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Alerstam, Thomas; Gudmundsson, Gudmundur A.; Green, Martin; Hedenström, Anders

Published in:
Science

DOI:
10.1126/science.291.5502.300

2001

Link to publication

Citation for published version (APA):

Total number of authors: 4

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Migration Along Orthodromic Sun Compass Routes by Arctic Birds
Thomas Alerstam,1* Gudmundur A. Gudmundsson,2 Martin Green,1 Anders Hedenström1

Flight directions of birds migrating at high geographic and magnetic latitudes can be used to test bird orientation by celestial or geomagnetic compass systems under polar conditions. Migration patterns of arctic shorebirds, revealed by tracking radar studies during an icebreaker expedition along the Northwest Passage in 1999, support predicted sun compass trajectories but cannot be reconciled with orientation along either geographic or magnetic loxodromes (rhem lines). Sun compass routes are similar to orthodromes (great circle routes) at high latitudes, showing changing geographic courses as the birds traverse longitudes and their internal clock gets out of phase with local time. These routes bring the shorebirds from high arctic Canada to the east coast of North America, from which they make transoceanic flights to South America. The observations are also consistent with a migration link between Siberia and the Beaufort Sea region by way of sun compass routes across the Arctic Ocean.

How birds use different compass systems based on the sun, stars, and geomagnetic field to orient along their migration routes is not fully understood (1–4). The region at the Northwest Passage where magnetic declination varies markedly close to the Magnetic North Pole provides a natural cue-conflict situation, in the sense that predicted flight trajectories differ in a very distinct way if birds orient by time-independent celestial rotation cues (predicted trajectories lie along geographic loxodromes) (2, 3, 5), the magnetic compass (predicted trajectories lie along magnetic loxodromes) (6), or the sun compass (7). The sun compass is sensitive to the time shift associated with longitudinal displacement (8–10), as long as the internal clock is not reset to local time, which apparently requires some period of stopover (11, 12). Such a natural time shift becomes substantial during migratory flights at polar latitudes, where distances between longitudes are small. At high latitudes, sun compass courses are expected to change by approximately 1° for each degree of longitudinal displacement, with little daily and seasonal variation. This corresponds to the change in sun azimuth associated with the difference in local time between longitudes (8). The course change along a great circle equals sin θ degrees for each degree of longitude intersected, where θ is the latitude (8). This means that at high latitudes, where sin θ approaches unity, sun compass routes constitute close approximations of orthodromes.

We have previously demonstrated regular and widespread east-northeast migration of shorebirds from northern Siberia toward North America across the Arctic Ocean (13). Evaluating predicted trajectories associated with different orientation principles showed orientation along sun compass routes to be most likely, although orientation along magnetic loxodromes could not be ruled out (14). In this study, we test this hypothesis of orientation along sun compass routes by investigating and evaluating the bird migration pattern in high arctic Canada, where there are extreme differences between predicted trajectories based on celestial and geomagnetic cues.

We used a tracking radar placed on board the Canadian Coast Guard icebreaker Louis S. St-Laurent to record the postbreeding bird migration pattern along the Northwest Passage during the period from 29 June to 3 September 1999 (15, 16). Radar observations were carried out when the ship was stationary (17), and more than 10 tracks of migrating birds were recorded at each of 11 sites between Baffin Island (66°W) in the east to Herschel Island (140°W) in the west. We focused on the dominating, high-altitude (mostly 400 to 3000 m above sea level), and broadband migration in easterly and southeasterly directions as recorded at seven of these sites (18). Field observations from the ship and at tundra sites indicated that shorebirds (such as the American golden plover Pluvialis dominica, semipalmated sandpiper Calidris pusilla, white-rumped sandpiper C. fuscicolis, and pectoral sandpiper C. melanotus) made up most of the migrants in this study, traveling in flocks up to about 100 individuals. The above-mentioned species of shorebirds have a wide breeding range in arctic North America, migrating mainly via the Atlantic region of North America to well-defined winter quarters in South America. Hence, the results from the different sites are expected to reflect, to a large extent, this major shorebird migration system in the New World (19).

The mean and scatter of flight directions are shown in Table 1. Track direction refers to the flight direction relative to the ground, as measured by radar, whereas heading direction was calculated by subtracting the wind vector from the birds’ track vector. We primarily refer to observed track directions in our evaluation. The differences between track and heading directions are generally small or modest (Table 1), and our conclusions will be valid irrespective of whether partial wind drift has influenced the track directions on some occasions.

