

Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds

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SUMMARY

Birds adjust their flight behaviour to the physical properties of the air. Lift and drag, the two major properties in aerodynamics, are highly dependent on air density. With decreasing air density drag is reduced and lift per wingbeat decreases. According to flight mechanical theory, wingbeat frequency and air speed should increase with decreasing air density, i.e. increasing flight altitude. Although wind tunnel experiments have shed light on many aspects of avian flight, the effect of air density remained ambiguous, because air density could not be adjusted in wind tunnels, until now. By means of radar we recorded tracks of several thousand free-flying individual birds during nocturnal migration. From these tracks we derived wingbeat frequencies and air speeds covering air densities from 0.84 kg m^{-3} to 1.13 kg m^{-3} , corresponding to an altitudinal range of about 3000 m. We demonstrate here with this sample of nocturnal migrants that: (1) wingbeat frequency decreases with air density (which corresponds to an increase in flap-gliding flyers by 0.4 Hz km^{-1} and in bounding flyers by 1.1 Hz km^{-1}), (2) reducing wingbeat frequency to equivalent sea level values did not abolish the dependency on air density, as expected by flight mechanical theory, and (3) bounding flyers show a higher response in their flight behavioural adjustments to changes in air density than flap-gliding flyers. With respect to air speed flap-gliding flyers increase their air speed by $1.0\text{ m s}^{-1}\text{ km}^{-1}$ and bounding flyers by $1.4\text{ m s}^{-1}\text{ km}^{-1}$.

Key words: flight, bird, wingbeat frequency, air speed, air density, altitude.

INTRODUCTION

Lift and drag, the two major properties in aerodynamics, are highly dependent on air density. To produce the same amount of lift, a given airfoil has to be moved faster through thin air than through dense air (Lighthill, 1977; Rayner, 1988). However, with a constant power output the reduced drag in thin air yields more thrust and, hence, higher air speed. If birds encounter decreasing air density, i.e. increasing flight altitude, they will adjust their flight behaviour to the changing physical properties of the air (Pennycuik, 1975; Rayner, 1979; Pennycuik, 1989; Norberg, 1990; Pennycuik, 2001; Rayner et al., 2001). Birds might either increase their (a) wingbeat frequency (Pennycuik, 2001; Hedenström et al., 2002), (b) stroke amplitude (Chai and Dudley, 1996) or (c) both (Chai et al., 1996). All of these adaptations will allow them to overcome the reduced lift and lead to an increase in air speed.

In order to compare field data with the predictions from flight mechanical theory at the individual level, body mass, wing span, wing area, wingbeat frequency, stroke amplitude, air speed, air density, and in bounding flyers power fraction, measurements are required (Pennycuik, 2001). Wind tunnels allow detailed investigations of the flight behaviour at the individual level and have produced important results improving our understanding of aerodynamics in birds, e.g. Pennycuik et al. estimated the body drag coefficient (Pennycuik et al., 1996), Rosén and Hedenström developed a model for calculating wingspan and wing area with respect to forward speed in gliding birds (Rosén and Hedenström, 2001), and Lentink et al. demonstrated that for slow glides and turns extended wings are favourable but swept wings are better for fast glides and turns (Lentink et al., 2007). Recent technical advances allowed the approach of estimating the aerodynamic (mechanical)

power by carefully investigating the wake structure induced by a flying bird (e.g. Spedding et al., 2003; Hedenström et al., 2006). Information about how birds adapt their flight behaviour to changing air densities is still lacking, because until now air density could not be adjusted in wind tunnels. Besides these constraints, Tucker conducted some very important flight experiments with house sparrows (*Passer domesticus*) and budgerigars (*Melopsittacus undulatus*) in hypobaric flight chambers investigating their flight behaviour at different air densities (Tucker, 1968). Tucker drew our attention to the aerodynamical problems birds face at high altitudes, i.e. low air densities. An alternative approach to wind tunnel or flight chamber experiments is the direct visual observation of identified species in free flight (Pennycuik, 1990; Pennycuik, 1996; Pennycuik, 2001) but the range of altitude covered and, hence, differences in air density are rather small. Thus, detecting behavioural flight adaptations are very limited and additionally the required individual dimensions (see above) of the observed birds are hardly available. Intensive studies on the flight performance of hummingbirds in respect of changing environmental factors demonstrated, among other important things, that wingbeat frequency remained relatively constant with decreasing air density whereas stroke amplitude increased (Chai and Dudley, 1996; Chai et al., 1996; Chai et al., 1997; Altshuler and Dudley, 2003). These studies focused, however, on hovering and not cruising flight, so that theoretically predicted flight adaptations with respect to air density are hardly tested empirically for birds performing cruising flights (Pennycuik, 1990; Pennycuik et al., 1996; Pennycuik, 2001; Hedenström et al., 2002).

By using tracking radar an extensive altitudinal range of birds in cruising flight can be covered; however, identification at the species

level is hardly possible. Nevertheless, general aerodynamic predictions (Alerstam et al., 2007) and air speed adjustments to altitude (Bruderer, 1971; Alerstam and Gudmundsson, 1999; Hedenström et al., 2002) have been tested for migrating birds detected by radar. Within a large set of tracking radar data collected from a wide range of altitudes, average trends in wingbeat frequency and air speed adjustment should follow the theoretically predicted ones. However, ignoring the effect of body mass, wing span, wing area and stroke amplitude can only be accepted, if we can credibly expect that species composition and body condition are independent of flight altitude.

We collected data on singly flying, nocturnal migrants crossing the Western Sahara during two spring seasons and one autumn season. Every night migrants crossing the Sahara are confronted with similar environmental conditions. Based on the fact that flight altitude of migrating birds is primarily governed by wind conditions (Liechti, 2006; Schmaljohann et al., 2008c; Schmaljohann et al., 2009), we presume that, at least within morphologically similar groups of birds (swifts, songbirds), the distribution of flight altitudes is governed by atmospheric conditions and not by species-specific flight levels. With the tracking radar 'Superfledermaus' we recorded the echo signature of birds, i.e. the temporal variation of energy reflected by the bird (Schmaljohann et al., 2008a; Zaugg et al., 2008). This variation in the received signal mirrored the wingbeat pattern of the bird and can, therefore, be used for echo identification (Houghton, 1969; Bruderer and Joss, 1969; Bruderer, 1997; Schmaljohann et al., 2008a; Zaugg et al., 2008). In doing so, recorded tracks were assigned to one of the three flight styles: (1) continuously flapping (flapping, such as waders and ducks), (2) irregular flapping and gliding (flap-gliding, such as swifts), and (3) regular flapping and bounding (bounding, such as songbirds). From these patterns we derived the wingbeat frequency and power fraction, defined as the proportion of flapping in flap-gliding and flap-bounding birds (Fig. 1). Individual ground speed and flight altitude were also recorded by radar. Atmospheric conditions experienced by migrants were measured by radiosondes at altitudes up to 3 km above ground level (a.g.l.) every night, allowing us to calculate the air density experienced by each bird and, hence, the dependency of wingbeat frequency and air speed on air density.

The two forces, lift and drag, are proportional to air density (Lighthill, 1977; Rayner, 1988) and, consequently, high flying birds encountering a lower air density than at sea level have to increase their wingbeat frequency (and air speed) to maintain the same amount of lift. To compare wingbeat frequencies as well as air speeds irrespectively of flight altitude, we 'reduced' them according to flight aerodynamic theory to the equivalent values that would have prevailed at sea level. These equivalent sea level values of wingbeat frequency (f_{SL}) and air speed (V_{SL}) are supposed to be independent of air density, because after the reduction to sea level, birds 'experience' the 'same' atmospheric conditions. Thus, they are supposed to behave similarly (Pennycuick, 2001; Hedenström et al., 2002; Alerstam et al., 2007).

