

## *The concepts and terminology of bird navigation*

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As understanding of the processes and mechanisms of bird navigation has increased, older conceptual frameworks and terminology have become inadequate. Terminology used to refer to orientation and navigation behaviour have acquired varied and divergent meanings. Here I present a unified set of terminology that I hope will help clarify thinking and communication in the field.

In any research field, effective communication requires a common vocabulary. Furthermore, as understanding in the field advances, older conceptual frameworks may no longer be adequate, and they and the associated terminology will have to be modified or replaced. Birds perform a diverse array of behaviours in situations that require navigation over distances of a few meters to thousands of kilometers. Navigational tasks performed by birds include central place foraging and other movements within a familiar area, foraging journeys by albatrosses that cover thousands of km, cache recovery in food-storing species, vector navigation by first-time migrants, and the long-distance homing navigation performed by migratory birds and homing pigeons. There exists a need for a unified set of terms to describe these behaviours that reflects current understanding of their underlying mechanisms.

Several attempts to define types of orientation mechanisms have been made in the past. Griffin's (1952) three types of orientational ability related to homing were of necessity descriptive because at the time very little was known about the mechanisms involved. Griffin's Type I orientation was defined as steering a course on the basis of familiar landmarks; Type II is the ability to head in a given compass direction independent of landmarks; and Type III is the ability to orient toward a goal, regardless of its direction, based on mechanisms other than recognition of landmarks. His scheme was adopted in numerous subsequent reviews because of its heuristic

value (e.g., Schmidt-Koenig 1965, Keeton 1974, Emmlen 1975, Able 1980), but increasing understanding of the behaviour of navigating birds has rendered its rather general framework obsolete, and even at the outset it was formulated only to explain homing processes. Other classifications have been proffered in various contexts (Jander 1975, Schöne 1984, Beugnon 1986, Papi 1990) and over the years the terms used to refer to various types of orientation and navigation behaviour have unfortunately acquired varied and divergent meanings.

One simple but important example should illustrate the confusion that can result. The map and compass model of homing navigation (Kramer 1953, 1957) remains the enduring hypothesis to explain homing from distant, unfamiliar sites and a great deal of empirical evidence supports it. As discussed below, it seems clear that Kramer intended the map to include only spatial information obtained at the remote release site of a displaced bird. His concept thus corresponded with Griffin's Type III orientation, the ability of a bird to choose the homeward direction when released in unfamiliar territory (Griffin 1952). Recently, the "map" of Kramer's map and compass model has been changed and expanded to include other phenomena, e.g. navigation based on information picked up along the displacement route and vector navigation (see below) (W. Wiltschko and Wiltschko 1998, R. Wiltschko and Wiltschko 1999, Gould 1998). Similar fundamental problems of definition afflict terms describing basic orientation behaviours such as piloting and route reversal.

Here I will define, describe and provide examples of the main types of orientation and navigation behaviour performed by birds. It is my (perhaps naive) hope that workers in the field might adopt a common set of terminology. I have made no attempt here to review the empirical evidence that either supports or refutes the various examples cited; they are used simply to illustrate the basic concepts discussed.

## Orientation and navigation

Even the two most ubiquitous terms in this field are used in a variety of contexts. *Orientation* can refer to orientation of parts of the body with respect to one another, orientation of the body in space based on internal signals, orientation of the body with respect to external stimuli, and compass orientation. Most of the behaviour discussed here falls under the category referred to as *distant orientation* by Schöne (1984:95): orientation that leads an animal to a goal that is beyond the limits of direct sensory perception. I will use *orientation* to denote *directed movement*; most often this will be synonymous with compass orientation.

*Navigation* has likewise been used in so many different ways that it no longer has any special, restricted meaning. With respect to homing in birds, Griffin's Type III navigation and Kramer's map and compass navigation subsequently came to be referred to as *true navigation* (e.g., Keeton 1974, Emlen 1975, Able 1980, Phillips 1996). Now it is probably best to abandon these once useful variants and adopt the general definition given by Schöne (1984:105): navigation is the theory and practice of charting a course to a remote goal. All of the examples of spatial behaviour cited above would fall easily within this definition.