Eastbound migration was massive at all three Beaufort sites (combined in Table 1), with similar mean track directions 100 km north of the coast (105° at 70.5°N, 139.0°W), 27 km north of the coast (87° at 69.8°N, 133.3°W), and only a few kilometers from Herschel Island (104° at 69.6°N, 135.9°W). Combining all eastbound tracks (0° to 180°) from these three sites, 33, 42, and 16% fell in the sectors 60° to 90°, 90° to 120°, and 120° to 150°, respectively. Selected courses within these sectors have been used to illustrate predicted trajectories to and from the Beaufort sites for different orientation principles, whereas corresponding trajectories were calculated on the basis of mean directions for the Wollaston, King William, and Baffin sites (Fig. 1). When evaluating the alternative trajectories, we rejected those that do not take the birds through the Hudson Bay region or the interior and east coast of North America, where these shorebirds are known to pass during autumn migration (19).

Long-distance orientation along constant geographic or magnetic courses can be ruled out, because the geographic and magnetic loxodromes (20) in most cases extend too far north, with some of the latter spiralling toward the Magnetic North Pole (Fig. 1, A through D). Geographic loxodromes from the Beaufort sites toward 60 to 110° (65% of the recorded tracks), as well as the loxodrome along the mean direction at Wollaston Peninsula, can be rejected (Fig. 1, A and B). All magnetic loxodromes except one (Baffin Island) can also be rejected (Fig. 1, C and D). Magnetoclinic orientation (21) is also invalid in many cases (14). It has been recently suggested, on the basis of experiments testing the interactions between celestial and magnetic compasses in birds, that the problem of a changing magnetic declination is solved by recalibration of magnetic orientation by celestial rotation cues at stopover sites along...
the route (2). This is probably not a feasible solution for the shorebirds in this study, because it necessitates very frequent recalibration (east-bound movement between 120° and 90°W at the 70°N parallel is perpendicular to densely spaced declination isolines involving a change in magnetic declination by about 70° per 1000 km of distance, and inclination is very steep, 85° to 88°) and still leads the birds along unrealistic loxodromes (Fig. 1, A and B) in many cases.

Sun compass trajectories (Fig. 1, E and F)
show an excellent agreement with known au-

tumn concentration of shorebirds at, for exam-

ple, James Bay and the east coast of North

America, and with the transatlantic migration to

South America (19, 22–25). These trajectories

also agree with a migration system between

Siberia and North America across the Arctic

Ocean (14). Only for the migration at Baffin

Island do all three orientation principles give

similar trajectories, and no conclusion about the

most likely alternative can be drawn for this site

(Fig. 1, B, D, and F). The fact that sun compass

routes are distance-efficient is illustrated in Fig.

2, showing trajectories on an equidistant azi-

muthal map projection (26). For this evalua-

tion, it is the predicted trajectories at northerly

latitudes that are critical. The birds may change
to other orientation principles and cues for the
transoceanic flights across the Atlantic Ocean
(23–25) and at more southerly latitudes, where
celestial and geomagnetic cues (and wind pat-
terns) are quite different from those at high

latitudes [sun compass trajectories in Figs. 1 and

2 are extended across the Atlantic Ocean and
to more southerly latitudes (8) without

implying any critical evaluation in relation to

alternative possibilities of orientation in these

latter regions].

Orientation along sun compass routes is

facilitated by long nonstop flights (common

among arctic shorebirds), when there is no
time for the birds to reset their internal clock in

phase with local time. To continue along the

same sun compass route after a stopover period

when the birds reset their internal clock to local
time requires that the arrival course at the stop-

over locality be transferred from the sun compass
to another cue system (such as magnetic compass or topography), to be transferred back
to the sun compass as the departure course after

resetting of the internal clock (8).

Although the radar tracks showed that mi-
gration takes place on a broad front, apparently

without responses to landmark features, large-
scale topographical guidance could play some

role in the birds’ flight routes (such as along the

south coast of the Beaufort Sea). However,

there are long passages, across ocean, barrans,
or low-level fog, where the migrants cannot
dependently on topographical orientation. Our analysis
does not exclude the possibility that the birds
use a more complex orientation program than

assumed in the alternative cases above, perhaps

involving changes of preferred compass course

and/or switching between different celestial and

magnetic orientation mechanisms during the

passage across arctic North America. Geneti-
cally programmed changes in migratory direc-
tion have been demonstrated for passerines (1, 5),

and it is also known that migratory birds may

switch between magnetic and celestial ori-

tentation cues (1–3). Even if feasible in princi-

ple, it is difficult to propose a complex orien-
tation program that accounts for the observed

migration patterns under the special geomag-

etic and environmental conditions at the

Northwest Passage. Furthermore, the orien-
tation from Siberia toward North America across