Adjustments of wingbeat frequency and air speed depend among other things on air density, the flight style of the bird [flapping, flap-gliding and bounding (Pennycuick, 2001; Rayner et al., 2001)] and the flight behaviour (e.g. power fraction). In the present study, we consider only flap-gliding and bounding flyers. Flap-gliding flyers descend only very little during the gliding phase and, hence, fly nearly horizontally whereas bounding flyers descend and ascend periodically during cruising flight (Rayner et al., 2001). Bounding flyers fold their wings against the body in regular phases, so that no useful aerodynamic force is produced, leading to a decrease in

lift, thrust and drag. During the subsequent flapping phase they must produce sufficient lift and thrust supporting their weight and overcoming drag for the whole flight phase (Rayner et al., 2001). When pulling up in the flapping phase to compensate for the loss in kinetic and potential energy during the pause phase, bounding flyers experience an additional value of gravity, as we do when ascending with an aeroplane (Pennycuick, 2001). The overall value of the additional gravity depends on the proportion of flapping and pause phases and can be modelled by the 'load factor', which is the inverse of the power fraction (Pennycuick, 2001). In a recent study on flight behaviour of common swifts (*Apus apus*), Henningsson et al. demonstrated that swifts increase their air speed not by an increase in the wingbeat frequency but by an increase in the wingbeat amplitude, actually resulting in a decrease of wingbeat frequency (Henningsson et al., 2008). Air density was constant during their wind tunnel experiment, and we can only speculate how the constant speed of contraction of the flight muscles is influenced by a reduced air density. Bounding flyers are supposed to increase their air speed by an increase in their wingbeat frequency (Stark, 1996; Bruderer, 1997) or power fraction (Stark, 1996), although wingbeat frequency might increase with a decrease in the power fraction when air speed remains constant (Pennycuick, 2001). Consequently, bounding flyers are supposed to show an overall higher increase in wingbeat frequency and air speed than flap-gliding flyers (Pennycuick, 2001).

In the present study, we test three fundamental predictions of the flight aerodynamic theory for flap-gliding and bounding flyers (Pennycuick, 2001): (1) wingbeat frequency and air speed increase with decreasing air density, i.e. increase with flight altitude. (2) When 'reducing' wingbeat frequency and air speed to the sea level equivalent values, they are supposed to be independent of air density and, hence, altitude. (3) Because of the differences in their flight styles and behaviours, bounding flyers are supposed to show a higher increase in their wingbeat frequency and air speed with decreasing air density than flap-gliding flyers.

MATERIALS AND METHODS

Study site

Bird migration was studied by tracking radar about 500 km east of the Atlantic coast in the Western Sahara during spring 2003 (from 6 March to 15 May), autumn 2003 (from 24 August to 10 October) and spring 2004 (from 14 March to 10 May). The study site was situated close to the oasis Ouadâne in Mauritania [20°56'N, 11°35'W, 420 m above sea level (a.s.l.)].

Radar data

Radar targets were recorded by an X-band tracking radar of the type 'Superfledermaus' (3.3 cm wavelength, 150 kW peak pulse power, produced by Oerlikon Contraves, Zürich, Switzerland [for further details about the characteristics of this radar, see Bruderer et al. and Bruderer (Bruderer et al., 1995a; Bruderer, 1997)]).

Quantitative data on the density and altitudinal distribution of bird migration were recorded in a fixed beam mode (Schmaljohann et al., 2008a). Every hour on the hour a fixed beam measurement was carried out at a low and high elevation angle (11 deg. and 79 deg., respectively) to survey high and low altitudes with comparable effort. The beam was directed towards west (270 deg.) and, thus, perpendicular to the main migratory direction (Schmaljohann et al., 2007). Detection range was restricted to 7.5 km and recording time was 4 min [for further details about these measurements, see Schmaljohann et al. (Schmaljohann et al., 2008a)]. These fixed beam measurements provided information on the altitude and wingbeat

pattern but not the flight speed of the targets. Between fixed beam measurements, tracks of single targets were recorded for at least 40 s. By tracking targets, data on flight directions, and horizontal and vertical speeds are obtained (Bruderer, 1994). With our radar system the smallest European bird, the goldcrest [*Regulus regulus* (Linnaeus 1758)] can be tracked in tail-on view slightly beyond 3 km (F.L., unpublished). All trans-Saharan bird migrants are larger than goldcrests. We, therefore, considered only birds that were detected at a distance of less than 3 km from radar. In doing so, we held the detection probability for small and large birds approximately constant (for tests about the detection probability, see Results).

Meteorological data

We launched radiosonde balloons at the study site before midnight every night to record altitudinal profiles of air pressure, air temperature and relative humidity at least up to 3 km a.g.l. Radiosondes (ZEEMET™ Mark II MICROSONDE, Sippican, England) transferred these meteorological data every second to our ground site. Depending on the vertical speed of the balloon this corresponds roughly to a height difference between two successive samplings of, on average, 4.0 ± 1.6 m (\pm s.d.) with a mean sampling size of 674 ± 150 (\pm s.d.) per night ($N_{\text{nights}}=182$) from ground level up to 3 km a.g.l. Because radiosonde measurements were performed only at midnight, we restricted our analyses to nocturnal migrants. Wind profiles were gathered simultaneously by tracking the radiosonde balloons with radar (Bruderer, 1994). We calculated air speed of tracked birds based on birds' flight and the corresponding wind vector. Because meteorological conditions change over time, in our analyses we have considered only birds that had a vertical distance to the nearest data point of our wind measurements of <100 m, a horizontal distance of <5 km and a temporal difference of <180 min.

Calculation of air density

The ideal gas law is:

$$PV = nRT, \quad (1)$$

where P is pressure (Pa), V is volume (m^3), n is number of moles, R is gas constant [$287.05 \text{ J}/(\text{kg} \times \text{K})$] and T is temperature (Kelvin). Air density (D) (kg m^{-3}) under dry conditions is simply the number of molecules of the ideal gas in a certain volume:

$$D = n / V. \quad (2)$$

Air density can consequently be calculated as:

$$D = P / RT. \quad (3)$$

Because air density is affected by humidity, real air density is a mixture of dry air and water vapour molecules, which can be expressed as:

$$D = \left(\frac{P_d}{R_d T} \right) + \left(\frac{P_v}{R_v T} \right), \quad (4)$$

where P_d is pressure of dry air (Pa), R_d is gas constant for dry air [$287.05 \text{ J}/(\text{kg} \times \text{K})$], P_v is pressure of water vapour (Pa) and R_v is gas constant for water vapour [$461.495 \text{ J}/(\text{kg} \times \text{K})$].

P_v can be calculated from saturation vapour pressure (P_{sat}) and relative humidity (ϕ):

$$P_v = \phi P_{\text{sat}}. \quad (5)$$

After Buck (Buck, 1981), P_{sat} can be calculated as:

$$P_{\text{sat}} = 6.1121 \exp [(17.502 T_C) / (T_C + 240.97)^{-1}], \quad (6)$$

where T_C is ambient temperature ($^{\circ}\text{C}$) [see also discussion in Elliott and Gaffen (Elliott and Gaffen, 1991) about vapour pressure formulas].

The absolute air pressure P in the system is the vapour pressure of water P_v plus the partial pressure of dry air P_d . Thus, P_d is:

$$P_d = P - P_v. \quad (7)$$

By simply combining Eqns 4, 5, 6 and 7 we calculated actual air density in steps of about 4 m up to 3 km a.g.l. for each night ($N_{\text{nights}}=182$). Radiosondes provided data on ambient temperature, relative humidity and pressure. Birds' flight altitude did not necessarily coincide with the precise altitude, for which air density was calculated. We calculated, therefore, mean air densities for 50 m height intervals per night and derived birds' ambient air density from the corresponding 50 m height interval and night.

