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PO Box 117
221 00 Lund
+46 46-222 00 00

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Do Arctic waders use adaptive wind drift?

Martin Green, Thomas Alerstam, Gudmundur A. Gudmundsson, Anders Hedenström and Theunis Piersma

Green, M., Alerstam, T., Gudmundsson, G. A., Hedenström, A. and Piersma, T. 2004. Do Arctic waders use adaptive wind drift? – J. Avian Biol. 35: 305–315.

We analysed five data sets of flight directions of migrating arctic waders in relation to winds, recorded by tracking radar and optical range finder, in order to find out if these birds compensate for wind drift, or allow themselves to be drifted by winds. Our purpose was to investigate whether arctic waders use adaptive wind drift strategies or not. The data sets were collected in Siberia (two sets) and Canada during post-breeding (autumn) migration, and in Mauritania and South Sweden during pre-breeding (spring) migration. Both significant drift and compensation effects were found in three of the data sets, Canada, Mauritania and South Sweden. Almost no compensation was found in birds departing in easterly directions from the Siberian tundra (complete drift), while no drift effect was found in birds departing in westerly directions (complete compensation). There were indications that at least some populations of waders may use an adaptive drift strategy consisting of drift at high altitude and/or in high wind speed combined with compensation at low altitude and/or in lower wind speeds, but support for this idea was rather weak and not consistent. Our results were instead more in accordance with the adaptive drift theory that predicts initial drift during the migratory journey, followed by compensation during later stages as the birds are approaching their destinations. Such a strategy implies that arctic waders, at least adult birds, have the capacity of true navigation. A comparison with earlier studies of migrating arctic waders from different parts of the world show that all results so far may be interpreted in accordance with this general adaptive drift strategy. An element of non-adaptive drift can, however, not be completely ruled out.

M. Green (correspondence), T. Alerstam and A. Hedenström, Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden. E-mail: martin.green@zooekol.lu.se. G. A. Gudmundsson, Icelandic Institute of Natural History, P.O. Box 5320, IS-125 Reykjavik, Iceland. T. Piersma, Department of Marine Ecology, Royal Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands and Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

Many arctic breeding waders fly impressively long distances between their summer and winter quarters. Overall migration distances exceeding 10 000 km are not uncommon (Morrison 1984, Pienkowski and Evans 1984, Piersma 1987). Some species or populations even make single non-stop flights that cover several thousands of km, in some cases both during spring and autumn migration (Morrison 1984, Drent and Piersma 1990, Piersma and Gill 1998, Battley et al. 2000). Conducting such long migrations and non-stop flights requires special adaptations to deal with the costs of endurance flight. Several studies have also shown that these birds have both physiological and behavioural adaptations that allow them to reduce their travel costs (Piersma 1998, Alerstam and Gudmundsson 1999a, Kvist et al. 2001). Arctic waders adjust the size and mass of internal organs and muscles in ways that make them more efficient foragers during fuel deposition, and

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more efficient flyers during episodes of migratory flight (Piersma 1998, Piersma and Lindström 1998, Piersma et al. 1999, Battley et al. 2000, Lindström et al. 2000). They migrate in flock formations (Noer 1979, Piersma et al. 1990a) with the possibility of achieving lower costs of transport due to reductions in drag (Hummel 1983, Weimerskirch et al. 2001), and they predominantly choose to migrate during days and at altitudes with favourable winds to increase their ground speeds and to reduce the cost of transport (Richardson 1979, Gudmundsson 1994, Alerstam and Gudmundsson 1999a, Green and Piersma 2003, Green in press).

In this contribution we analyse whether arctic waders also deal with the problem of wind drift in an adaptive way, thus allowing savings in both time and energy. Whether migrating birds compensate for wind drift or allow themselves to be drifted has been a matter of much discussion (see reviews by Alerstam 1976, Richardson 1990a, Alerstam and Hedenström 1998). Results from field studies have not shown any general unambiguous pattern. Instead behaviour seems to vary greatly between bird species, areas and environmental circumstances. Several ideas about adaptive drift and compensation have been put forward (Williams and Williams 1978, Alerstam 1979a, b, 1981, Stoddard et al. 1983, Williams 1991, Williams and Webb 1996), and some of the results about the response of migrants in relation to wind have been interpreted in the light of these ideas (Alerstam 1985, Williams 1985, Helbig et al. 1986, Hilgerloh 1991, Liechti 1993, Liechti and Bruderer 1995, Zehnder et al. 2002). However, few studies have shown consistent results supporting adaptive drift strategies. Furthermore, the analyses of whether birds drift or not have suffered from analytical inconsistencies where some of the methods used may lead to spurious results (Green and Alerstam 2002). Here we analyse whether arctic waders compensate for wind drift or allow themselves to drift with the wind, and if the latter is true, we evaluate whether they are likely to use adaptive drift strategies or not. We do this by using methods recently demonstrated to produce reliable results (Green and Alerstam 2002).

