

1.1**Avian Migration and Navigation**

Among other aspects of bird migration, such as aerodynamics, energetics and associated migratory strategies, including remarkable ecological adaptations, the aspect of spatial orientation is certainly the most striking one. Consequently, migratory orientation has been investigated in great detail. It is known that birds can determine compass directions by means of the geomagnetic field, the stellar sky or the sun, which are globally available as directional references. Using their compasses, the birds can select genetically encoded directions which lead them to their winter quarters. An endogenous time programme gives the appropriate distance of flight in a temporal scale. Experimental data suggest that such bearing-and-distance programmes, which are roughly adapted to, and modified by, topographical and ecological conditions of the covered regions, and which in some species include even directional changes, are the general bases of many or most population-specific migratory routes. Applying in this way its endogenous intentions to the external world, even a young bird, leaving its birth place for the first time, eventually arrives in the far distant wintering range of its population. With larger birds, such as waterfowl or storks, which migrate in flocks during the daytime, also guidance of juveniles by adults along traditional routes is involved. Such guidance can be excluded in most of the smaller birds, particularly in the many passerine species migrating predominantly at night. Detailed reports on bird migration and migratory orientation can be found in other books (see Alerstam 1990; Berthold 1996, 2000, 2001; Berthold et al. 2003).

In spring, the bearing-and-distance programme can be expected to operate analogously to its operation in autumn; only the directions need to be reversed. A bird may return thereby to its population-specific breeding range. It is hardly imaginable, however, that a redstart can reach, on this basis alone, the village and the garden in which it had bred the year before. Migrating at night and exposed to drift-causing winds, simply keeping the body axis on a genetically encoded compass course would be insufficient. In fact, the birds can perform better. It has been shown that birds of many species (e.g. starlings, cowbirds, blackbirds, swallows, swifts, terns, gulls, storks, shearwaters, petrels and albatrosses) are able to find a familiar home site by goal-related navigation from far distant unfamiliar areas to which they had been passively displaced (for lists of such experiments and for references see Matthews 1955; Wiltschko

1992; Åkesson 2003). To achieve this performance, the animals must have more than a compass. Only if a bird is aware that it is north (and not south, east or west) of home, can it usefully apply a compass in order to steer a southward course guiding it home.

The process of birds finding their way back from a position in a distant unfamiliar area (where the animals have never been before) to a familiar geographical position (which has been established, during longer-lasting previous presence, as a 'home site') has often been called *navigation* in a narrow sense (Sect. 1.3). There is hardly any doubt that birds commonly apply goal-related navigation in the course of their migrations (Sect. 10.2.2) and that, without this capability, bird migration patterns would never have achieved their present overall character. Nevertheless, as substantial parts of migratory orientation, homing mechanisms are usually not closely inspected in books and articles dealing with bird migration. In fact, these mechanisms have not been closely investigated in migratory species. However, they have been intensely investigated in a non-migratory domesticated bird. I feel confident that the knowledge gained from pigeon homing can largely be considered as knowledge about avian homing in general and hence also of goal-finding in the course of bird migration.

1.2

Why Investigate Domestic Homing Pigeons?

In research on avian navigation, the homing pigeon acts as a kind of laboratory rat. Without the experiments conducted with this domestic animal, only a small fraction of our present knowledge about the mechanisms used by birds to find their way home from remote areas would have been achieved. The advantages of homing pigeons, as compared to any wild species, are obvious. Hundreds or even thousands of pigeons can be kept in man-made lofts at man-selected locations. Over the whole year the birds are easily available for experimental use without laborious and stressful trapping procedures. Individual returns from releases can be precisely recorded, usually by only one observer. Homing pigeons are always motivated to return to their loft, not only during the short breeding season. Due to their strong homing drive, they fly off mostly immediately after release, thus giving opportunity to observe their initially selected courses, whereas most other birds tend to land on nearby trees or in meadows etc. before starting homeward movements some time later. Over short and median distances, many pigeons return in a non-stop flight, so that the time they need for homing reflects, by and large, the length of the route they have flown. Even many of the pigeons that fail to home provide information about their orientation: Due to their social impulses, they tend to enter one or another of the pigeon lofts which are, in some countries, quite densely scattered over the land. Reports by pigeon fanciers contribute instructive spatial distributions of recovery sites. Finally, pigeons are very handy, their size is neither too small nor too large. They are large enough to be observed with bin-

oculars over approximately 2 km and large enough to carry the weight of a small transmitter for telemetry or some other apparatus apt to record their flight paths. They are small and tame enough to be confined in large numbers together in manageable crates for transport.

These outstanding advantages resulted in in-depth investigations on homing capabilities of birds being almost exclusively conducted with homing pigeons. Thus, the question arises whether pigeon homing can be seen as a model case of bird homing in general. At least there are good reasons to assume that it can. It appears extremely unlikely that, in the course of domestication from the rock pigeon (*Columba livia*) and selective breeding, an entirely novel navigation mechanism that did not exist before in the genus *Columba*, has been implanted into the strains of homing pigeons. The fact that the rock pigeon is usually sedentary implies no argument against the assumption that navigation mechanisms detected in homing pigeons can indicate mechanisms used by other birds during migration. Closely related species (e.g. *Columba palumbus*) do migrate, and Berthold et al. (1990) have shown that offspring of partially migratory birds of a given species can be genetically transformed, by means of selective breeding, to either full migrants or non-migrants within only a few generations. It is uncertain whether selection performed by man noteworthy affected the navigational capabilities of pigeons. Much more obvious is improvement of the homing drive, which appears less highly developed in the rock pigeon (Alleva et al. 1975; Visalberghi et al. 1978) and in other wild birds (e.g. Able et al. 1984). In pigeon races, the breeder is concerned with getting a maximum number of pigeons homed at maximum speed. The fastest homers are then preferentially selected for breeding. Homing speed in such races, however, is not primarily a result of outstanding navigation but rather of motivation, physical strength and persistence. The birds are usually trained to return in large flocks from always the same direction. Thus, the ability to find their way home from novel directions and sites by making individual decisions is not a criterion for selection.