Because air density is a function of air temperature, pressure and relative humidity, it can change considerably at the same altitude. At an altitude of 500 m a.g.l., air density varied from 1.03 kg m^{-3} to 1.08 kg m^{-3} during our study, because air temperature, pressure and relative humidity reach values from 20.0°C to 32.9°C , from 903.5 to 912.9 mbar and from 6.3% to 75.5%, respectively.

Flight styles

In both recording modes (fixed beam and tracking), we could sample echo signatures of the targets, which enabled us to distinguish between birds and insects on the basis of their echo signatures. In birds, the echo signature mirrors their wingbeat pattern (Bruderer, 1969; Bruderer, 1997) whereas in insects the complicated structure of the echo signature consists probably of a mixture of wing and other body movements (Schmaljohann et al., 2008a; Zaugg et al., 2008). Bird echoes can be assigned to groups of different flight styles according to their wingbeat pattern (Bruderer, 1969; Bruderer, 1997; Schmaljohann et al., 2008a; Zaugg et al., 2008): (a) continuously flapping flyers (waders, waterbirds, gulls, terns, rails, etc.), (b) flap-gliding flyers with irregularly long flapping and gliding phases, between which speed undulates but height does not [swifts (Bruderer and Weitnauer, 1972), bee-eaters and small raptors (Stark and Liechti, 1993)], (c) bounding flyers with regular alternation of flapping and bounding [passerines without swallows and corvids but also small owls, woodpeckers, and hoopoes (Rayner et al., 2001)], and (d) soaring flyers [raptors, storks, etc. migrating only diurnally (Bruderer and Boldt, 2001; Pennycuik, 2001)]. For this study we considered only echoes of single birds that could be doubtlessly assigned to flap-gliders or bounding flyers (Schmaljohann et al., 2008a; Zaugg et al., 2008). Identification of bounding flyers was straightforward because of the regular alternation of flapping and pause phases. In this study, the group of bounding flyers consisted mostly of songbirds, because they outnumbered other candidates like hoopoes [*Upupa epops* (Linnaeus 1758)], scops owls [*Otus scops* (Linnaeus 1758)] and wrynecks [*Jynx torquilla* (Linnaeus 1758)] by far (H.S. and F.L. personal observation) (Hahn et al., 2009). Therefore, the vast majority of this bird group had similar morphological prerequisites, at least with respect to aerodynamics. This is even more appropriate for flap-gliding flyers, where swifts [mainly common *Apus apus* (Linnaeus 1758), pallid *Apus pallidus* (Shelley 1870) and some alpine *Apus melba* (Linnaeus 1758) swifts] made up the huge part of the sample with only a few bee-eaters and perhaps some small raptors migrating at night. Because the group of continuously flapping flyers did not contain a homogeneous set of birds, mostly waders, ducks, gulls, rails, etc. but probably also turtle doves and some songbirds (Cochran et al., 2008), we excluded these from our analyses. Echo

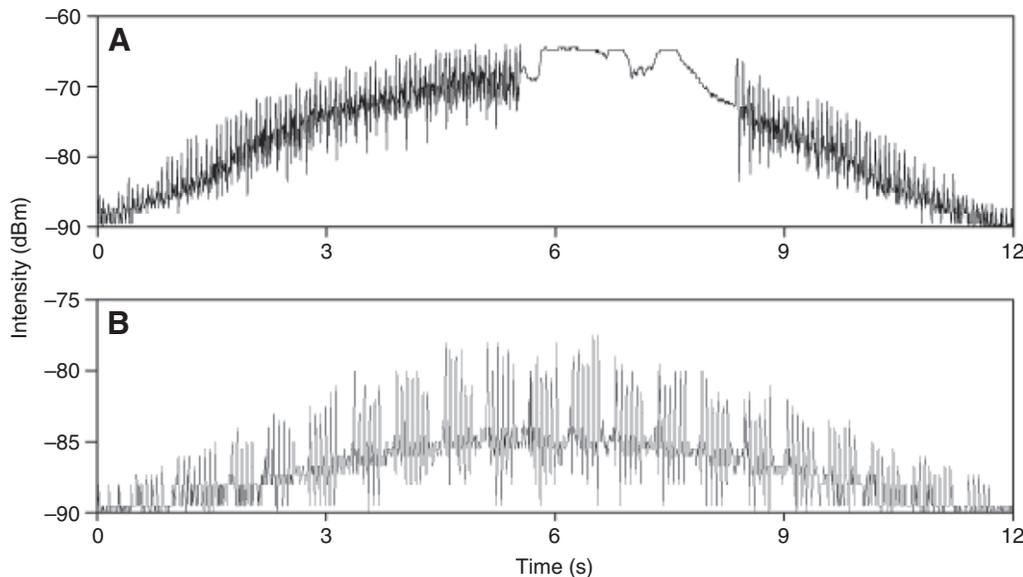


Fig. 1. Echo signatures of a flap-gliding (A) and bounding flyer (B) as recorded with the 'Superfledermaus'. Each graph shows the temporal variation of echo's intensity (y-axis) in relation to time (x-axis). The long pause phase in the flap-gliding flyer is recognisable by the low variation of the echo intensity. The echo signature of the bounding flyer is characterised by the regular alternation of flapping and pause phases. Fast Fourier transformation resulted in a wingbeat frequency of 7.6 Hz for the flap-gliding and 14.0 Hz for the bounding flyer.

signatures of a flap-gliding and bounding flyer are given in Fig. 1. Additional bird and insect echo signatures can be found in different publications (Schaefer, 1968; Bruderer and Joss, 1969; Bruderer and Steidinger, 1972; Demong and Emlen, 1978; Cochran et al., 2008; Schmaljohann et al., 2008a; Zaugg et al., 2008).

Wingbeat frequency

Among others the strength of the echo signal depends on the size of the target (= radar cross section) (Bruderer, 1997; Schmaljohann et al., 2008a). This radar cross section varies with a bird's wingbeats (Fig. 1) (Bruderer, 1969; Bloch et al., 1981; Bruderer, 1997), so that its variation mirrors the wingbeat pattern of the bird (echo signature). We recorded the echo strength with a sampling rate of 130 Hz, which is by far sufficient to detect wingbeat frequencies within the expected range of 5–25 Hz (Zaugg et al., 2008). We defined the wingbeat frequency as the frequency within the flapping phase (Pennycuick, 2001) and not as the mean number of wing-flaps over flapping and pause or gliding phases. We determined the first dominant frequency within the flapping phase by applying fast Fourier transforms. All fast Fourier transforms were checked manually by H.S. The fixed beam and tracking mode qualitatively sampled the same birds, because wingbeat frequencies did not differ significantly between the same bird groups of the two recording modes (flap-gliding flyers: Welch two-sample *t*-test: $t=0.4$, $P=0.7$, $N_{\text{fixed beam}}=188$, $N_{\text{tracking}}=1481$; bounding flyers: $t=1.4$, $P=0.15$, $N_{\text{fixed beam}}=1782$, $N_{\text{tracking}}=2316$). Hence, the species composition considered was not influenced by the recording mode.

Power fraction

Because ascending and descending influence the flight behaviour, especially the length of flapping and pause phases in bounding flyers (Renevey, 1981; Bloch et al., 1981; Pennycuick et al., 1996; Hedenström and Liechti, 2001; Cochran et al., 2008) (F.L. and H.S., unpublished), we considered only birds flying horizontally in cruising flight and omitted birds with a vertical speed of less than -0.5 ms^{-1} or more than $+0.5 \text{ ms}^{-1}$. Such a selection was limited to tracks, because the fixed beam mode does not provide information of a bird's vertical speed. However, we omitted all echoes from the fixed beam measurements where distance varied within the track.

