Evolutionary aspects of orientation and migration in birds

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Summary. Evolutionary aspects of avian migratory orientation and navigation are reviewed. A theoretical approach to the evolution of complex (endogenously programmed) migratory behavior is presented using the comparative method of ordering a progression in existing behavioral characteristics from dispersal, to facultative migration, to obligate migration.

Key words. Orientation; migration; navigation; evolution of behavior; dispersal.

Introduction

The constant interactions between organisms and their environment represent fundamental exchanges essential for survival and reproduction. Orientation processes have to do with the spatial and temporal aspects of these interactions[64]. Each movement an organism makes has its associated costs and benefits[41] and thus, natural selection should select for mechanisms that enhance the ability to orient correctly within these dimensions.

In a sense, every behavior is oriented in some way simply because the behavior is organized relative to spatial and temporal aspects of the environment[64]. For the purpose of reviewing natural selection and oriented movements by birds, however, I will be primarily concerned with a more restrictive sense of orientation as a behaviorally mediated process that results in a nonrandom pattern of locomotion. Thus, I will be omitting an entire category of orientation behavior involving stationary placement of body axis relative to the environment[8].

In recent decades, the emphasis of research on avian orientation, navigation, and migration has focused primarily on mechanistic aspects[30] which, of course, is quite appropriate. Nevertheless, our understanding of these complex behaviors would be enhanced by studies of evolutionary and ecological aspects as well[27, 30, 72, 77], and relatively more research in this direction has recently been initiated.

I have organized this overview along two fundamental lines of evolutionary inquiry with respect to migration: 1) the evolution of orientation mechanisms and the ability to use specific cues to orient and, 2) the selective factors that led to movements that necessitated use of these mechanisms.

In no way is this contribution intended to be an exhaustive review. Because the majority of the contributions contained within this issue are concerned, in detail, with mechanisms of orientation, I will confine my discussion to a brief overview of evolutionary aspects of avian orientation, and devote relatively more theoretical treatment to the evolution of migratory behavior. Where appropriate, I refer the reader to more exhaustive reviews of relevant subject matter.

Evolutionary aspects of avian orientation

General overview

Because orientation is a fundamental necessity of mobile life, the ability to orient is found in even the most primitive organisms[8]. Organisms at the simplest known organizational level have been shown to possess two functionally distinct subcellular systems, one for dealing with resources, the other for dealing with information. The latter system detects chemical gradients and controls movements in space[8].

The earliest forms of life were probably limited to using chemical and energy gradients for orientation (taxis)[8]. As organisms became increasingly complex, more sophisticated locomotion was necessarily coupled with an increased ability to orient. More complex orientation behavior, including navigation and homing, is often divided into three categories[1, 9, 35]: 1) piloting, the ability to use fixed, known reference points ('landmarks') to orient or navigate; 2) compass orientation, which represents orienting in a given compass direction without reference to known landmarks; and 3) true navigation (which has been demonstrated in only a few species[1]), referring to the ability of an organism to select the appropriate direction to a particular goal in completely unfamiliar territory without any form of sensory contact with the goal[1].

In some cases, these categories have been considered a reflection of increasing levels in complexity through evolutionary time[12]. Other authors, however, have pointed out that this may not be the case[85]. For example, compass orientation may well have preceded the ability to memorize and utilize landmark information.

At this time, we can only speculate about the evolution of orientation abilities and, of course, the acquisition and development of orientation mechanisms may have varied considerably between taxa. Indeed, it is often assumed that functional similarities in orientation mechanisms between taxonomically distant groups are the result of convergence. On the other hand, we should not dismiss the possibility that such similarities occur because they represent phylogenetically ancient traits[4]. A general approach to this problem involves three levels of inquiry: a) theory;

i.e., what cues were, and are, available and how might they be used to determine direction, and what are the selection pressures for using particular cues; b) use of behavioral assays to determine which cues are used, and in the case of multiple cue usage, establishment of the relationships between the cues, including the ontogeny and development of cue usage in individuals; and c) establishment of the neurophysiological basis for the detection and processing of cue information. The second level is necessary, but not sufficient, to make strong inferences concerning the phylogeny of orientation mechanisms. This level is necessary to establish which cues are being used and, to a certain extent, how they are being utilized. However, even in the case of identical cues being used in the same manner by two or more distinct taxa, if it turns out that different integrating centers are involved, or different receptors are used, then the commonality may well be the result of analogy rather than homology. Thus, the third level of inquiry (c) is quite important in constructing an accurate picture of the evolution and phylogeny of orientation mechanisms.

For the most part we are still involved in levels (a) and (b), and even the most basic studies of orientation are entirely lacking for the huge majority of animal species. Level (b) is a long and tedious process, especially in light of the complexities that have arisen due to multiple cue usage, but based on the studies that have been undertaken (primarily on birds) several common themes are emerging[1,4,85,86]: 1) many of the same orientation cues are utilized by distantly related groups, and characteristics of these cues are being utilized in the same manner; 2) orientation is a highly complex system of multiple cue integration and apparent redundancy; 3) a great deal of learning and plasticity is involved in integrating and calibrating the usage of these various cues, and; 4) at least in birds, the basic information for orientation utilizing one or more cues is transmitted genetically. This information is then used as a baseline for learning and integrating information concerning those and other cues. All the known compass mechanisms, including those involving heritable information concerning direction, are subject to a greater or lesser degree of environmental modification during the first few months of life[6].

The adaptive significance of this redundancy and plasticity is probably somewhat complex. It has been suggested that pooling information from multiple cues would result in improved directional performance[4] and, indeed, exposure to multiple cues, both in the laboratory and in nature, substantially reduces variance around the directional mean[86]. A second adaptive aspect is that cue redundancy hedges against spatial and temporal variability in access to cue information and in spatial and temporal changes in aspects of the cues themselves. The integration and ontogeny of multiple cue usage is discussed in more detail elsewhere[4,5].

Adaptive aspects of spatial orientation and memory

Spatial orientation refers to all movements and states that are actively ordered in space. The concept refers to the ability of organisms to relate the position and movement of their bodies, body parts, and even foreign objects to spatial cues[64]. *Spatial memory* is memory for places and spatial relationships between them[68].