Adaptive drift, non-adaptive drift and predictions

Birds in migratory flight could either keep their headings (the direction of their body axis) constant in their intended migratory directions and be subjected to wind drift, or they could adjust their headings to compensate for the effect of the wind, i.e. keep the tracks (resulting flight directions over the ground) constant. Which of the two, or any intermediate strategy of partial drift and compensation, that will be adaptive depends on wind patterns, the distance remaining to the goal of migration and the distribution of suitable staging areas. a) If winds remain stable throughout the migratory journey, compensation will always be the most beneficial strategy. Similarly, if specific staging areas have to be visited, compensation will probably also be the best choice, unless the birds have the capacity of true navigation to these staging areas, as the risk of missing vital staging areas will increase when allowing drift. b) In variable winds migrating birds have the possibility to gain both time and energy by allowing drift in certain situations. Alerstam (1979a) proposed that if winds are variable, birds should allow initial drift to increase ground speed and then increase compensation when approaching the destination. This strategy allows energy savings if different crosswinds are encountered along the route. This is also true for long non-stop flights between specific stopover sites if the birds are capable of true navigation. c) Similarly, drift will be beneficial in terms of time and energy if there is a large difference in wind speed between altitude layers. In such circumstances, it will be rewarding to drift at altitudes with high wind speeds (usually higher altitudes) combined with compensation or even overcompensation at altitudes with low wind speeds (usually lower altitudes Alerstam 1979b). d) A third situation when drift is beneficial is when winds from one side are succeeded by winds of similar magnitude from the other side. In such situations it will pay to allow complete drift during the whole flight (Williams and Williams 1978, Alerstam 1981). Such a strategy will work if departures occur under specific synoptic situations. A closely related idea is that birds depart on fixed headings, but do so only in situations when the drift effect is small, i.e. due tailwinds or weak winds (Cochran and Kjos 1985). If migratory flights occur only in such situations, the cumulative effect of drift is small and the birds will thus not face the problem of getting drifted too far away from their intended destinations.

Drift could also occur as a result of constraints in the capacity of birds to compensate, i.e. the birds try to compensate but can not, for one reason or the other, do so to full extent, and become subjected to drift (cf. Alerstam and Pettersson 1976, Green 2001). This has been termed non-adaptive drift. The obvious case would be when wind speed exceeds the birds' airspeed, and thus prevents the birds from maintaining certain track directions. Other cases include flight at high altitude, over open sea or above fog and clouds when the birds do not have proper access to a visual, stationary ground-based reference system that may be required for achieving compensation for wind drift (Alerstam and Pettersson 1976, Alerstam 1990, Richardson 1990a). If the capacity to compensate is something that birds have to learn, e.g. by means of an acquired map (navigation) sense, non-adaptive drift should be more obvious in young inexperienced migrants than in older birds.

From these basic ideas we can formulate different predictions about the behaviour of migrating arctic waders if they use one strategy or the other. a) If the birds are aiming for specific, localised stopover sites at relatively close ranges, our first prediction is that these birds should use a complete compensation strategy at all times to make sure that they do not miss these important sites (cf. Alerstam and Gudmundsson 1999a). A drift strategy would be adaptive only if the birds have the capacity of true navigation to these sites, or if they can use predictable synoptic situations, that will bring the birds to their destinations irrespective of drift. If the flights are rather long and/or the immediate goals more flexible, we can make the following predictions according to the ideas above: b) Birds that just have departed from a staging area should drift while birds close to destinations should compensate (cf. Alerstam 1979a). c) Birds flying in higher wind speeds (usually at high altitude) should allow drift while birds flying in lower wind speeds (usually at lower altitude) should compensate or overcompensate (cf. Alerstam 1979b). d) Birds using specific synoptic situations and departing on fixed headings should drift at all times (cf. Williams and Williams 1978). e) If drift only occurs in very strong winds or in fog, above clouds, over open sea or during periods when juvenile birds dominate, the drift could possibly be attributed to non-adaptive drift, i.e. the birds are for different reasons prevented from detecting the true amount of wind drift and thus from compensating for it.

Methods

Study areas and earlier analyses

The data analysed in this contribution originate from five different data sets of flight trajectories of arctic breeding waders. Three sets have been recorded during