For bounding flyers we determined the lengths of the flapping and pause phases by applying an algorithm using wavelet transforms

(Torrence and Compo, 1998; Carmona et al., 1998; Addison, 2002) and additional correction tools (S. Zaugg, unpublished), which could only be applied to fixed beam echoes. To test whether the algorithm determined the length of the flapping and pause phases correctly, we verified manually for a randomly selected sample of 300 bounding flyers the flapping and pause phases. The median of either phase was correctly identified in 93% of the cases. Because we could not apply this algorithm to tracks, we measured manually the median flapping and pause phase for a randomly selected sample of 200 tracks. In 3% of the sample the flapping or pause phases could not be measured owing to high noise level. Power fraction (q) was calculated as the flapping phase divided by the sum of the flapping and pause phases as in Pennycuick (Pennycuick, 2001). We included only bounding flyers, of which at least a whole flapping phase and a whole pause phase were recorded. Although power fractions determined for the fixed beam [0.78 ± 0.09 (mean \pm s.d.), range=0.49–0.96, $N=1180$, 95% CI=0.775–0.781] and tracked bounding flyers [0.76 ± 0.11 (mean \pm s.d.), range=0.50–0.93, $N=194$, 95% CI=0.750–0.767] differed significantly (Welch two-sample *t*-test: $t=2.3$, $P=0.02$, $N_{\text{fixed beam}}=1180$, $N_{\text{tracking}}=194$), this difference of 0.02 (or 3%) between the means was regarded as not of biological relevance. Therefore, we pooled the two data sets.

Predicted effect of air density on wingbeat frequency

After Pennycuick (Pennycuick, 1996; Pennycuick, 2001; Pennycuick et al. 1996), the benchmark wingbeat frequency of a given bird depends on body mass, gravity, wing area, wing span and air density (equivalent sea level value), see Eqn 2 in Pennycuick (Pennycuick, 2001). The equivalent wingbeat frequency at sea level (f_{SL}) is supposed to be a function of the measured true wingbeat frequency (f_i) at any altitude and the ratio (σ) of ambient (ρ) to standard air density (ρ_{SL}):

$$f_{\text{SL}} = f_i \sigma^{3/8}, \quad (8)$$

with:

$$\sigma = \rho / \rho_{\text{SL}}, \quad (9)$$

after Eqns 4 and 6 in Pennycuick (Pennycuick, 2001).

To compare wingbeat patterns between different species or individuals, but collected under different atmospheric conditions, values were 'reduced' to reference conditions (following

aeronautical convention); air density at sea level in the standard atmosphere is 1.23 kg m^{-3} (Pennycuick, 2001). This value is used as the reference air density and has been applied in many aerodynamic papers (e.g. Rayner, 1979; Pennycuick, 1989; Pennycuick, 1990; Pennycuick, 2001; Bruderer and Boldt, 2001; Hedenström et al., 2002; Alerstam et al., 2007). To calculate equivalent sea level wingbeat frequency for flap-gliding flyers, we corrected for the increase in wingbeat frequency with lower air density by multiplying the wingbeat frequencies by $\sigma^{3/8}$.

Because bounding flyers are pulling up in the flapping phase, they experience an additional value of gravity, which grows by the inverse of the power fraction. Consequently, equivalent sea level wingbeat frequency was calculated from the wingbeat frequency by multiplying it by $\sigma^{3/8} q^{0.5}$ following Eqn 10 in Pennycuick (Pennycuick, 2001).

Although gravity changes with altitude, it does not play an important role here, because an altitudinal difference of 3000 m in flight altitude would result in a decrease of gravity of about 0.1%, which is negligible in comparison with the effect of air density, i.e. altitude (see Results).

We compared the body mass of different songbird species mist-netted in close vicinity to the radar site during spring and autumn seasons to identified possible differences in their body mass, which might have an influence on birds' wingbeat frequency. The eighth most common songbirds were subalpine warbler (*Sylvia cantillans*, Pallas 1764), orphean warbler (*Sylvia hortensis*, Gmelin 1789), willow warbler (*Phylloscopus trochilus* Linnaeus 1758), reed warbler (*Acrocephalus scirpaceus*, Hermann 1804), garden warbler (*Sylvia borin*, Boddaert 1783), redstart (*Phoenicurus phoenicurus*, Linnaeus 1758), nightingale (*Luscinia megarhynchos*, Brehm 1831) and spotted flycatcher (*Muscicapa striata*, Pallas 1764).

Predicted effect of air density on air speed

According to Pennycuick (Pennycuick, 1997; Pennycuick, 2001) the benchmark air speed of a given bird depends on body mass, gravity, frontal area, wing span, drag coefficient of the body, induced power and air density and is an equivalent sea level value. The equivalent sea level air speed (V_{SL}) is a function of the measured true air speed (V_t) and the ratio (σ) of ambient (ρ) to standard air density (ρ_{SL}):

$$V_{SL} = V_t \sigma^{0.5}, \quad (10)$$

after Eqn 5 in Pennycuick (Pennycuick, 2001).

We reduced air speed to the equivalent sea level air speed for the flap-gliding flyers by multiplying the air speed by $\sigma^{0.5}$ (Pennycuick, 1989; Pennycuick, 2001; Hedenström et al., 2002) and for the bounding flyers by $\sigma^{0.5} q^{0.5}$ (Pennycuick, 2001).

Statistics

In regressions the residual analyses did not show any serious deviation from normal distribution. Therefore, data were not transformed. Statistics were calculated using the statistical software package R (R Development Core Team, 2008).

RESULTS

Detection probability

In general, large birds have lower wingbeat frequencies than small birds but higher air speeds (Pennycuick, 1969; Pennycuick, 1990; Welham, 1994; Bruderer and Boldt, 2001; Pennycuick, 2001; Alerstam et al., 2007; Schmidt-Wellenburg et al., 2007), and large birds are detected at farther distances than small ones by radar (Bruderer, 1997). Because we considered birds only up to a distance

of 3 km from the radar, we needed to confirm that detection probability was nearly constant for large and small birds within this range, otherwise there would be an artificial decrease in the wingbeat frequency and an increase in the air speed over distance. To test this, we considered only birds of both flight styles from low altitudes, so that we can rule out an effect of altitude here. Because we set wingbeat frequency and air speed in relation to air density and not altitude directly, we selected only birds that encountered a high air density above the 95% quantile of the encountered air density of all birds. Thus, only birds from low altitudes were considered; corresponding altitudinal ranges were given.

Considering such flap-gliding flyers, wingbeat frequency did not vary with distance in either recording mode (linear regression fixed beam: $F_{1,8}=0.2$, $P=0.7$, $N=10$, distance range=330–2490 m, altitudinal range a.g.l.=640–906 m; tracking: $F_{1,73}=0.1$, $P=0.7$, $N=75$, distance range=622–2735 m, altitudinal range a.g.l.=600–1392 m). There was also no dependence of distance on detected wingbeat frequency in bounding flyers (linear regression fixed beam: $F_{1,87}=1.9$, $P=0.2$, $N=89$, distance range=330–2940 m, altitudinal range a.g.l.=473–874 m; tracking: $F_{1,115}=0.3$, $P=0.6$, $N=117$, distance range=405–2514 m, altitudinal range a.g.l.=508–1139 m). Air speed did change over distance neither in tracked flap-gliding (linear regression: $F_{1,73}=0.0$, $P=1.0$, $N=75$, distance range=622–2735 m, altitudinal range a.g.l.=600–1392 m) nor in bounding flyers (linear regression: $F_{1,115}=1.5$, $P=0.2$, $N=117$, distance range=405–2514 m, altitudinal