Complex spatial orientation and memory are of fundamental importance to all birds, from life-time residents to long-distance migrants. Although migrant birds have often been considered to possess more advanced mechanisms for spatial orientation and memory[12] than nonmigrants, or short-distance migrants, there is no real basis of support for this concept. On the contrary most of the evidence (albeit sparse) indicates that birds in general (regardless of the presence or absence of migratory behavior) have highly sophisticated spatial orientation and memory systems[42,46,54,61,69] and rapid learning of spatial memory tasks suggests that birds are 'biologically prepared' to process complex spatial information[83]. Although many more species groups need to be examined, the data currently indicate that abilities to interpret, process and store complex spatial information is widely distributed among the class Aves and, if this is indeed the case, probably represent phylogenetically ancient mechanisms. Thus, migrants may not possess special adaptations for orientation and navigation, only complex requirements for their use.

In nature, spatial orientation within the familiar area (e.g., home range) is a basic and fundamental necessity for an animal to track its position relative to the position of important aspects of the environment (such as the location of resources[51]) and to determine the location of resources relative to one another[9,10,85]. Thus, spatial memory is used to construct 'mental maps' of familiar areas[10] and such an ability appears to be relatively widespread among animals[1,4,9,32]. It is important not only to remember relative locations of significant sites within the familiar area, it is also advantageous to use the spatial map to calculate the fastest (and safest) routes between sites without necessarily retracing previous routes[9,10,80]. This ability has obvious implications for conserving travel time and energy and thus would enhance efficient utilization of resources within the familiar area. Overall then, selection should promote the development of mental maps that comprise 1) the location of important sites; 2) the landmarks by which the sites can be recognized; 3) the spatial relationships between the sites; and 4) the ability to calculate the most efficient routes between sites[10,81,85].

In addition to utilizing landmarks for orientation, many animals, from a large variety of phyla, are known to be capable of using a 'compass' (e.g., solar compasses, stellar compass, magnetic compasses; see under 'cues' below) for orientation. Biological compasses have been defined as any mechanism that tells an animal a constant direction and provides it with a nonchanging directional reference system[85]. The selective advantages of using a compass (with or without landmarks) have been previously described in detail[9, 10, 80, 81, 85, 86]. One of the basic advantages is that a compass can be used independently of landmarks. It also would reduce the number of sites and site relationships that would have to be memorized to construct a mental map. Such an ability would greatly reduce the amount of time and energy necessary to develop cognitive spatial maps and allow an organism to more easily return to its familiar area should it be displaced. Finally, mental 'mosaic' maps utilizing compasses and landmarks might be supplemented with (or even replaced by) 'gradient maps' utilizing not landmarks, but environmental factors that assumed gradient qualities[85] (e.g., magnetic field, olfactory gradients, etc.). In the case of two or more gradients at sufficiently large angles to one another, 'bicoordinate navigation'[81, 85] would be theoretically possible (see recent reviews[10, 86] for discussions of the evidence for navigational maps in birds). Such a map would have the following advantages: 1) it would allow orientation within the home range (if the gradient is detectable over short distances); 2) it would enable the organism to orient outside the home range in completely unfamiliar territory which would greatly facilitate efficient exploration and rapid return to the home territory; and 3) selection should favor a navigation system that is functional on a large scale, rather than being restricted to a local level. Of course, in long-distance migrants, the problem of orientation is global and cues must be available and reliable over vast distances[4].

The Wiltschkos[85] argue that an early evolutionary step from a mosaic map of landmarks to a gradient map utilizable in bicoordinate navigation is theoretically more plausible than the assumption that more complex navigational capabilities evolved independently, numerous times, for example, as distance of migration increased in a particular lineage[12]. More experimental work is necessary to address this question, but initial results tend to support the Wiltschkos' hypothesis. For example, the sedentary rock dove, *Columba livia* (ancestor of the artificially selected homing pigeon) shows homing abilities that are as sophisticated as those of homing pigeons[78] indicating that the capacity for long-distance orientation is present in nonmigratory as well as migratory species. Rapid, long-distance homing has been found in nonmigratory dark-eyed juncos (*Junco hyemalis*)[54]. Displaced neotropical residents showed homing abilities similar to those of displaced neotropical migrants[58, 59]. Finally, one of the arguments that resident birds lack the navigational abilities of migrants is based on slower return rates following displacement generally found for nonmigrants[12]. Several studies have demonstrated that homing ability appears to be independent of homing rates[7, 10, 78].

Orientation cues

Since the use of orientation and navigation cues is discussed in detail in other contributions in this issue, I will only briefly summarize adaptive aspects of the major cues that birds use for migratory orientation. For more detailed information, the reader is also referred to recent reviews elsewhere[1, 4, 5, 10, 86]. Although, in the interest of brevity, I often discuss the use of these cues in a general sense, the information available is extremely limited.

A) Landmarks. The use of landmarks is widely distributed among animal groups[8], and is often considered to be the most primitive means of orientation[12, 85]; however, as was mentioned previously, there is no a priori reason that landmark usage should have preceded compass orientation or the use of nonvisual gradients. Landmarks are utilized by birds that also use other means for orientation (e.g., sun and magnetic compasses) including pigeons[63] and even nocturnal migrants[22].

B) Sun compass. The use of a time-compensated sun compass has been demonstrated in a wide variety of animals[1, 8]. Recent experiments involving scrub jays (*Aphelocoma coerulescens*) have produced some very interesting results[84]. These birds preferentially use their sun compass to relocate food caches (storage sites) even when conspicuous landmarks are visible. A similar phenomenon has been observed in homing pigeons that ignore familiar landmarks and instead use their sun compass to home if the sun is visible[43]. Both scrub jays and pigeons have been demonstrated to be fully capable of using landmarks for these tasks as well. These findings indicate that the sun compass may indeed play an important role in fundamental spatial orientation and not just in special cases like homing and migration. The reason for the preferential use of the sun for orientation, even over very short distances in familiar areas (cages!), is unclear. It may be that the birds consider the sun compass to be more reliable, or it may be easier to encode, or recall, or both[84]. The widespread presence of a time-compensated sun compass in a diversity of animals, coupled with its use in very fundamental tasks, indicate that this compass ability may be very basic and phylogenetically quite old within Vertebrata (because sun-compass ability appears in organisms that have independently evolved visual systems, e.g., Arthropoda and Chordata, it has apparently evolved independently within Animalia).

It appears that no animal inherits an ability to compensate for the sun's movement[4, 10]. Rather it is the predisposition to learn the path of the sun as it relates to compass directions and integrate this information with the animal's circadian clock that is passed on genetically.

