

Understanding the Migratory Orientation Program of Birds: Extending Laboratory Studies to Study Free-Flying Migrants in a Natural Setting

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From the symposium "Integrative Migration Biology" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2010, at Seattle, Washington.

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Synopsis For many years, orientation in migratory birds has primarily been studied in the laboratory. Although a laboratory-based setting enables greater control over environmental cues, the laboratory-based findings must be confirmed in the wild in free-flying birds to be able to fully understand how birds orient during migration. Despite the difficulties associated with following free-flying birds over long distances, a number of possibilities currently exist for tracking the long distance, sometimes even globe-spanning, journeys undertaken by migrating birds. Birds fitted with radio transmitters can either be located from the ground or from aircraft (conventional tracking), or from space. Alternatively, positional information obtained by onboard equipment (e.g., GPS units) can be transmitted to receivers in space. Use of these tracking methods has provided a wealth of information on migratory behaviors that are otherwise very difficult to study. Here, we focus on the progress in understanding certain components of the migration-orientation system. Comparably exciting results can be expected in the future from tracking free-flying migrants in the wild. Use of orientation cues has been studied in migrating raptors (satellite telemetry) and thrushes (conventional telemetry), highlighting that findings in the natural setting may not always be as expected on the basis of cage-experiments. Furthermore, field tracking methods combined with experimental approaches have finally allowed for an extension of the paradigmatic displacement experiments performed by Perdeck in 1958 on the short-distance, social migrant, the starling, to long-distance migrating storks and long-distance, non-socially migrating passerines. Results from these studies provide fundamental insights into the nature of the migratory orientation system that enables experienced birds to navigate and guide inexperienced, young birds to their species-specific winter grounds.

Introduction

The migration routes of birds span the entire globe with the typical movement, at least for terrestrial species, from higher to lower latitudes and avoiding hostile areas such as deserts or seas, but several alternative migration patterns exist. Nevertheless, the ability to orient is a central part of the migratory strategy and the migratory orientation program is considered to be very important for the survival of individual birds and to have a strong impact on the

evolution of migration routes (Alerstam and Hedenström 1998; Alerstam et al. 2003).

The easiest way to perform migration is probably to learn from experienced conspecifics. Such a strategy is well documented for several species, e.g., geese (Sterbetz and Szijj 1968; Essen 1982) and storks (Schüz 1951). However, in many species both long and short distances are presumably travelled alone at night (Larkin 1982; Zuur 1984), and if true, these birds cannot follow conspecifics easily. The most

obvious example is the cuckoo *Cuculus canurus*, in which the parents leave long before the young cuckoo has left the nest of its foster parents. Nevertheless, even young cuckoos manage to perform migrations to wintering areas in sub-Saharan Africa, proving the innate nature of the migration program (Sutherland 1988). True navigation has been shown to occur in experienced birds of many species, e.g., in homing pigeons (see e.g., Wallraff 2000; Wiltschko and Wiltschko 2000) and albatrosses over thousands of kilometers (Kenyon and Rice 1958) and also in long-distance migrants with high rates of return to specific breeding and wintering sites. In some species, return rates suggested that almost all individuals returned (references in Newton 2008) requiring returning individuals to be able to precisely pin-point their goal.

According to Wallraff (1991), there are only two possible hypotheses explaining how the migration routes can be followed without guidance from other birds: birds are either programmed to (1) fly in a specific direction or (2) to reach a specific geographic location. In each case, controlling the orientation requires three conditions to be met: (1) suitable physical structures, (2) ability to sense these structures by the bird, and (3) strategies enabling the bird to make adequate use of the signals. Furthermore, he lists five possible mechanisms that could potentially be used by a migrant to terminate its' migration: recognizing that it has reached a certain (1) geographic location or (2) habitat, after a certain (3) distance, (4) amount of flying, or (5) amount of motivation.

Most of our understanding of the migratory orientation program comes from laboratory-based settings in which the birds' location does not change and the enormous changes encountered along the migration route are extremely hard to simulate. Generally, it is recognized that although we have well-documented knowledge of how the migratory orientation program is expressed in captive birds, we still lack knowledge about how it is carried out in free-flying migrants (Alerstam 1996). Here, we focus on the progress in understanding components of the migration system that has been achieved and can be expected in the future from tracking free-flying migrants in the wild.