## Orientation behaviour employed independent of homing

### (1) Non-compass orientation

During migration, birds often orient their flight with respect to topographic features (coastlines, mountain ridges, rivers) or the wind. These environmental cues do not, of themselves, provide compass directions, but in many cases they constitute the primary stimulus by which the bird's movement is directed. Even in cases where visual landmarks are used, this type of orientation should not be termed *piloting* (see below; cf. Schöne 1984) because it is not goal-directed in any strict sense. For example, a first-time migrant is apparently not navigating toward a specific, defined goal area. Such a bird might nonetheless depart from its vector navigation course to follow, e.g., a coastline.

### (2) Compass orientation

This type of orientation is the ability to head in a given compass direction (either a true compass direction based on celestial cues or a magnetic compass direction) without reference to landmarks. The orientation direction is not related to a specific known goal. To do this, the animal must possess a compass. This corresponds to Griffin's (1952) Type II orientation. There are nu-

merous examples. Racing pigeons are typically trained to fly from progressively greater distances in one direction from home. If released at a site in some other direction from home, the birds will show a strong tendency to fly in the now incorrect fixed compass direction learned during the training sessions and races. Similar behaviour has been found in homing trials with Bank Swallows *Riparia riparia* (Giunchi et al. 1999). Population-specific and apparently innate fixed orientation directions have been described in a number of species. Griffin and Goldsmith (1955; Goldsmith and Griffin 1956) released adult Common Terns *Sterna hirundo* displaced from their nesting colonies. In both New England and the U.S. Great Lakes, the birds showed a strong tendency to fly SE regardless of the direction back to the colony. Bellrose (1958) found that Mallards *Anas platyrhynchos* displaced and released in autumn tended to fly away toward NNW, again irrespective of the actual direction back to the capture site. Matthews (1961) found similar behaviour among Mallards in England and termed it "nonsense orientation". These fixed orientation directions differ from population to population, are apparently innate, are based on visual compasses, and if they provide any adaptive advantage to the ducks it is not yet demonstrated (Matthews and Cook 1982 and references cited therein). The birds fly the fixed courses for only a short time. Another example of simple fixed compass orientation was documented in Adelie Penguins *Pygoscelis adeliae*. Displaced long distances from several breeding colonies (including to the geographic South Pole) all consistently walked off toward NE (Emlen and Penney 1964, Penney and Emlen 1967). In this case, the direction makes sense in that it provides the birds with the shortest seaward route toward offshore feeding areas that may be many km away across featureless ice and snow fields.

### (3) Vector navigation

Young birds of many species embarking on their first migration possess inherited information about the direction to the population-specific winter range and information that is correlated with the distance to that range. The implementation of this direction and distance 'program' was termed vector navigation by Schmidt-Koenig (1970). It has also been called *vector orientation*, *genetically-based orientation* (Papi 1990), or a *spatio-temporal* or *time-and-direction program* (Berthold 1996). Schmidt-Koenig's original term has been widely used and I think it is preferable to continue to use vector navigation. Papi (1990, 1992) has classified vector navigation as a homing mechanism but this seems inappropriate inasmuch as there is no goal defined on the basis of innate information or through experience, only information about direction and distance.

The clear difference between the orientation behaviour of first-time migrants employing vector navigation and experienced birds performing goal-directed orientation was demonstrated in the classic displacement experiments of Perdeck (1958): young European Starlings *Sturnus vulgaris* on their first migration did not compensate for the displacement, but continued to fly in the SW direction typical of their population and for a distance that approximated that of the remaining portion of their migratory flight. Experienced adults reoriented toward NW and navigated back toward the traditional winter range of their population. Without prior migratory experience, the young birds could only proceed in the direction and for the distance dictated by vector navigation. In species that migrate in social groups, the coded direction of vector navigation may be influenced by the behavior of other flock members.