C) Polarized light. The ability to perceive polarized light is widespread among animals, both vertebrates and invertebrates[1]. The widespread use of polarized light in vertebrates may be an example of analogy since amphibians use extraoptical intracranial receptors for detection of polarized light. The ability to utilize polarized light for orientation is adaptive because it (the e-vector) can be used as an axis of orientation and as a reference to determine the position of the sun (for sun-compass orientation) when the sun is not directly visible. The majority of experimental work on polarized light as an orientation cue has been performed on nocturnal migrants during sunset[2, 3, 52], a time of day that seems to be particularly important in migratory decision making[50]. Results of some of these experiments indicate that migrants preferentially use sunset position over skylight polarization for directional information when presented with conflicting cue information[52].

D) Stars. In spite of the fact that a wide variety of animals are mobile at night, stellar orientation has been demonstrated only in birds and thus, may be an avian phenomenon[1]. The star compass of birds is not based upon an innate knowledge of directional relationships of stellar configurations per se, as was initially believed[62]. Rather, it appears that star configurations as directional cues are learned using the axis of stellar rotation as the polar direction, which is innate[4, 28]. Thus, in this aspect it is fundamentally similar (in terms of inherited propensity to develop directional information based on celestial rotation) to diurnal compass (sun and/or polarized light) development.

One question of evolutionary interest is why birds (which are generally diurnal and have access to other functional cues) have a stellar compass at all. This question is, in turn, associated with perhaps the larger question of why most migrants migrate nocturnally in the first place. In a few cases the answer is rather obvious: some species migrate over vast distances where they are unable to land for a prolonged period which requires flight during the night. This explanation, however, is not applicable in the majority of cases. Kerlinger and Moore[44] determined that several factors involving atmospheric structure should select for nocturnal migratory behavior because they promote a faster, and more energetically favorable, migration. These factors take into account that: 1) less energy is required to fly in cool, dense air (night) than in warm air (day); 2) horizontal winds at night are slower than during the daytime, so birds are less likely to be blown off course or to have to fight crosswinds; 3) there is decreased variation in wind direction at night; and 4) there is decreased turbulence in vertical winds at night. Kerlinger and Moore find little support in the oft-cited hypothesis that avoidance of predation during migratory flight is a primary selective force underlying nocturnal migration. They do find theoretical merit in 'the diurnal feeding hypothesis' which simply states that the extreme energetic demands of migration necessitate feeding en route, which can only take place (for many, but not all nocturnal migrants) during daylight hours. They conclude that the diurnal feeding hypothesis coupled with the energetic savings associated with migrating at night would be a potent selective force for nocturnal migration. It should be noted, however, that some species migrate exclusively during the daytime and many species are known to migrate day and night, even when not forced to. Thus, there appears to be a great deal of flexibility in the system, and a complex of selective factors leading to diel timing of migratory flight.

E) Magnetic field. The possibility that organisms might use the magnetic field of the earth for orientation was initially proposed by Middendorff during the middle of the last century and for many years this possibility was entirely dismissed by the scientific community[86]. We now know that the use of the magnetic field for orientation is extremely widespread in animals, from the most primitive prokaryotes on up through Vertebrata[86], and the large number of organisms with the ability to biologically precipitate magnetite (the likely contender for magnetic receptivity) suggests that this ability, and perhaps perception of the magnetic field, is phylogenetically primitive, probably evolving prior to the major radiation of animal phyla in the late Precambrian[48].

In terms of natural selection for a magnetic compass, the following factors are noteworthy. First, the earth's magnetic field provides a very reliable, global orientation cue[86]. Second, compass orientation using celestial cues requires sophisticated mechanisms to compensate for temporal changes in the position of cues, whereas perception of a (basically) constant field provides animals with a complete and unchanging reference system[85]. The magnetic compass represents, in this respect, the simplest functional compass[85, 86]. This aspect of the magnetic compass may be a major contributing factor to its being the genetically transmitted (primary), directional information source in birds[86]. Third, magnetic cues can be used both day and night regardless of weather conditions, so there are no restrictions on the time of day during which oriented movements can take place (and this benefit should extend from home-range use on up to long-distance migration).

A magnetic compass has been found in all avian species examined, and birds have developed systems based on perception of inclination, rather than polarity, for migratory orientation[86]. Such a system would appear to have disadvantages, for example, a loss of functional usage near the equator[10], and migrants crossing the equator would have to reverse their inclination goal 180 degrees, or switch to some other cue entirely. On the other hand, use of inclination, rather than polarity, should be strongly selected for because the polarity of the earth has reversed itself frequently in evolutionary time[10]. Thus, for example, each time a reversal occurs, northern hemisphere migrants using a polar compass in autumn would migrate north, an obviously disadvantageous trait, whereas migrants with an inclination compass would continue to migrate towards the equator. It is, perhaps, of evolutionary interest that the same magnetic orientation rules would apply to both northern hemisphere and southern hemisphere temperate migrants (i.e., 'poleward' for breeding, 'equatorward' for wintering rather than 'north' or 'south' per se).

Of considerable current interest is the possibility that migrant birds may use different magnetic systems for migratory orientation and homing[85, 86]. Migrants often return to the same exact breeding and wintering sites after traveling thousands of kilometers[53] and they may switch from migratory orientation to goal-area navigation (which would require completely different levels of receptive sensitivity[86]). Homing pigeons become disoriented when exposed to magnetic anomalies where the magnetic field is distorted from its normal values for the region[86] which indicates that there may be a distinct magnetoreception pathway involved in homing. Radio tracking of displaced wood thrushes, *Hylocichla mustelina* (a migrant species), during the breeding season indicated that these birds use true navigational ability to home, even under total overcast[7]. Of interest are the results of recent experiments on newts (*Notophthalmus viridescens*)[57]. Migrating newts use an axial (inclination) compass for simple-compass orientation similar to that used by migrating birds; however, a distinct receptive system with polar response may be involved in homing. This result, coupled with work done on birds, suggests the possibility that two distinct magnetoreceptive pathways might be evolutionarily widespread.

