

## Airspeed of the Song Thrush in relation to the wind during autumnal nocturnal migration

Alexandra Sinelschikova\*, Martin Griffiths, Michael Vorotkov, Victor Bulyuk & Casimir Bolshakov

*A. Sinelschikova, St. Petersburg State University, 7/9 Universitetskaya nab., St. Petersburg 199034, Russia.\* Corresponding author's e-mail: Sinelsch@mail.ru*

*M. Griffiths, Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent. CT2 7NS. UK*

*M. Vorotkov, The Central Astronomical Observatory at Pulkovo RAS, Pulkovskoye road. 65/1, 196140 Saint Petersburg, Russia*

*V. Bulyuk, C. Bolshakov, Biological Station "Rybachy", Zoological Institute of the RAS, Rybachy 238535, Kaliningrad reg., Russia*

*Received 28 March 2018, accepted 17 November 2018*

Birds possess behavioural and physiological adaptations which permit them to minimize time and energy expenditure during migration in a broad spectrum of winds, for instance, by varying their airspeed. Nocturnally migrating birds were recorded by an optical-electronic matrix system, which permitted recording their images and flight parameters in the dark. Among medium size birds, Song Thrushes (*Turdus philomelos*) were identified by their silhouette, linear size, wing-beat pattern, and phenology. The equivalent airspeed at sea level ( $V_{Eq}$ ) of the observed thrushes without wind assistance (mean value 14.4 m/s) was close to the maximum range speed ( $V_{mr}$ ) predicted from flight mechanical theory. This indicated an energy-selected migration strategy of the thrushes in autumn. The characteristic speed  $V_{mr}$  is wind-dependent: it increases with increasing velocity of head- and sidewinds. The airspeeds of the Song Thrushes showed a similar pattern of wind-dependence. The birds significantly increased their airspeed with increasing headwind component, relative to its value in still air, and decreased it with increasing tailwind component. We also found an effect of cross winds on airspeed: those birds that compensated for wind drift completely along the leading line of the Courish Spit, which coincided with general migratory direction, increased their airspeed with increasing sidewind component. The flying birds tended to maintain their airspeed close to the speed of minimal cost of transport under various winds. Nevertheless, this trend was more in qualitative than quantitative agreement with Pennycuick's flight model: migrating thrushes varied their airspeed in a smaller range than expected and their airspeed was significantly slower under calm and headwinds than the model predicted.



## 1. Introduction

The ground speed and airspeed of birds are basic parameters important for our comprehension of the time and energy required by birds to perform their seasonal migrations (Norberg 1990, Hedenström & Ålerstam 1995, Ålerstam & Hedenström 1998, Pennycuik 2008). Field observations have shown that migration occurs not only under favorable tailwinds and in calm weather, but also under side- and headwinds, which may hamper the birds or deflect them from their intended migratory routes (Liechti 2006, Baushev & Sinelschikova 2007, Karlsson *et al.* 2011). It is obvious that birds should possess behavioural and physiological adaptations which permit them to minimize time and energy expenditure during migration in a broad spectrum of winds, for instance, by varying their airspeed. The principle of such adaptations has theoretical support in flight mechanical theory.

The fundamental theoretical function that establishes the relationship between mechanical flight power and airspeed applied to a bird in flapping flight has been verified for over 40 years by empirical data (Tucker 1973, Rayner 1979, 1990, Pennycuik 1968, 1978, 2008). Two key characteristic speeds for a bird with given flight parameters, mass and fuel amount can be derived from this relationship:  $V_{mp}$  – the minimum power speed at which a bird can fly for the longest time on a given amount of energy, and  $V_{mr}$  – the maximum range speed (cruising speed) at which a bird can cover the longest distance on a given amount of energy.  $V_{mp}$  is constant under any wind while  $V_{mr}$  varies depending on wind direction and velocity: it decreases under tailwinds and increases under headwinds.

In order to reduce energy expenditure when meeting a variety of wind conditions migrating birds are expected to adjust their flight speed so that they increase their airspeed in headwinds and decrease it in tailwinds (Tucker & Schmidt-Koenig 1971, Pennycuik 1978, Rayner 1991). Birds are also expected to increase their airspeed with increasing sidewind component. This is considered to be a mechanism of compensation for wind displacement (birds shift their headings into the winds and increase airspeed) and energy minimization (Liechti *et al.* 1994, Liechti 1995).

Optimal migration theory (Ålerstam & Lind-

ström 1990) predicts optimal flight speeds of birds depending on the ecological situation and on which optimization criteria are used: energy or time (Hedenström & Ålerstam 1995, 1996, Ålerstam & Hedenström 1998). Speed  $V_{mp}$  is not considered to be relevant during migration. But  $V_{mr}$  is predicted to be optimal in autumn and when fuel economy during migration is of great importance. Time minimizing speed  $V_{mt}$  (which does not arise from the power curve directly but can be defined if the fuel deposition rate for a bird at stopover sites is taken into account) is predicted during spring migration or when the currency is the resulting overall migration speed.

The surest way to verify whether, during autumn or spring migration, birds adjust their speed in accordance to theoretical predictions, and to what extent they do, is to collect field data on free flying birds. Observation of the combined nocturnal bird stream confirmed that airspeed was faster under headwinds and slower under tailwinds (Bloch & Bruderer 1982, Liechti 1995, Hedenström *et al.* 2002, Nilsson *et al.* 2014). Tracking radar estimates of the speed of particular species were mainly recorded for diurnal migrants identified by telescope or binoculars (Bruderer & Boldt 2001, Mateos & Bruderer 2012), caught and released nocturnal migrants (Griffiths 1970, Bruderer & Boldt 2001); or for free flying birds equipped with radio-transmitters (Cochran & Wikelski 2005, Cochran *et al.* 2008).

The authors of these investigations noted that in some cases the behaviour of the treated birds could not be typical of their free migratory flight. In rare cases species identification is possible at night using tracking radar where the major criterion is the wing-beat pattern, such as in Common Swifts (*Apus apus*) in Scandinavia (Bäckman & Ålerstam 2001, Henningson *et al.* 2009, Karlsson *et al.* 2010). Hence, field data on the speed of free flying nocturnal passerine migrants of particular species are far from being numerous yet.

Application of the Optical-Electronic Matrix System and a complex of methods of nocturnal passage investigation made it possible to obtain the speed characteristics of free flying nocturnal migrants in autumn. Recorded medium sized passerine birds were assumed to be mainly thrushes and about 1/3 of them were assumed to be the Song Thrushes (*Turdus philomelos*) by their

wing-beat pattern, linear size and phenology. Our data allowed us to consider the following questions:

1) At what ground- and airspeeds do the Song Thrushes migrate in autumn? 2) Over what range do the birds vary their airspeed in relation to winds of different direction and velocity (tail-, head- and sidewinds)? 3) Can they maintain their airspeed close to the speed of the minimal cost of transport ( $V_{mr}$ ) under both tail- and head winds in autumn, in agreement with the theoretically predicted wind-dependence?

## 2. Methods

All the data were collected on the Courish Spit of the Baltic Sea (South-Eastern Baltic region) at the Biological Station Rybachy (55°05' N, 20°44' E) in September and October 2008–2010 and 2013.

### 2.1. Optical-Electronic Matrix System

Flight characteristics of the birds were received by the Optical-Electronic Matrix System (OEMS) especially designed for investigation of nocturnal migration. The detailed description of this device, advantages and limitations of its application for nocturnal migration study have already been published (Vorotkov *et al.* 2009, Bolshakov *et al.* 2010, 2013) and are available in open access (<https://www.zin.ru/journals/aeb/contents.asp>).