Subsequent studies on a number of species have demonstrated the components of vector navigation in hand-raised birds tested in orientation cages. Such birds orient in the appropriate direction when they come into migratory condition for the first time. The first such studies by W. Wiltschko and Gwinner (1974; Gwinner and W. Wiltschko 1978) on the Garden Warbler *Sylvia borin* showed that not only did birds hand-raised in isolation from all visual orientation information orient in the expected migratory direction when tested in the earth's magnetic field, but the well-known shift in direction from SW to SE also occurred at approximately the expected time during the migration season. Extensive breeding experiments with Blackcaps *S. atricapilla* have shown that the population-specific orientation during the first migration is heritable and comparative studies of a host of *Sylvia* species have documented a heritable relationship between aspects of migratory restlessness (*Zugunruhe*) and migration distance (Gwinner 1968, Helbig 1991, recent review in Berthold 1996).

## Orientation behaviour involved in homing

A bird attempting to return to a nest, roosting site, foraging place or some other "home" might do so by any of several methods. The bird might be in sensory contact with the goal as by being able to see the goal or by following the gradient of an odour originating from home. It might use various strategies to log its journey away from home, thereby enabling it to retrace that route or even to estimate a shorter, more direct return route. It might be able to record and integrate the signals generated by its own motion and compute the direction back home by inertial navigation. Or it might employ some kind of map or positioning system to fix its location relative to home. Lacking any of these more complicated abilities, it might simply wander at random or move in some type of organized searching pattern

until it encounters familiar terrain. These strategies are, of course, not mutually exclusive and we should expect the birds to bring to bear as many abilities as are relevant to the navigational task at hand.

## (1) Route-based navigation

Route-based navigation is a general term used to describe homing navigation performed on the basis of information perceived during the outward journey from its beginning to the point at which the return is begun (Baker 1981, 1984). The outward journey may be passive or active. Route-based navigation is a general descriptor in that no specific type of outward journey information is specified. Depending upon the information involved and mechanisms employed, three types of route-based navigation may be identified. Although each fits the general definition of route-based navigation given here, they are based on fundamentally different processes.

### (a) *Piloting*

Piloting has been used in many different ways. It was apparently introduced by Schmidt-Koenig (1965) as a synonym for Griffin's Type I orientation. Griffin (1952) actually defined Type I orientation in more general and mechanistically vague terms: reliance on visual landmarks within familiar territory and some type of systematic search or random wandering until familiar areas are encountered when released in unfamiliar territory. Schmidt-Koenig (1965: 218) defined piloting as the ability "to find a goal with reference to familiar landmarks." In neither case was the way in which landmarks are employed to find the goal specified. Baker (1984: 17) confined piloting to situations in which the goal is reached by retracing steps past landmarks learned during the outward journey, placing it unequivocally in the category of route-based navigation. The situation became even more complicated when Papi (1990) used the term *route-reversal* for piloting *sensu* Baker and defined piloting (p. 13) as occurring "when an animal is familiar with an array of landmarks . . . and is able to switch from one to the other in the appropriate order to reach any known site without the use of a compass. The mechanism is used by many vertebrates over familiar areas and presupposes an acquired topographic map that psychologists . . . would recognize as being an example of a cognitive map." The critical component of Papi's definition is the preclusion of use of a compass in the goal orientation process. This restriction is necessary if piloting is to be distinguished from map and compass navigation involving a *mosaic map* (see below). Others (e.g., Wallraff and Neumann 1989, Wallraff 1991, Wallraff et al. 1994) use piloting as synonymous with goal navigation using a mosaic map.

The fluidity of the definition of piloting reflects our lack of empirical understanding of exactly how birds use landmarks. In my opinion, we do not need a synonym for navigation using a mosaic map. I propose that piloting be used only to refer to goal-directed orientation based upon following a sequence of familiar landmarks of any type. The critical criterion is that the landmarks themselves provide a route to the goal, they do not define the animal's position with respect to the goal as a compass direction (see *mosaic map* below). Distinguishing between these two possibilities can be done empirically. Clock shifts should have no effect on initial orientation of homing pigeons if piloting, as defined here, is taking place. The sequence of landmarks used in piloting might be learned during an immediately preceding outward journey (either active or passive), or the memory of the landmarks might be accumulated and remembered over longer periods of time. Because landmarks of at least some types can be sensed at distance, piloting should not require that the animal retrace the route exactly: some shortening or straightening could be accomplished (Baker 1984).