F) Wind. Because prevailing wind patterns often seasonally covary with meteorological cues, it has been suggested that birds might be able to predict, fairly accurately, wind direction based on these cues[1]. Thus, a bird might be able to select a particular time for migration based only on meteorological cues and have a relatively high probability of migrating in the seasonally appropriate direction. The observation that the same species of migrants fly downwind regardless of the direction at some localities, but not in others[1], indicates that there is geographic variability in the degree to which birds use wind direction as an orientation device. The majority of data indicates that it is generally the case that birds wait for favorable tailwinds to migrate in seasonally appropriate directions[60]. Thus, migrants utilize tailwinds to conserve energy, but apparently do not frequently use winds per se, to orient. Of evolutionary interest is the likely possibility that prevailing wind patterns have played an important role in the evolution of migratory routes, the distribution of migrants, and in the establishment of new populations.

Physiological mechanisms of orientation

Because the same basic orientation problems are common to all animals, it may be that the fundamental neurophysiological mechanisms involved in many aspects of spatial memory, spatial orientation and the construction of spatial maps, are phylogenetically ancient, but at this time much more experimental work is necessary to address this problem. Recent experiments with pigeons indicate that it is likely that homologous regions of the central nervous system (i.e., the hippocampal complex) are involved in spatial orientation in pigeons and rodents[21]. The hippocampus plays an important role in complex spatial memory in the tits (Paridae)[67].

As was mentioned earlier, the ability to precipitate magnetite is widespread in animals and this substance is considered a contender for magnetoreception[79]. Magnetically sensitive materials have been found in the head regions of both mammals[10, 87] and birds[11, 79]. Current evidence suggests that detection of the magnetic field may occur within the visual system[86].

Evolutionary aspects of migratory behavior

General

Bird migration is usually defined as a movement from the breeding (natal) grounds followed by subsequent return to the same breeding area for the next reproductive effort. Most recent theories consider migration an adaptive response that allows birds to exploit high levels of food for reproduction in areas that offer low probabilities of survival between reproductive efforts[75]. Some of these movements are quite spectacular, taking birds thousands of kilometers each year. Just as amazing, perhaps, is that the timing, distance and direction of these journeys are, at least in some species, transmitted genetically[15, 16]. How did natural selection shape these complex behavioral systems?

Whereas orientation and navigational abilities, and mechanisms, may not have evolved independently many times in birds[85], migratory behavior has probably evolved independently in numerous avian lineages and is being constantly modified by natural selection. For example, variation in migratory orientation in blackcaps (*Sylvia atricapilla*) has provided the raw material for the very recent development of a new wintering population that is growing rapidly in size[18]. Other examples include situations in which species that are normally resident may develop migratory populations when expanding their range[82] (e.g., the serin, *Serinus canarius* in Europe), or when members of a resident species are introduced into a new region (e.g., the house finch, *Carpodacus mexicanus* in eastern North America).

Current theories of the evolution of migration (for recent summaries of historical and current theories of the evolution of migration see reviews by Gauthreaux[30] and Dingle[27]) often invoke an ordered sequence of evolutionary steps proceeding from residency and relatively local movements, to partial migration (only a portion of a population migrates), to short-distance migration (by an entire population) and finally, to long-distance migration[24, 25, 31]. This order seems to make intuitive sense, and the scenario probably accurately summarizes the evolution of many migratory patterns. It should be noted, however, that this evolutionary sequence is not unidirectional and that steps may be skipped. It has been recently demonstrated empirically that partial migrant populations can be artificially selected to become entirely migratory or entirely resident in a very few generations[16], and residency has developed in previously migratory populations in nature[82]. For example, formerly migratory fieldfares (*Turdus pilaris*) have recently become residents on Greenland. Thus, habits of migration and residency may vacillate within a lineage, in both directions, through evolutionary time as a function of changing spatial and temporal characteristics of resource availability. The potential for complex migratory behavior may be quite primitive in Aves. Indeed, the ability to explore large areas offered by powered flight, and hence the opportunity to more efficiently exploit ephemeral, patchy resources on a large scale, may have been a selective factor in the evolution of flight itself.

In the following section, I outline a theoretical sequence of evolutionary events leading to endogenously programmed, long-distance migration. I follow with a brief summary of the evidence, based on both field and experimental studies, for such a sequence. Finally, I close with the suggestion that research into the regulation of intratropical movements may help to further test the model.

Evolution and the regulation of migratory behavior

One way to address evolutionary questions about behavior is by the 'comparative method'. When comparative studies indicate that species can be arranged in such a way that they form a progression in a behavioral characteristic, it can be theoretically assumed that since intermediate forms are possible (and still exist), evolution might have proceeded through a similar progression[23]. Indeed, lacking a fossil record of behavioral characteristics, or the neurophysiological mechanisms underlying them, comparative studies may comprise the most accurate (albeit indirect) information available for constructing the evolutionary sequence of behavior. In this respect we have a convenient comparative situation in avian migration, and that is a continuum in the degree to which endogenous and exogenous factors regulate migratory behavior between species, populations and even within individuals[74]. This continuum ranges from highly *facultative* migratory behavior that represents proximate responses to immediate changes in ecological factors, to *obligate* migratory behavior in which the fundamental stimulus to migrate is not environmental but programmed endogenously[13, 36, 38, 71, 72, 77]. It may be that the relative degree to which migratory behavior is regulated by exogenous and endogenous stimuli can tell us something about the evolution of complex migratory behavior. It is important to keep in mind, throughout this discussion, the assumption that natural selection should result in migratory behavior that maximizes the probability of overwinter survival while minimizing migratory distance[31, 45, 73].

When discussing movements by birds, it is useful to make a distinction between the concepts of dispersal and migration[31]. The distinction is simply this: 'dispersal' is movement away from a particular locality without returning to the point of origin, while 'migration' involves a return movement to the original location. Another important difference is that dispersal is often random in direction, while migration usually comprises consistently oriented movements in a given direction[31]. Adaptive aspects of dispersal are varied, but often cited factors include: a) exploration (finding the best habitats); b) avoidance of inbreeding; and c) escape from detrimental ecological or social conditions. Dispersal is highly relevant to population genetics and evolutionary theory because it can affect gene flow, the colonization of new areas, genetic drift and speciation[33]. The majority of animals, including birds, disperse during some period (or periods) of the life cycle, although relative degrees of dispersal within populations may vary greatly between years or seasons, between populations, or (prominently) between different age, sex or social classes within a population or group. In birds, the dispersal of young is greater than that of adults, and females disperse farther than males (and the same patterns are often characteristic of migration as well[31]). A very interesting question is why selection has favored the opposite pattern (i.e., males disperse more than females) in mammals[34]. For a comprehensive review of dispersal in birds and mammals see Greenwood[34].