The OEMS permits the detection and recording of small nocturnal aerial targets flying within the range from 100 to 700–1,000m (depending on the bird's size). The device consists of the recording unit (optical-electronic system) and the illumination system. The flying targets were illuminated from the ground by narrow faint light from searchlights. In 2008–2010 we used white searchlight beams (5°, 250–400W) but in 2013 we used infrared light panels composed of light-emitting diodes (500 LEDs, each 1.5°, 3 W) with the wave length 805 nm which is invisible to birds (Hart 2001). The images of the birds are received by the recording unit.

The recording unit is installed vertically and consists of three channels with parallel optical axes. Each channel includes long-focus or wide-

angle objective and CCD matrix. Most of the measurements are based on the parallax computation of the altitude of the target simultaneously observed from two or three channels separated from each other at a fixed distance. On high-sensitivity CCD matrices long-focus channel forms instantaneous sequential images (silhouettes) of flying birds with, for example, open and folded wings aligned in a series of beats and pauses typical of passerine birds. The wide-angle channel permits tracking of birds up to 50 m. This allows for calculation of the target linear size from known distance and its angular dimensions; the ground speed from the angular displacement for the known time interval of exposition; the dynamic characteristics of the target and its orientation.

As a result, the main flight parameters of each recorded bird include altitude, linear size (wing span and body length), direction of flight (track), orientation of the body axis (heading), ground speed (GS), wing-beat frequency, number of wing-beats in each series of beats, duration of the pause between series of wing-beats, and the shape of the flight trajectory. The error of groundspeed and consequently airspeed estimation at the altitude of 500 m is 5% (Bolshakov *et al.* 2010).

There was no possibility to measure the vertical speed of the birds. To minimize the climbing or descending effect we considered only birds observed from 3h after sunset until –3h before sunrise. This is a period of transit passage when the fewest number of thrushes tends to take off or descend (Bolshakov *et al.* 2002), although some of them may go up or down all over the night.

For airspeed calculation we used wind profiling data collected by equipment similar to the OEMS (Bolshakov *et al.* 2010). The principle used here is computation of 3D coordinates of the helium filled pilot-balloon of fixed size with a light-emitting diode installed inside. Reliable wind data were available for the altitudes between 100 m and 700 m. We launched the balloons 2–3 times a night. Wind effect was estimated by tail-wind and sidewind components (twc and swc).

The measurements of True airspeed ( $V_{Tr}$ ) were converted to Equivalent airspeeds at sea level (Pennycuik 2008):  $V_{Eq} = V_{Tr} \sqrt{\sigma}$  but  $\sigma = \text{Airden}(h) / \text{Airden}(0)$ , where  $\text{Airden}(h)$  is the air density at the bird's altitude and  $\text{Airden}(0)$  is air density at 0 m a.s.l. (1.23 kg/m<sup>3</sup>). Finally, we compared the re-

ceived values of  $V_{Eq}$  with the model values of  $V_{mp}$  and  $V_{mr}$  at sea level.

## 2.2. Identification of the Song Thrushes

We assumed that the recorded flight characteristics belonged to a particular species, the Song Thrush, although the exact species identification of birds flying in darkness at considerable height is practically impossible by regular field methods. The criteria for identifying the Song Thrushes among the recorded images were as follows: shape of the silhouette “typical of passerine bird”, linear size (wing span (WS) and body length (BL)), wing-beat pattern (WBP), wing-beat frequency, and phenology. Data selection was rigorous. High demands were made of the quality of images.

We chose only birds with a straight trajectory of flight longer than 20 m, sharp silhouettes with clear heading which could be precisely measured, and WBP typical of the passerine transit flight – wing beat series separated by pauses. Further, we included the birds with real (measured) heading differing by no more than  $5^\circ$  from the calculated heading. This helped to avoid possible errors in the wind profiling data (gusts of wind). The OEMS was operated every night without rain, but nights with high air humidity or dense lower overcast, when white light beams could affect the bird’s behaviour (Bolshakov *et al.* 2013), were excluded. Birds that changed their ground speed during tracking within the field of vision were also excluded.

The thrushes and the Skylarks (*Alauda arvensis*) are the most numerous large passerines during autumn migration at the Courish spit (Bolshakov *et al.* 2002, 2010). The size of the Song Thrush (BL 20–24 cm, WS 33–38 cm) and the Redwing (*Turdus iliacus*) (BL 19–21 cm, WS 33–37 cm) strongly overlap. However, the passage of the Song Thrush begins in early September and that of the Redwings as late as October 5, and even as late as November 15 in some years (Bolshakov *et al.* 2002). From September until early October Song Thrushes make up to 96% of this group (Bolshakov *et al.* 2010). The passage of other species of thrushes usually begins after mid-October. These species are considerably larger than the Song Thrush and Redwing, making confusion unlikely. Blackbirds *Turdus merula* (BL 22–27 cm,

WS 37–44 cm) also have a very specific silhouette of a “bird in black”. The Fieldfare (*Turdus pilaris*) (BL 22–26 cm, WS 40–46 cm) and the Mistle Thrush (*Turdus viscivorus*) (BL 24–28 cm, WS 44–49 cm) do not migrate annually in considerable numbers. The wing spans of these species and the Song Thrush overlap, with only a 5–6% error when measuring birds flying above 500 m (Bolshakov *et al.* 2010).

A marked nocturnal passage of Skylarks occurs in October. These birds are a little smaller than Song Thrushes or Redwings (BL 15–19 cm, WS 30–37 cm). They can be separated, but not always, by the proportion of their wing span to body length. For the Skylark this is about 2.0. For the Song Thrushes and Redwings it is ca. 1.6–1.7.

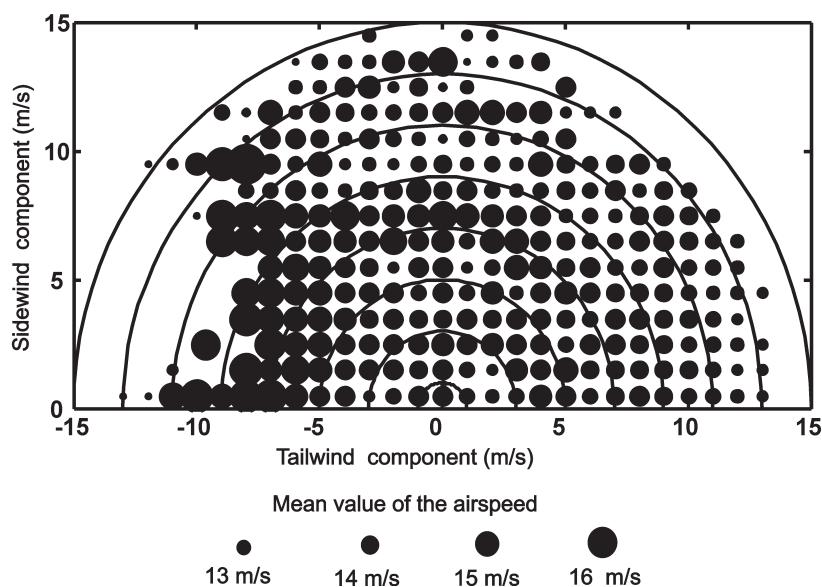
Therefore, we considered as Song Thrushes large passerine birds, recorded in September and the first ten days of October with WS 32–38 cm, BL 20–24 cm, the proportion of WS/BL  $\leq 1.7$  and WBF from 8 to 12 Hz, mean value 10.14 Hz (Griffiths 1970, Bolshakov *et al.* 2010, Bruderer *et al.* 2010). In our opinion, among the birds selected in this way the proportion of the “non Song Thrushes” did not exceed 5%. In total, during three of the autumn seasons, 2008–2010, when white illumination was used, about 7,000 birds were recorded and 2,770 of them were identified as thrushes. Only 954 of them completely satisfied the demands listed above and were declared Song Thrushes. During one autumn, 2013, when IR illumination was used, about 2,000 birds were recorded but only 170 of them were classified as Song Thrushes.