Orientation during migration

The migration strategies in birds are commonly (e.g., Berthold 1996) assumed to differ between adult and first-time migrants, in that young birds are guided by a bearing-and-distance program

(called a clock-and-compass strategy), whereas adult birds navigate toward the previously visited wintering grounds or breeding grounds. Some very impressive experiments performed by Perdeck (1958, 1964, 1967) and involving displacement of thousands of birds on migration form the basis of this view, and later work by Mewaldt (1964) confirmed the navigational ability in adult migrants. Perdeck displaced more than 11,000 European starlings from The Netherlands to Switzerland. These included adults that had had previous experience with migration as well as juveniles migrating for the first time. In general, the banded adults were recovered in directions toward their normal wintering grounds whereas the recoveries of first-time migrants indicated that they had continued in their normal direction of migration. Later, Mewaldt (1964) displaced adult white-crowned sparrows caught on their wintering grounds in California to Eastern United States with the rather high rates of return in subsequent winters confirming the navigational ability of experienced migrants.

The orientational responses in displaced first-time migrants have been studied in detail in white storks (Chernetsov et al. 2004), teals (Wolff 1970), sparrowhawks (Drost 1938) and starlings (Perdeck 1958, 1967), all social, daytime migrants with pronounced flocking behavior, and in which juveniles mostly follow adults. In no case was a general navigation toward the wintering area found in these species. The sparrowhawks apparently compensated for the displacement and significant, but much smaller, differences were found also in the displacements of white storks and starlings; these differences, however, could easily be the result of different topographies at the release site.

The orientational response of white storks (Schüz 1949; Wallraff 1977; Katz et al. 1988; Chernetsov et al. 2004) and blue-winged teals (Bellrose 1958) when detained during migration but later released when conspecifics had already migrated, has been investigated in detail. These species are also social migrants with pronounced flocking behavior. However, in teals, juveniles travel independently from adults and at the time of release no wildfowl species, blue-winged or other, with similar routes of migration were present (Bellrose 1958). Generally, white storks did not migrate in the direction of conspecifics, whereas blue-winged teals chose the proper direction.

The innate migratory orientation program of juveniles has a temporal and a spatial component. Most of the remaining work supporting this view has a rather descriptive nature and most is based

on studies of the temporal component of the postulated program in captive birds. Much experimental evidence has accumulated regarding the temporal component of the clock-and-compass program in captive migrants. Many studies have shown that initiation, duration and termination of migratory restlessness (or *Zugunruhe*) is controlled by an endogenous circannual clock (Gwinner 1977, 1996, 2003; Berthold 1996, 2001) that is under direct genetic control (Berthold and Querner 1981; Berthold et al. 1990). Generally, onset, duration and termination of migratory restlessness correspond reasonably well with that observed in wild conspecifics (Berthold 1975, 2001) as do directional changes during the migration period (Gwinner and Wiltschko 1978). Furthermore, Berthold (1973, 1984) suggested a correlation between the amount of migratory restlessness and distance migrated.

Much less work has been conducted on the spatial component of the clock-and-compass orientation system. Kramer (1949) discovered that migratory restlessness was directed in approximately the normal direction of migration. In experiments in which inexperienced migrants were detained until conspecifics had moved south, the released birds (teals and crows) in general migrated in approximately the normal direction of migration (e.g., Rowan 1946, Bellrose 1958).

By manipulating potential cues, migrating birds have been shown to be able to use most of the potential compass cues, including the sun (reviewed by Schmidt-Koenig 1990), stars (reviewed by e.g., Emlen 1975) and the geomagnetic field (reviewed by Wiltschko and Wiltschko 1995). Wehner (2001) suggested that birds use all kinds of available information for guidance. Additionally, Emlen (1970) showed how orientation developed in inexperienced migrants. Young indigo buntings *Passerina cyanea* in their first fall oriented in their normal direction of migration (southward) in reference to stellar rotation (oriented away from the point of rotation). The interaction between magnetic and celestial cues in migrants has been much debated. According to Wiltschko et al. (1998) and Wiltschko and Wiltschko (1999), naïve migrants use celestial rotation as a reference direction and the magnetic field provides the population-specific deviation, whereas experienced migrants use the magnetic field as the dominant cue. However, Able and Able (1996) believed that celestial rotation provides the primary cue for both naïve and experienced migrants and Cochran et al. (2004) also argues that *Catharus* thrushes in spring apparently calibrate their magnetic compass using celestial cues.

Apart from the experiments by Perdeck (1958) and Mewaldt (1964), few experiments have focused on the navigational ability of adults. Interestingly, crows displaced in the spring did not, in general, appear to compensate for displacement (Rüppell 1944).