If resource availability changes more or less continuously, or unpredictably, in space and time, dispersal can be relatively continuous and involve entire populations[26]. In these cases, the term 'nomadism' is probably more appropriate. Examples include species that more or less wander continuously in Africa and stop long enough to breed if the conditions become lush enough to support reproduction[26]. If spatial and temporal changes in resource availability become relatively predictable (cyclic), and are within an appropriate time frame (i.e., cycles occur within the reproductive lifespan of the organism), the selective conditions for migration are met. Dispersal and nomadism are typically treated as evolutionary precursors to migratory behavior.

Facultative migration is probably the most primitive type of migratory behavior. It begins as movement away from an area in direct response to a decrease in the probability of survival if the bird remains at that locality. Examples of factors that induce the outward journey include decreases in resources, increased resource demand due to harsh climatic conditions, increased population size, and restricted access to resources as mediated through social dominance[31, 70]. If decreased resource availability at the point of origin is short-term, and the benefits of returning to the original area outweigh the costs of staying at the dispersal site, or dispersing further, then migratory behavior is selected for. In any case, an important characteristic of facultative migration is that the total distance of migration is apparently a function of resource availability during the entire outward journey. Facultative migrations range from short-distance movements, for example, downslope in elevation [55, 58] to relatively large-scale movements [31]. Classic examples of the latter include 'irruptive' migrations, where large numbers of individuals of particular species, or groups of species, will appear far outside the normal range.

Facultative migration is more complex than typical dispersal due to the return trip, which is usually delayed until resources on the breeding grounds are renewed. Short-distance facultative migrants, for example, elevational migrants, may be able to assess the favorability of the breeding areas more or less directly and return accordingly. Migrants traveling relatively long distances would find it difficult to accurately assess conditions on remote breeding grounds and therefore, timing of the return trip in these birds may be related to some indirect measure of resource availability, such as increasing daylength, or consistently increasing temperatures. For temperate migrants, photoperiod is the most reliable cue of seasonality [36] and thus, a return trip fundamentally timed by changes in photoperiod, and perhaps fine-tuned by other factors, such as temperature, would offer a selective advantage. Although, I believe, the question of which stimuli are actually used by facultative migrants to time their return to the breeding grounds is entirely open, photoperiod has been repeatedly demonstrated to be of basic importance in the timing of initiation of both vernal and autumnal migration in obligate migrants (see below). This observation, coupled with the fact that even resident birds rely heavily on photoperiod in the temporal organization of their annual cycles (including reproduction), suggests that vernal migration synchronized by photoperiodic cues in facultative migrants may provide an important evolutionary step toward obligate migration.

It appears that, although the initial stimulus to migrate is triggered exogenously, the direction of the *outward* journey may be programmed endogenously (inherited) in many facultative migrants (another important step in the evolution of obligate migratory behavior). This prospect would make sense if resources were more consistently available in one general direction relative to others. Individuals that tended to move in the favorable direction in response to stress would be at a selective advantage relative to individuals that dispersed in other directions.

The persistence of facultative migratory behavior in a population should be a function of high variance in resource availability during the nonreproductive period, either between years, or between members of the population. Thus, for example, if the probability of any particular winter being a good winter is approximately equal to it being a poor winter, it would be advantageous to remain at the breeding grounds unless exogenous factors indicated that staying would be more costly than moving during that particular winter [49]. Underlying this concept is the assumption (and in some cases demonstration [65]) that, when it is possible to do so, remaining on the breeding area is reproductively advantageous over leaving (due to access to better territories, an early start on breeding, etc.). If the costs and benefits for staying vary for different members of the population, for example if subordinates are less likely to obtain resources than dominants [31], then *facultative partial migration* [76] may occur. Decreases in resource availability may be of a nature that individuals which spontaneously leave the breeding grounds in the preprogrammed direction before resources diminish may be at an advantage relative to individuals that attempt to remain in the area (post-breeding dispersal may be an evolutionary precursor to this behavior because it often appears to be undertaken while resources are still generally abundant). For example, if sudden, severe, prolonged crunches in resource availability occur, individuals that had emigrated while food was still plentiful during such years would be at an advantage relative to those that attempted to remain on the breeding grounds and were unable to secure the resources necessary to migrate. If nonreproductive periods that select for this type of behavior are interspersed with more benign periods, *obligate partial migration*, in which the migratory impetus is endogenous, might come about. That is, if years in which obligate migratory behavior is favored over facultative migratory behavior (or residency) are regularly interspersed between years that favor the latter behavior(s), obligate migratory behavior may persist in partial migratory populations (for a detailed discussion of obligate partial migration see Berthold [14, 16]).

There is ample evidence for both facultative partial migration [70] and obligate partial migration [14]. In fact, there is evidence for partial migrant populations comprising both facultative and obligate migrants; central European populations of the European blackbird (*Turdus merula*) [66] are an example. Complex situations involving partial migration may be the reflection of very dynamic evolutionary processes, for example, populations changing from migratory to resident (or vice versa) as appears to be happening in the central European populations of the European blackbird (Berthold, pers. comm.). Or, it might be possible that such complexes are the result of cycles in resource availability that are too short, or too variable, to allow fixation of resident or particular migratory behaviors. The possibility of variations in aspects of resource availability selecting for different migratory behaviors (i.e., facultative and obligate) in partial migrant populations would be a worthwhile area of research.

If the unsuitability of the breeding area during the nonreproductive period increases enough in frequency and/or severity, then entire populations will begin to migrate annually. If the area the birds need to traverse to reach favorable regions increases in extent (for example, due to long-term climatic changes) selection should favor individuals that move through these regions as quickly and efficiently as possible; i.e., obligate migratory behavior. Contrary to facultative migrants then, obligate migrants generally migrate from the breeding area (and migratory stopover sites) when resource availability is still extremely favorable, at least in the short term[29]. This would seem to be a rather unusual situation, at least in terms of optimal foraging theory. How was this behavior selected for?

Obligate migrants generally leave, and travel across, regions in which in the probability of survival between reproductive efforts is consistently very low[73-75]. They perform these movements while food is still plentiful enough to sustain the high energetic demands of such a journey. Simply put, individuals within this region that had waited for environmental cues to indicate an ('inevitable' seasonal) decrease in resource availability to stimulate further migration may have waited too long to obtain the resources necessary to arrive at more favorable regions. Thus, the behavior of utilizing fat stores and available resources to continue movement in a particular direction was selected over utilizing resources to remain in a given area as long as possible. In addition, there may be other selective pressures to traverse, as rapidly as possible, an area that will be uninhabitable between reproductive seasons; one example is the establishment of territories in the wintering area.

