The Use of Low-Level Jets by Migrating Birds

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Abstract Birds flying at high altitudes have occasionally been observed above mountain areas and the open sea. For the first time the regular occurrence of migrating birds flying within a low-level jet at heights of 5000 to almost 9000 m asl. have now been verified by radar above the Negev desert in southern Israel. Tracks of rather large birds with wing-beat frequencies of 5–6 Hz were measured to have horizontal flight speeds up to 50 m/s. Visual observations, seasonal occurrence, and wing-beat frequencies allowed to associate them with small species of the order Ciconiiformes (mainly Ardeidae) and possibly with members of the Laro-Limicolae group. These wading birds seem prone to continuing nocturnal migration into daytime under favorable conditions and to make use of high wind speeds at sometimes extreme altitudes.

Bird migration takes place in the highly variable, continuously moving airspace of the troposphere. Wind speeds often reach or exceed the birds' air speeds (10–15 m/s). Thus wind has an important effect on a bird's flight path and is a relevant selective force for behavioral adaptations to minimize energy and time demand (Alerstam 1990). Jet-streams are strong winds (25–70 m/s) in the upper troposphere which wobble back and forth as they move generally eastward within the middle latitudes (30–60°). In the northern latitudes the vast majority of migration is known to take place generally within 1000 m above ground level, which by most means corresponds to heights below 2000 m above sea level (asl; Able 1970; Bruderer 1971). Regular migration at 2000–6000 m asl has been recorded in the subtropical zone over Israel (Bruderer and Liechti 1995), the western North Atlantic ocean (Richardson 1976), and the Caribbean Sea (Williams and Williams 1978). Reports of birds at very high altitudes (>6 km) exist from accidental observations by pilots and from mountain climbers in the Himalayan. A single flock of swans (*Cygnus* sp.) has been reported flying from Iceland towards the British islands at 8.2 km with a ground speed of 38 m/s (Stewart 1978), confirming that at least some birds are able to fly under the extreme physiological conditions of very high altitudes. Here we report the rare but regular occurrence of birds migrating at altitudes above 5 km that take advantage of very strong tailwinds, enabling them to travel with speeds of up to 50 m/s (180 km/h).

In spring 1992 we recorded bird migration in southern Israel (30°53′N, 34°47′E) by radar, which allows the tracking of single birds and the recording of their wing-beat patterns (Bruderer and Liechti 1995). The technical basis of radar ornithology and its major achievements (e.g., on temporal and spatial distribution of bird migration) have been reviewed by Bruderer (1997a,b). The present data show that some migrants may regularly reach altitudes above 5000 m asl under appropriate conditions (Fig. 1). The fingerlike pattern of the shaded areas in Fig. 1, indicating increasing wind speeds, are typical effects of a jet-stream, which accelerates winds at lower altitudes during unstable atmospheric conditions. Maximum wind speeds (71 m/s) were reached at altitudes of 10–12 km. Most birds above 6 km flew with speeds of more than 25 m/s, taking advantage of the strong SW winds. The strong winds between 7 and 10 April were mostly unfavorable NW winds and therefore not exploited by migrants.

The regular pattern of recorded tracks below 3 km shows the well known rhythm of migration, with intense nocturnal and relatively week diurnal migratory activity within this region. Due to the operating mode of the radar and the limit in detection range for small birds, Fig. 1 does not represent a proper quantitative distribution. Quantitative measurements give an even more pronounced concentration of migration during night-time and below 4 km. Less than 2% of nocturnal migrants make the transition