Even after rigorous removing of the tracks that could be influenced by white light beam a matter of dispute remained, despite the general light pollution of the coastal zones in recent time (Gauthreaux & Belser 2006). We compared two samples of birds recorded under white and IR light by F-test and no significant difference in airspeed between two samples was found ( $F = 1.25$ ,  $n1 = 954$ ,  $n2 = 170$ ,  $p > 0.05$ ), so we pooled them together. In total, our combined sample was 1,124 thrushes.

## 2.3. Characteristic speeds

Basic theoretical characteristic speeds  $V_{mp}$  (minimum power speed) and  $V_{mr}$  (maximum range speed) were calculated using Program Flight Ver-

Fig. 1 Airspeed of the Song Thrushes in relation to tailwind and sidewind components. Mean values of the equivalent airspeed  $V_{Eq}$  shown by the dots are calculated on both axes (twc and swc) for clusters  $2 \times 2$  m/s. The diameter of the dot is proportional to the mean airspeed value for the correspondent cluster. Concentric semicircles indicate wind velocity with a step 2 m/s.



sion 1.24 (2008) (<http://www.bio.bristol.ac.uk/people/pennyquick.htm>), the software written by Colin Pennyquick (2008). In order to compute the power curve and get the values of  $V_{mp}$  and  $V_{mr}$  we input body mass and fat mass of the Song Thrushes trapped by the high mist-nets on the Courish Spit at the beginning of night from the 1st until the 4th hour after sun set (Bolshakov *et al.* 2000, 2002).

The sample of the departing birds was small – 28 immature birds. The fuel mass was estimated according to the method proposed by Ellegren and Fransson (1992). Our values of the body and fuel mass were rather close to those of 13 sample birds from Ottenby given in the program interface as a “preset bird” in the last Pennyquick’s model correction (2008). We selected for “bounding flight style” (power fraction, i.e. the proportion of the cycle period during which the bird is flapping, 0.8). All the other flight characteristics were put in as proposed for the sample birds in Pennyquick’s program.

We also relied on program Flight 1.24 for modeling the dependence of distance covered by the Song Thrush on its airspeed under various wind conditions. A bird covers the maximum distance if it flies at airspeed  $V_{mr}$ . First, the distance ( $D$ ) vs airspeed ( $V_{air}$ ) curve was received for still air as  $D(V_{air})$ . When we added the wind expressed in tail component ( $V_w$ ) the distance covered by bird be-

came  $D_w(V_a, V_w) = D(V_a)/V_a \cdot (V_a + V_w) = D(V_a) \cdot (1 + V_w/V_a)$ . Using this approach we got the family of such curves for different winds with twc from  $-7$  to  $12$  m/s and with a step 1 m/s. On each curve of distance vs airspeed the point of maximum indicates the values of  $V_{mr}$  under the corresponding wind. Connecting these points of maximum we finally received the curve that showed  $V_{mr}$  under head- and tail winds.

### 3. Results

#### 3.1 Migratory direction, ground speed and airspeed

In the autumn, the general direction of the nocturnal passage of thrushes (*Turdus spp.*) at the Courish Spit on calm nights was  $218^\circ$  (moon-watching data) (Bolshakov *et al.* 2002). The mean track direction of the Song Thrushes (OEMS method) was  $220^\circ$  ( $n = 1,123$  birds,  $SD = 16$ , Rayleigh test  $r = 0.91$ ,  $p < 0.001$ ). The mean heading direction was  $221^\circ$  ( $n = 1,123$  birds,  $SD = 25$ , Rayleigh test  $r = 0.85$ ,  $p < 0.001$ ). It coincides with a very pronounced leading line of the Courish Spit ( $220^\circ \pm 5^\circ$ ) and the mean direction to the winter quarters  $223^\circ$  according to ringing recoveries of the Song Thrushes caught at the Spit (Payevsky *et al.* 2005). Consequently, north-easterly winds from  $30$ – $50^\circ$

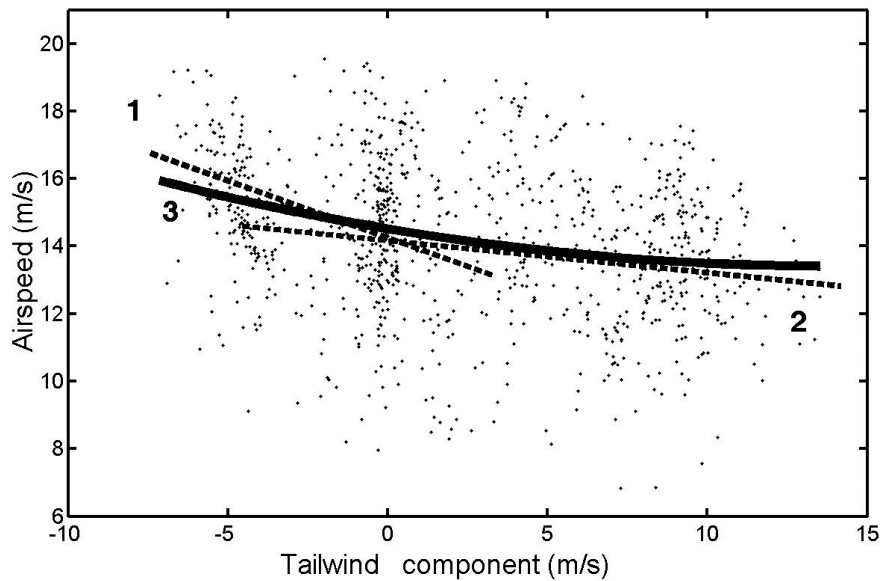


Fig. 2 Airspeed of the Song Thrushes in relation to the tailwind component. Dash line 1 – Regression of airspeed  $V_{Eq}$  against headwinds from  $-7$  to  $0$  m/s. Results of regression analysis:  $R^2 = 0.09$ ,  $F = 36.2$ ,  $n = 288$ ,  $p < 0.0001$ . Dash line 2 – airspeed  $V_{Eq}$  vs tailwinds from  $0$  to  $12$  m/s:  $R^2 = 0.12$ ,  $F = 20.1$ ,  $n = 667$ ,  $p = 0.0016$ . Solid line 3 – airspeed in the integral range of tailwind component values: polynomial  $^2$  approximation ( $y = 0.0057x^2 \pm 0.16x + 14.4$ ),  $R^2 = 0.21$ ,  $F = 11.3$ ,  $n = 955$ ,  $p = 0.0002$ .

are tailwinds in autumn in the SE Baltic region for the Song Thrushes, and the strict tailwind is 40.