What we still do not understand

Since the early descriptive work on how migration unfolds in the wild, many laboratory experiments have increased our understanding of the underlying mechanisms of the migratory orientation program. Nevertheless, there are several observations regarding the orientation system in naïve migrants that are difficult to reconcile with our current understanding. Furthermore, how the actual migration is carried out in experienced birds has hardly been explored.

In a few cases, a very high precision of migration has been suggested which is surprising when assuming a clock-and-compass strategy. The very narrow corridor used by migrating marsh warblers in East Africa and the restricted wintering grounds of barred warblers (Thorup and Rabøl 2001) are examples of this. The recently published migration routes of juvenile Eleonora's falcons (Fig. 1a; Gschwend et al. 2008) revealed by satellite-based radio-tracking strongly emphasize this point: despite a complex migration route, all individuals reach the wintering grounds on Madagascar apparently without any guidance from experienced conspecifics.

A re-analysis of 109 published displacement experiments indicated that even juvenile birds were able to detect and react to displacements, including those in which displacement was simulated in a planetarium (Thorup and Rabøl 2007). Additionally, results by Åkesson et al. (2005) indicate that juvenile white-crowned sparrows may be able to correct for displacements. A few other observations cannot easily be accommodated within a clock-and-compass strategy. In marsh warblers, migratory restlessness recorded by Berthold and Leisler (1980) does not terminate in fall when free-flying conspecifics reach their winter grounds (Dowsett-Lemaire and Dowsett 1987; Pearson 1990; but see Berthold 1996). Also the lack of termination of migration by a number of Siberian vagrants turning up in Europe might possibly indicate a lack of some external cue for termination of migration in addition to the migration in the wrong direction away from their winter grounds (Thorup 1998, 2004).

It is still not clear whether an endogenously controlled direction, combined with the simple rules of response to some (more or less well defined)

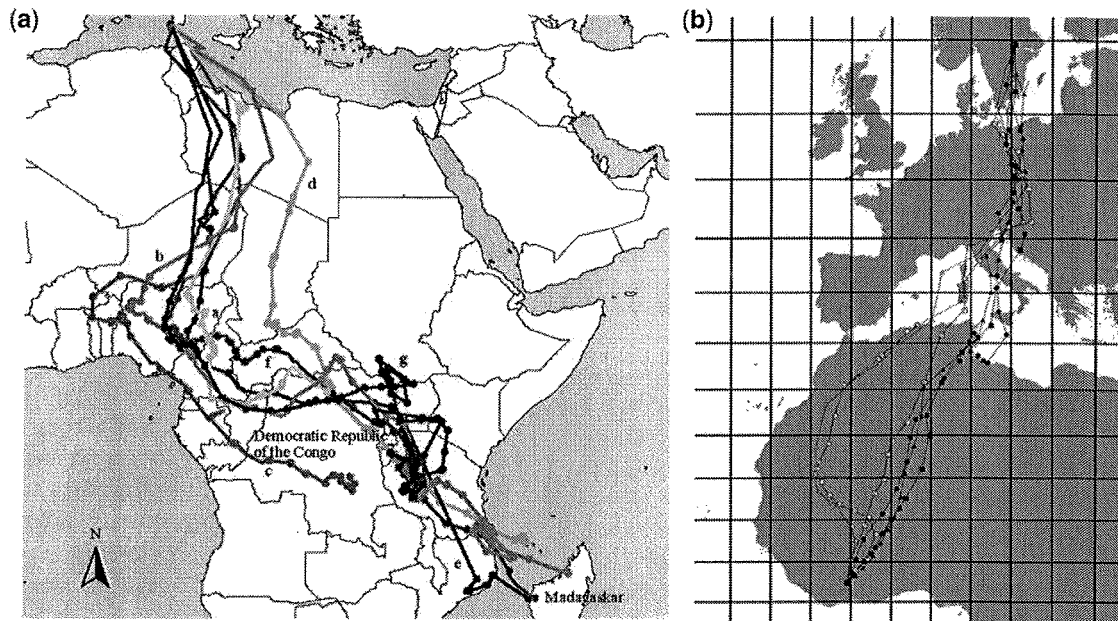


Fig. 1 Migration trajectories of (a) several juvenile Eleonora's falcons (Gschweng et al. 2008) and (b) repeated journeys of one adult osprey (Alerstam et al. 2006). The juvenile falcons all converge toward Madagascar. The adult osprey seems to have several intermediate destinations or goal areas along the route. (a) Reprinted from Gschweng M, Kalko EKV, Querner U, Fiedler W, Berthold P. 2008. All across Africa: highly individual migration routes of Eleonora's falcon. *Proc R Soc Lond B* 275:2887–96 with permission from The Royal Society and (b) Reprinted from Alerstam T, Hake M, Kjellen N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys, *Animal Behaviour* 71:555–66, with permission from Elsevier.