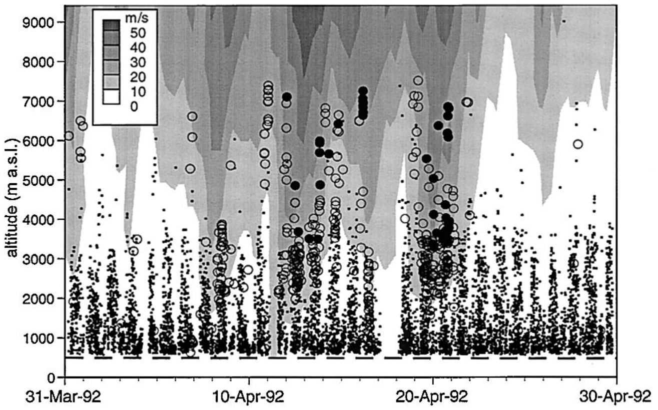

Fig. 1. Distribution of the recorded tracks (*symbols*; $n = 9078$) and the wind velocities (*shaded areas*) in time and altitude over the Negev desert. Birds are grouped into three classes according to ground speed: *small squares* <25 m/s; *open circles* 25–40 m/s; *large black dots* >40 m/s (max. 52 m/s). *Dashed line* height of the radar station above sea level (470 m). The gaps in tracks on 12 and 17–18 April were caused by technical problems

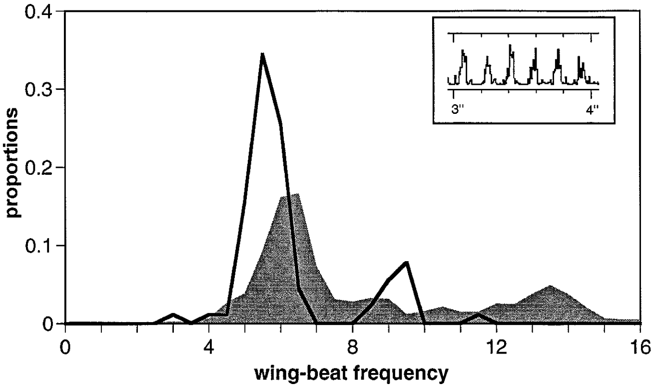

Fig. 2. Distribution of wing-beat frequencies of birds with continuous flapping flight (wader-waterfowl-type birds). *Black line* birds flying above 4 km asl ($n = 90$); *shaded area* birds below ($n = 1270$). *Inset* an example of 1 s of the raw echo fluctuation from a tracked bird with continuous wing-beats. The bird was flying at 7030 m asl with an average wing-beat frequency of 5.8 Hz

between nocturnal migration and diurnal migration in these areas (Bruderer 1994). The passerines, as by far the largest group of migrants (60%), adhere to either pure nocturnal (most trans-Saharan migrants) or more or less pure diurnal migration (e.g., swallows). Some raptors may continue migration into the night (Spaar et al. 1998), while other nocturnal migrants (e.g., waterbirds), finding no suitable resting areas but optimal flight conditions at dawn, may continue migration into the day.

Corresponding to the west and southwesterly winds, the tracks of high flying birds (>4 km) were highly concentrated towards NE (45±21°, $n = 208$), indicating well oriented migratory movements. For these birds, wing-beat patterns, recognizable only from birds flying singly, showed mainly continuous flapping at frequencies between 5 and 6 Hz, but some also at 9–10 Hz (Fig. 2). Continuously beating birds at lower levels showed wider variation in frequencies, with some concentrations at 6–7 and 13–14 Hz. While the clear frequency peaks at high flight levels are unambiguous indications of a narrow spectrum of species involved, the lack of small birds (with frequencies above 10 Hz) may be due partly to the declining detection probability of small birds as the result of radar characteristics. Nevertheless, selecting only birds tracked at distances farther than 4 km ($n = 220$), similar numbers of large birds were observed above and below 4 km altitude asl (41% and 37%), whereas only 2 of 48 (1%) small birds flew above 4 km. Thus, small birds flew generally at lower altitudes than large ones. According to visual observations by a telescope mounted parallel to the radar antenna, 20% of the high altitude tracks were from flocks, and 60% were determined as single birds by visual observation or wing-beat pattern; the remaining 20% could neither be seen nor identified by wing-beat pattern. Species identification was usually not possible at such large distances, but observers have often reported "large white birds." Differences in silhouettes have been attributed by the observers to heron-type birds, spoonbills (*Platalea leucorodia*), and glossy ibis (*Plegadis falcinellus*).