Defined in this way, there is remarkably little empirical evidence concerning the role of piloting in bird navigation, although it is intuitively appealing to imagine that birds must often employ piloting when moving between sites within the home range. The importance of landmarks and exactly how they might be involved in pigeon homing have been controversial (e.g. Wallraff et al. 1994). Some have concluded that piloting exclusively by landmarks does not occur at all (Wiltschko and Wiltschko 1998), but recent studies on homing pigeons implicate a role of familiar landmarks, although precisely how they are being used remains unclear (Braithwaite and Guilford 1991, 1995, Braithwaite 1993, Burt et al. 1997, Wallraff et al. 1999). It has also been suggested that olfactory and other features of the open ocean surface might be temporally and spatially stable enough to provide seabirds with a means of piloting on very large scales (Nevitt 1999).

#### (b) *Beaconing*

Goal orientation of a different sort was described in storm-petrels (Grubb 1974, Minguez 1977). Leach's *Oceanodroma leucorhoa* and British *Hydrobates pelagicus* Storm-petrels used odours specific to their own nests to find the entrances to burrows when they returned at night from foraging trips at sea. Characteristically the birds landed downwind of the burrow entrance and then walked upwind, apparently following the gradient of the learned odour. Following a gradient in some stimulus originating from the goal has been termed beaconing (Collett 1987). At sea, a number of species of procellariiform seabirds follow odour cues upwind as a mechanism for localizing ephemeral patches of food (Grubb 1972, Hutchinson and Wenzel 1980, Nevitt et al. 1995, Nevitt and Veit 1999).

#### (c) *Path integration*

Also termed 'dead reckoning', an animal performing path integration uses outward journey information to constantly update its position relative to its point of departure. Even if the outward journey is circuitous, the animal is able to return home by the straight path direct route. Theoretically, path integration may be based on external reference information (*allothetic path integration*), or upon internal signals such as inertial signals generated by the vestibular system, somatosensory feedback and efference copies, or counting steps (*ideothetic path integration*). Path integration over complex routes requires the animal to monitor both direction and distance of movement or passive displacement and hybrid systems employing both internal and external reference information are possible. *Reverse displacement navigation* (Schmidt-Koenig 1965) includes both ideothetic and allothetic path integration.

For individuals that have had limited or no exploratory experience in their home range and therefore little opportunity to develop a navigational map of any kind, path integration may provide a useful homing strategy. An important disadvantage is that there is no mechanism by which errors in the necessary estimations may be corrected. Unless compensated by chance opposing errors, the effect of such mistakes will accumulate over the course of the journey. For this reason, path integration should become less efficient as the distance and complexity of the outward journey increase.

(i) *Allothetic path integration*. Foraging ants use sun-based compasses to measure the angles turned during travel and retinal image flow during motion to estimate distance traveled (Wehner et al. 1996; they also use ideothetic path integration to estimate distance). This constitutes allothetic path integration. Schmidt-Koenig (1975) applied the term *route reversal* to this behaviour and Papi (1990) subsequently used *course reversal* to describe this process. Route reversal is potentially misleading in that the wording implies that the outward route is retraced rather than integrated (Papi 1990). Although both of these terms have been used more or less synonymously with allothetic path integration, communication will be facilitated if we use path integration as a general descriptor and its specific cases when the mechanisms are known.

The Wiltschkos (R. Wiltschko and Wiltschko 1978a, W. Wiltschko and Wiltschko 1982, 1987) adopted the term *route reversal* to describe the behaviour of young homing pigeons. Using their magnetic compass, the pigeons apparently monitor the direction of displacement during passive transport and use this information to estimate a direct return course. Homing will be facilitated if the bird can also estimate the distance to home along the determined course, but there is no

evidence that they can do that. The possibility of path integration of this kind has been questioned by Wallraff (2000a).