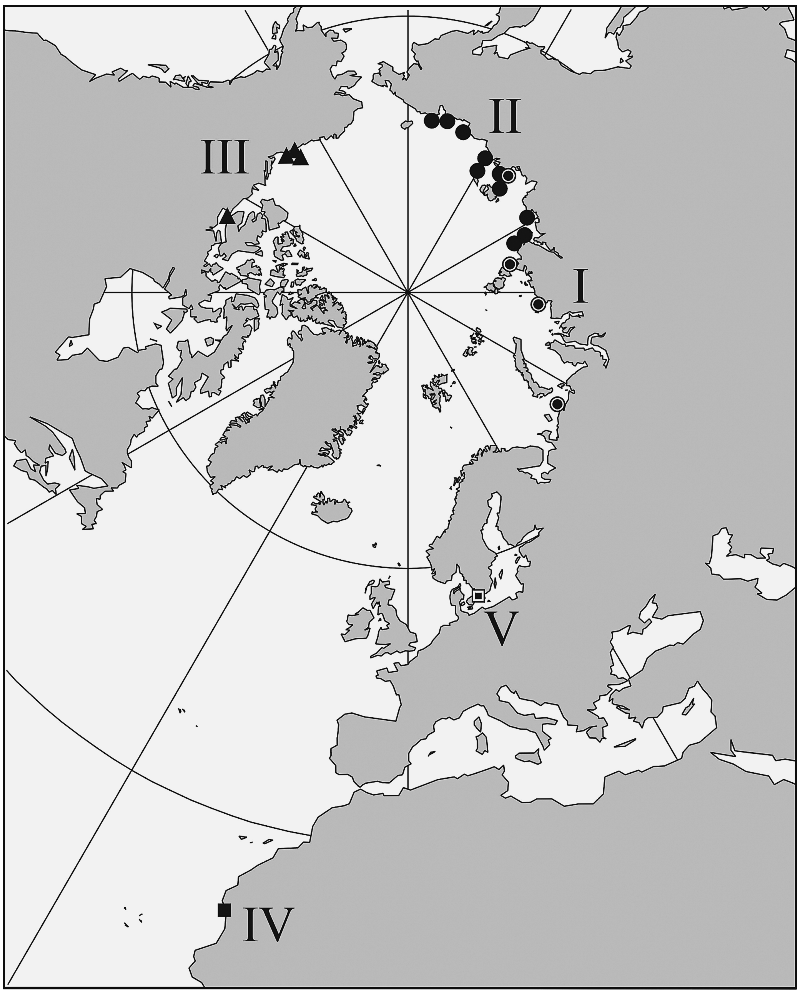

Fig. 1. Map showing the study sites (Azimuthal Equidistance Projection). Sites where westbound migrants in Siberia were tracked are shown with dotted circles (I), sites where eastbound waders were tracked in Siberia are shown with filled circles (II), Canadian sites are shown with filled triangles (III). Baie d'Aouatif, Banc d'Arguin, Mauritania is shown with a filled square (IV) and Lund, South Sweden is shown with a dotted square (V).

post-breeding (autumn) migration and two during pre-breeding (spring) migration. The three autumn data sets were collected in the Arctic, two along the NE Passage in Siberia and one along the NW Passage in Canada (Fig. 1). The two data sets covering spring migration were collected at (a) departure from wintering grounds in Mauritania, West Africa, and (b) relatively close to departure from the last major spring staging area preceding the final flight towards arctic breeding areas, in south Sweden, NW Europe, (Fig. 1). Three of the data sets evaluated here have been previously analysed and published with respect to drift and compensation. These are the data sets from Mauritania and Siberia (Piersma et al. 1990a, Alerstam and Gudmundsson 1999a, b). As the methods used in the earlier analyses have been shown to produce spurious results (Green and Alerstam 2002), we here re-analyse these data sets with robust methods. Previously published results (Piersma et al. 1990a, Alerstam and Gudmundsson 1999a, b) are hence replaced by the ones presented in this contribution.

Data collection

Flight paths of post-breeding migrating birds were recorded with a tracking radar placed on the Russian ice-going expedition vessel "Akademik Fedorov" at 15 sites along the coast of the Arctic Ocean in northern Siberia, the NE Passage, in July and August 1994 (Alerstam and Gudmundsson 1999a) during the Swedish-Russian "Tundra Ecology" expedition. In the same way flight paths of post-breeding migrants were recorded with a tracking radar placed on the Canadian Coast Guard Icebreaker "Louis S. St-Laurent" at 23 sites in arctic Canada, along the NW Passage, in July and August 1999 during the expedition "Tundra Northwest 1999" (Gudmundsson et al. 2002). For details about overall patterns of migration concerning flight directions, speeds, altitudes and species composition, as well as details about radar operation, data collection and data handling from these two studies see Alerstam and Gudmundsson (1999a) and Gudmundsson et al. (2002).

Flight paths of birds departing on spring migration from West Africa were recorded at Baie d'Aouatif, Banc d'Arguin, Mauritania (19°53′N, 16°17′W, Fig. 1), with an optical range-finder in April and May 1988. For details about the Mauritania study see Piersma et al. (1990a, 1997). Tracks of spring migrating flocks of waders were recorded at Lund, south Sweden (55°42′N, 13°12′E Fig. 1), using a tracking radar on the roof of the Ecology Building, Lund University, in late May-early June 1998–2001. A detailed summary of the Lund study and the methods used there is given in Green (in press).

Radars and optical range finders measure track directions and groundspeeds (the resulting flight directions and flight speeds over the ground, the flight vector relative the ground). In order to calculate airspeeds (the birds' flight speeds relative the surrounding air) and headings (the directions of the birds' body axis) of migrating birds, helium-filled weather balloons with aluminium foil reflectors were released and tracked by the radars within 2 h of each bird track record to measure wind direction and speed at different altitudes (Siberia, Canada, Sweden). In Mauritania weather balloons were tracked with a theodolite (details in Piersma et al. 1990a). Airspeeds and headings were then calculated by vector subtraction of horizontal wind velocities, at the altitudes where the birds were flying, from the birds' flight vectors relative the ground.

From the data collected in Siberia and Canada (Alerstam and Gudmundsson 1999a, Gudmundsson et al. 2002) three main samples of migrating birds were extracted, two from Siberia and one from Canada, to make the data within each analysis as homogenous as possible regarding species (population) composition and thus the birds' intended flight directions, a prerequisite for any meaningful analysis of drift or compensation. As a first step, the bird track records from Siberia were divided into two groups: (a) birds flying in easterly directions (both track and heading between 0 and 180°) and (b) birds flying in westerly directions (both track and heading between 180 and 360°). Secondly, we included data only from sites with more than 10 bird track records, for which wind data were available, per direction category.

