

## **Influence of the vertical light beam on numbers and flight trajectories of night-migrating songbirds**

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In this paper we analyse the data obtained in the automatic regime by the Optical Electronic Device (OED, Vorotkov et al. 2009; Bolshakov et al. 2010) for autumn nocturnal passage of passerines on the Courish Spit on the Baltic Sea and estimate: (1) numbers aloft under different types of wind (following wind, opposing wind and calm conditions); (2) flight trajectories in the 5° cone of white light. We found that under natural nocturnal illumination conditions, the vertical cone of white light impacts the detectable numbers aloft and disturbs straight flight trajectories. The OED data obtained throughout the night suggest, after correction for ground speed and the mean flight altitude, the actual number of birds in the light cone peaks at calm conditions, is halved under following winds which are optimal for passage and is 21 times lower under unfavourable headwinds. It is assumed that high numbers in the light cone under calm conditions is an artefact of bird attraction by light and their concentration around the searchlights. The OED data obtained for midnight  $\pm 1$  hour, flying migrants respond to the vertical light cone under all types of wind conditions by altering their straight flight trajectories. However, this response is most apparent in still air conditions. The proportion of birds that change their flight track reaches 43%. We assume that under such conditions some birds are not only attracted to the illuminated zone at low altitudes, but, besides slowing down their ground speed, change their trajectories to the degree of flying in circles. To determine combinations of factors and to test for their possible impact on the probability of response to light, we used a binary logistic regression. The presence of birds with straight vs. curved tracks was used as the dependent variable. Final logistic models obtained for midnight  $\pm 1$  hour for calm conditions and headwinds, suggest that occurrence probability of songbirds with curvilinear flight tracks is higher for small birds, when no or just a small part of Moon disk is visible and under high air humidity. Under headwinds the probability of occurrence of birds flying curvilinear tracks is also higher under overcast. For following winds, the probability of occurrence birds flying curvilinearly was higher when many small birds were aloft, when air humidity was high and when wind was not strictly following. Unlike other wind situations, this model did not include the size of visible part of the Moon disk as a significant factor. The increase of occurrence of curvilinear flight tracks through the light beam when winds were not exactly following was probably caused by the problems with compensating the lateral component of tailwinds under high velocities, especially by small birds.

*Key words:* nocturnal migration, light pollution, numbers, flight track, extrinsic factors

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## 1. Introduction

In the recent decades many avian nocturnal migrants encounter light pollution more and more frequently, which is caused by anthropogenic lights or various intensity, that illuminate the airspace at night (Verheijen 1985). In the zone of such photopollution which interferes with the natural light environment, mass bird mortality events from collisions with different man-made structures often occur (Avery *et al.* 1980; Verheijen 1981a, b; Evans Ogden 1995; Gauthreaux & Belser 2006; Gehring *et al.* 2009; Longcore *et al.* 2012, 2013; Loss *et al.* 2012).

In spite of significant progress in studies of response of nocturnal avian migrants to anthropogenic lights, especially in North America (Avery *et al.* 1980, Larkin & Frase 1988, Evans Ogden 1996, Bruderer *et al.* 1999, Jones & Francis 2003, Gauthreaux & Belser 2006, Evans *et al.* 2007), many aspects remain poorly studied. In particular, it remains unclear (1) which extrinsic factors cause behavioural changes in night-migrating birds in the areas with artificial illumination; (2) what are the responses of flying birds to artificial light and at what altitudes do they occur; (3) whether anthropogenic lights attract birds from the vicinity, what is the scale of this event and if it is weather-dependent; (4) whether responses vary with the wavelength of light and avian taxa; (5) whether response to artificial light varies with the phase of nocturnal flight, i.e. at take-off, during mid-flight and at landing. Answers to these questions are essential for understanding of the basics of behaviour and orientation of avian nocturnal migrants and for conservation purposes (see review by Gaston *et al.* 2012).

Here we analyse the numbers of birds aloft at night and especially their tracks when crossing a limited zone of vertical white light beam estimated from the data collected by the Optical Electronic Device in the automatic regime (Vorotkov *et al.* 2009, Sinelschikova *et al.* 2009, Bolshakov *et al.* 2010). We analysed the importance of (1) primary weather factors; (2) size of the visible part of the Moon disk; (3) flight altitude for the numbers. The analysis was done for autumn migration and was restricted to songbirds.

## 2. Study area, material and methods

Our study was performed on Cape Rossitten on the Courish Spit on the Baltic coast (55°09'N, 20°51'E). Cape Rossitten experiences no light pollution from three sides. Only from the west the village of Rybachy is located where street lights and mainly one-storey houses produce some night lights. These light sources even in dense fog do not create any noticeable sky glow over the adjacent area. The nearest areas with anthropogenic lights are located on the Courish Spit (10 km to the NE and 20 km to the SW) and on the eastern shore of Courish Lagoon (30 km to the E; Fig. 1).