The best evidence for allothetic path integration in birds comes from geese that were able to walk in the homeward direction from release sites up to 1500 m from home. When the outward journey was circuitous, the birds returned via the straight line course. They were able to do this whether they walked to the 'release' point, followed a human to whom they were imprinted, or were passively transported in a hand-pulled cart. The homeward orientation persisted under overcast skies and when the top of the cart was covered, but disappeared when both the top and upper one-third of the sides of the cart were covered (Saint Paul 1982). These results certainly suggest that the geese were relying on external information to perform path integration.

(ii) *Ideothetic path integration.* Ideothetic path integration employs signals generated by locomotion to enable an animal to constantly update its position relative to its point of departure (Mittelstaedt and Mittelstaedt 1982). Internal information such as inertial signals generated in the vestibular system, somatosensory feedback and efference copies may be integrated to yield a direct homeward course. Mammals performing short-distance goal orientation under their own powers of locomotion perform ideothetic path integration (Etienne et al. 1996); the ability disappeared when they were displaced passively (Etienne et al. 1988).

Remarkably little work has been done on ideothetic path integration in birds navigating at any scale. Merkel (1978) showed that Painted Quail *Excalfactoria chinensis* could compensate for angular deviations imposed during either active or passive transport through a gangway of up to 10 m length leading into an open arena. The birds compensated for smaller angular deviations better and overall were much poorer than rodents at performing similar tasks.

That birds might use path integration based on inertial signals for long-distance homing navigation was suggested many years ago by Barlow (1964). In strict terms, it is a difficult hypothesis to test because regardless of the treatment, pigeons are alive during transport and their nervous systems may be logging some information despite our attempts to block them or overwhelm them with noise. However, a variety of attempts have produced entirely negative results. These include transporting pigeons on rotating turntables, within rotating and tilting drums, while under deep anesthesia, and releasing pigeons after surgical removal of the vestibular apparatus (summarized in detail in Keeton 1974; see Wallraff 1980). Of course, showing that a capability such as inertial navigation is not necessary for homing does not imply that it might not be used when available. The best we can say at the moment is that the evidence does not support a role for ideothetic

path integration, whether by inertial signals or otherwise, in long-distance homing.

## (2) Map-based navigation

Map-based navigation, also called *location-based* and *site-based navigation*, denotes the situation in which a bird determines its spatial position relative to home (or at least the direction toward home) solely on the basis of information available at the distant release point. *Map-based navigation* is a less ambiguous term than the two synonyms because some types of information (e.g. odours) that might be accessed in transit (and therefore considered to fall under *route-based navigation*) are site- or location-dependent (Wallraff and Sinsch 1988). That homing pigeons have the ability to perform map-based navigation was demonstrated most convincingly by Wallraff (1980), and the rapid, very long-distance homing of seabirds and others suggests that the ability may be widespread among birds. Of course, the capacity to perform map-based navigation does not preclude the simultaneous use of route-based navigation techniques, but while perhaps often sufficient, it seems clear that route-based navigation is not necessary for homing. At least since Kramer (1953), the system by which birds determine spatial position from distant sites has been termed a "map". Inasmuch as there is scant evidence that the distance from home is indicated (but see Holland et al. 2000), the term map may not be strictly applicable but it has been used widely and remains a convenient shorthand (Wallraff 1974). Based on fundamental differences in the information upon which they might be based and their mode of operation, we distinguish between two types of map.

### (a) *Mosaic map*

The term *mosaic map*, introduced by Wallraff (1974), has also been called a *familiar area map* (Baker 1978) or *topographical map* (Wallraff 1988). The mosaic map is formed from the learned spatial relationships among features of the landscape and their relation to home. These relationships are presumed to be learned as compass directions as the animal explores increasingly large portions of its home range (W. Wiltschko and Wiltschko 1978b, Wallraff et al. 1994). As such, the extent of the learned map is a function of the range of exploration. Although the range of the map might be extended somewhat beyond that actually visited by the bird (visual landmarks, at least, can be seen for some distance), a mosaic map will be of no use at sites far removed from the familiar area.

