ANIMAL BEHAVIOUR, 2008, **76**, 1133–1138
doi:10.1016/j.anbehav.2008.05.024

Available online at www.sciencedirect.com
ScienceDirect

ARTICLES

Sustained bird flights occur at temperatures far beyond expected limits

HEIKO SCHMALJOHANN, BRUNO BRUDERER & FELIX LIECHTI
Swiss Ornithological Institute

(Received 18 February 2008; initial acceptance 8 April 2008;
final acceptance 25 May 2008; published online 21 July 2008; MS. number: D-08-00106)

Migratory birds deposit fat and protein before passing ecological barriers and must economize these during such crossings. Birds crossing the western Sahara during autumn face a trade-off between cold and humid air along with head winds at high altitudes versus warm and dry air along with tail winds at low altitudes. Since water loss rate increases with temperature, migrants should avoid warm and dry air to save water and hence fly at high altitudes. By quantifying nocturnal songbird migration across the western Sahara with radar, we found that more than 60% of the songbirds migrated below 1000 m above ground level. Thus, the majority of songbirds performed sustained migratory flights in much warmer and drier conditions than predicted (weighted means: 30 °C; relative humidity: 27%; water vapour density: 7.8 g/m^3). Based on the metabolically available water from fat and protein catabolism, we estimated the maximum possible overall water loss rate of a flying model bird, the garden warbler, *Sylvia borin*, for the entire Sahara crossing at 0.29 g/h. This is considerably lower than water loss rates for the same model bird passing our study site, 0.62 g/h at 30 °C, based on applied calculations of physiological studies. Our results clearly show that migrating songbirds can fly at much higher temperatures, and have considerably lower water loss rates, than predicted. This new insight based on observations under natural conditions will have substantial impact on the development of new physiological models for birds and other animals with restricted access to water.

Keywords: bird; flight; garden warbler; humidity; migration; Sahara; *Sylvia borin*; temperature; water loss

Migratory birds crossing large ecological barriers, such as deserts or oceans, have to prepare for extended periods of fasting. Therefore, they accumulate large amounts of fat and increase their flight muscles in advance (Jenni & Jenni-Eiermann 1998). The amounts of energy and water consumed during such passages depend on the size of the barrier, but are highly influenced by wind (Liechti 2006), temperature and humidity (Torre-Bueno 1978; Biesel & Nachtigall 1987; Carmi et al. 1992; Klaassen et al. 1999; Kvist 2001; Klaassen 2004; Engel 2005). Since these parameters change with time and space, bird migrants are thought to adjust their energy expenditure and water loss by choosing the right time and altitude for their flight (Carmi et al. 1992; Bruderer et al. 1995; Klaassen et al. 1999; Klaassen 2004; Liechti 2006). Most songbirds migrate nocturnally across the Sahara (Schmaljohann et al. 2007), thus avoiding the highest diurnal temperatures and reducing water loss (Klaassen 2004). In autumn, favourable winds (trade winds) coincide with high nocturnal temperatures and low humidity at low altitudes, whereas low temperatures occur with unfavourable winds (antitrades) and high humidity at high altitudes. Consequently, birds face a trade-off between minimizing energy expenditure and water loss. Physiological models (Carmi et al. 1992; Klaassen et al. 1999) and several studies (Tucker 1968; Torre-Bueno 1978; Biesel & Nachtigall 1987; Wolf & Walsberg 1996; Giladi & Pinshow 1999; Tieleman et al. 1999, 2002b; Williams & Tieleman 2000;

Correspondence and present address: H. Schmaljohann, Institute of Avian Research, An der Vogelwarte 21, 26386 Wilhelmshaven, Germany (email: heiko.schmaljohann@ifv.terramare.de). B. Bruderer and F. Liechti are at the Swiss Ornithological Institute, Luzernerstrasse 6, 6204 Sempach, Switzerland.

0003–3472/08/$34.00/0

Kvist 2001; Michaeli & Pinshow 2001; Engel 2005) have shown that, in general, water loss increases with temperature. According to these results, immense water loss would prevent birds from flying for longer than 2–4 h at high temperatures (Biesel & Nachtigall 1987; Giladi & Pinshow 1999; Ward et al. 1999; Michaeli & Pinshow 2001; Engel 2005). In addition, in most experiments birds refrained from flying at high temperatures, that is, in most cases above 25 °C (Torre-Bueno 1976; Biesel & Nachtigall 1987; Ward et al. 1999; Engel 2005). Based on this current knowledge, we would predict that (1) birds do not perform sustained migratory flights in air layers of such high temperatures along with low relative humidity and (2) they would cross the Sahara at high altitudes in autumn.

We quantified the altitudinal distribution of songbird migration by radar during autumn migration (Schmaljohann et al. 2007). We then chose the garden warbler, *Sylvia borin*, as a model songbird and calculated its water loss rate at the meteorological conditions encountered when actually crossing the Sahara based on our current physiological knowledge (Torre-Bueno 1976, 1978; Biesel & Nachtigall 1987; Carmi et al. 1992; Adams et al. 1997; Giladi & Pinshow 1999; Ward et al. 1999; Kvist 2001; Michaeli & Pinshow 2001; Engel 2005). We compared this rate with the maximum possible water loss rate based on the metabolically available water of the model songbird given different fuel loads.

