J Ornithol (2012) 153:1261–1265
DOI 10.1007/s10336-012-0883-6

SHORT NOTE

Orientation of vagrant birds on the Faroe Islands in the Atlantic Ocean

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Received: 26 October 2011 / Revised: 6 May 2012 / Accepted: 12 July 2012 / Published online: 15 August 2012

Abstract Migratory birds are frequently found far outside their normal range but the phenomenon is poorly understood. We used radio telemetry to track individual migratory flights of several species of songbirds on the Faroe Islands, far west of their normal migration route. Birds with expected easterly and south-easterly migration direction departed westwards out over the Atlantic Ocean, indicating that these birds are actively flying in the "wrong" direction and that their occurrence is not caused by wind drift. This is in contrast to the apparently normal south-westerly to easterly departure directions in birds expected to migrate south or southwest.

Communicated by H. Mouritsen.

Electronic supplementary material The online version of this article (doi:10.1007/s10336-012-0883-6) contains supplementary material, which is available to authorized users.

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Keywords Vagrancy · Migration · Orientation and navigation · Songbirds

Zusammenfassung

Orientierung bei verdrifteten Vögeln auf den Faröer Inseln im Atlantik

Zugvögel sind regelmäßig außerhalb ihres normalen Verbreitungsgebiets zu finden, aber dieses Phänomen ist wenig untersucht. Wir verwendeten Radiotelemetrie, um individuelle Flüge bei verschiedenen Singvogelarten auf den Faröer Inseln zu untersuchen, weit westlich der normalen Zugroute. Vögel mit erwartungsgemäß östlicher und süd-östlicher Zugrichtung flogen westwärts hinaus auf den Atlantik, was darauf hindeutet, dass diese Vögel aktiv in die „falsche"Richtung flogen und nicht vom Wind verdriftet wurden. Dies steht im Kontrast zu der anscheinend normalen süd-westlichen bis östlichen Abflugrichtung bei Vögeln, von denen man annimmt, dass sie nach Süden oder Süd-Westen ziehen.

Introduction

In general, juvenile migrants reach population-specific wintering grounds with surprising precision (Thorup and Rabøl 2001), and perhaps only a small fraction end up as vagrants outside the normal distribution range. Nevertheless, the migratory behaviour of vagrants can be surprisingly stable for long distances and often fitting a reverse (Rabøl 1969, 1976; Richardson 1982) or mirror (Diamond 1982; DeSante 1983) image of their expected orientation.

In principle, we expect vagrancy to occur in all populations as the most extreme cases of natural scatter. The establishment of a new wintering area of blackcaps is assumed to have arisen from this (Berthold et al. 1992; Bearhop et al. 2005). Currently, there is increasing appreciation that extreme events, i.e. the "tail" of the normal distribution, can have disproportional large effects for ecological and evolutionary processes. The underlying causes of vagrancy are, however, poorly understood.

A lack of understanding of the causes of vagrancy is in part because the behaviour of vagrants is inherently difficult to study. Not only does vagrancy only occur in a small fraction of the population, but the small size of most bird species also makes following the behaviours leading to vagrancy very difficult to study (Wikelski et al. 2007). Several terrestrial songbird species occur regularly as vagrants on most islands in the North Atlantic Ocean.

To study the behaviour of vagrant individuals, we deployed small radio transmitters to record the orientation of juvenile passerine vagrants during autumn migration on the Faroe Islands, 600 km off the coast of Norway. We tracked easterly breeding populations with a normal, standard south-easterly orientation and compared these with migrants from Northern Europe with a normal, standard migration direction between southwest and south-southeast (Fig. 1) reported in Thorup et al. (2011). We used recordings of the departure flight orientation of the vagrants to test if birds were consistently migrating in the wrong direction and whether this orientation could have led the birds directly to the Faroe Islands from their breeding grounds.

Materials and methods

We tested the migratory orientation of juvenile vagrant passerine migrants with small radio transmitters during September–October 2009 on the southernmost island in the Faroese archipelago. General methods followed Thorup et al. (2011).

In addition to the migratory flights of eight birds from Northwest Europe reported by Thorup et al. (2011), we tracked the migratory flights of nine individuals of four species of naturally occurring vagrants (see Supplementary Materials and methods). The species are long-distance nocturnal migrants breeding in temperate and subarctic regions of Eurasia and wintering in tropical and subtropics regions of East Africa (two species) and Southeast Asia (two species).

