consequences of bird orientation

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Summary. An advanced orientation capability offers possibilities for birds to optimize movement patterns in a wide variety of ecological situations. The adaptive significance of different patterns of angular dispersion and of orientation responses to topography and sociality are elucidated. The orientation capacity is characterized by flexibility, exemplified by reorientation promoting safety and restoration of fat reserves during migration. There are also limitations to the orientation process, leading to costs of migration through mis- or disorientation, and to constraints on the evolution of routes and timing of migratory flights. Young migrants may acquire an erroneous compass sense, and misorient several thousands of kilometers off their normal course. Widespread and dense fog of long duration causes disorientation and mortality among land birds migrating over the sea. Orientational constraints in the evolution of migration routes may be most easily disclosed at high geographic and magnetic latitudes. Here the birds are faced with special difficulties in using their celestial as well as their magnetic compasses. The sun compass could be used for great circle orientation, but observed spring flight trajectories of high arctic shorebirds and geese seem to conform with rhumbline routes.

Key words. Bird migration; orientation; angular dispersion; leading-lines; flocking; reorientation; misorientation; disorientation; great circle routes; timing of flight.

Introduction

Orientation is a part of all types of bird movement; domestic movements in a local familiar area, dispersal and exploration, migration, homing and compensation for displacement. There are also other well-oriented movements, the meaning of which is less well understood, like escape orientation by ducks (Einar 1977), and penguins (1985, 1987) (fig. 1). In the latter case, it is believed that the adaptive significance of the penguins' northward orientation is to guide them out of ice entrapment to offshore feeding grounds. The easterly component of their orientation may represent a compensation for a westward ice drift by coastal Antarctic currents (1985). This serves to illustrate the fundamental fact that ecological premises are decisive for a correct interpretation of adaptive values of orientation behaviour.

Birds have an advanced compass sense, based on celestial and geomagnetic cues (1987). Within the home range, landmark recognition seems to be integrated within a compass frame. Hence, the sun compass plays an important role for pigeon orientation also over very familiar terrain close to the lofts (1987), and for seed-cache relocation by scrub jays (1987). With the compass framework serving to align as yet unknown mosaic or gradient cues extending beyond the home range also, birds may navigate home from unfamiliar sites, as do homing pigeons.

Migratory orientation is not only determined by the birds' celestial or magnetic compass systems, but is also directly influenced by environmental, social and physiological factors. Among environmental factors, wind is of paramount importance (cf. review by Richardson), but topography, weather, and ecological barriers are also of great significance. How and why is the orientation affected by these proximate ecological factors?

The orientation capability has its limitations, and birds sometimes misorient or completely lose their orientation. How does this come about, and do the risks for mis- or disorientation represent a significant cost of migration? What do these phenomena tell us about the function of the birds' complex orientation systems? Orientational constraints may have important effects on the evolution of migratory habits. To what extent are routes and timing of migratory flights determined by factors related to orientation?

These and similar questions will be addressed in this review of ecological causes and consequences of orientation.

Figure 1. Mean orientation of Adelie penguins Pygoscelis adeliae transported from their home rookery at Cape Crozier and released on featureless snow-ice surfaces at various Antarctic localities. The birds used a time-compensated sun compass, with their internal clocks remaining in phase with local home time, to orient consistently towards NNE/NE with respect to their home longitude. Birds from a rookery at Mirnyj, released at long. 180°, also oriented NE in relation to their home longitude (dotted short arrow). After their circadian rhythms were reset to the solar cycle at the new longitude, they changed to the same orientation as the Cape Crozier birds. In addition to this fixed escape orientation response, Adelie penguins have a navigation system allowing them to return home after considerable longitudinal and latitudinal displacement.
Angular dispersion

In figure 2 ringing data are used to exemplify different patterns of orientation with respect to the angular dispersion.

A more or less random or uniform circular distribution is typical of dispersal orientation. Dispersal occurs widely among young birds, soon after independence, in resident as well as migratory species. This behaviour is important for exploration (for example for possible future breeding opportunities), competition avoidance and, possibly, inbreeding avoidance. Griffin presented a theoretical analysis of exploration, and discussed optimal search patterns. Movement and orientation strategies adopted by birds during their dispersal phase remain to be investigated in the light of this theory.

There is an indication of an axial orientation for the long-distance dispersal of Swedish ravens in figure 2 (r² = 0.46, p < 0.01), presumably an effect of the topography of the Scandinavian peninsula. In a more extensive analysis of movements by Finnish ravens, no important deviations from a random scatter were found.

Quite a different pattern of post-breeding movement, Zwischenzug, is found in juvenile starlings. The summer moult they travel 100 km or more. In some populations the orientation is close to the normal migratory direction later in autumn, while other populations show an orientation distinctly divergent from the autumn migratory direction, sometimes almost reversed. Still other populations exhibit widely scattered movements, influenced by topography in mountain regions.

Wide-angle orientation is illustrated in figure 2 by recoveries of ospreys ringed in Sweden. Juveniles as well as adults fan out widely across Europe on a broad-front migration to African winter quarters. Östrolöf found that environmental rather than hereditary influences are responsible for this wide scatter. Siblings show large angular differences in migratory bearings as do young from neighbouring broods.

Narrow-angle orientation is exemplified by the song thrush migrating from Sweden to winter quarters in SW Europe (fig. 2). Similar narrow-angle orientation has been reported, on the basis of ringing recoveries, for, e.g., spotted flycatcher Muscicapidae trioctis (angular deviation 8–18° for adults, 13–23° for juveniles), willow warbler Phylloscopidae trochilus (from Finland; ang. dev. 9° for adults, 21° for juveniles), ortolan bunting Emberiza hortulana (ang. dev. 5–8°) and honey buzzard Pernis apivorus (ang. dev. about 8° for adults, 12° for juveniles).

Which factors determine the angular concentration of migratory orientation? Within species there is often an important difference between age groups, with young and inexperienced migrants showing a wider orientation scatter than adults (cf. above). Stabilizing selection may operate to maintain the orientation within narrow limits. On the basis of experiments with Savannah sparrows Passerculus sandwichensis, Moore demonstrated a greater within-individual variability in migratory orientation, both between and within test nights, for juveniles (first autumn) as compared to adults. In contrast, between-individual variability was larger among adults. With en route experience and stopover and winter site attachment, the orientation capability of adult birds may differ fundamentally from that of naive migrants. Populations at migratory divides show a wide angular scatter of recoveries, and analyses of selection pressures on migratory orientation in such transition populations are desirable.

The concentration of orientation can differ markedly between species, even between closely related species. The song thrush can be contrasted with the redwing Turdus iliacus; individual redwings may winter as far west as

![Figure 2. Angular distribution of ringing recoveries of raven Corvus corax (resident species), osprey Pandion haliaetus (migrant to Africa), and song thrush Turdus philomelos (migrant to SW Europe) from Sweden. Mean vectors and angular deviations are calculated according to Batschelet. The data refer to birds ringed as nestlings and recovered > 100 km away, during their first year of life (raven, n = 27), during the first autumn migration and winter season Sept.–March (song thrush, n = 42). Based on annual reports 1972–1984 from Bird Ringing Centre, Swedish Museum of Natural History.](image-url)