Experiments, primarily with *Sylvia* warblers, have demonstrated that the fundamental stimulus for the timing, distance and direction of obligate migration is endogenous[13,15,36]. The migratory program is organized within the framework of an endogenous, circannual rhythm that is entrained to the natural year by annual cycles in photoperiod[36]. Hand-raised birds that have access to unlimited food and are held under constant conditions display spontaneous migratory activity (Zugunruhe). Zugunruhe is oriented in a seasonally appropriate direction during both outward and return migratory periods, and temporal patterns (e.g., initiation in autumn and spring and duration in autumn) correlate significantly with relevant aspects of migratory behavior in freeliving conspecifics[13,15,16,36]. Furthermore, these elements of migratory behavior have been shown to be highly heritable[15-17].

I have attempted to outline, theoretically, how long-distance obligate migration might be an evolutionary extension of facultative migration and dispersal. The basic aspects of these behavioral 'links' have, for the most part, been demonstrated in nature, and/or experimentally, utilizing a species-level, or population-level approach[74]. Of further evolutionary interest is the observation that characteristics of facultative migratory behavior have been found in several species of obligate migrants[20,37,39,40,47,71-77]. In these birds, the relative importance of ecological and endogenous stimuli in releasing overt migratory behavior appears to change with time and distance of the autumnal migration. More specifically, the fundamental stimulus for migration changes from primarily endogenous (the 'obligate phase') to primarily environmental (the 'facultative phase')[39,56,71-77]. Theoretically, the obligate phase takes birds from, and across, regions where the probability of overwinter survival has been consistently low for generations (see above). The distance and duration of the obligate phase should be a function of the probability of overwinter survival along the migratory route[73-75]. As this probability increases, the birds switch to a facultative mode in an attempt to track variable resource availability (between years) along the migratory route and minimize migratory distance in any given year.

Based on several field[19,20] and experimental studies[19,37,39,56] it appears that in some species the change from an obligate migratory phase to a facultative migratory phase involves the dropping of a single decission rule that is superimposed over basic facultative migratory rules: migration from areas with favorable resource availability. The results of these studies suggest that during the obligate phase the impetus to migrate is 1) expressed when migrants are in an energetic state favorable for meeting the metabolic demands of migration and conditions (e.g., climatic conditions) are appropriate for migration; 2) expressed, or enhanced, when birds are confronted with poor prospects for maintaining or improving energy budgets; and 3) inhibited when migrants are in a poor energetic state, but wind up in an area favorable for gaining weight – and, upon doing so, the birds return to condition (1) above. The facultative mode is expressed when condition (1) is somehow switched off with time and distance of migration while decision rules (2) and (3) remain operational. Recent experiments, however, on blackcaps (Terrill and Berthold, in prep.) indicate that early in the autumn migration (the obligate phase), whether the birds show normal, increased, or decreased migratory activity in response to food deprivation depends on several factors such as severity of food deprivation, time of day food is available, and experience. Dark-eyed juncos have failed to show evidence of condition (2) during the obligate phase (Holberton, unpublished data). Although much work is still needed in this area, it appears that the relative roles of obligate and facultative migratory behavior probably vary greatly between populations and species depending on the distance of migration[13], stability of resource base[73] and other factors.

In closing, I would like to suggest, as have others[26,58,59] that intratropical movements may represent a productive testing ground for further research concerning basic regulation and evolutionary aspects of migratory behavior. Although we know relatively little of intratropical movements by tropical species or wintering migrants, it is becoming apparent that much more movement than was previously thought to be the case is occurring[26,59]. These movements span the spectrum from highly irregular to very predictable[26]. Of particular interest is the observation that at least some of these movements are not only highly predictable with respect to timing and direction, but are nocturnal as well, at least in Africa[26] (as far as I know, no comparable data exist from other major tropical regions). Thus, it would be of interest to examine, for example, to what degree these movements are environmentally regulated versus endogenously programmed (inherited) for timing, direction, and distance, and how these aspects relate to spatial and temporal characteristics of resource availability and perhaps to taxonomic groupings. Finally, it would be very interesting, from an evolutionary perspective, to discover what orientation cues are used for the various levels of movement.