Often, the normal migration directions differ markedly among populations. Based on the assumption that most individuals originate from the breeding grounds closest to the Faroe Islands, the four species had an initial population-specific standard migration direction in autumn to the east of south (SE-group, $N = 9$). For the species reported in Thorup et al. (2011), the standard migration direction in autumn of the nearest breeding population was to the west of south (SW-group, $N = 8$). Lesser whitethroat *Sylvia curruca* is the only species in the SE-group that also breeds in Northwest Europe close to the Faroe Islands. Thus, we also tested the difference between the SE-group and the SW-group with this species excluded.

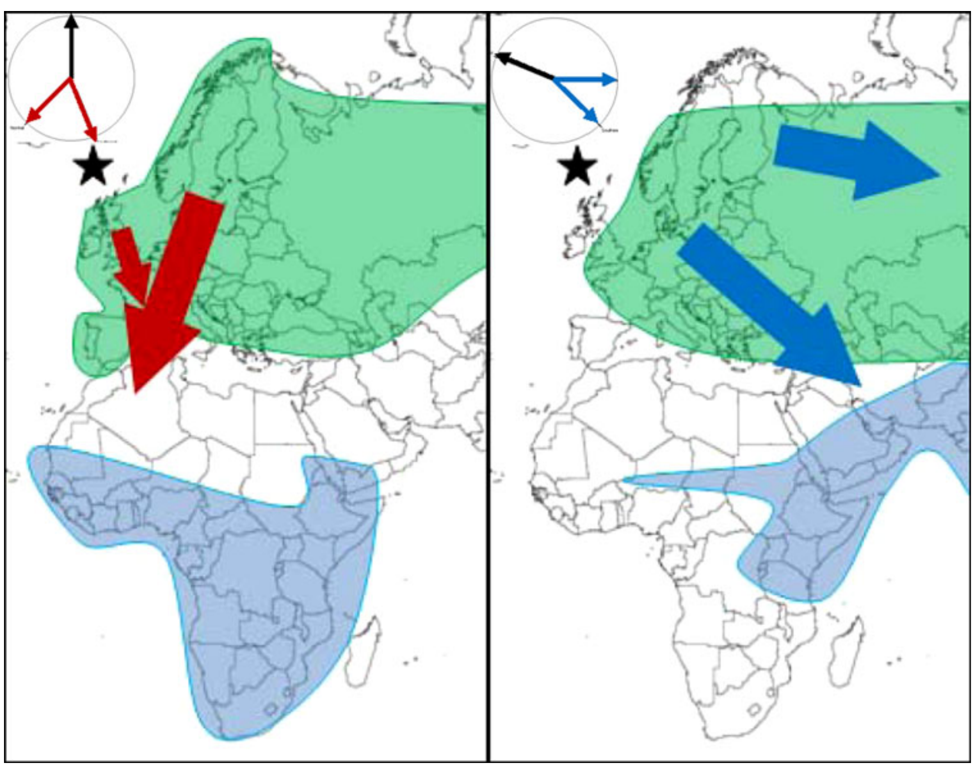

Fig. 1 Distribution and migration directions of species from SW-group (*left*) and SE-group (*right*). Shown are the combined breeding and wintering distributions for the species in each group. Migration directions are shown for the populations breeding nearest to the Faroe Islands. The position of the Faroe Islands is indicated with a *black star*. Breeding grounds are *shaded green*, wintering areas *blue*. *Inset circle* shows possible migration directions for birds on the Faroe Islands: expected normal migration direction is indicated by *red arrows* for SW-group and *blue arrows* for SE-group. *Black arrows* indicate reverse orientation (colour figure online)