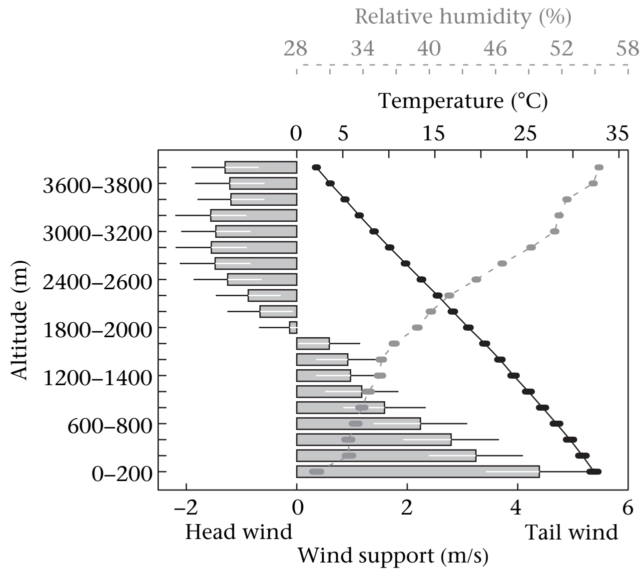

Figure 1. Altitudinal profiles of wind support (as tail wind component in grey bars), air temperature (unbroken line) and relative humidity (broken line) at Ouadâne above ground level around midnight ($N_{nights} = 62$). Means are shown ± SEM. The tail wind component was defined as cos (wind direction − main migration direction) × wind speed. The main migration direction was defined as the mean heading direction of tracked songbirds (177°, $\rho = 0.764$, $N = 1524$), which we simplified to 180°. Meteorological data were provided by nightly radiosonde measurements.

METHODS

Radar Study

Bird migration was quantified by a fixed-beam radar method (Schmaljohann et al. 2008) in Mauritania close to the oasis Ouadâne, about 500 km east of the Atlantic coast (20°56′N, 11°35′W, 420 m above sea level; 23 August to 24 October 2003). Songbirds passing our radar site had already covered about 1500–1700 km of the 2000 km Sahara crossing. We carried out radar measurements ($N = 484$) every hour on the hour at both low and high elevation angles (11° and 79°) to survey high and low altitudes with nearly the same effort. The recording time per measurement was 4 min and the detection range for songbirds was restricted to 7500 m (Schmaljohann et al. 2008). The radar beam was directed towards the west (270°), perpendicular to the main migration direction (Fig. 1). We considered only fixed-beam measurements from 2100 to 0100 hours GMT and thereby excluded the large number of songbirds departing after sunset; the altitudinal distribution of songbirds did not change after 0100 hours (unpublished data). The echo signature of each target crossing the beam was registered; this enabled us to distinguish between birds ($N_{echoes} = 2307$) and insects ($N_{echoes} = 13\,357$; Schmaljohann et al. 2008). To quantify songbird passage of nocturnal migrants, we selected only identified songbirds ($N_{echoes} = 1172$) according to their echo signature, that is, wing beat pattern, and we also excluded hirundines and corvids because they are not typical nocturnal songbird migrants. Migration intensity is given as migration traffic rate in birds/km per h per night and 200 m height intervals (Schmaljohann et al. 2008). Launching sounding balloons around midnight every night provided altitudinal profiles of air pressure, temperature, relative humidity and wind up to 6000 m above ground level (Bruderer 1994).

Model Songbird

We chose the garden warbler, a well-studied songbird of the Palaearctic–African migration system (Bairlein 1991), as a model songbird to estimate water loss rates. Model birds were provided with hypothetical fuel loads of 75, 100 and 125% of their lean body mass (15 g, Bairlein 1991) consisting of 95% fat and 5% protein (Jenni & Jenni-Eiermann 1998) prior to the Sahara crossing. The highest load is about the upper limit of recorded fuel loads in songbirds and would provide sufficient energy to fly far more than 2000 km without refuelling (Dierschke et al. 2005). Model birds were assumed to cross the 2000 km of desert with an intermittent flight strategy, that is, by nocturnal flights and diurnal rests but without feeding or drinking (Schmaljohann et al. 2007). Thus, fuel loads would decrease with ongoing migration across the Sahara. We assumed the shortest possible time to cross the Sahara was 4 nights of 10 h flights, because the average ground speed of singly tracked songbirds at our study site was about 50 km/h. Hence, for the 2000 km crossing, a songbird would need to fly for 40 h. This comprises 4 nights combined with three daytime rests of 14 h each (Schmaljohann et al. 2007).

To obtain the model bird's body mass when passing our study site, we used two methods. (1) Model birds were assumed to lose 1% of their body mass during a 1 h flight, which is a realistic figure for small songbirds (Delingat