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1 Able, K. P., Mechanisms of orientation, navigation, and homing, in: Animal Migration, Orientation, and Navigation, pp. 283–373. Ed. S. A. Gauthreaux Jr. Academic Press, New York 1980.
2 Able, K. P., Skylight polarization patterns at dusk influence the migratory orientation of birds. Nature *299* (1982) 550–551.
3 Able, K. P., Skylight polarization patterns and the orientation of migratory birds. J. exp. Biol *141* (1989) 241–256.
4 Able, K. P., Common themes and variations in animal orientation systems. Am. Zool., in press.
5 Able, K. P., and Bingman, V. P., The development of orientation and navigation behavior in birds. Q. Rev. Biol. *62* (1987) 1–29.
6 Able, K. P., and Bingman, V. P., The development of migratory orientation, in: Acta XIX Congr. int. Ornith., vol. 2, pp. 1932–1940. Ed. H. Quellet. University of Ottawa Press, Canada 1988.
7 Able, K. P., Gergits, W. F., Cherry, J. D., and Terrill, S. B., Homing behavior of wood thrushes (*Hylocichla mustelina*). A radio tracking study. Behav. Ecol. Sociobiol. *15* (1984) 39–43.
8 Adler, H. E., Ontogeny and phylogeny of orientation, in: Development and Evolution of Behavior, Essays in Memory of T. C. Schneirla, pp. 303–336. Eds L. R. Aroson et al. Freeman, San Francisco 1970.
9 Baker, R. R., The Evolutionary Ecology of Animal Migration. Hodder and Stoughton, London 1978.
10 Baker, R. R., Bird Navigation, the Solution of a Mystery? Holmes and Meier, New York 1984.
11 Beason, R. B., and Nichols, J. E., Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. Nature *309* (1984) 151–153.
12 Bellrose, F. C., Possible steps in the evolutionary development of bird navigation, in: Animal Orientation and Navigation, pp. 223–258. Eds S. A. Galler et al. NASA SP-262. U.S. Govt Print. Off., Washington D.C. 1972.
13 Berthold, P., Migration: control and metabolic physiology, in: Avian Biology, vol. V, pp. 77–128. Eds D. S. Farner and J. R. King. Academic Press, New York 1975.
14 Berthold, P., The control of partial migration in birds: a review. Ring *10* (1984) 253–265.
15 Berthold, P., The control of migration in European warblers, in: Acta XIX Congr. int. Ornith., vol. I, pp. 216–249. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.
16 Berthold, P., Evolutionary aspects of migratory behavior in European warblers. J. evol. Biol. *1* (1988) 195–209.
17 Berthold, P., and Querner, U., Genetic basis of migratory behavior in European warblers. Science *212* (1981) 77–79.
18 Berthold, P., and Terrill, S. B., Migratory behavior and population growth of Blackcaps wintering in Britain and Ireland: some hypotheses. Ringing Migration *9* (1988) 153–159.
19 Biebach, H., Sahara stopover in migratory flycatchers: fat and food affect the time program. Experientia *41* (1985) 695–697.
20 Biebach, H., Friedrich, W., and Heine, G., Interaction of bodymass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. Oecologia *69* (1986) 370–379.
21 Bingman, V. P., The avian hippocampus: its role in the neural organization of the spatial behavior of homing pigeons, in: Acta XIX Congr. int. Ornith., vol. II, pp. 2073–2082. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.
22 Bingman, V. P., Able, K. P., and Kerlinger, P., Wind drift, compensation, and the use of landmarks by nocturnal bird migrants. Anim. Behav. *30* (1982) 49–53.
23 Brown, J. L., The Evolution of Behavior. W. W. Norton and Co., New York 1975.
24 Cox, G. W., The role of competition in the evolution of bird migration. Evolution *22* (1978) 180–192.
25 Cox, G. W., The evolution of avian migration systems between temperate and tropical regions of the New World. Am. Nat. *126* (1985) 451–474.
26 Curry-Lindahl, K., Bird Migration in Africa. Academic Press, London 1981.
27 Dingle, H., Ecology and evolution of migration, in: Animal Migration, Orientation, and Navigation, pp. 2–101. Ed. S. A. Gauthreaux Jr. Academic Press, New York 1980.
28 Emlen, S. T., Migration: orientation and navigation, in: Avian Biology, vol. V, pp. 129–219. Eds D. S. Farner and J. R. King. Academic Press, New York 1975.
29 Farner, D. S., The annual stimulus for migration: experimental and physiologic aspects, in: Recent Studies in Avian Biology, pp. 198–237. Ed. A. Wolfson. University of Illinois Press, Urbana 1955.
30 Gauthreaux, S. A. Jr, Priorities in bird migration studies. Auk *96* (1979) 813–815.
31 Gauthreaux, S. A. Jr, The ecology and evolution of avian migration systems, in: Avian Biology, vol. VI, pp. 93–168. Eds D. S. Farner, J. R. King and K. C. Parkes. Academic Press, New York.
32 Gould, J. L., The locale map of honey bees: do insects have cognitive maps? Science *232* (1986) 861–863.
33 Grant, V., Organismic Evolution. W. H. Freeman and Co., San Francisco 1977.
34 Greenwood, P. J., Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. *28* (1980) 1140–1162.
35 Griffin, D. R., Bird navigation, in: Recent Studies in Avian Biology, pp. 154–197. Ed. A. Wolfson. University of Illinois Press, Urbana 1955.
36 Gwinner, E., Circannual rhythms in the control of avian migrations. Adv. Study Behav. *16* (1986) 191–228.
37 Gwinner, E., Biebach, H., and von Kries, I., Food availability affects migratory restlessness in caged garden warblers (*Sylvia borin*). Naturwissenschaften *72* (1985) 51.
38 Gwinner, E., and Czeschlik, D., On the significance of spring migratory restlessness in caged birds. Oikos *30* (1978) 364–372.
39 Gwinner, E., Schwabl, H., and Schwabl-Benzinger, I., Effects of food-deprivation on migratory restlessness and diurnal activity in the garden warbler (*Sylvia borin*). Oecologia, in press.
40 Haila, Y., Tiainen, J., Vespsalainen, K., Delayed autumn migration as an adaptive strategy of birds in northern Europe: evidence from Finland. Ornis fenn. *63* (1986) 1–9.
41 Jander, R., Ecological aspects of spatial orientation. A. Rev. ecol. Syst. *6* (1975) 177–188.
42 Kamil, A. C., and Balda, R. P., Spatial memory in Clark's nutcrackers (*Nucifraga columbiana*), in: Acta XIX Congr. int. Ornith., vol. II, pp. 2100–2106. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.
43 Keeton, W. T., The orientational and navigational basis of homing in birds. Adv. Study Behav. *5* (1940) 47–132.
44 Kerlinger, P., and Moore, F. R., Atmospheric structure and avian migration, in: Current Ornithology, vol. 6, pp. 109–142. Ed. D. M. Power. Plenum Press, New York 1989.
45 Ketterson, E. D., and Nolan, V. Jr, Intraspecific variation in avian migration: evolutionary and regulatory aspects, in: Migration: Mechanisms and Adaptive Significance. Contributions in Marine Science, suppl. vol. 27, pp. 553–579. University of Texas Press, Marine Science Institute, Port Aransas, Texas 1985.
46 Ketterson, E. D., and Nolan, V. Jr, Site-attachment and site-fidelity: experimental evidence from the field and analogies from neurobiology in: Bird Migration: Physiology and Ecophysiology. Ed. E. Gwinner. Springer-Verlag, Berlin, in press.
47 Lack, P., The movements of Palaearctic landbird migrants in Tsavo East National Park, Kenya. J. Anim. Ecol. *52* (1983) 513–524.
48 Lowenstam, H. A., and Kirschvink, J. L., Iron biomineralization: a geobiological perspective, in: Magnetite Biomineralization and Magnetoreception in Organisms, pp. 3–16. Eds J. L. Kirschvink, D. S. Jones and B. J. MacFadden. Plenum Press, New York 1985.

49 Lundberg, P., Partial bird migration and evolutionarily stable strategies. J. theor. Biol. *125* (1987) 351–360.

50 Moore, F. R., Sunset and the orientation behavior of migrating birds. Biol. Rev. *62* (1987) 65–86.

51 Moore, F. R., and Osadchuk, T. E., Spatial memory in a passerine migrant, in: Avian Navigation, pp. 319–325. Eds. F. Papi and H. G. Wallraff. Springer-Verlag, Berlin 1982.