the Arctic Ocean (14) would require the as-

sumption of an analogous complex system pro-
grammed in relation to quite different geomag-
netic and environmental conditions, which

seems highly unlikely. Also, the long flights

and rapid postbreeding migration from the tun-
dra to temperate staging areas, which are com-

mon features among shorebirds (the passage

across the Arctic Ocean from Siberia to North

America is presumably completed in a single

flight), make a division of the journey into a

series of differently programmed orientation

steps unlikely. Before considering such intricate

solutions, we investigated whether fixed orien-
tation on the basis of any of the birds’ funda-

mental compass mechanisms may suffice to

explain the long-distance orientation and migra-
tion routes at high magnetic and geographic

latitudes.

This analysis supports the hypothesis of

sun compass routes as an explanation for the

long-distance orientation of many tundra shore-
birds between Siberia, arctic North America, and

the east coast of North America, whence

the birds continue by transatlantic flights to-

toward South American winter quarters. An

important feature of this migration system is the

fact that the resulting sun compass routes con-

form closely to distance-saving orthodoxes.

The sun compass has probably provided the

basis for the evolution of the above-mentioned

extraordinary migration system in a region with

an exceptional geomagnetic field. Along routes

where magnetic declination is less variable,
birds may use their interacting compass senses
differently (27, 28). The sun compass has been
demonstrated to be important to Adelie pen-
guins (Pygoscelis adeliae) in Antarctica (9, 10)—another case of polar orientation. The fact

that the arctic shorebirds in this study do not

return in spring along the same routes as used in

autumn [spring migration mostly occurs

through the interior of North America (19)]
testifies to the complexity of the global orien-
tation performance of migrating birds.

References and Notes

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16. The icebreaker route extended from Iqaluit on Baffin

Island (29 June 1999) through Hudson Strait, Foxe Basin, and northward to northern Bathurst Island, where

the ship turned south- and westward, passing south of Victoria Island to Herschel Island at the Beaufort Sea as

the westemmost position (3 to 5 August). The ship then sailed eastward by another route north of Banks Island

via the Magnetic North Pole at Elles Ringnes Island (79°N, 105°W), returning to Iqaluit (3 September)

along the east coast of Baffin Island.

17. A tracking radar (3 cm wavelength, 200 kW peak

power, 0.25/1.0 μs pulse duration, and 1.5° nominal

pencil beam width) was placed on board the CGG

icebreaker Louis St-Laurent (radar antenna 21

meters above sea level) and operated when the ship was stationary in pack ice or open

water, most often 2 to 8 km from the nearest tundra

shores, except at two sites in the Beaufort Sea, 27

and 100 km north of the coast, respectively.

The position of a target was recorded every 2 s by

the radar operated in automatic tracking mode. Radar

data were corrected for the heading, motion, and

leveling of the ship recorded simultaneously with the

radar tracking. Mean track direction, ground speed,

vertical speed, and altitude were calculated for flocks

or individual birds tracked for at least 30 s (mean

tracking time was 160 s) within 10 to 12 km from

the radar. Wind measurements at different altitudes

were obtained within 2 hours of bird track records by

radar tracking of helium-filled balloons. Mean head-

ing direction and airspeed of the birds were calculat-

ed by subtraction of the wind vector from the birds’

track vector. For some tracks, heading directions
could not be calculated because of missing wind data.

18. A grand total of 692 radar tracks of birds was recorded

during 494 hours of radar operation during the journey.

In this analysis, we focused on a well-defined and

intensive east- and southbound migratory passage re-
corded at seven sites, excluding sites with sparse (<10

radar tracks) or widely scattered movements (three

sites at Banks and Melville Islands) or mainly low-

altitude (<200 m) movements over the sea (Arnundsen

Gulf). Included in our analyses are three sites at the

Beaufort Sea with massive easterly migration (279

tracks toward 0° to 180°; 23 tracks toward 180° to 360°

excluded), one site at Wollaston Peninsula (21 tracks

toward 0° to 180°; 4 tracks toward 180° to 360°

excluded), one site at King William Island (18 tracks

Fig. 2. Flight trajectories along sun compass routes extrapolated from the mean Beaufort position (for geographic courses 75°, 90°, 105°, 120°, and 135°) on an equidistant azimuthal projection with the Beaufort position as projection center. This map projection shows ortho-
dromes through the projection center as straight lines (26).
A Ribonucleotide Reductase Homolog of Cytomegalovirus and Endothelial Cell Tropism