Of course, there may be differences among pigeons and other species in many details of homing behaviour, for instance in the motivation to fly home at all, in the hierarchy in which different navigational cues are used or in the effectiveness with which such cues are exploited. It seems most likely, however, that once we understand pigeon homing we are able to understand the principles of avian goal-oriented navigation in general. Nevertheless, this assumption remains merely an assumption unless it can be actually shown that at least the most substantial conclusions drawn from experiments with homing pigeons can in fact be generalized and are valid for other bird species as well. Some supporting evidence is already available (Chap. 10).

Although the carrier pigeon is a unique subject for research on animal homing, the huge amount of data obtainable from millions of homing flights performed in the course of pigeon races has only a minor value as a source of information in the context of this research. As mentioned above, races take place in large flocks, usually comprising thousands of birds, so that, in a statistical

sense, an individual bird is not an independent unit. Moreover, the pigeons of a given region are usually displaced towards a standard compass direction with distances increasing in the course of the season. Only homing speeds are measured. By multiple correlation analyses using such data (e.g. Dornfeldt 1996) it is hardly possible to isolate causal relationships concerning navigational processes. To analyse these processes, it is necessary to conduct specifically designed experiments using individually flying pigeons released at sites in varying directions around home. Thus, researchers have no choice but to install their own 'scientific' pigeon lofts in order to gather suitable data.

1.3

On Terms and Definitions

Homing and *navigation* are the key terms used in this book. It is self-evident that a precondition for homing is the creation of a home to which an animal is willing to return from a distant site, whether it has moved to this site voluntarily or been displaced passively by man. Any adult bird usually makes its breeding territory a home site. Domestic pigeons feel bound to a loft in which they were living over several weeks postfledging (Sect. 3.1). Any act of return movement to this site may be called homing, but not any such act is commonly called navigation. If a pigeon or a starling returns from an accustomed feeding area some hundred metres or even a few kilometres away, we may hardly speak of navigation. However, if an albatross returns from a foraging flight covering some thousand kilometres, its homing to a small island in the midst of the ocean is undoubtedly an outcome of a remarkable navigational performance. So what is navigation? I refrain from giving a sharp definition. Attempts to do so, as attempted earlier, have never been successful. Usage of the term has even been broadened in recent years (navigation through the brain, the Internet etc.). Nevertheless, in the present context and in a narrower sense, the term *true navigation* is frequently used for goal-related orientation towards a given position on earth, usually a home site, towards which no direct sensory contact is available at the current position of an animal. In its strictest sense, the term is only applied if not even familiar landmarks surrounding the goal can be recognized, or are used, which potentially can guide to the goal. Such guidance by familiar landmarks is often called *piloting*.

Another pair of terms to mention are *compass* and *map*. These are tools used by human navigators and it is frequently implicated that animals also make use of such instruments. In fact, applying these terms in the field of animal orientation and navigation is very convenient, as they describe particular functions in a vivid and succinct way. While speaking about compasses and maps, however, we should be aware that we are using anthropomorphic metaphors. A flying bird might perhaps have an equivalent of a map exhibiting explored topographical features, but certainly it does not have a chart showing isolines of physical quantities that might correspond to a grid of coordinates. However, an animal navigator must have some representations in the brain referring to spa-

tial structures in the environment and must evaluate them in a way so that the outcome is comparable to the outcome of our use of such instruments. Thus, in order to avoid long-winded circumscriptions of neural processes which are largely unknown, I shall use the terms *compass* and *map* as metaphoric short-cuts of such processes. As I do so with some reluctance, however, the terms should always be thought of as between quotation marks, although they are mostly not labelled that way because of their frequent occurrence.

Further words of caution concern the attributes often preceding the word 'map'. If I speak of a 'gradient map' (Sect. 4.2.2), for instance, I do not presume that a pigeon is in any way aware of spatial gradients or that such gradients are 'mapped' to some brain region. The term merely implies that the bird's navigational system exploits scalar values of relevant environmental parameters that increase or decrease more or less monotonically over some distance in a given direction. The bird is thought to make use of gradients that could be drawn (by man) on a map, but the bird is not thought to 'have' such a map (Sect. 7.9.3). The attributes connected with a 'map' may belong to quite different categories. They may refer to the physical or sensory nature of input signals (magnetic map, olfactory map), to the spatial structure of evaluated cues (gradient map, mosaic map, topographical map), to the application of 'true navigation' as opposed to piloting (navigational map), to the spatial experience of an individual bird (familiar area map) or to a psychological category (cognitive map). Concerning the latter, I do not take a position on whether or not pigeons have a cognitive map (Sects. 4.2.2 and 9.1) (cf. Bennett 1996; Mackintosh 2002).

Generally, I have no ambition to get into debates on terminology. Classifications of terms and definitions rarely find unrestricted acceptance by all researchers working on different topics within a given field. Lines of demarcation separating natural phenomena from each other may appear appropriate in one context but are often inappropriate when seen from another point of view or when thus far unconsidered circumstances have to be included. By and large, my notions are roughly, but not always literally, consistent with the terminological classifications as proposed by Papi (1992b) and Able (2000).

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