The recorded values of ground speed varied about 6-fold from 5 to 29 m/s. The median value was 17.6 m/s ( $n = 1,124$  birds), and about 70% of birds passed at a speed between 11 and 24 m/s. Mean true airspeed ( $V_{Tr}$ ) was 14.6 m/s and it varied from 7 to 20 m/s. Most of the birds (70%) flew in a rather narrow speed corridor between 11 and 17 m/s (variation 1.5 fold). Mean equivalent airspeed at 0m a.s.l. ( $V_{Eq}$ ) was 14.3 m/s ( $SD = 2.3$ ,  $n = 1,112$ ) and in still air (wind velocity 0–2 m/s) it was 14.4 m/s ( $SD = 1.6$ ,  $n = 260$ ).

### 3.2. Wind-dependence of the airspeed

The dependence of airspeed ( $V_{Eq}$ ) on wind direction and velocity (tail-, head- and sidewinds) is shown in the diagram Fig. 1, where the diameter of the dots is proportional to the airspeed value. The wind is presented here in coordinates of the tail / head-wind component (t/hwc) versus the sidewind component (swc). The contribution of the winds on the left and on the right relative to the general direction of autumn migration was assumed to be

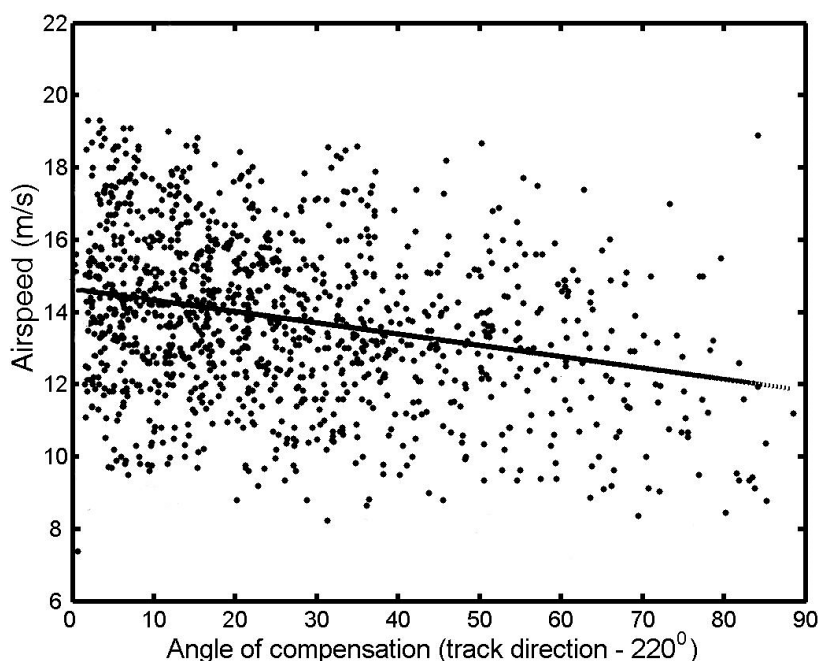
equal as the birds were observed flying above the narrow spit (about 1km wide) surrounded by the water and in accordance with theory (Liechti *et al.* 1994).

Hence, on the y-axis the absolute values of the swc (both positive and negative) are plotted to assess the magnitude of this parameter. First, we tested the influence of wind assistance (difference between ground speed and airspeed) on airspeed ( $V_{Eq}$ ) and found significant effect ( $R^2 = 0.13$ ,  $F = 9.3$ ,  $n = 955$ ,  $p = 0.0011$ ). Then, the effects of tail/head and sidewinds were considered separately.

About 30% of the sampled birds (380 thrushes) passed in weak winds and calm air (0–3 m/s). Half the birds (47%, 505 thrushes) passed with tailwinds. The passage was not intensive under moderate headwinds (4–8m/s); only 20% (220 birds) were recorded under such winds. The general tendency was obvious: the airspeed of the thrushes decreased with increasing twc relative to its value in calm air and considerably increases with the increasing headwind component ( hwc is i.e. negative values of twc).

The airspeed ( $V_{Eq}$ ) depended significantly on

Fig. 3 Airspeed of the Song Thrushes in relation to the angle of compensation for wind drift. Angle of compensation is  $\text{abs}(\text{track direction of bird} - 220^\circ)$  ( $220^\circ$  – general direction of autumn migration of the Song Thrush). Weak  $< 3\text{m/s}$  and strong  $> 10\text{m/s}$  winds are excluded. Results of regression analysis:  $B = 15.14$ ,  $b = -0.03$ ,  $R^2 = 0.12$ ,  $F = 42.1$ ,  $n = 467$ ,  $p < 0.0001$ .



twc (Fig. 2, see figure text). Tail- and headwinds were analyzed separately. The regression of  $V_{\text{Eq}}$  against the negative values of twc (i.e. hwc) with a step  $1\text{m/s}$  from  $0$  to  $-7\text{m/s}$  (at least 20 points per step) showed that  $V_{\text{Eq}}$  varied from  $14.4$  to  $16.4\text{m/s}$  (Fig. 2, line 1). The increment of the airspeed was  $0.29\text{m/s}$  for every  $1\text{m/s}$  increase of the hwc. Under tailwinds, from  $12$  to  $0\text{m/s}$  (Fig. 2, line 2)  $V_{\text{Eq}}$  ranged from  $13.1$  to  $14.4\text{m/s}$ . This indicated a decrease in  $V_{\text{Eq}}$  by  $0.11\text{m/s}$  for every  $1\text{m/s}$  increase of the twc. Both relationships were significant but headwinds influenced the airspeed twice as strong as tailwinds. Under strong headwind over  $10\text{m/s}$ , which is comparable with the thrushes' airspeed, the passage was negligible.

The dependence of the airspeed ( $V_{\text{Eq}}$ ) on the sidewinds was not obvious (Fig. 1). When we selected thrushes flying in winds with tail component and then regressed their airspeed ( $V_{\text{Eq}}$ ) against swc we did not find a significant relationship ( $F = 3.01$ ,  $n = 756$ ,  $p = 0.069$ ). The effect was also not significantly pronounced when we checked the residuals from tailwind-airspeed regression against swc ( $F = 3.49$ ,  $n = 753$ ,  $p = 0.053$ ). The expected reaction of the birds to cross winds (increasing of airspeed with increasing velocity of sidewinds) was predicted for birds compensating for wind drift (Liechti *et al.* 1994).

The problem we encountered was that the flux of thrushes consisted of birds that compensated for wind drift completely, partly or did not compensate at all (Sinelschikova & Vorotkov 2013). We found a negative relationship between  $V_{\text{Eq}}$  and the angle of compensation for wind drift, defined as an angle between the track direction of the bird and the general (intended) migratory direction (Fig. 3). As the general direction of autumn migration for thrushes coincided with the orientation of the Courish Spit and birds tended to keep the Spit we considered their intended direction to be  $220^\circ$ . The smaller the angle  $\text{abs}(\text{track} - 220^\circ)$ , the higher was the degree of compensation. We investigated dependence of the  $V_{\text{Eq}}$  on moderate sidewinds, weak ( $< 3\text{m/s}$ ) and strong winds ( $> 10\text{m/s}$ ) were excluded. In Fig. 3 we see that birds significantly increase their airspeed to augment the degree of compensation (i.e. decreasing angle between the track and  $220^\circ$ ).