The group of easterly migrants consisted of 628 bird track records from ten localities in eastern Siberia, spread out from eastern Taymyr peninsula (113.5°E) eastwards to Cape Shelagski (170.5°E; Fig. 1). Visual observations of tracked flocks, and of birds at stopover sites close to the radar tracking sites, confirmed that the majority of the radar echoes were waders including grey plover *Pluvialis squatarola*, Pacific golden plover *P. fulva*, red knot *Calidris canutus*, curlew sandpiper *C. ferruginea*, dunlin *C. alpina*, sanderling *C. alba*, pectoral sandpiper *C. melanotos*, sharp-tailed sandpiper *C. acuminata*, bar-tailed godwit *Limosa lapponica*, grey phalarope *Phalaropus fulicarius* and turnstone *Arenaria interpres*. These cohorts represent birds on their way towards wintering areas around the Pacific Ocean, in some cases with destinations on or around the American continent (Alerstam and Gudmundsson 1999a, b).

The westerly migrant group contained 183 bird track records from four sites ranging from Yana (138.9°E) westwards to Pechora (53.5°E; Fig. 1). Visual identification of radar echoes and ground observations on nearby stopover sites showed that this group of migrants also consisted mainly of waders with species such as grey plover, red knot, curlew sandpiper, dunlin, sanderling, little stint *Calidris minuta*, ruff *Philomachus pugnax*, bar-tailed godwit, grey phalarope, red-necked phalarope *Phalaropus lobatus* and turnstone. These populations have staging and wintering areas in W Europe and Africa. Both Siberian data sets did to a smaller extent contain records of birds other than waders, including skuas *Stercorarius* spp., terns *Sterna* spp., geese and ducks (Anseriformes).

From Canada we selected bird track records from four sites around the Beaufort Sea, all with more than 10 bird track records per site with flight directions (both track and heading) between 0 and 180°. This data set consisted of 281 records and the localities were spread from Wollaston peninsula (115°W) to Herschel Island (140°W; Fig. 1). The Canadian data set probably to a large extent refers to waders on their way to intermediate staging areas in eastern North America, and eventually bound for wintering areas in South America. In part, the Canadian data set also contains birds arriving at stop-over areas along the coast of the Beaufort Sea after a longer flight from eastern Siberia (cf. Alerstam and Gudmundsson 1999b). Identified radar echoes and observations made in this study area showed that waders such as grey plover, American golden plover *Pluvialis dominica*, red knot, pectoral sandpiper, semipalmated sandpiper *Calidris pusilla*, Baird's sandpiper *C. bairdii*, white-rumped sandpiper *C. fuscicollis*, buff-breasted sandpiper *Tryngites subruficollis* and red-necked phalarope took part in these movements (Gudmundsson et al. 2002). Also in the Canadian data set a small proportion of radar tracks probably refer to other types of birds besides waders, such as skuas and terns.

The data set from Mauritania contained only visually identified waders, (grey plovers, red knots, dunlins, sanderlings and bar-tailed godwits) departing from their wintering area on a 4000 km flight towards W Europe, where their final spring staging before the flight to the arctic breeding areas take place (Piersma et al. 1990a).

The Lund data set to a large extent consisted of records of the same species and populations as the Mauritania data set, but referring to a situation when the birds recently have departed from Western Europe on their final flight towards the breeding area. Visual observations of tracked birds confirmed that grey plovers, red knots, dunlins, sanderlings and bar-tailed godwits took part in the movements. A small proportion of the tracked flocks in Lund refer to brent geese *Branta bernicla* en route to the same destinations as the waders.

Data and statistics

Calculations of mean directions and angular deviations of flight directions and winds were made according to standard circular statistical methods (Batschelet 1981). To evaluate if these birds were compensating for drift or not, we divided each sample into two groups according to whether winds were coming from the right or the left of the average flight (track) direction of the whole sample (Green and Alerstam 2002). If the birds compensate for drift, we expect that tracks will be similar for the two groups irrespective of where the winds are coming from, while the headings will differ between the groups, being shifted into the wind (to compensate for the effect of winds, more to the right in winds from the right and *vice versa*). On the other hand, if the birds are drifting with the wind, we expect tracks to change with the wind but headings to remain the same irrespective of what direction the wind is coming from. Differences between flight directions (tracks and headings) in different wind situations were tested with the Watson-Williams test (Batschelet 1981). The relative magnitude of drift and compensation were calculated as follows. We denote mean track directions in winds from the left and right T_1 and T_2 respectively, and the corresponding mean heading directions H_1 and H_2. The difference between track and heading is denoted α, then α_1 will be $T_1 - H_1$ and α_2 will be $T_2 - H_2$. The estimated magnitude of drift is then,

$$B_{track} = \left(\frac{T_1 - T_2}{\alpha_1 - \alpha_2}\right)$$

With $B_{track} = 0$ there is no drift and complete compensation. If $B_{track} = 1$ there is full drift and no compensation. When $0 < B_{track} < 1$ there is partial drift and partial compensation. When $B_{track} < 0$ there is overcompensation and when $B_{track} > 1$ there is overdrift (Green and Alerstam 2002).