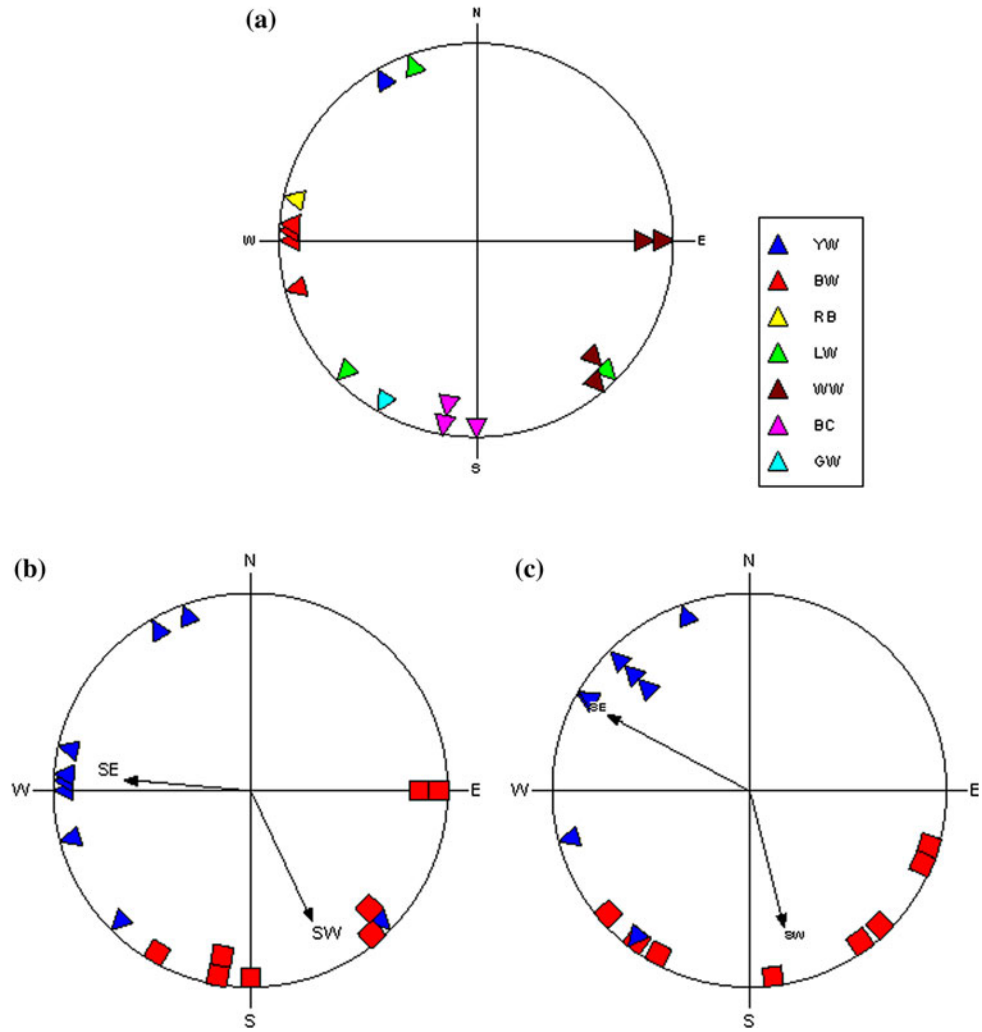

Fig. 2 Migratory orientation at Sumba, the Faroe Islands. **a** Vanishing bearings of all individuals according to species. **b** Difference in vanishing bearings between the SE- (*blue triangles*) and SW- (*red squares*) group. **c** Difference in calculated headings between the SE- (*blue triangles*) and SW- (*red squares*) group. *YW* Yellow-browed warbler *Phylloscopus inornatus* ($n = 1$), *BW* barred warbler *Sylvia nisoria* ($n = 4$), *RB* red-flanked bluetail *Tarsiger cyanurus* ($n = 1$), lesser whitethroat *Sylvia curruca* ($n = 3$), *WW* willow warbler *Phylloscopus trochilus* ($n = 4$), *BC* blackcap *Sylvia atricapilla* ($n = 3$), *GW* garden warbler *Sylvia borin* ($n = 1$). Data on WW, BC and GW are from Thorup et al. (2011) (colour figure online)

Inferring the migratory orientation from the vanishing bearings of free-flying passerine migrants is complicated by the influence of wind drift. The tested vagrants took off in highly variable wind conditions approaching, or even exceeding, their intrinsic flight speed. Overall, wind conditions were not likely to have a profound influence on the migration directions of the SE-group. In contrast, the south-easterly orientation in the SW-group could well have been a result of the generally westerly winds. We calculated headings using an intrinsic flight speed of 10 m/s (Thorup et al. 2011).

Using ORIANA vers. 3, we tested if the orientation of samples could be considered random with the Rayleigh test, and differences in orientation between and among samples were tested with Watson-Williams test (Batschelet 1981) as well as circular–circular correlations (Fisher 1995).

Results

Overall, departures from the Faroe Islands were widely scattered (Fig. 2a). The orientation of the SE-group differed significantly from the SW-group reported in Thorup et al. (2011) (vanishing bearings: $F = 19.65$, $df = 15$, $P = 0.0004$; headings: $F = 30.92$, $df = 14$, $P = 0.00007$; Watson-Williams F tests, Fig. 2b, c) with SE-migrants on average departing toward west ($\alpha = 275°$, $r = 0.644$, $P = 0.019$) and SW-migrants toward south-southeast ($\alpha = 155°$, $r = 0.734$, $P = 0.009$; Rayleigh test). Headings differed only slightly from vanishing bearings (SE-group: $\alpha = 298°$, $r = 0.816$, $P = 0.002$; SW-group: $\alpha = 166°$, $r = 0.714$, $P = 0.012$). Vanishing bearings and headings within the two groups, SE- and SW-migrants, did not differ (SE-group: $F = 0.929$, $df = 15$, $P = 0.35$. SW-group: $F = 0.198$, $df = 14$, $P = 0.663$, WW test).