The negative relationship indicates that the high values of the angles between the tracks and the leading line of the Spite are associated with low airspeeds and vice versa. As a further step, we selected only those birds that compensated for wind drift completely, i.e. kept their track direction close to  $220^\circ (\pm 5^\circ)$  and, as a result, moved along the Courish Spit. To maintain this track direction the

birds first of all had to shift their heading (body axis) into the wind. We regressed their airspeed ( $V_{Eq}$ ) against the swc but only for the positive values of the twc from 0 to 14 m/s (i.e. headwinds were excluded). Even after such rigorous selection the dependence of  $V_{Eq}$  on the swc was not highly significant ( $B=4.43$ ,  $b=0.13$ ,  $R=0.06$ ,  $F=5.09$ ,  $n=128$ ,  $p=0.025$ ). Under sidewinds within the range of the values of the swc from 0 to 14 m/s with a step 1m/s the airspeed  $V_{Eq}$  varied from 13.2 to 16.9 m/s. This indicates an increase in  $V_{Eq}$  by 0.264 m/s for every 1m/s increase in the swc.

### 3.3. The observed airspeed of the Song Thrushes and theoretical characteristic speeds $V_{mp}$ , $V_{mr}$ and $V_{mt}$

In order to plot the power curve (Fig. 4 a, b) and calculate the characteristic speeds  $V_{mp}$  and  $V_{mr}$  according to Pennycuick's model (Flight 1.24) we used the input parameters of Body Mass and Fuel deposition for Song Thrushes caught on the Courish Spit at the moment of their taking off at the beginning of night (Bolshakov *et al.* 2002). Our "statistical average model Song Thrush" had a body mass of 70.1g (SD = 5.4, n = 28) and fuel mass 5.7 g (SD = 1.4), wing span 354 mm (SD = 14), altitude of flight 0m. These values were very close to those received in Ottenby and used by C. Pennycuick in his last model (2008).

In Fig. 4 a,b the power curve and theoretical values of  $V_{mp}$  and  $V_{mr}$  were calculated with the parameters of the trapped birds that had been starting their night voyage, while the mean value of the airspeed ( $V_{Eq}$ ) without wind assistance (14.4 m/s) plotted in the same figure, was obtained for the flying birds observed by OEMS. Most of the birds were recorded by OEMS in the first half of night, probably after 1–3 hours of flight. They were assumed to be in the physiological condition rather close to the birds caught at the beginning of night. It is worth adding that the power curve is most sensitive to change in wing geometry and body mass load but to a lesser extent to fat amount change.

The bottom point on the curve of the mechanical power (gray solid thick line in Fig.4a) gives the value for  $V_{mp}$  9.6 m/s. It should be noted that within the range of its minimal values the curve is so flat that power increase of 8% (from 4.4 to 4.8W)

allows the bird to fly at the observed mean speed of 14.4 m/s. Nevertheless, it is hard to say to what extent such an increase in power is sensitive and perceptible to the birds. The minimal value of  $V_{Eq}$  recorded under strong tailwinds, 13.1 m/s, is much higher than the theoretical  $V_{mp}$  (Fig.4 b).

The distance a bird can cover depends not only on its flight parameters and the amount of fuel but also on its airspeed. The family of curves (thin costal arches) in Fig 4b shows dependence of distance that "our model Song Thrush" can cover on airspeed ( $V_{Eq}$ ) under tail- and headwinds with the twc from -7 to 12m/s. The peak points on these arches indicate the maximum distance the bird can cover flying with the corresponding airspeed. The values of these airspeeds are just the values of  $V_{mr}$  for the respective winds. If we connect these peak points we receive the  $V_{mr}$  curve for our model bird under different winds (shown in Fig 4b by a bold black dash line). The  $V_{mr}$  lies within the range between 14.1 and 20.0 m/s. In still air its value is 17.4 m/s, whereas  $V_{Eq}$  of the observed thrushes in still air is 14.4 m/s. Both  $V_{Eq}$  and  $V_{mr}$  are increased with increasing headwind component.

When the model  $V_{mr}$  and the observed  $V_{Eq}$  curves were compared we found that this trend was qualitative but not quantitative. The  $V_{Eq}$  of the observed birds did not differ from the model  $V_{mr}$  under strong tailwinds over 7m/s ( $\chi^2 = 8.9$ ,  $df = 4$ ,  $n = 345$  birds,  $p > 0.05$ ). In calm air (0–2 m/s) the model  $V_{mr}$  (17.4 m/s) significantly exceeded the value of the observed airspeed 14.4 m/s ( $\chi^2 = 25.2$ ,  $df = 1$ ,  $n = 265$  birds,  $p < 0.01$ ). Under headwinds the model gave significantly higher values of  $V_{mr}$  (for twc from -2 to -7 m/s:  $\chi^2 = 153.5$ ,  $df = 4$ ,  $n = 135$  birds,  $p < 0.001$ ). The values of the model  $V_{mr}$  and the observed  $V_{Eq}$  differed by a factor of 1.3 under headwinds, by 1.2 in still air and were very close only under strong tailwinds (difference by a factor of 1.05).

## 4. Discussion

Flight speed measurements of free flying nocturnal migrants of particular species are known only from a few publications (Stark 1996, Bruderer & Boldt 2001, Cochran & Wikelski 2005, Henningson *et al.* 2009) mainly because of difficulties of species identification in the dark. In our investiga-