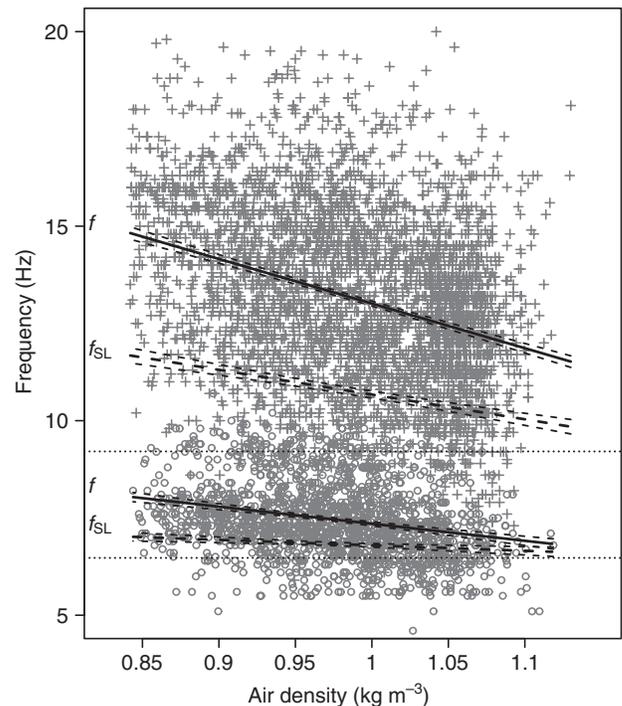


Fig. 2. Observed wingbeat frequencies (f) plotted against air density of flap-gliding (o) and bounding (+) flyers. For flap-gliding flyers the slope of wingbeat frequency is $-4.39 \text{ Hz kg}^{-1} \text{ m}^{-3}$, $F_{1,1667}=103.4$, $P<0.0001$, $N=1669$ (solid lower line) and for bounding flyers is $-11.47 \text{ Hz kg}^{-1} \text{ m}^{-3}$, $F_{1,4096}=525.6$, $P<0.0001$, $N=4098$ (solid upper line). Reducing true wingbeat frequency to equivalent sea level values (f_{SL}) produced slopes of $-1.40 \text{ Hz kg}^{-1} \text{ m}^{-3}$, $F_{1,1697}=12.54$, $P<0.0001$, $N=1699$ for flap-gliding (lower broken line) and $-6.36 \text{ Hz kg}^{-1} \text{ m}^{-3}$, $F_{1,1372}=114.7$, $P<0.0001$, $N=1374$ for bounding flyers (upper broken line). Thin broken lines show the 95% confidence bands around regressions. The dotted lines represent the expected lines for the equivalent sea level wingbeat frequencies for flap-gliding (lower) and bounding (upper) flyers.

range a.g.l.=508–1139 m). This lack of a decrease in wingbeat frequency or an increase in air speed over distance confirmed that detection probability was constant within 3000 m from the radar. Because there are no differences between recording modes in the comparisons made above, we pooled the data accordingly.

Wingbeat frequency in relation to air density

In flap-gliding flyers, the wingbeat frequency decreased significantly with air density (linear regression: $F_{1,1667}=103.4$, $P<0.0001$, $N=1669$, slope= $-4.39 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI = -5.23 to -3.54 ; Fig. 2) and also in bounding flyers (linear regression: $F_{1,4096}=525.6$, $P<0.0001$, $N=4098$, slope= $-11.47 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI = -12.45 to -10.49 ; Fig. 2). The decrease in wingbeat frequency with air density was significantly more pronounced in bounding than in flap-gliding flyers (Figs 2 and 3), because their corresponding 95% CI did not overlap.

Equivalent sea level wingbeat frequency in relation to air density

Wingbeat frequencies were adjusted to the equivalent sea level values but the correlations with air density remained: flap-gliding flyers (linear regression, wingbeat frequency: $F_{1,1697}=12.54$, $P<0.001$, $N=1699$, slope= $-1.40 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI = -2.18 to -0.63 ; Fig. 2) and bounding flyers (linear regression: $F_{1,1372}=114.7$, $P<0.0001$, $N=1374$, slope= $-6.36 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI = -7.52 to -5.19 ; Fig. 2). The decrease in equivalent sea level wingbeat frequency was significantly stronger in bounding than in flap-gliding flyers (Figs 2 and 3).

Air speed in relation to air density

Air speed of flap-gliding flyers increased significantly with decreasing air density (linear regression: $F_{1,1479}=48.87$, $P<0.0001$, $N=1481$,

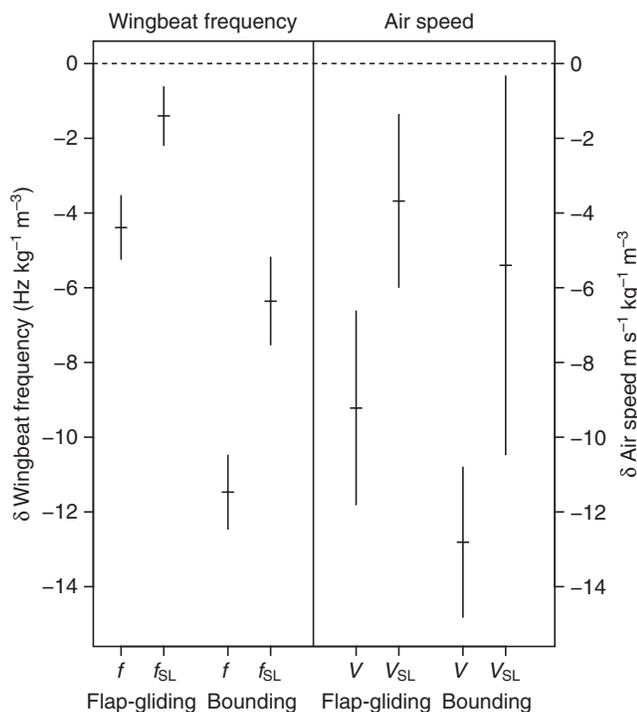


Fig. 3. 95% confidence intervals for the decrease of true wingbeat frequency (f) and its equivalent sea level values (f_{SL}) (on the left) and of true air speed (V) and its equivalent sea level values (V_{SL}) (on the right) with air density for flap-gliding and bounding flyers. Non-overlapping confidence intervals indicate significant differences between the slopes.

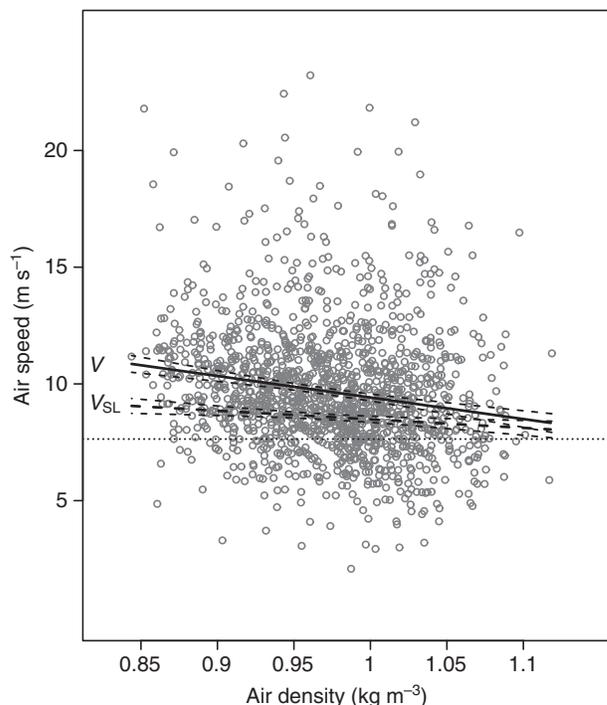


Fig. 4. Observed air speed (V) plotted against air density of flap-gliding flyers (tracking mode only). The slope of air speed is $-9.22 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, $F_{1,1479}=48.87$, $P<0.0001$, $N=1481$ (solid line). Reducing true air speed to the equivalent sea level (V_{SL}) produced a slope of $-3.68 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, $F_{1,1479}=9.80$, $P=0.0018$, $N=1481$ (broken line). Thin broken lines show the 95% confidence band around regressions. The dotted line represents the expected line for the equivalent sea level air speed for flap-gliding flyers.

slope= $-9.22 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, 95% CI = -11.80 to -6.63 ; Fig. 4) and also of bounding flyers (linear regression: $F_{1,2314}=157.9$, $P<0.0001$, $N=2316$, slope= $-12.81 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, 95% CI = -14.81 to -10.81 ; Fig. 5). The decrease in air speed with air density tended to be stronger in bounding than in flap-gliding flyers (compare Fig. 4 with Fig. 5) but not significantly owing to overlapping 95% CI (Fig. 3).