The corresponding magnitude of compensation is,

$$B_{heading} = \left(\frac{H_1 - H_2}{\alpha_1 - \alpha_2}\right)$$

If $B_{heading} = 0$ there is full drift and no compensation. When $B_{heading} = -1$ there is full compensation and no drift. Values of $B_{heading}$ between 0 and -1 indicates partial drift and partial compensation. If $B_{heading} < -1$ there is overcompensation and when $B_{heading} > 0$ there is overdrift (Green and Alerstam 2002).

In a supplementary step we calculated linear regressions of the average track and heading directions on the average difference between track and heading directions (α) for different wind situations in each sample (Alerstam 1976, Green and Alerstam 2002). Here we used all bird track records from each 10-degree interval of wind direction for the Siberian (eastbound birds), Canadian and Lund data sets, and from each 20-degree interval of wind direction for the westbound Siberian data set (because of the smaller size of this latter sample). Only intervals with more than 10 records were used in the regression analysis. The Mauritanian sample was too small to allow a regression analysis under these restrictions. Statistical testing was made with conventional linear regression methods in the statistical package SPSS for Windows (version 10.0.5). The regression coefficient, B_{track}, for track on α corresponds to the magnitude of drift (B_{track}) and when it is equal to 1 there is full drift, if $B_{track} = 0$ there is full compensation. Values between 0 and 1 indicate partial drift and partial compensation. If $B_{track} > 1$ there is overdrift and if $B_{track} < 0$ there is overcompensation. Corresponding regression coefficients for heading ($B_{heading}$) on track-heading (equivalent to the magnitude of compensation, $B_{heading}$) are 0, -1, > 0 and < -1 (Alerstam 1976).

Results

Summary statistics of flight directions and winds for the different samples are shown in Table 1. In all cases the migratory movements were concentrated in seasonally appropriate directions with relatively little scatter (angular deviations ranging between 14 and 37 degrees).

Significant differences between track directions in winds from left and right of the overall mean direction of the sample were recorded in all but one case (westbound migrants in Siberia, Fig. 2 and Table 2). The significant differences in heading directions between birds flying in winds from the left and right (Table 2 and Fig. 2) indicate that in most cases the drift was partial, i.e. there was a significant element of compensation as well. Only in the data set of migrants flying in easterly directions in Siberia did this analysis indicate drift close to full drift (Table 2 and Fig. 2), with very similar headings in winds from left and right (Fig. 2). The regression method yielded similar results as the comparison between birds flying in winds from left and right of the overall mean direction, apart from the case of eastbound migrants in Siberia where the regression method indicated a small but significant compensation element as well. The confidence interval of the regression coefficient for track on the difference between track and heading did, however, not exclude a full drift scenario (95% C.I. = 0.36–1.00).

For the two largest data sets (eastern migrants in Siberia and spring migrating birds in south Sweden) we compared the magnitude of drift and compensation in two altitude layers (above or below 1 km height) and in three different wind strength intervals (weak, moderate and strong winds). In Siberia a significant drift effect was found in all cases (Table 3). The results indicated full drift with no significant compensation for all groups except for birds flying in moderate winds at high altitude (Table 3). In birds passing southern Sweden evidence for significant drift was only found at high altitudes or the presence of strong winds. Drift was only partial drift with significant compensation as well. The results for the lower wind speed and/or altitude layers were somewhat inconclusive, but an overcompensation effect was indicated at low altitude in weak winds. However, only the differences in headings were significant (Table 3).

Discussion

True drift, pseudo-drift or non-adaptive drift?

Most birds prefer to migrate in following winds (Richardson 1978, 1990b) and arctic waders certainly do so if they have the possibility (Gudmundsson 1994, Alerstam and Gudmundsson 1999a, Green and Piersma 2003). As a consequence, departures will be biased towards tailwind conditions. If departure and destination areas differ between populations within the studied sample, such selective departures will give rise to patterns similar to the ones expected with wind drift, even if all birds participating in these movements actually compensate completely for drift (Evans 1966, Nisbet and Drury 1967). Such 'pseudo-drift' is most likely to occur when one deals with multi-species, multi-population data sets with large variation in preferred migratory directions and destinations within the sample. In the present analysis we find it unlikely that pseudo-drift has affected the results from Mauritania and Sweden to any important degree. Both data sets were homogenous regarding bird species and consisted completely (Mauritania), or almost completely (Sweden), of records of species with known departure and destination areas. These populations are known to migrate along narrowly defined routes between winter and summer quarters (Piersma and Jukema 1990, Green et al. 2002). In the other cases (Siberia and Canada) we cannot completely rule out pseudo-drift. Eastern Siberian and Canadian birds probably also migrate along relatively narrow routes (Morrison 1984), but at least for eastern Siberian

Table 1. Summary statistics of bird track records of migrating waders. Average flight and wind directions of each sample are shown together with angular deviations (a.d.).