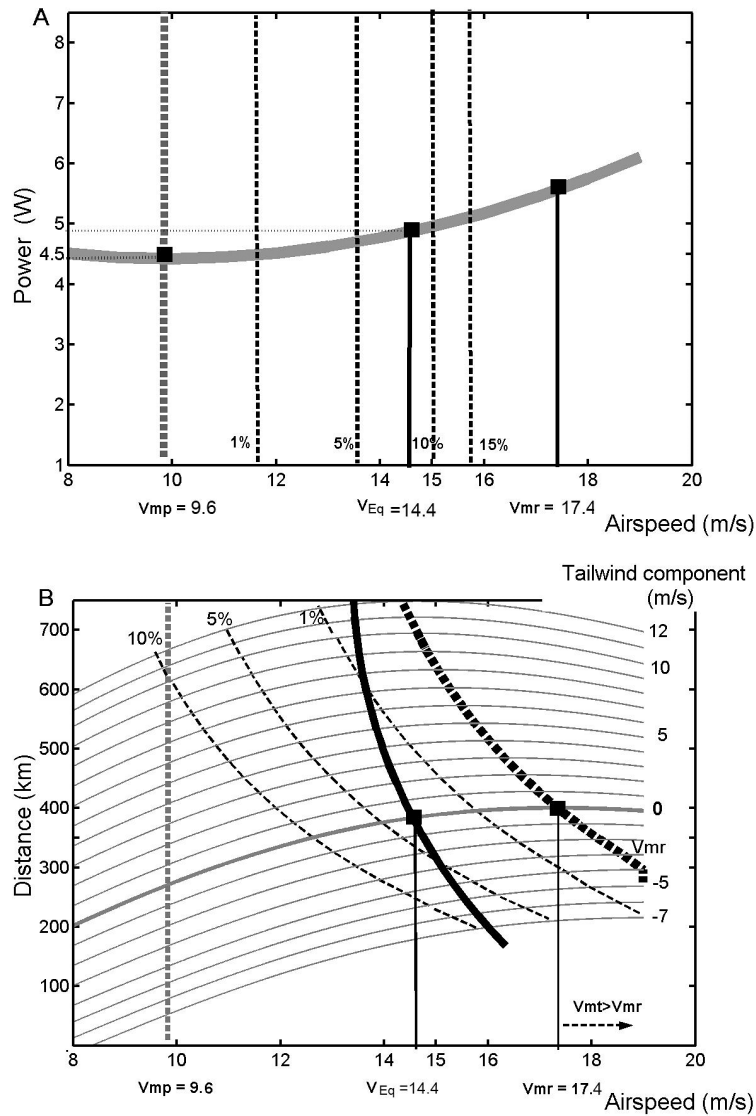


Fig. 4 The relationship between theoretical minimal power speed ( $V_{mp}$ ), maximum range speed ( $V_{mr}$ ) and observed airspeed of the flying Song Thrushes during autumn migration. a) Power curve (thick solid gray curve) and characteristic speeds  $V_{mp}$  and  $V_{mr}$  resulting from this curve are plotted for parameters of the model Song Thrush starting nocturnal flight according to Pennycuik's flight model (Flight 1.24). The mean value of the airspeed without wind assistance  $V_{Eq}$  is pointed on the curve for the observed flying at night birds. The theoretical  $V_{mp}$  – bottom point on the power curve marked by a vertical bold dash gray line (9.6 m/s). Vertical thin dash lines indicate the airspeed of the model bird if it increases mechanical power of flight by 1%, 5%, 10% and 15%. The values of  $V_{mr}$  (17.4 m/s) and mean value of airspeed (14.4 m/s) are given for still air. b) The same power curve (thick solid gray curve) is super-imposed on the family of curves of flight on airspeed of the model Song Thrush under various winds. Wind is presented by the values of tailwind component from -7 to 12 m/s with a step of 1 m/s. The values of tailwind component on the right of the scheme are given for each curve of dependence of distance on airspeed (thin costal arches). Bold black dash curve connects the peak points on these costal arches and forms  $V_{mr}$  curve under head- and tail winds. Thin dash curves indicate the airspeed at which the bird would fly under correspondent wind to cover a distance by 1%, 5% and 10% less than its maximum possible. Mean value of airspeed of all sampling thrushes under different winds is shown as in Fig. 2 by bold black approximation curve.

tion the mean true airspeed of the nocturnally migrating Song Thrushes measured by OEMS (14.6 m/s) was in surprising agreement with radar observations: the airspeed of 51 Song Thrushes migrating in autumn identified by wing-beat frequency and phenology varied between 12.8 to 16.7 m/s, with an average of 14.6 m/s (Stark 1996). Released and tracked Song Thrushes showed slightly lower airspeeds from 10 to 15 m/s with the mean value of 12.65 m/s, which might be explained as an artifact (Bruderer & Boldt 2001).

We found a 1.5-fold difference of airspeed among the observed birds which could be explained on the one hand by individual size-load variations and on the other hand by the ability of birds to change their airspeed under different winds, or by both. Numerous wind tunnel tests showed that birds of different species and orders are capable of varying their airspeed in a wide range depending on the velocity of the opposing air flow (Bruderer *et al.* 2001, Park *et al.* 2001, Hedenström *et al.* 2006, Tobalske *et al.* 2007, Henningson *et al.* 2008). It is assumed that a similar reaction to winds allows free flying birds to reduce their energy expenditure when they met a variety of wind conditions during migration (e.g., Tucker & Schmidt-Koenig 1971, Pennycuik 1978, Rayner 1991). It has also been repeatedly shown on combined groups of free flying passerines (Bloch & Bruderer 1982, Liechti 1995, 2006), or e.g., arctic birds (Hedenström *et al.* 2002), long- and short-distance migrants (Nilsson *et al.* 2014), that the birds significantly increase their airspeed with increasing headwinds and decrease it with increasing tailwinds. The same trend was also observed in some seabird species (Mateos & Bruderer 2012) and free flying individuals of particular species such as Swainson's Thrushes (Cochran & Wikelski 2005). Our study confirms the significance and omnitude of this already known phenomenon of airspeed adjustment with respect to tail/headwind component on a large sample of free flying Song Thrushes during nocturnal migration.

In autumn, westerly winds (side and head-side for migrating thrushes) are prevailing in Europe (Liechti & Bruderer 1998). Insufficiency of favorable winds makes the thrushes regularly fly in cross winds (Baushev & Sinelschikova 2007). An increase of airspeed with increasing velocity of sidewinds was expected as a drift compensation

measure and theoretically predicted for birds minimizing energy cost per unit of distance covered (Liechti *et al.* 1994, Liechti 1995) in the case when the birds compensate for the possible wind drift completely. Nevertheless, it was not an easy task to reveal this effect. A. Hedenström with colleagues (2002) analyzed 6 papers where the possible adjustment of the airspeed in relation to the sidewinds was investigated but did not find any empirical confirmation.

Since then, a significant effect of sidewind on airspeed was found in a mixed group of long- and short-distance passerine migrants (Nilsson *et al.* 2014) and in Swifts – a species adapted to a life in the air and capable of compensating for wind drift without pronounced landscape leading lines (Karlsson *et al.* 2010). It was supposed that a potential problem to get field support of the theoretical prediction was to find a situation where birds migrate along coastlines or some other topographical feature, where they could compensate completely for wind drift (Green & Alerstam 2002, Hedenström *et al.* 2002). The Courish Spit is a narrow strip of land surrounded with water and is thus a perfect place for such a kind of investigation: we know the general migratory direction of the thrushes by ringing recoveries and moon-watching and it coincides with the orientation of the Spit. But when we regressed the airspeeds of sampling birds against the sidewind component we did not get the expected result, probably because the flux of thrushes consisted of birds that compensated for wind drift completely, partly or did not compensate at all (Sinelschikova & Vorotkov 2013).

When we considered only those birds that compensated for wind drift completely (mainly low flying birds < 300m a.s.l.) we found that in order to keep along the Spit (i.e., to reduce the angle between the track and the leading line of the Spit) thrushes did significantly increase their airspeed with the increasing velocity of sidewinds. Thereby, they achieved compensation for wind drift not only by shifting their heading into the wind but also by increasing their airspeed.

Although the effect was significant, the model explained only 6% of the variance ( $R^2 = 0.06$ ). Low  $R^2$  is explained either by other factors or due to unmeasured variance. Probably this could be explained by a wide variety of possible combinations of adjusting the direction into the wind and

airspeed adjustments that permit birds to compensate for wind displacement, especially taking into account the reaction of young birds dominating in the night flux in autumn. Our investigation in general confirms that the thrushes (at least flying along pronounced leading lines) do not keep a constant airspeed but can control it and adjust it according to the current winds of overall direction and speed: we found a significant effect of the head/tailwinds and sidewinds on airspeed and they were of similar magnitude.

In autumn the thrushes (*Turdus spp.*) migrate under tail- and headwinds (usually with side component) in a quantitative ratio of 2:1 respectively (Baushev & Sinelschikova 2007). Under any winds they tend to minimize energy expenditure of flight by varying their airspeed. According to the theory of optimal migration (Alerstam & Lindström 1990) when the optimization criterion is minimizing energy consumption per unit of distance (Hedenström & Alerstam 1995, Alerstam & Hedenström 1998), as it is relevant in autumn, the appropriate flight speed becomes the maximum range speed ( $V_{mr}$ ).

In autumn Skylarks, Swifts, and birds of other species flew at speeds associated with maximum range  $V_{mr}$  which was considerably lower than  $V_{mt}$  ( $V_{mt}$  is relevant mainly during spring migration) (Alerstam 1981, Wege & Raveling 1984, Rayner 1985, Bruderer & Bold 2001, Nilsson *et al.* 2013). We also expected the speed of the Song Thrushes migrating in autumn to be close to  $V_{mr}$  and like  $V_{mr}$  to increase with increasing headwind component relative to its value in calm air (Hedenström & Alerstam 1996).