Equivalent sea level air speed against air density

When adjusting air speeds to equivalent sea level values significant relationships remained for flap-gliding flyers (linear regression: $F_{1,1479}=9.80$, $P=0.0018$, $N=1481$, slope= $-3.68 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, 95% CI = -5.98 to -1.37 ; Fig. 4) and for bounding flyers (linear regression: $F_{1,192}=4.4$, $P=0.04$, $N=194$, slope= $-5.40 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, 95% CI = -10.46 to -0.34 ; Fig. 5).

DISCUSSION

Birds in cruising flight increased their wingbeat frequency and air speed with decreasing air density as expected by flight mechanical theory (Pennycuik, 2001). When adjusting wingbeat frequencies of birds to the equivalent sea level values, they still increased significantly with decreasing air density and, hence, are more pronounced than theoretically predicted (Pennycuik, 2001). In the present study, we demonstrate that the response of wingbeat frequency and air speed adjustment to air density is generally more distinct in bounding flyers than in flap-gliding flyers.

Sources of possible errors

We could rule out that differences in detection probability between small and large birds have impeded our results. A bird's wingbeat

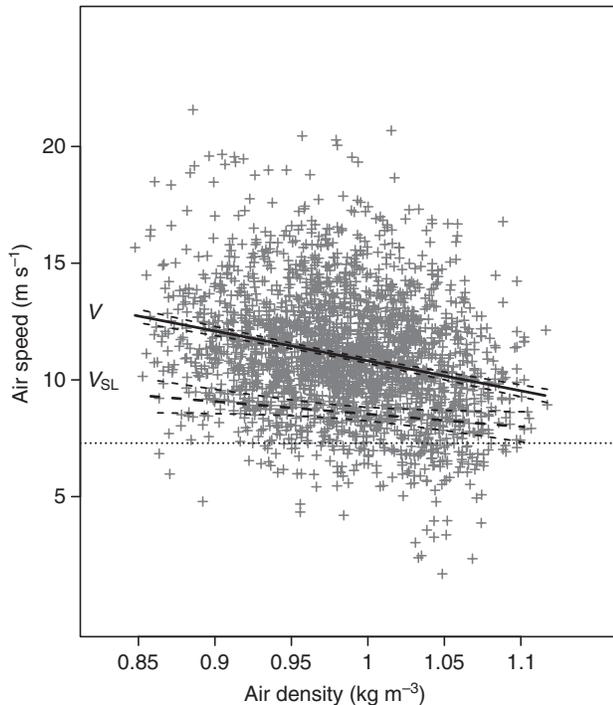


Fig. 5. Observed air speed (V) plotted against air density of bounding flyers detected in the tracking mode. The slope of true air speed is $-12.81 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, $F_{1,2314}=157.9$, $P<0.0001$, $N=2316$ (solid line). Reducing true air speed to the equivalent sea level air speed (V_{SL}) produced a slope of $-5.40 \text{ m s}^{-1} \text{ kg}^{-1} \text{ m}^{-3}$, $F_{1,192}=4.4$, $P=0.04$, $N=194$ (broken line). Thin broken lines show the 95% confidence band around regressions. The dotted line represents the expected line for the equivalent sea level air speed for bounding flyers.

frequency is expected to decrease relative to its body size (mass) (Rayner, 1979; Pennycuick et al., 1996; Schmidt-Wellenburg et al., 2007) whereas air speed is expected to increase (Pennycuick, 1969; Pennycuick, 1990; Welham, 1994; Bruderer and Boldt, 2001; Pennycuick, 2001; Hedenström et al., 2002; Alerstam et al., 2007). A bird's cruising flight altitude is predicted to be lower in larger than in smaller birds, because water loss and costs of climbing are expected to increase with size (Hedenström and Alerstam, 1992; Klaassen et al., 1999; Green and Alerstam, 2000; Hedenström et al., 2002; Green, 2003). This raised the question whether the observed decrease in wingbeat frequency with air density (Fig. 2) might be spurious due to a higher ratio of small to large birds at lower than at higher air densities. The vast majority of flap-gliding flyers crossing the Western Sahara consisted of swifts. Only five swift species could have passed our study site, i.e. common (*A. apus*), pallid (*A. pallidus*), alpine (*A. melba*), house [*Apus affinis* (Gray 1830)] and white-rumped [*Apus caffer* (Liechtenstein 1823)] swifts. The latter two could have occurred only in very low numbers because of their restricted breeding ranges and small population sizes in Spain and Morocco (Cramp, 1985), and were never visually identified crossing our site. Alpine swifts passed the study site infrequently (38 alpine swifts were visually identified during diurnal migration but 2902 common or pallid swifts were identified). Hence, the sample of flap-gliding flyers consisted of mainly two species, common and pallid swifts, having nearly the same body size (Cramp, 1985), wingbeat frequency (H.S. and F.L., unpublished data) and air speed (Bruderer and Boldt, 2001). In flap-gliding flyers, the observed effect of air density on wingbeat frequency and air speed

is, consequently, a real response of the birds (Figs 2 and 4) and not an artefact owing to larger and, therefore, more slowly flapping birds closer to the ground.

Bounding flyers passing our study site comprised more species than flap-gliding flyers. Based on bird species mist-netted in close vicinity of the radar site and during the same time as the radar study, we estimated that at least 34 songbird species, hoopoe and scops owl were included in the group of bounding flyers passing our study site. Although body mass of mist-netted bounding flyers ranged from 4.4 g to 80.0 g [14.4 ± 7.1 (mean \pm s.d.), $N=1938$], 99% of birds' body mass were below 40 g [14.0 ± 5.6 g (mean \pm s.d.), $N=1919$]. Because climbing rate, which might influence the chosen flight altitude, decreases with body mass, larger birds might tend to migrate at lower altitudes than smaller birds (Hedenström and Alerstam, 1992). However, Hedenström and Alerstam showed that in three species of bounding flyers, having a body mass range of 10–60 g, the climbing rate did not differ significantly. In our study body mass range of the bounding flyers was even smaller (Hedenström and Alerstam, 1992). Hence, there is good evidence that our bounding flyers would have similar climbing rates and the same potential to use high altitudes for migratory flights. This assumption seems reasonable, because even much larger birds, like herons and gulls, perform cruising flights at altitudes 4500 m a.s.l. (Liechti and Schaller, 1999; Schmaljohann et al., 2008b), which is higher than the maximum flight altitude considered in this study. Furthermore, bounding flyers did not prefer different flight altitudes due to differences in body size and mass but simply selected the altitude with the best meteorological conditions for their migratory flights (Bruderer et al., 1995b; Liechti et al., 2000; Schmaljohann et al., 2008c; Schmaljohann et al., 2009). Although we cannot categorically exclude any size effect on flight altitude, the substantial changes in wingbeat frequency and air speed are a result of behavioural adjustments of the birds to changing meteorological conditions, mainly air density.