Site/Area	Season	Track ± a.d.	Heading ± a.d.	Wind direction ± a.d.	Wind speed ± s.d.	Flight altitude median	N
I. Siberia (westbound)	Autumn	265 ± 32	259 ± 29	139 ± 65	6.9 ± 4.0	654	183
II. Siberia (eastbound)	Autumn	103 ± 22	106 ± 26	277 ± 49	8.4 ± 4.6	1347	628
III. Canada	Autumn	97 ± 24	114 ± 24	203 ± 53	7.4 ± 3.1	853	275
IV. Mauritania	Spring	350 ± 37	343 ± 27	338 ± 37	8.2 ± 2.5	N.a.*	57
V. Lund, Sweden	Spring	64 ± 14	59 ± 19	254 ± 36	10.1 ± 4.2	1800	888

* N.a. = Not applicable. The Mauritania material refers to climbing birds flying between ground level and up to a maximum of 1000 m.

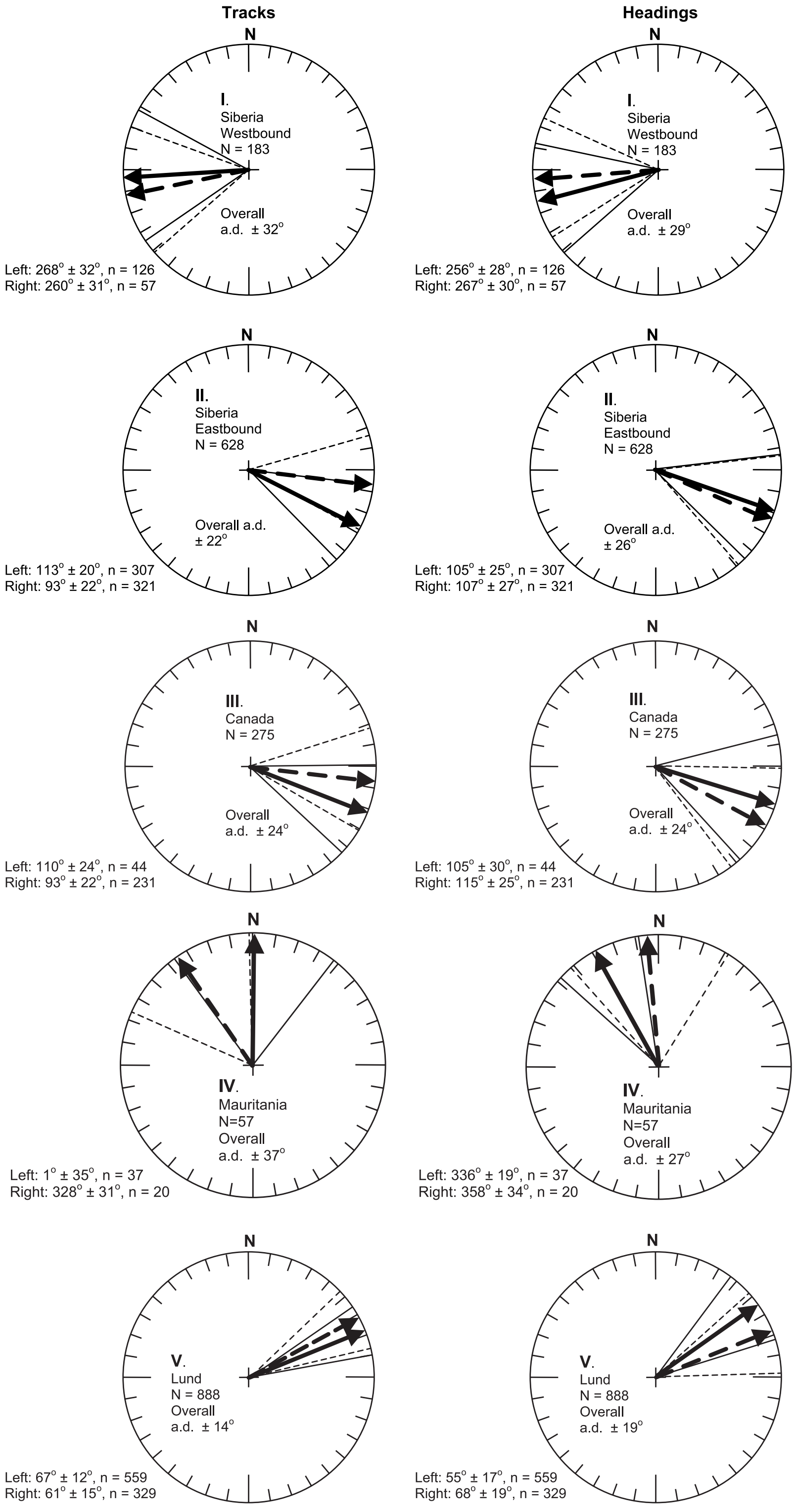

Fig. 2. Average flight directions, tracks and headings, in winds from the left (unbroken bold arrows) and right (broken bold arrows) of the mean direction of the total sample. Angular deviations (a.d.) are shown with unbroken lines for flight directions in winds from the left, and broken lines for flight directions in winds from the right. N-values given are the total sample sizes, the combined values for both groups together (see also Table 2). Mean directions ± angular deviations for each group are given below each panel.