This type of map is often referred to as a *cognitive* or *mental* map (e.g., Papi 1992), but it is not clear that, as currently conceived, it meets the criteria set forth by Tolman (1948) and O'Keefe and Nadel (1978) when

they coined the term. In their view, a cognitive map is a mental representation in which spatial, possibly geometric, relationships among places are coded with respect to distance and direction and an animal possessing a cognitive map must be able to make novel short-cuts between points. In the case of the mosaic maps proposed for birds, it is not clear that information about distance between points is coded (Wallraff 1974) and there is little evidence that birds can navigate readily between any two points within the range of the mosaic map as opposed to between any given point and home (Bingman 1998). Because the term cognitive map has been used in a variety of ways (e.g. Gallistel 1990) and because he felt there was no compelling evidence for the existence of cognitive maps as originally defined, Bennett (1996) argued that the concept is no longer useful and that the term should be avoided. I am inclined to agree that arguing about whether what we currently understand about how birds represent spatial relationships fits or does not fit a definition of cognitive map is not particularly useful.

Most research on homing navigation in birds has been devoted to discovering what physical information forms the basis of the navigational map. One type of mosaic map might be based on visually perceived features of the landscape. It has often been assumed that homing pigeons rely on such a map when released within the familiar area (e.g., Wallraff 1991) and there is some evidence that they do use landmarks in some way in such situations (see piloting above). What is not clear is whether landmarks are being used to define a route (piloting) or to define spatial position (i.e., as a map). The fact that clock shifts produce large deflections of vanishing bearings even at very familiar release sites is at least consistent with the possibility that landmarks are being used as a map which yields the homeward course as a compass bearing (see Bingman 1998). However, the consistent observation that clock shifts at very familiar release sites yield a reduced deflection and increased scatter of homeward bearings suggests that landmarks may be used in addition to (and in this case, conflicting with) a map and compass system (Wallraff et al. 1999).

Another type of mosaic map that has been widely discussed is the olfactory map of Papi and his colleagues (Papi et al. 1972, Papi 1976, 1982). Here the 'landmarks' consist of qualitatively different odours which are detected by pigeons near the home loft and associated with the directions of winds that carry them past the loft. This is a peculiar type of mosaic map because the 'landmarks' move past the animal instead of the animal moving past the landmarks as it explores. But because winds and the odours they carry may arrive from beyond the area with which the bird is directly familiar, the range of the map's effectiveness could be considerably greater than the familiar area based on direct exploration. Wallraff (1991) has dis-

cussed numerous conceptual problems with an olfactory mosaic map.

### (b) Gradient map

It is hard to imagine that even an extended mosaic map of the sort proposed by Papi could be used over distances of 300 km or more (Wallraff 1981, Wallraff et al. 1981, Ioalè et al. 1983) unless the pigeons had previous experience with such distant release sites and at least some of the intervening terrain. For goal orientation from very distant unfamiliar places a more general and much more extensive map would seem to be required. *Gradient* or *grid* maps are thought to be based on at least two gradients of any physical substrate that vary systematically over sufficiently large regions. A bird could learn the gradients of the relevant physical variables within the familiar area. Assuming that these gradients extend monotonically beyond the familiar area, a displaced bird could obtain an estimate of its position relative to home by comparing the remembered values of the variables at home with the values at the release site. In theory, the range of such a map is unlimited; in practice its range and accuracy would depend on the spatial extent of the gradient fields and their uniformity. Wallraff (e.g. 1974, 1991) has extensively explored the details of gradient maps and how they might function in bird navigation.

Homing in any animal based on a gradient map remains hypothetical. For many years, various astronomical parameters were considered as possible sources of information upon which a gradient map might be based because they are familiar indicators of latitude and longitude. There has been little or no experimental support for these hypotheses and more recently maps based on parameters of the earth's magnetic field have become popular (e.g. Gould 1982, 1998, Walcott 1991, Phillips 1996, Walker 1998). Because pigeons can home using only map-based information from distances that would seem to exceed any conceivable olfactory mosaic map, Wallraff (1989a, b, 1991, 2000b) has speculated on the existence of a map based on gradient fields of airborne odours and explored theoretically how such a map might work.