For quantitative comparison of the observed airspeed and theoretically predicted characteristic speed  $V_{mr}$ , the latest Pennycuick's aerodynamic model (2008) was used. Airspeed ( $V_{Eq}$ ) of the flying birds did not differ significantly from the predicted  $V_{mr}$  under strong tailwinds, but it was lower in still air and under head winds. As any model it has many uncertainties and it seems to give a very high value of  $V_{mr}$  (17.4 m/s) calculated for the parameters of the birds caught at the Courish Spit or in Ottenby (17.7 m/s) given as an example in the program Flight 1.24, while the mean airspeed  $V_{Eq}$  of the observed by OEMS thrushes in still air was 14.4 m/s.

The strategy of time minimization is more rele-

vant in spring than in autumn, especially in short-distance migrants (Nilsson *et al.* 2013, 2014), but it seems doubtful that in spring the Song Thrushes are capable of attaining a speed higher than 17.4 m/s in calm air. For comparison, the previous version Flight 1.1 (1992) gave significantly lower theoretical predictions for  $V_{mp}$  (7.6 m/s) and  $V_{mr}$  (13.3 m/s) for the Song Thrush (Bruderer & Bold 2001). The field data presented here would be useful for improvement models in the future. Despite the fact that the model and the observed wind-dependence patterns of airspeed were different our data are in qualitative agreement with Pennycuick's flight model. The birds apparently tend to maintain the cheapest cost of transport under any wind in autumn.

*Acknowledgements.* The authors are grateful to anonymous referees and the editor for critical comments. We thank Felix Liechti for his valuable comments and suggestions on the previous version of this manuscript. We also thank T. Gunf and E. Hawkins for the language review. This study was financially supported by the Russian Foundation for Basic Research (grants to V. Bukyuk no. 19-04-00807 and to J. Bojarinova no. 19-04-00900). The authors acknowledge support from the Zoological Institute RAS (registered research project No 01201351182).

### **Tuulien vaikutus laulurastaiden lentonopeuteen syysmuutolla**

Lintujen käyttäytymisen ja fysiologian sopeumat mahdollistavat niitä minimoimaan ajan ja resurssien käytön muuton aikana erilaisissa tuuliolosuhteissa. Tässä tutkimuksessa selvitimme laulurastaiden yömuuttoa opti-elektronisella matriisilaitteistolla, joka mahdollistaa yöllä muuttavien lintujen havainnoinnin ja lennon analysoinnin. Laulurastaiden tunnistettiin silhuetin, koon, siipien liikkeiden ja fenologian perusteella. Havaitimme, että rastaiden lentonopeus ilman myötätuulia ( $V_{Eq} = 14.4$  m/s, merenpinnan tasolla), oli lähellä lentomekaniikan teoreettista maksiminopeutta ( $V_{mr}$ ). Tämä viittaa siihen, että rastaiden muutto syksyllä perustuu energian minimointiin.  $V_{mr}$  on riippuvainen tuulista: se kasvaa vasta- ja sivutuulen myötä.

Rastaiden lentonopeudessa oli samanlainen kaava: lentonopeus kasvoi lisääntyvien vastatuulien myötä (suhteessa tyyneen ilmaan), ja väheni myötätuulissa. Havaitimme myös, että sivutuuli

vaikuttaa lentonopeuteen: linnut, jotka kompensoivat tuulen aiheuttaman ajautumisen muuttorei-tillään Kuurinkyntäällä, nostivat lentonopeuttaan kun sivutuulet lisääntyivät. Linnut pyrkivät len-tonopeuksiin, jotka minimoivat energian kulutuk-sen kaikissa tuuliolosuhteissa. Verrattuna nk. Pen-nycuick-lentomekaniikan malliin, vaihelua oli kuitenkin enemmän ja lentonopeus hitaampi tyy-nellä ilmalla ja vastatuulella.

## References

- Alerstam, T. 1981: The course and timing of bird migra-tion. — In: Aidley, D. J. (ed.), *Society for Experimental Biology Ser.*: 9–54. Cambridge Univ. Press.
- Alerstam, T. & Hedenström, A. 1998: The development of bird migration theory. — *Journal of Avian Biology* 29: 343–369.
- Alerstam, T. & Lindström, Å. 1990: Optimal bird migra-tion: the relative importance of time, energy, and safe-ty. — In *Bird migration: Physiology and Ecophysiology* (ed. Gwinner, E.): 331–351. Springer, Berlin.
- Bäckman, J. & Alerstam, T. 2001: Confronting the winds: orientation and flight behaviour of the roosting swift, *Apus apus*. — *Proceedings of Royal Society B* 268: 1081–1087.
- Baushev, A.N. & Sinelschikova, A. 2007: On a probabilis-tic model for the numerical estimation of the nocturnal migration of birds. — *Mathematical Bioscience* 205: 44–58.
- Bloch, R. & Bruderer, B. 1982: The airspeed of migrating birds and its relationship to the wind. — *Behavioral Ecology and Sociobiology* 11: 19–24.
- Bolshakov, C.V., Bulyuk, V.N. & Sinelschikova A. 2000: Study of nocturnal departures in small passerine mig-rants: retrapping of ringed birds in high mist-nets. — *Vogelwarte* 40: 250–257.
- Bolshakov, C.V., Žalakevičius, M. & važas, S. 2002: Noc-turnal Migration of Thrushes in the Eastern Baltic Re-gion. — Publishing House “AKSTIS”, Vilnius.
- Bolshakov, C.V., Bulyuk, V.N., Sinelschikova, A. & Vo-rotkov, M. 2013: Influence of the vertical light beam on numbers and flight trajectories of night-migrating songbirds. — *Avian Ecology and Behaviour* 24: 35–49.
- Bolshakov, C.V., Vortkov, M., Sinelschikova, A., Bu-lyuk, V.N. & Griffiths, M. 2010: Application of the Optical-Electronic Device for the study of specific aspects of nocturnal passerine migration. — *Avian Ecology and Behaviour* 18: 23–51.
- Bruderer, B. & Bold, A. 2001: Flight characteristic of birds: I. radar measurements of speed. — *Ibis* 143: 178–204.
- Bruderer, B. & Weitnauer, E. 1972: Radarbeobachtungen über Zug und Nachtflüge des Mauerseglers (*Apus apus*). — *Revue Suisse de Zoologie* 79: 1190–1200. (In German)
- Bruderer, B., Liechti, F. & Bilo, D. 2001: Flexibility in flight behaviour of Barn Swallow (*Hirundo rustica*) and House Martin (*Delichon urbica*) tested in a wind tunnel. — *Journal of Experimental Biology* 204: 1473–1484.
- Bruderer, B., Peter, D., Boldt, A & Liechti, F. 2010: Wing-beat characteristics of birds recorded with tracking ra-dar and cine camera. — *Ibis* 152, 2: 272–291.
- Cochran, W.W. & Wikelski, M. 2005: Individual migrato-ry tactics of New World *Catharus* thrushes: current knowledge and future tracking options from space. — In *Birds of Two Worlds: Ecology and Evolution of Mi-gration* (ed. Greenberg, R. & Marra, P.): 274–289. Johns Hopkins Univ. Press, Baltimore.
- Cochran, W.W., Bowlin, M.S. & Wikelski, M. 2008: Wingbeat frequency and flap-pause ratio during natu-ral migratory flight in thrushes. — *Integrative and Comparative Biology* 48, 1: 134–151.
- Ellegren, H. & Fransson, T. 1992: Fat loads and estimated flight-ranges of four *Sylvia* species during autumn mi-gration at Gotland, South-east Sweden. — *Ring and Migration* 13: 1–12.
- Gauthreaux, S. A.Jr. & Belser, C.G. 2006: Effects of arti-ficial night lighting on migrating birds. — In *Ecological consequences of artificial night lighting* (ed. Rich, C. & Longcore, T.): 67–93. Island Press, Washington, Covelo, London.
- Green, M. & Alerstam, T. 2002: The Problem of Estima-ting Wind Drift in Migrating Birds. — *Journal of Theoretical Biology* 218: 485–496.
- Griffiths, M.E. 1970: Wing-beat frequencies and flight patterns of the more common migrant birds of the Bri-tish Isles and Europe. Report No. 9. — AT/2170/08/RDI. Ministry of Technology, London.
- Hart, N.S. 2001: The Visual Ecology of Avian Photorecep-tors. — *Progress in Retinal and Eye Research* v 20, 51: 675 — 703.
- Hedenström, A. 1993: Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. — *Philosophical Transactions of the Royal Society B* 342: 353–361
- Hedenström, A. & Alerstam, T. 1995: Optimal flight speed of birds. — *Philosophical Transactions of the Royal Society B* 348: 471–487.
- Hedenström, A., & Alerstam, T. 1996: Skylark optimal flight speeds for flying nowhere and somewhere. — *Behavioral Ecology* 7: 121–126.
- Hedenström, A., Rosén, M. & Spedding, G. R. 2006: Vor-tex wakes generated by robins *Erithacus rubecula* du-ring free flight in a wind tunnel. — *Journal of the Royal Society, Interface* 3: 263–276.
- Hedenström, A., Alerstam, T., Green, M., & Gudmunds-son, G.A. 2002: Adaptive variation of airspeed in rela-tion to wind, altitude and climb rate by migrating birds in the Arctic. — *Behavioral Ecology and Sociobio-logy* 52: 308–317.