Wingbeat frequency

According to flight mechanical theory (Pennycuick, 2001), flap-gliding and bounding flyers significantly increased their wingbeat frequency with decreasing air density (Fig. 2), although the increase was more pronounced than predicted (Figs 2 and 3). We first discuss a possible seasonal effect in our data set, and then go into detail about the general flight behaviour and how birds could adjust their flight behaviour to varying air densities by other means than wingbeat frequency.

Birds are highly selective for favourable wind conditions during migratory flights (Liechti, 2006; Schmaljohann et al., 2008c; Schmaljohann et al., 2009). The prevailing trade and anti-trade wind system over western Africa leads to migration at high altitudes in spring but low altitudes in autumn (Schmaljohann et al., 2007; Schmaljohann et al., 2008c; Schmaljohann et al., 2009). In autumn, songbirds passing our study site had covered a longer distance (about 1500 km) across the Sahara than in spring (about 300 km) so autumn migrants might have lower fuel reserves than spring migrants. Because wingbeat frequency increases with body mass, which was demonstrated theoretically (Pennycuick, 1990; Pennycuick, 1996; Pennycuick, 2001) and empirically (Chai et al., 1996; Bruderer and Boldt, 2001; Tobalske, 2001; Altshuler and Dudley, 2003; Schmidt-Wellenburg et al., 2007), fat spring migrants might have a somewhat higher wingbeat frequency than lean autumn migrants. We suppose, therefore, that at least a part of the difference between the predicted and observed wingbeat frequencies could be a seasonal effect because of differences in the body masses of the migrants. To test this hypothesis, we compared body mass, corrected for size by

Table 1. Body size corrected body mass (body mass divided by wing length) of the eighth most common songbirds mist-netted in close vicinity to the radar site during spring 2003 and 2004 and autumn 2003

	Subalpine warbler <i>Sylvia cantillans</i>	Orphean warbler <i>Sylvia hortensis</i>	Willow warbler <i>Phylloscopus trochilus</i>	Reed warbler <i>Acrocephalus scirpaceus</i>	Garden warbler <i>Sylvia borin</i>	Redstart <i>Phoenicurus phoenicurus</i>	Nightingale <i>Luscinia megarhynchos</i>	Spotted flycatcher <i>Muscicapa striata</i>
N_{spring}	730	493	305	156	161	126	49	12
N_{autumn}	21	12	15	119	18	13	21	10
$\alpha_{\text{Bonferroni}}$	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063	0.0063
P -value	0.0000	0.0039	0.0213	0.5959	0	0.2516	0	0.0517
W	2385	1514	1481	8935	455	660	44	30
Body mass _{spring} (g)	10.3±1.5	21.0±2.7	8.5±1.4	11.2±1.5	21.6±3.2	14.8±2.3	23.9±2.9	15.2±2.1
Body mass _{autumn} (g)	8.7±0.9	19.0±1.9	7.7±1.0	10.9±1.2	17.6±1.7	14.2±2.0	18.3±2.3	12.9±1.9

We applied multiple tests and consequently, decreased the alpha-level according to the Bonferroni-correction. Alpha-level was $0.05/8=0.006$. P -values lower than the Bonferroni-corrected alpha-level; therefore, significant differences between body size corrected body mass between spring and autumn, are in bold. Wilcoxon signed rank tests were applied throughout. Body mass not corrected for body size are given in the two lowest rows.

dividing by wing length, of the eighth most common mist-netted songbirds at the ringing area in close vicinity of the radar site: no flap-gliding flyers were mist-netted. Half of these songbird species were indeed heavier in spring than in autumn (Table 1). To investigate whether this difference might explain the stronger increase in the equivalent sea level frequency than predicted, we calculated regressions of sea level equivalent frequency against air density for autumn and both spring seasons separately. In autumn, the relationship did not remain between sea level equivalent frequency and air density (linear regression: $F_{1,727}=1.66$, $P=0.20$, $N=729$, slope= $1.43 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI= -0.75 – 3.61) whereas in spring it remained nearly as strong as before (linear regression: $F_{1,643}=17.12$, $P<0.0001$, $N=645$, slope= $-4.16 \text{ Hz kg}^{-1} \text{ m}^{-3}$, 95% CI= -6.13 to -2.18). Because of the clear result in spring and only a body mass difference in four out of the eight songbird species, a significant seasonal effect on our analysis is unlikely. We suppose that the lacking relationship in autumn was caused by the restricted height range in autumn (75% of data below 1000 m a.g.l.) compared with spring (75% above 1800 m a.g.l.).

To compensate for decreasing air density, birds with an intermittent flight style can adjust either their wingbeats (frequency, stroke amplitude and/or angle of attack) or increase their power fraction, i.e. add some flaps and reduce the pause phase. We are only aware of studies from Dudley's lab dealing intensively with wingbeat frequencies and varying air densities (Chai and Dudley, 1995; Chai and Dudley, 1996; Chai et al., 1996; Chai et al., 1997; Chai et al., 1998; Altshuler and Dudley, 2003). The outcomes of these studies seem difficult to compare with our data, because (a) hummingbirds were in hovering and not cruising flight so that hummingbirds did not have to produce thrust, (b) the bird's morphology, wing kinematics and the overall flight style of hummingbirds and birds considered in the present study are different (Pennycuik, 1975; Tobalske et al., 2003), and (c) hummingbirds are supposed to modulate their wingbeat frequency only slightly (reviewed by Chai et al., 1998). Nevertheless, they demonstrated clearly that wingbeat frequency remains relatively constant with decreasing air density whereas stroke amplitude increased considerably. Thus, we must also be aware that other birds might compensate for a decrease in air density by an increase in their stroke amplitude. This might especially apply for flap-gliding flyers like common swifts. While flying under constant atmospheric conditions in a wind tunnel, they increased their air speed by an increase in their stroke amplitude and not in their wingbeat frequency. Because the speed of muscle contraction remains constant in swifts, their wingbeat frequency decreased with higher stroke amplitude and,

thus, higher air speed (Henningsson et al., 2008). We found the same phenomenon (increase in air speed with a decrease in wingbeat frequency) in our data, when correlating sea level equivalent values of air speed and wingbeat frequency (Pearson correlation: $t_{1,1479}=-4.8$, $P<0.0001$, $N=1481$, $R=-0.12$, 95% CI= -0.17 to -0.07). However, whether this significant correlation is superimposed by the well known effect of body size on air speed and wingbeat frequency remained unknown to us (Pennycuik, 1969; Rayner, 1979; Pennycuik, 1990; Welham, 1994; Pennycuik et al., 1996; Bruderer and Boldt, 2001; Pennycuik, 2001; Hedenström et al., 2002; Alerstam et al., 2007; Schmidt-Wellenburg et al., 2007). By contrast, we must be aware that in the wind tunnel an increase in air speed implies an increase in power output (within the range above the speed of minimum power) whereas an increase in air speed with decreasing air density might occur even when power output remains constant. If swifts contracted their flight muscles with a constant power (rate of ATP consumption), the downstroke speed would increase with decreasing air density (reduced drag). Maintaining this regime also in the upstroke would result in a higher wingbeat frequency (and thus air speed) without any increase in power output.