There was no obvious correlation between vanishing bearings and wind direction (non-significant circular-circular correlations $r = 0.04$ and 0.03 for SW and SE-group, respectively). The variation in orientation within the SE-group was generally low (interval 10°–50°), except for the lesser whitethroat (205°). Excluding this species, the two groups still show very significant differences in orientation. The barred warbler *Sylvia nisoria* made up the largest sample of one species in the SE-group ($N = 4$). This species invariably departed westwards (mean $\alpha = 268°$; interval = [255°, 275°]) in mild winds below their intrinsic flight speed ($U = 5.4$ m/s).

Discussion

The observed free-flying orientations among songbird migrants on the Faroe Islands differed according to presumed standard migratory orientation. Species with expected orientation east of south (SE-group) had a general westward orientation whereas species with orientation around or west of south (SW-group) had a general southerly orientation. The observed grouping of directions according to standard orientation indicates that our initial pooling of several species is well justified.

Lack (1962) concluded that failure to correct for wind drift could not provide a full explanation for the occurrence of long-distance vagrancy and rather that "either their innate headings or their star-compasses were astray". Since then such vagrancy has been explained variously by birds' migration directions being on the edge of the normal variation in inherited migratory direction (Alerstam 1990; Gilroy and Lees 2003), by the influence of external factors such as wind (Baker 1977), or by malfunction of the migratory orientation system (Rabøl 1969; Alerstam 1991). The latter can have very different origins in nocturnal migrants. Malfunction in the sensory apparatus or the cognitive processing of compass cue information could lead to erroneous orientation. Misorientation in nocturnal migrants has also been suggested to arise by abnormal compass cue exposure during early development (Alerstam 1991).

On basis of the observed behaviours, the origin for westward orientation (SE-group) is explained most easily by misorientation whereas the southerly orientation (SW-group) is likely to be caused by wind drift alone because the orientation on average did not show a large-angle deviation from the standard orientation and not in a direction that would guide them to the Faroe Islands. The basis for the movement to the Faroe Islands thus appears to differ fundamentally between the groups. The misorientation in the SE-group seems maladaptive as birds continue out over the Atlantic Ocean where they have almost no chance of survival. The high variation in vanishing bearings for the lesser whitethroat might indicate that occurrences of this species could be caused both by misorientation as in the other species in the SE-group but also by wind drift from closer breeding grounds as in the SW-group.

In an earlier experiment on the Faroe Islands, Rabøl (1985) tested the orientation in cages of similar species but for the SE-group his experiments were inconclusive because of the small sample sizes. In contrast, Thorup (1998) showed that Siberian vagrants on the island of Christiansø in the Baltic in cages oriented towards west-southwest similar to the departure directions of Siberian species on the Faroe Islands.

In general, only long-distance migrating species are likely to occur as vagrants far from the breeding grounds as shown for Siberian species by Pfeifer et al. (2007). Additionally, Thorup (2004) showed that the propensity for long-distance reverse migration in European birds depends on their normal population specific orientation. Species with an easterly orientation (e.g. barred warbler and yellow-browed warbler) occurred more frequently in Northern Europe during autumn than species with a southward orientation. According to our assignment of initial standard orientation, the orientation of the SE-group seems to support these patterns at the behavioural level, and suggests that migrants with a more east-west migration may have trouble separating east from west. The hypothesis that the occurrences are the result of reversed migration caused by an inability to separate east from west would explain not only the occurrence in Northwest Europe of Siberian species but also explain the proposed mirror-image migration occurrences observed in North America (Diamond 1982; DeSante 1983).

Acknowledgements We are grateful to Jens-Kjeld Jensen for catching birds on Nolsoy, and to Dorete Bloch, Aksal Poulsen and several local Faroese for much help during field work on the Faroe Islands. We thank Bill and Jim Cochran for technical help. K.T. was supported by a grant from the Danish Council for Independent Research. This study was carried out in strict accordance with Guidelines to the use of wild birds in research of the Ornithological Council (Fair et al. 2010). Animal work was approved by the Faroese Food and Environmental Agency (J.nr. 2009-00101-43) and the Danish Forest and Nature Agency by permission to the Copenhagen Bird Ringing Centre (J.nr. SN 302–009).

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