Wolfram Brune,1,2* Carine Ménard,2 Jürgen Heesemann,2 Ulrich H. Koszinowski2

Human cytomegalovirus (HCMV) establishes a persistent lifelong infection. Infection of the immunocompetent individual is usually subclinical, but the virus may cause severe and life-threatening disease in transplant patients and people with acquired immunodeficiency syndrome (AIDS). HCMV infects a wide variety of cells and tissues (1). Several studies have implicated HCMV in the genesis of arteriosclerosis, and particularly in rapidly progressing coronary artery disease and endothelialitis in cardiac transplant patients, and in the development of coronary restenosis after angioplasty (2). Migration of vascular smooth muscle cells stimulated by a CMV-encoded chemokine receptor has been proposed to promote vascular destruction by cellular apoptosis. The genomes of HCMV and HCMV laboratory strains have lost the ability to grow on vascular endothelial cells, indicating that the BAC clone retains the capacity to propagate MCMV for vascular endothelial cells.

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1Department of Molecular Biology, Princeton University, Princeton, NJ 08544, USA. 2Gesellschaftzentrum and Max von Pettenkofer-Institut, Ludwig-Maximilians-Universität München, Pettenkoferstrasse 9a, 80336 Munich, Germany.

*To whom correspondence should be addressed. E-mail: wbrune@princeton.edu

of arteries (4). This suggests a mechanism by which a viral inhibitor of apoptosis contributes to vascular disease. Moreover, HCMV-infected endothelial cells circulate in the blood of patients with CMV disease and contribute to viral dissemination (3).

Studies on the interaction of HCMV with vascular tissues could clarify the contribution of HCMV to vascular disease. Unfortunately, the HCMV laboratory strains do not replicate in endothelial cell cultures. Clinical isolates, by contrast, can be propagated in endothelial cells, but this property is lost after virus propagation in fibroblasts (6, 7). Although there is evidence for a genetic basis of cell tropism (6), the gene(s) responsible are difficult to find, owing to the large genome of CMV, the lack of candidate genes, and the difficulty generating mutants of clinical HCMV isolates.

The HCMVs and murine CMVs (MCMVs) share a similar pathobiology and have collinear genomes. In the mouse, endothelial cells are known to play a role in viral dissemination, latency, and vascular disease (8). The genomes of the MCMV and HCMV laboratory strains were recently cloned as infectious bacterial artificial chromosomes (BACs) in Escherichia coli (9, 10), where they can be mutated rapidly particularly with the use of random transposon (Tn) mutagenesis (11). MCMV derived from the BAC clone retains the capacity to propagate on cultured endothelial cells. In this work, we focused on the genetic basis of the tropism of MCMV for vascular endothelial cells.

In the absence of specific candidate genes, we constructed a library of virus mutants randomly mutated at a single position by combining a refined Tn mutagenesis procedure with a phenotypic screening approach. MCMV Tn mutants were generated by a single-step procedure using a Tn derivative, TnMax16, bearing the enhanced green fluorescent protein (GFP) gene (12). To convert mutant genomes into a library of mutant viruses rapidly for phenotypic analysis, we directly transferred BAC DNA from E. coli to mammalian cells. The transfer of small multicopy plasmids can be done using naturally invasive bacteria or E. coli expressing the invasive gene of Yersinia pseudotuberculosis and the listeriolysin O gene of Listeria monocytogenes from the plasmid pGB2Inv-hly (13). We adapted this approach for the transfer of the 240-kb MCMV BAC into fibroblasts (14, 15). A library of 576 E. coli clones, each carrying the MCMV BAC, TnMax16, and pGB2Inv-hly, was deposited in six 96-well microtiter plates. Two microtiter plates of each bacterial culture was used to inoculate NIH-3T3 fibroblasts grown in 96-well tissue culture plates. Viable mutant viruses were easily detected because only MCMV with a Tn forms green fluorescent plaques, whereas wild-type MCMV or nonviable MCMV mutants do not. In this way, we retrieved 199 viable mutants.

Fibroblast and endothelial cells were infected in parallel with individual virus mutants to screen for loss of ability to grow on endothelial cells (16). Viral growth was assessed visually by observation of green fluorescent plaques and by titration. We identified six mutants that did not grow and spread in endothelial cells but did grow well in fibroblasts (Fig. 1). Using BAC DNA extracted from the corresponding E. coli clones we determined the Tn insertion sites by direct sequencing from within the Tn (11). Remarkably, the insertions in all six mutants mapped to two adjacent open reading frames

28 August 2000; accepted 13 November 2000

www.sciencemag.org SCIENCE VOL 291 12 JANUARY 2001

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