Intermittent flight style can be regarded as a trade-off between generating the necessary lift and thrust but minimising drag produced by the flapping wings (profile drag). Quantitative analyses on the flapping wing have just begun (e.g. Hedenström and Spedding, 2008), and whether power fraction should change or not with respect to air density is not yet solved. In our bounding flyers, power fraction decreased significantly with air density (linear regression: $F_{2,1235}=5.6$, $P=0.018$, $N=1237$, slope= $-0.08 \text{ kg}^{-1} \text{ m}^{-3}$, 95% CI= -0.14 to -0.01). With decreasing air density birds are forced to move their wings faster through the air to provide the same amount of lift. Bounding flyers could either increase flapping frequency or the flapping phase. Now, we have found that both are true and that the flapping frequency increases even more than expected. This is surprising but indicates that other parameters might have changed like a decrease in stroke amplitude or angle of attack.

We believe that the lack of predicting the full increase in wingbeat frequency observed is possibly caused by: (1) insufficient knowledge of the estimated coefficients with respect to lift and drag, (2) our ignorance about birds' possible aerodynamic adjustments (stroke amplitude and angle, constant muscle contraction) other than wingbeat frequency, and (3) the subtle interaction of the forces in flap-bounding flight, e.g. wing area does not necessarily vary proportionally with body mass (willow warbler, *Phylloscopus trochilus*, and chiffchaff, *Phylloscopus collybita*) (Tiainen and Hanski, 1985). Although we

are convinced that bounding flyers would use the altitudinal range regardless of their body mass, wing morphology and wing load, birds might adjust their wingbeat frequency to varying air densities differently in respect of their specific wing morphology or load. These three arguments might explain the discrepancy between the observed and predicted increase in wingbeat frequency with decreasing air density.

Air speed

As predicted by flight mechanical theory (Pennycuik, 2001), birds significantly increased their air speed with decreasing air density (Fig. 3–5), which is generally in line with other studies where air speed increased with altitude (Bruderer, 1971; Alerstam and Gudmundsson, 1999; Hedenström et al., 2002).

To quantitatively compare the amount of response in air speed of these three studies with our results, we calculated a linear regression of air speed against altitude instead of air density for our flap-gliding (linear regression: $F_{1,1479}=70.8$, $P<0.0001$, $N=1581$, slope= $1.0\text{ m s}^{-1}\text{ km}^{-1}$, 95% CI= $0.75\text{--}1.21$) and bounding flyers (linear regression: $F_{1,2314}=242.6$, $P<0.0001$, $N=2316$, slope= $1.37\text{ m s}^{-1}\text{ km}^{-1}$, 95% CI= $1.20\text{--}1.54$). Based on the predicted mean air speed at sea level of 7.9 m s^{-1} and 8.6 m s^{-1} and its rise of about 1.0 m s^{-1} and 1.37 m s^{-1} per km in altitude, birds increased their air speed by 13% and 16% per km in altitude, respectively. These values are considerably higher than the observed increases in air speed of about 5% (Hedenström et al., 2002) and 2.5% (Alerstam and Gudmundsson, 1999) in Arctic bird migrants but closer to the increase of 12% observed in central Europe (Bruderer, 1971). One source of difference might be that flapping, flap-gliding and bounding flyers were analysed together in these three radar studies. However, if we combine these three flight styles of our data together, air speed will increase even stronger per km in altitude, i.e. by about 20% (linear regression: $F_{1,5629}=606.8$, $P<0.0001$, $N=5631$, slope= $1.67\text{ m s}^{-1}\text{ km}^{-1}$, 95% CI= $1.54\text{--}1.80$, mean air speed at sea level= 8.0 m s^{-1}).

An important difference might be that Bruderer (Bruderer, 1971), Alerstam and Gudmundsson (Alerstam and Gudmundsson, 1999) and Hedenström et al. (Hedenström et al., 2002) related air speed with altitude and not air density. In general, the decrease in air temperature with altitude is more pronounced with increasing latitude. If air pressure is constant, air density increases with decreasing temperature, i.e. cold air is denser than warm air. Without these measures we cannot decide whether or not differences in atmospheric conditions could explain the discrepancies between our results and the former studies.

For flap-gliding flyers our calculated equivalent sea level air speed of 7.9 m s^{-1} corresponds well to the predicted maximum range speed (V_{mr}) of 8.6 m s^{-1} and 9.1 m s^{-1} for common and pallid swifts, respectively, presented by Bruderer and Boldt (Bruderer and Boldt, 2001). Considering the theoretically assumed maximum range speed of bounding flyers encountered in abundance at our study site ($N=998$), for which such data were available (14 species) in Bruderer and Boldt (Bruderer and Boldt, 2001), we computed the weighted maximum range speed, which averaged 10.2 m s^{-1} . This was slightly higher than the equivalent sea level air speed of 8.6 m s^{-1} calculated from our data.

Some general variation in air speed might be due to the limited information on wind conditions at the bird's flight time and altitude. To increase the accuracy in this respect, we analysed a sub-sample by reducing the allowed temporal and spatial distance between bird records and their corresponding wind measurements (vertical distance $<50\text{ m}$, horizontal distance $<2\text{ km}$ and temporal $<60\text{ min}$); thus, air speed measured by radar was more precise. Also in this

sub-sample [bounding flyer's air speed increased with decreasing air density (linear regression for such bounding flyers: $F_{1,324}=35.7$, $P<0.0001$, $N=326$, slope= $-14.0\text{ Hz kg}^{-1}\text{ m}^{-3}$, 95% CI= $-18.6\text{ to }-9.4$)] the conclusion remained the same but the smaller sample size generated lower statistical power.

In both groups the increase in air speed was higher than predicted, which goes along with the stronger than predicted increase in wingbeat frequency. Air speed in bounding flyers was positively correlated with power fraction (linear regression: $F_{2,192}=518.7$, $P<0.0001$, $N=194$, slope= 5.33 m s^{-1} , 95% CI= $2.9\text{--}7.8$), i.e. bounding flyers at high altitudes had higher speeds and a elevated proportion of flapping time than at low altitudes.

Difference between flap-gliding and bounding flyers

Although birds of both flight styles showed a similar response to changes in air density, the magnitude of their responses differed. Bounding flyers increased their wingbeat frequency and air speed significantly more than flap-gliding flyers (Fig. 3). The reason for this difference seems manifold. First, bounding flyers experience a higher acceleration during the flapping phase than flap-gliding flyers and, hence, have an overall higher wingbeat frequency and air speed (Pennycuik, 2001). Second, our data of flap-gliding flyers were dominated by two very similar species (*A. apus* and *A. pallidus*), which mainly excludes effects due to differences between species. In flap-bounding flyers, many more species were involved consequently producing a higher variation in body mass, wing shape and wing load, which might affect the comparison with the flight mechanical theory.

Bird migrants crossing the Sahara corroborated the predicted increase of wingbeat frequency with decreasing air density and revealed the predicted difference in this increase between flap-gliding and bounding flyers. Moreover, the effect of air density on wingbeat frequency was higher than predicted. Fundamental aerodynamics explains well the dependency of lift force on lift coefficient (Lighthill, 1977; Rayner, 1988). If this lift coefficient is equal among bird species (Lighthill, 1977; Alerstam et al., 2007), birds' migratory flight speed is supposed to scale with body mass and wing load. Because larger birds tend to have a proportionately larger wing area and span, resulting in a lower wing load, than smaller birds (Rayner, 1977; Rayner, 1995), migratory flight speeds and wingbeat frequencies did differ from their theoretical predictions. Furthermore, phylogeny seemed to explain a high variation of such deviations from theoretically predicted flight speeds (Alerstam et al., 2007) and possible wingbeat frequencies. It seems that evolutionary and ecological flight adaptations have an influence on the flight behaviour of birds (Alerstam et al., 2007), which might explain why air speed and wingbeat frequency did increase more strongly than predicted by fundamental aerodynamic models. The field data presented here might stimulate studying bounding flight under different air densities to disentangle the interactions of lift, thrust, and the different drag components in relation to optimal flight speed.

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