According to flight theory, the wing-beat frequency of an individual bird should increase by almost 4% per 1 km of altitude because of the decreasing air density (Pennycuick 1996). Within the peak of 4–7 Hz in our data on high flying birds (Fig. 2) wing-beat frequency increased significantly by 2% per 1 km ($P < 0.05$). Thus at sea level wing-beat frequencies of these birds might be 0.5-1 Hz below of those actually measured. According to visual observations, distribution of wing-beat frequencies, and phenological data from long-term surveys (Shirihay 1996), these high tracks can be associated with small species of the order Ciconiiformes, mainly small egrets, such as squacco heron *Ardeola ralloides*, little egret *Egretta garzetta,* night heron *Nycticorax nycticorax*, and possibly spoonbill and glossy ibis. Nevertheless, some species of the Laro-Limicolae group cannot be excluded (e.g., large species of the Scolopacidae, Laridae, and Sternidae) and possibly Anatidae.

These birds are confronted with dramatically reduced air densities and oxygen partial pressure (about 40% at 7 km compared to sea level) and temperatures between –20° C and –30° C. Mean air speeds of all birds with wing-beat frequencies between 2 and 8 Hz was 14.4 ± 3.9 m/s ($n = 1046$; calculated by subtracting the wind vector at the corresponding height from the flight vector). Air speeds were not positively correlated with decreasing air density as predicted by flight mechanical theory (Pennycuick 1989). We might speculate that these birds keep their power output constant regardless of their flight altitude. For a bird such as a little egret maximum range speed (minimum costs per unit distance) at sea level is close to minimum power speed (minimum costs per unit time) at 7 km asl, and also power output is roughly the same. Nonetheless, even to fly with minimal power it must increase respiratory volume or oxygen extraction by a factor of 2–3. Increased ventilation in cold air can strongly increase water loss and might therefore limit flight duration at high altitudes (Klaassen et al. 1999). Under the extremely low temperature the bird's exhaled air temperature probably also decreases considerably ($<10°$ C) (Schmidt-Nielsen 1997). Saturated water vapor pressure increases exponentially with temperature. Thus the amount of water to saturate cold air, even when it is very dry, is only a fraction of that of warm (e.g., 20° C) and dry air. Therefore water loss due to increased ventilation is markedly reduced, and it is a moot point whether this at all is a limiting factor for the high flying birds.

Although these fast flying birds can cover up to 2000 km within 12 h, it is unlikely that they are on a nonstop flight from their winter quarters to the breeding grounds. The jet-streams do not occur much further south than 30°N and therefore do not bring them over the Sahara-desert. However, moving on with these low level jets northeastward would bring them to potential breeding or good refueling areas in the region of the Caspian Sea within 10–20 h. Making profit of these winds reduces energy demands to less than one-third of those of flights in still air. We believe that the occurrence of birds at such heights is not due to a specific selectivity of these migrants for high altitudes and extreme wind speeds, but that some particular species prolong nocturnal migration into the day when conditions on the ground are unfavorable for resting and conditions aloft are favorable for migration. After takeoff, nocturnal migrants climb up to search for the heights with the most favorable tailwinds. Depending on individual or species-specific physiological limits and on the length of the intended flight some birds may climb higher and higher when winds grow better and better (Bruderer et al. 1995). For flights in daytime high altitude flights may be advantageous for flapping flyers because of a more stable laminar air flow compared to the disturbances at low levels caused by thermal convection. However, proper measurement of ground speed becomes more difficult with increasing height, and when flying above clouds the risk of being blown off course is high.

Data on migrants overshooting their breeding range in spring, as often observed in the species mentioned above (del Hojo et al. 1995) might reveal a correlation with the specific wind conditions observed in this study. Undoubtedly, general wind patterns play an important role for energetic considerations of bird migration. To learn more about migratory strategies further investigations may ask whether evolution has favored an adaptation according to site specific seasonal wind patterns or, more likely to us, an evolution of behavioral rules to be able to cope with varying conditions encountered en route.

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