Table 2. The magnitude of drift and compensation (calculated according to Green and Alerstam 2002) for the comparison between flight directions in winds from the left and right (see text and Fig. 2). When the magnitude of drift (B_{track}) equals 1 there is full drift and when it is 0 there is full compensation. Intermediate values indicate partial drift. Similarly, when then the magnitude of compensation ($B_{heading}$) equals −1 there is full compensation and when it is 0 there is full drift, intermediate values indicate partial compensation. If B_{track} is significantly different from 0, full compensation can be rejected. If $B_{heading}$ is significantly different from 0, full drift can be rejected. Levels of significance for tests of difference between average directions in winds from the left and right (see text): *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Statistical testing was made using the Watson-Williams test (Batschelet 1981). Significant drift (B_{track}) and compensation ($B_{heading}$) effects indicated in bold.

Site/Area	Season	Magnitude of drift B_{track}	Magnitude of compensation $B_{heading}$	Recorded behaviour
I. Siberia (westbound)	Autumn	0.42, P > 0.25	− 0.58*	Full compensation/partial drift
II. Siberia (eastbound)	**Autumn**	**0.91*****	− 0.09, P > 0.25	Full drift/partial drift
III. Canada	**Autumn**	**0.60*****	**− 0.40***	**Partial drift**
IV. Mauritania	**Spring**	**0.60***	**− 0.40***	**Partial drift**
V. Lund, Sweden	Spring	0.32***	− 0.68***	Partial drift

birds there may be a variation in destination areas and hence in preferred departure directions (cf. Alerstam and Gudmundsson 1999b). We conclude that the drift patterns found in this study, in most cases, refer to true drift and that pseudo-drift may explain only a limited part.

Could the observed drift be attributed purely to non-adaptive drift? We cannot rule out this possibility but several circumstances argue against it. In most cases the birds could see the ground, although part of the birds tracked in the Arctic (Siberia and Canada) were flying over open ocean, pack ice and/or over low altitude fog. Birds flying over the ocean were not very far off the coastline and may have had access to this cue for compensation. Drift was recorded in strong as well as weak winds, and at high and low altitude (Table 3), indicating that it was not forced drift under special conditions. All Arctic samples contained a mixture of young and adult birds, while the spring migration data obviously recorded birds with experience of at least one migratory journey. The fact that the sample, probably holding the largest proportion of young inexperienced migrants (Siberia W), showed significant compensation and that drift was recorded also in spring migrating birds, argue against any age dependent effect acting in the way that young, naive birds lack the capacity to compensate while adult, experienced ones have such a capacity.

Adaptive strategies?

A comparison between observed patterns and predictions from theories of adaptive drift and compensation are shown in Table 4. The waders did not use complete compensation strategies (prediction a), as some drift was recorded in most situations. Neither were they generally subjected to full drift (prediction d), as there was some amount of compensation involved as well (except possibly for the eastbound migrants in Siberia). Furthermore, they did not choose to fly only in due tailwinds or in weak winds (cf. Piersma et al. 1990b, Alerstam and Gudmundsson 1999a, Gudmundsson et al. 2002, Green in press) in order to minimise drift (cf. Cochran and Kjos 1985). Instead the results indicate partial drift/partial compensation strategies.

Most of the data (Siberian, part of the Canadian, Mauritanian and Lund data sets) used in the present analysis refer to birds that recently had departed on shorter or longer flight steps. The finding of some drift in most cases is thus in accordance with prediction b (Alerstam 1979a), of drift during the initial part of migration. The only data set probably reflecting a significant proportion of birds arriving at stopover areas was the Canadian data set (Gudmundsson et al. 2002) and some of the compensation recorded there (Table 2) may be a result of this, as birds about to arrive at a destination are expected to compensate (Alerstam 1979a).

The results from the westbound migrants in Siberia indicate a significant amount of compensation, perhaps even full compensation. According to prediction b) these birds should be expected to show some drift as well if they used an adaptive drift strategy. Adaptive drift strategies involving both drift and compensation (i.e. prediction b and c) requires true navigation skills from the birds, or at least the ability to detect a displacement and correct for it during some later stage of the migratory journey (or even single flight). As young birds in general are thought to migrate by an inherited simple vector navigation programme (Berthold 1988), such strategies seem implausible in young inexperienced migrants. Older birds may have gained knowledge about topographical features, staging areas etc and may thus be more likely to use adaptive drift strategies. Seen in this perspective the absence of drift in late migrants (westbound) in Siberia may be explained by differences in age composition among tracked birds. In arctic breeding waders the adults typically depart before the juveniles (Pienkowski and Evans 1984, Morrison 1984). As the data set from western Siberia was collected later in the season than the other data sets from the Arctic (Alerstam and Gudmundsson 1999a, Gudmundsson et al. 2002) it is likely that it contained a higher proportion

Table 3. The magnitude of drift and compensation at different altitudes and wind forces for the two largest data sets (eastbound migrants in Siberia and migrants over Lund south Sweden, see text). Magnitude of drift and compensation calculated according to Green and Alerstam (2002). When the magnitude of drift (B_{track}) equals 1 there is full drift, when it is 0 there is full compensation. Intermediate values indicate partial drift. A magnitude of drift below zero indicates overcompensation. Similarly, when then the magnitude of compensation ($B_{heading}$) equals –1 there is full compensation and when it is 0 there is full drift, intermediate values indicate partial compensation. A magnitude of compensation below –1 indicates overcompensation. Differences between average flight directions evaluated with the Watson-Williams test (Batschelet 1981) and the statistical results have been Bonferroni corrected. N-values (both groups of winds from left and right combined) are shown with parentheses. Levels of significance: $*P<0.05$, $**P<0.01$, $***P<0.001$. Significant drift (B_{track}) and compensation ($B_{heading}$) effects indicated in bold.