immediate exogenous influences, e.g., features of topography or habitat, and simple responses, e.g., reorientation at dawn when flying over water (Myres 1964), can be sufficient for guidance, or whether more detailed pre-programmed responses to cues along the migration route are needed. Nevertheless, it is difficult, even theoretically, to imagine how such a program could work for extremely precise routes such as observed in marsh warblers (Thorup and Rabøl 2001).

Relationships to external factors may account for some of the observed limitations (Klein 1980). Photoperiod may be useful in correct termination of migration in the fall: short days (as expected at lower latitude) will advance termination of migratory restlessness, whereas long days will delay termination (e.g., Gwinner et al. 1971; Berthold et al. 1972). However, late in the season longer photoperiods cause the reverse reaction (Gwinner 1977), perhaps because the program at this time has advanced to the type of reaction characteristically occurring in spring (Klein 1980); alternatively, the longer photoperiods help speed up birds that have travelled far south into the southern Hemisphere (Gwinner and Helm 2003).

Winds could potentially cause great variation in the distance covered on basis of an endogenous program, although Klein (1980) estimated that the

displacement would usually be less than 10% of the distance covered by long-distance migrants. Numerous radar and field studies during several decades have investigated whether migrants drift or compensate for wind, but the picture is highly complex and partly contradictory, with reported patterns of drift, partial drift, compensation, or even over-compensation (reviewed by Alerstam 1990a; Richardson 1991; Alerstam and Hedenström 1998).

For many diurnal migrants, coastlines and mountain-ranges like the Alps serve as leading-lines (Alerstam 1990b; Meyer et al. 2000). For nocturnal migrants, Bruderer (1982) reported that birds change direction according to both local and regional topography in the area of the Alps, and Fortin et al. (1999) showed that nocturnal migrants not only fly in their endogenously fixed direction, but adjust their directions more or less to their geographical position, the configuration of a coastline in relation to their innate direction, and their motivation to continue across a barrier.

Little is known about the actual termination of migration in free-flying long-distance migrants. Studies have shown that migrants can also perform facultative movements during the winter (Terrill 1990), and suitable habitat in the last part of migration may induce termination (Klein 1980; Perdeck

1964). Any possible reactions to specific topographies or wintering habitat have not been shown.

Pre-programmed responses to external geographic cues might be part of the orientation system. Such responses have been suggested by experiments with hatchling loggerhead sea turtles (Lohmann et al. 2001), and there are indications that geomagnetic cues, characteristic of certain latitudes or regions, affect the orientation (Beck and Wiltschko 1988) or the deposition of fuel (Fransson et al. 2001; Kullberg et al. 2003) of juvenile birds on their first migratory journey.

Very little information exists regarding the navigational system responsible for guiding experienced birds on migration. Navigation toward a known goal requires at least two coordinates. While detecting latitude is considered a relatively simple task, longitude is more difficult (Gould 2008) but little experimental evidence exists about how either longitude or latitude is determined (Thorup and Holland 2009). Only recently have detailed tracks showing how such migration is carried out been published. The tracks of several adult hobbies converged in Central Africa after large differences in routes from Sweden (Strandberg et al. 2009) and the repeated journey of ospreys suggest that adult, long-distance migrants may have several intended destinations along the route (Fig. 1b; Alerstam et al. 2006).

How to solve the migration-orientation enigma: going wild!

To fully understand how migration is carried out in the wild, one needs to be able to integrate the different behaviors observed at different points in time and space. This is necessary in order to confirm that what has been observed in the laboratory is also relevant in the wild and that it may lead to new insights into bird migration that may not have been apparent in the laboratory. Thus, a promising way to solve the mysteries of bird migration is "going wild" as suggested by Wikelski et al. (2007). This task has been pioneered by Bill Cochran (1972) but has only recently become modified and more widely used, thus enabling investigators to follow migrating birds over longer distances (Wikelski et al. 2007).