### Kramer's map and compass model – the enduring paradigm

Kramer (1950) discovered the sun compass in birds. This initial discovery was made in experiments on migratory European Starlings, but Kramer was at the same time studying the homing behaviour of pigeons. During this period, Matthews (1951, 1953) proposed his hypothesis of bicoordinate navigation in homing pigeons based solely on the sun. At least in part in reaction to Matthews' sun-arc hypothesis, Kramer out-

lined what came to be called the "map and compass" model of homing navigation (Kramer 1953, 1957). Kramer believed that the sun was involved in homing only as a compass, and thus he described navigation as a two step process. In the first step, a displaced pigeon estimates its position in space relative to home; this yields the homeward direction as a compass bearing, e.g., something like "I am south of home." In the second step, a compass is employed to identify the actual direction of the homeward bearing, e.g., something like "That way is south." Kramer's first description of the map and compass hypothesis (1953) was in German, but in 1961 he described the model in these words (pp. 356–357): "The first [step] would consist of establishing the geographic position of the release site relative to the home site, including the 'theoretical' homing direction. The latter is an immediate deduction from the first: both, therefore, are considered as one step and are called the 'map' constituent. The second step would consist of ascertaining the deduced homing direction in the field. This in the analogous human performance, is usually done by means of a compass; it is therefore called the 'compass' step."

The hallmarks of the map and compass hypothesis are three: (1) it is a two-component process dependent upon a position-fixing system and an independent compass capability; (2) the positioning system or "map" yields the solution to the homing problem as a compass course; and (3) a biological compass is employed to identify in the field the direction of this homeward course. The first criterion distinguishes this model from all others that were under discussion at the time (e.g., the sun-arc hypothesis of Matthews, Yeagley's (1947, 1951) model based on coordinates defined by the magnetic field and Coriolis force, and systematic search or piloting by familiar landmarks). In all other models, the same information that provides the animal with the spatial location of its release following displacement also communicates, *per se*, the appropriate direction of travel. The inclusion of a compass as an independent component of the navigation system not only set Kramer's model apart from others, it provided a critical means by which important aspects of the hypothesis might be tested.

Kramer hypothesized that the sun compass provided the mechanism underlying the compass of the two-step process in pigeon homing and this was subsequently shown to be the case (Schmidt-Koenig 1958, 1960, 1961). Since that time, scores of clock-shift experiments have been performed on homing pigeons. The robust and consistent result has been the demonstration that the sun is used by pigeons in the homing process only as a compass. It is clear from the clock-shift experiments that the map component of homing navigation is not disturbed: the pigeons know in what direction home lies; their sun compass simply identifies an incorrect, but predictable, direction as the homeward bear-

ing. This experimental manipulation provides the strongest evidence that map-based homing navigation does in fact involve a position-finding component and an independent compass component.

During Kramer's lifetime, the sun compass was the only known animal compass. Thus he naturally assumed that the sun compass was both the necessary and sufficient compass component of his model. When data accumulated indicating that pigeons could home perfectly well under solid overcast skies and at night, this was thought to perhaps challenge the map and compass model (Keeton 1974). Later discovery of the magnetic compass and elucidation of its role in pigeon homing provided an alternative compass mechanism that could be employed when the sun is not visible, a result entirely consistent with Kramer's basic conception if allowance is made for the possibility of more than one compass.

Whereas Kramer's original description of the map and compass model was quite specific as regards the compass, he was essentially silent with respect to the nature and basis of the map. Because of this vagueness, "map" has been used in a number of fundamentally different ways. In earlier years, the map was generally considered to refer only to positional information obtained at a distant, usually unfamiliar, site. More recently, the Wiltshkos (R. Wiltshko and Wiltshko 1979, W. Wiltshko and Wiltshko 1998) argued that any case in which the bearing toward a goal is coded as a compass direction should be considered true navigation based upon a map. This includes cases such as allothetic path integration based on a reading of compass bearings during an outward journey and vector navigation in which the compass direction is given by innate information and there is no defined goal. Gould (1998) adopted a similar very broad definition. Although Kramer was not explicit in the matter, his writing suggests strongly that in his mind "map" referred only to information obtained at the release site. In 1961 he stated (p. 360): "In a more general way it may be said that all evidence pointing to the map-and-compass concept . . . militates against a suggestion of direct perception of the home, or of the retracing of the route of transportation" [italics mine].