52 Moore, F. R., and Phillips, J. B., Sunset, skylight polarization and the migratory orientation of yellow-rumped warblers, *Dendroica coronata*. Anim. Behav. *36* (1988) 1770–1778.

53 Moreau, R. E., The Palaearctic-African Bird Migration Systems. Academic Press, London 1972.

54 Nolan, V. Jr, Ketterson, E. D., and Wolf, L., Long-distance homing by nonmigratory dark-eyed juncos. Condor *88* (1986) 539–542.

55 Orr, R. T., Animals in Migration. MacMillan Co., New York 1970.

56 Perdeck, A. C., An experiment on the ending of autumn migration in starlings. Ardea *52* (1964) 133–139.

57 Phillips, J. B., Two magnetoreception pathways in a migratory salamander. Science *233* (1986) 765–767.

58 Ramos, M. A., Seasonal movements of bird populations at a neotropical study site in southern Veracruz, Mexico. Unpublished Ph.D. dissertation, University of Minnesota 1983.

59 Ramos, M. A., Eco-evolutionary aspects of bird movements in the northern Neotropical region, in: Acta XIX Congr. int. Ornith., vol. I, 251–293. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

60 Richardson, W. J., Timing and amount of bird migration in relation to weather: a review. Oikos *30* (1978) 224–272.

61 Roberts, W. A., Foraging and spatial memory in pigeons, in: Acta XIX Congr. int. Ornith., vol. II, 2083–2093. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

62 Sauer, E. G. F., Die Sternorientierung nächtlich ziehender Grasmücken (*Sylvia atricapilla, borin* und *curruca*). Z. Tierpsychol. *14* (1957) 29–70.

63 Schlichte, H.-J., Untersuchungen über die Bedeutung optischer Parameter für das Heimkehrverhalten der Brieftauben. Z. Tierpsychol. *32* (1973) 257–280.

64 Schone, H., Spatial Orientation. Princeton University Press, Princeton, New Jersey 1984.

65 Schwabl, H., Ausprägung und Bedeutung des Teilzugverhaltens einer südwestdeutschen Population der Amsel *Turdus merula*. J. Orn. *124* (1983) 101–116.

66 Schwabl, H., and Silverin, B., Control of partial migration and autumnal behavior, in: Bird Migration: Physiology and Ecophysiology. Ed. E. Gwinner. Springer-Verlag, Berlin, in press.

67 Sherry, D. F., Food storage in the Paridae. Wilson Bull. *101* (1989) 289–304.

68 Sherry, D. F., and Balda, R. P., Introduction to 'Spatial memory in birds', in: Acta XIX Congr. int. Ornith., vol. II, pp. 1066–2068. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

69 Shettleworth, S. J., and Krebs, J. R., Spatial memory in food-storing *Parus* species, in: Acta XIX Congr. int. Ornith., vol. II, pp. 2094–2099. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

70 Smith, H. G., and Nilson, J.-A., Intraspecific variation in migratory pattern of a partial migrant, the blue tit (*Parus caeruleus*): and evaluation of different hypotheses. Auk *104* (1987) 109–115.

71 Terrill, S. B., Social dominance and migratory restlessness in the dark-eyed junco (*Junco hyemalis*). Behav. Ecol. Sociobiol. *21* (1987) 1–11.

72 Terrill, S. B., The relative importance of ecological factors in bird migration, in: Acta XIX Congr. int. Ornith., vol. II, pp. 2180–2190. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

73 Terrill, S. B., Food availability, migratory behavior, and population dynamics of terrestrial birds during the nonreproductive season, in: Food Exploitation by Terrestrial Birds. Studies in Avian Biology, Cooper Ornithological Society, in press.

74 Terrill, S. B., The regulation of migratory behavior: interactions between exogenous and endogenous factors. J. Orn., in press.

75 Terrill, S. B., Ecophysiological aspects of movements by migrants in the wintering grounds, in: Bird Migration: Physiology and Ecophysiology. Ed. E. Gwinner. Springer-Verlag, Berlin, in press.

76 Terrill, S. B., and Able, K. P., Bird migration terminology. Auk *105* (1988) 205–206.

77 Terrill, S. B., and Ohmart, R. D., Facultative extension of fall migration by yellow-rumped warblers (*Dendroica coronata*). Auk *101* (1984) 427–438.

78 Visalberghi, E., Foa, A., Baldaccini, N. E., and Alleva, E., New experiments on the homing ability of the rock pigeon. Monitore zool. ital. *12* (1978) 199–209.

79 Wallcot, B., The cellular localization of particulate iron, in: Magnetite Biomineralization and Magnetoreception in Organisms, pp. 183–196. Eds J. L. Kirschvink, D. S. Jones and B. J. MacFadden. Plenum Press, New York 1985.

80 Wallraff, H. G., Über das Heimfindevermögen von Brieftauben mit durchtrennten Bogengängen. Z. vergl. Physiol. *50* (1965) 313–330.

81 Wallraff, H. G., Das Navigationssystem der Vögel. Ein theoretischer Beitrag zur Analyse ungeklärter Orientierungsleistungen. Oldenbourg, München 1974.

82 Welty, C. J., The Life of Birds. W. B. Sanders Co., Philadelphia, PA. 1975.

83 Wilke, D. M., Delayed matching of key location: a useful paradigm for the study of short-term spatial memory in birds, in: Acta XIX Congr. int. Ornith., vol. II, pp. 2069–2074. Ed. H. Ouellet. University of Ottawa Press, Canada 1988.

84 Wiltschko, W., and Balda, R. P., Sun compass orientation in seed-caching scrub jays (*Aphelocoma coerulescens*). J. comp. Physiol. A *164* (1989) 717–721.

85 Wiltschko, W., and Wiltschko, R., A theoretical model for migratory orientation and homing in birds. Oikos *30* (1978) 177–187.

86 Wiltschko, W., and Wiltschko, R., Magnetic orientation in birds, in: Current Ornithology, vol. 5, pp. 67–121. Ed. R. F. Johnston. Plenum Press, New York 1988.

87 Zoeger, J., Dunn, J. R., and Fuller, M., Magnetic material in the head of the common pacific dolphin. Science *213* (1981) 892–894.

0014-4754/90/040395-10$1.50 + 0.20/0