Site/Area	Season	Magnitude of drift B_{track} or compensation $B_{heading}$	11Weak winds (<5 m s^{-1}) <1000 m altitude	Weak winds (<5 m s^{-1}) >1000 m altitude	Moderate winds (5–10 m s^{-1}) <1000 m altitude	Moderate winds (5–10 m s^{-1}) >1000 m altitude	Strong winds (>10 m s^{-1}) <1000 m altitude	Strong winds (>10 m s^{-1}) >1000 m altitude
Siberia (eastbound)	Autumn	B_{track}	**1.13***(62)	**0.69**** (95)	**1.24**** (106)	**0.55**** (181)	**0.87**** (71)	**1.47**** (113)
Siberia (eastbound)	Autumn	$B_{heading}$	0.13 ns (62)	−0.31 ns (95)	0.24 ns (106)	**−0.45*** (181)	−0.13 ns (71)	0.47 ns (113)
Lund, Sweden	Spring	B_{track}	−1.00 ns (48)	0.08 ns (53)	0.38 ns (67)	**0.20*** (294)	**0.41*** (45)	**0.44**** (376)
Lund, Sweden	Spring	$B_{heading}$	**−2.00*** (48)	−0.92 ns (53)	−0.62 ns (67)	**−0.80**** (294)	−0.59 ns (45)	**−0.56**** (376)

of juvenile birds. If juvenile birds do not have the capacity to use adaptive drift strategies that require true navigation skills (an idea proposed already by Alerstam 1979a), we would expect to find a higher degree of compensation within this group.

While results from birds overflying Lund were broadly in agreement with prediction c (overcompensation at low altitude in low wind speed, combined with drift at high altitude and in high wind speed), the results from Siberia showed drift at all altitudes and in all wind categories (Table 3). Furthermore, we would not expect drift in moderate winds as found both in the Lund and Siberia samples, according to this prediction. In order to give significant energy savings, the strategy of combined drift and compensation/overcompensation requires that wind speed amounts to at least 75% of the birds' airspeed (Alerstam 1979b). Waders generally fly with airspeeds in the interval 13–20 m s^{-1} (Gudmundsson 1994, Alerstam and Gudmundsson 1999a, Green in press). Wind speed then has to be in the order of 10–15 m s^{-1} for this strategy to be beneficial. We thus conclude that support for this prediction was at best weak, and only found in the Lund data set.

Adaptive drift in other studies?

Waders departing from Nova Scotia, East Canada, for a non-stop flight over the Atlantic to wintering areas in South America were found to drift at least partially (Richardson 1979). Records of the same cohort of birds when passing over the Caribbean area, midway between departure and destinations, did also show a large amount of wind drift (Richardson 1976, Williams 1985). Studies in the Pacific area showed extensive drift by birds passing Guam on their way from north-east Asian breeding grounds to wintering areas in the South Pacific islands, Australia and New Zealand (Williams and Williams 1988). Birds close to arrival at wintering and staging areas on Hawaii on the other hand showed compensatory behaviour (Williams et al. 1986). European studies have shown a significant drift component for waders departing from Iceland in spring on a flight towards breeding areas in Greenland and Canada (Gudmundsson 1993) and for red knots passing over south Sweden bound for breeding areas in northern Siberia (Gudmundsson 1994). Both the latter studies were in part analysed with methods liable to produce spurious results (cf. Green and Alerstam 2002), but the data sets here were also analysed with alternative, more robust, methods still indicating significant and true drift effects.

Taken together the results about arctic waders and wind drift seem to be in best accordance with the prediction that birds far away from their destinations, close to departure or midway between departure

Table 4. Interpretation of the analysis of drift and compensation in migrating arctic waders in relation to adaptive drift and compensation strategies. + denotes support for the strategy, − denotes that the results do not support that the birds use the strategy in question. Strategies: 1) Complete compensation, 2) Adaptive drift depending on distance to destination, 3) Adaptive drift with combined drift/compensation or overcompensation at high and low altitudes/wind speeds, 4) Full drift (see text for further details). Blank cells means that no analysis of this strategy was possible. Parentheses mean that support for the strategy in question was weak.

Strategy	Siberia W	Siberia E	Canada	Mauritania	Sweden
1	+	−	−	−	−
2	(+)	+	+	+	+
3		−			(+)
4	−	+	−	−	−

and destination show drift, while birds close to the destination show compensatory behaviour (prediction b; Alerstam 1979a). It could be argued that at least some of the studies reflect birds flying over open ocean, at high altitudes or in high wind speeds with limited possibilities of compensation (Alerstam and Pettersson 1976). This is perfectly right but does on the other hand not contradict the indication of adaptive drift strategies. The finding that arctic waders may use adaptive drift strategies that involve partial drift and partial compensation implies that these birds (at least the adults) have the capacity of true, goal-oriented navigation. Without doubt there still remain a lot of unsolved questions about how these birds, as well as birds in general, tackle the problem of drift and compensation. With satellite telemetry becoming more and more used in bird migration research and allowing detailed individual tracking during whole migratory journeys, there are good prospects for much new interesting information to emerge in the near future.

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