Despite the fact that directions of movement may be represented as compass bearings in each case, the processes of navigation involved in route-based navigation and vector navigation (which does not involve a defined goal) are fundamentally different from those based on a system in which spatial position is defined by stimuli perceived only at the release site. Clarity of communication and of thinking require, I believe, concepts and terminology that distinguish these behavioural mechanisms. I suggest, therefore, that map and compass navigation and map be used only to refer to situations in which spatial position relative to some specific goal can be determined solely on the basis of information

Table 1. Definitions and recommended terminology for the mechanisms of bird navigation.

Phenomenon	Definition	Notes
<i>(1) Orientation behaviour not goal-oriented</i>		
(a) Non-compass orientation	Oriented movement based on external environmental stimuli that do not provide compass directions (e.g., topographic features)	Not piloting (see 2.a.i below)
(b) Compass orientation	Ability to orient in a compass direction (either true or magnetic)	Synonymous with Griffin's (1952) Type II orientation
(c) Vector navigation	Compass orientation in directions dictated by heritable endogenous information about the direction of the first migration; some correlate of distance may also be coded	Synonyms: genetically-based orientation (Papi 1990); spatio-temporal or time-and-direction program (Berthold 1996)
<i>(2) Goal-oriented orientation behaviour</i>		
(a) Route-based navigation	Homing based on unspecified information perceived during active or passive displacement; can result in learned routes used repeatedly	Synonym: reverse displacement navigation (Schmidt-Koenig 1965)
(i) Piloting	Goal-directed orientation based upon following a sequence of familiar landmarks of any type	More or less synonymous with Griffin's (1952) Type II orientation; used here sensu Baker (1984); do not confuse with mosaic map (see 2.b.i below)
(ii) Beaconing	Goal-directed orientation based upon following a stimulus gradient emanating from the goal	
(iii) Path integration	Goal-directed orientation based upon unspecified outward journey information that updates position relative to point of departure; novel, more direct return routes possible	Synonyms: dead reckoning; reverse displacement navigation (Schmidt-Koenig 1965)
Allothetic path integration	Path integration based upon external information	Synonyms: route reversal (Schmidt-Koenig 1975); course reversal (Papi 1990)
Ideothetic path integration	Path integration based upon internal signals generated by motion	Includes inertial navigation (Barlow 1964)
(b) Map-based navigation	Ability to determine spatial position re home (or at least direction toward home) based solely on information at a distant place. Empirical data consistent with map and compass model in which position re home is given as a compass direction.	Synonyms: location-based navigation and site-based navigation; map and compass navigation; Griffin's (1952) Type III orientation; true navigation
(i) Mosaic map navigation	Goal orientation based upon learned spatial relationships among features of the landscape and their relation to home. Landmarks define position re home as a compass direction, not a route home (as in piloting)	Synonyms: familiar area map (Baker 1978); topographic map (Wallraff 1988)
(ii) Gradient map navigation	Goal orientation based upon values of at least two gradients of any physical variable that vary systematically over sufficiently large regions and define spatial positions re home; can work in unfamiliar places	Synonyms: Grid map; bicoordinate navigation if two gradients involved

available at a distant site (map-based navigation as defined here). This includes navigation based on mosaic maps and gradient maps.

Kramer's map and compass hypothesis has provided a strong conceptual framework for understanding bird navigation. A wealth of experimental data is consistent with its basic tenets and to date, no repeatable experi-

ment has refuted it. It is likely to remain the central explanatory paradigm for the foreseeable future.

Table 1 summarizes the definitions and salient features of the basic concepts of bird navigation and of the terminology proposed herein.

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