- Henningsson, P., Spedding, G.R., & Hedenström, A. 2008: Vortex wake and flight kinematics of a swift in cruising flight in a wind tunnel. — *Journal of Experimental Biology* 211: 717–730.
- Henningsson, P., Karlsson, H., Bäckman, J., Alerstam, T. & Hedenström, A. 2009: Flight speeds of swifts (*Apus apus*): seasonal differences smaller than expected. — *Proceedings of Royal Society B* 276: 2395–2401.
- Karlsson, H., Nilsson, C., Bäckman, J. & Alerstam, T. 2011: Nocturnal passerine migration without tailwind assistance. — *Ibis* 153: 485–493.
- Karlsson, H., Henningsson, P., Bäckman, J., Hedenström, A. & Alerstam, T. 2010: Compensation for wind drift by migrating swifts. — *Animal Behavior* 80: 399–404.
- Liechti, F. 1995: Modeling optimal heading and airspeed of migrating birds in relation to energy expenditure and wind influence. — *Journal of Avian Biology* 26: 310–316.
- Liechti, F. 2006: Birds: blowin' by the wind? — *Journal of Ornithology* 147: 202–211.
- Liechti, F. & Bruderer, B. 1998: The relevance of wind for optimal migration theory. — *Journal of Avian Biology* 29: 561–568.
- Liechti, F. & Bruderer, B. 2001: Flexibility in flight behaviour of Barn Swallow (*Hirundo rustica*) and House Martin (*Delichon urbica*) tested in a wind tunnel. — *Journal of Experimental Biology* 204: 1473–1484.
- Liechti, F., Bruderer, B. & Paproth, H. 1995: Quantification of nocturnal bird migration by moon-watching: comparison with radar and infrared observations. — *Journal of Field Ornithology* 66: 457–468.
- Liechti, F., Hedenström, A. & Alerstam, T. 1994: Effects of sidewinds on optimal flight speed of birds. — *Journal of Theoretical Biology* 170: 219–225.
- Mateos, M., & Bruderer, B. 2012: Flight speeds of migrating seabirds in the Strait of Gibraltar and their relation to wind. — *Journal of Ornithology* 153: 881–889.
- Nilsson, C., Bäckman J. & Alerstam T. 2014. Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short- and long-distance migrants. — *Behavioral Ecology and Sociobiology* 68 (11):1799–1807. doi:10.1007/s00265-014-1789-5
- Nilsson, C., Klaassen, R. & Alerstam, T. 2013: Differences in speed and duration of bird migration between spring and autumn. — *American* 181(6): 837–45. doi: 10.1086/670335.
- Norberg, U.M.L. 1990: Vertebrate Flight: mechanics, physiology, morphology, ecology and evolution. — *Zoophysiology Series*, vol. 27, Springer-Verlag, Berlin.
- Park, K.J., Rosén, M. & Hedenström, A. 2001: Flight kinematics of the barn swallow *Hirundo rustica* over a wide range of speeds in a wind tunnel. — *Journal of Experimental Biology* 204: 2741–2750.
- Payevsky, V.A., Shapoval, A. & Vysotsky, V.G. 2005: Spatial distribution of thrushes migrating through the Eastern Baltic area as shown by ring recoveries. — *OMPO Newsletters* 25: 5–12.
- Pennycuik, C.J. 1968: Power requirements for horizontal flight in the pigeon *Columbia livia*. — *Journal of Experimental Biology* 49: 527–555.
- Pennycuik, C.J. 2008: *Modelling the Flying Bird*. — Academic Press, Amsterdam.
- Rayner, J.M.V. 1979: A new approach to animal flight mechanics. — *Journal of Experimental Biology* 80: 17–54.
- Rayner, J.M.V. 1985: Flight, speeds of. — In *A dictionary of birds* (ed. Campbell, B. & Lack, E.): 224–226. Poyser, Staffordshire, England.
- Rayner, J.M.V. 1990: The mechanics of flight and bird migration performance. — In *Bird migration* (ed. Gwinner, E.): 283–299. Springer-Verlag, Berlin.
- Rayner, J.M.V. 1991: On the aerodynamics of animal flight in ground effect. — *Philosophical Transactions of the Royal Society B* 334: 119–128.
- Sinelschikova, A. & Vorotkov, M. 2013: Compensation for wind drift by thrushes during autumn nocturnal migratory flight. — 9th Conference of the EOU: 212. Norwich, UK.
- Stark, H. 1996: *Flugmechanik Nachts Ziehender Kleinvögel*. — PhD Thesis, Universität, Basel. (In German)
- Tobalske, B.W., Warrick, D.R., Clark, C.J., Powers, D.R., Hedrick, T.L., Hyder, G.A. & Biewener, A.A. 2007: Three-dimensional kinematics of hummingbird flight. — *Journal of Experimental Biology* 210: 2368–82.
- Tucker, V.A. 1973: Bird metabolism during flight: evaluation of a theory. — *Journal of Experimental Biology* 58: 689–709.
- Tucker, V.A. & Schmidt-Koenig, K. 1971: Flight speeds of birds in relation to energetics and wind direction. — *Auk* 88: 97–107.
- Vorotkov, M., Sinelschikova, A. & Griffiths, M. 2009: Optical Matrix Device: Technical aspects of a new tool for the detection and recording of small nocturnal aerial targets. — *Journal of Navigation* 62: 1–9.
- Wege, L.M. & Raveling, D.G. 1984: Flight speed and directional responses to wind by migrating Canada Geese. — *Auk* 101: 342–348.