Such experiments can be natural, based on variation in seasonal or daily behavior or to variation along the migration route, or can involve experimental manipulations in which access to potential cues is manipulated or birds are physically displaced, or both (Table 1). These types of experiments require unbiased tracking, with no spatial bias as would be the result if one had to recapture individuals to

retrieve the data as is the case with light-loggers (called geolocators, Stutchbury et al. 2009). A remarkable result of this "going wild" approach was achieved when we recently confirmed Perdeck's (1958) finding that a long-distance migrant in an experiment in which white-crowned sparrows were transferred from western to eastern North America and showed the expected difference in behavior between adult and juveniles (Thorup et al. 2007).

Several studies have successfully used tracking for investigating reactions to external factors such as displacement by wind and the use of orientation cues. For example, Cochran and Kjos (1985) tracked *Catharus* thrushes in spring in northern United States and found that headings were more or less constant, irrespective of wind direction, indicating that these birds did not compensate for displacement by wind. Thorup et al. (2003b) found that juvenile ospreys and honey buzzards drifted in crosswinds, whereas adult birds compensated for wind.

Studying the use of cues along the whole migration route, Thorup et al. (2006) showed that migration routes of three raptor species fit constant geographic compass routes better than they did constant geomagnetic compass routes, suggesting importance of celestial cues for overall guidance. The interaction between stellar and magnetic cues has been studied in a free-flying setting by Cochran et al. (2004), who found that *Catharus* thrushes, followed by radio telemetry in spring, apparently calibrate their magnetic compass using celestial cues at sunset. Interestingly, however red-eyed vireos *Vireo olivaceus*, northern waterthrushes *Seiurus noveboracensis*, indigo buntings *Passerina cyanea* and grey catbirds *Dumetella carolinensis* followed for only short distances with light sticks apparently calibrated their celestial compass using geomagnetic cues (Sandberg et al. 2000). The discrepancy between these two experiments is striking and warrants further investigation to ascertain whether it is due to differences among species, to availability of cues (e.g., differences in declination, Bingman et al. 2003) or to the experimental setup.

Despite intensive studies of navigation and homing in birds, the navigational system of homing pigeons is still controversial. Given this background it is perhaps not surprising that so few studies have focused on the navigational system in long-distance migratory birds (Thorup and Holland 2009). Nevertheless, Holland et al. (2009) performed experimental manipulation of cues in displaced adult and juvenile catbirds. The most striking result from their study was that adult birds with the olfactory sense impaired migrated in the same direction as

Table 1 Experimental approaches to the study of bird migration in the wild with examples of each use

Type of experiment		Conventional tracking	Satellite tracking
Natural experiments			
Seasonal, daily, or geographic variation	External factors: wind compensation	Thrushes (Cochran and Kjos 1985)	Ospreys and honey buzzards (Thorup et al. 2003b)
	External factors: magnetic orientation	Magnetic cue use (Sandberg et al. 2000; Cochran et al. 2004)	Importance of magnetic compass (Thorup et al. 2003a)
True experiments			
Cue manipulation	Orientation mechanisms	Catbirds (Holland et al. 2009)	
Displacements	Navigational ability	White-crowned Sparrows (Thorup et al. 2007)	White storks (Chernetsov et al. 2004)
Cue manipulation and displacements	Navigation mechanisms	Catbirds (Holland et al. 2009)	Lesser black-backed gulls (Wikelski et al. in preparation)

"Natural experiments" rely on naturally occurring variation, whereas "true experiments" involve deliberate manipulation.

juveniles, southwards, towards Cape May, New Jersey in clear contrast to non-manipulated adults and to adults subjected to a strong magnetic pulse which oriented southwest. No effects of manipulations were seen in juveniles.

The near future: what can be expected?

The size of satellite tags is constantly decreasing and within the next decade we are likely to be able to track globally the migrations of even the smallest songbirds. The most likely candidates for such achievement are tags designed for the current ARGOS system (<http://www.argos-system.org>), but several other initiatives pursue this task, notably the ICARUS initiative (<http://www.icarusinitiative.org>). Despite this development of tags, it is doubtful whether currently available satellites can accomplish the task in the foreseeable future. Furthermore, other technologies, such as cell phones, might prove more promising. When such a global small-animal tracking system is operational, a large-scale collaboration between research groups will hopefully enable a quantum step forward in our understanding of bird migration.

In the meantime, innovative applications of satellite and conventional tracking for doing experimental work are necessary to reach the goal of solving the mysteries of bird migration.

Funding

The Danish National Research Foundation through support to the Center for Macroecology, Evolution and Climate [to K.T. and A.P.T.].

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