Birds flying at night were recorded by the original Optical Electronic Device (OED). The device consists of two main components: the recording unit (electronic optical system) and the illumination system. The image of an object, under artificial illumination of white light in the visible range of wavelength, is received on two high-

sensitivity CCD matrices. The illumination system is installed 40 m apart from the recording unit and system consists of three searchlights with parabolic mirrors. They have differing luminance (OSRAM lamps of 250–400 W) and angular size (3–5°). The working zone of illumination by white light has a shape of inverted cone with an open angle of 5°, is limited to altitudes 100–1000 m a.g.l. where a relatively uniform field of light is formed (see Vorotkov et al. 2009, Sinelschikova et al. 2009, Bolshakov et al. 2010) for more technical details.

OED makes it possible to perform a continuous automatic recording of birds flying in the darkness, including estimates of the main flight characteristics: (1) flight altitude above ground level (up to 1000 m in large songbirds in clear nights); (2) flight tracks in the illuminated zone; (3) body size of birds (body length and wing span); (4) flight direction and body axis orientation; (5) ground and air speed; (6) wingbeat frequency; (7) quality of recorded silhouettes (Vorotkov et al. 2009, Sinelschikova et al. 2009, Bolshakov et al. 2010). To analyse the impact of the cone of white light on birds aloft at night we used the data obtained by OED during three autumn migratory seasons: 23/24.9–26/27.10 in 2008 (31 nights with observations out of 33); 12/13.09–23/24.10 in 2009 (27 nights with observations out of 42); 22/23.09–26/27.10 in 2010 (35 nights with observations out of 37). Of the total 112 nights between 12 September–26 October during 17 nights observations were not possible due to technical limitations.

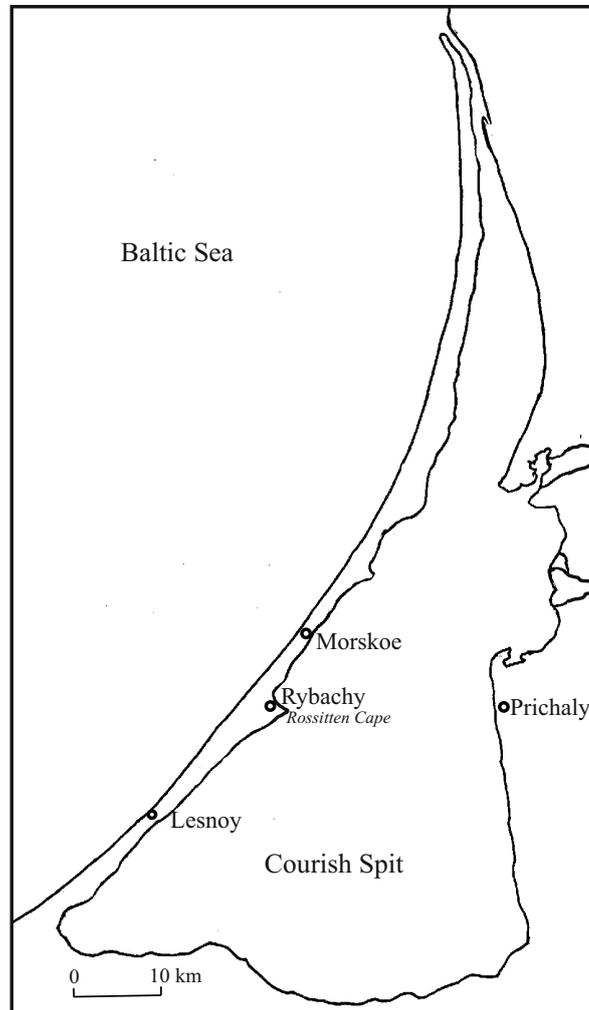


Figure 1. Schematic map of the study area. The sites with small anthropogenic light pollution closest to Cape Rositten are shown by open circles (see text).

### 3. Limitations of the method and data analysis

#### 3.1. Limitations of the method

This study is based on data collected by continuous automatic monitoring of nocturnal avian migration on the Courish Spit by OED. Taking the aims of study into account, it is essential to emphasize the existing limitations of the method.

First, under certain weather conditions (rain, dense fog and low overcast) observations were not possible due to technical limitation of the recording method (Vorotkov *et al.* 2009, Bolshakov *et al.* 2010). This limitation did not make it possible to perform observations during some of nights or parts of certain nights and, importantly, to include dense fog, precipitation and low overcast in the predicting factors. The existing data suggest that under such conditions the impact of anthropogenic light on behaviour of flying birds is most pronounced (Bolshakov 1981).

The second limitation is due to the narrow beam of light which results in the restricted zone of recording flight path, especially in birds flying at low altitudes. To improve the estimates of numbers and responses of flying birds to the light beam the device needs to be updated, mainly by using lenses with broader angle of vision that would make it possible to obtain data on birds flying low, in fog, under low visibility, precipitation and below the edge of low clouds (Bolshakov & Bulyuk 1978, Bolshakov 1981).

The third limitation concerns the time of night for which flight tracks were analysed. In this study, we only analyse this parameter for the two-hour period between one hour before midnight and one hour after midnight (00:00  $\pm$  60 min Eastern European summer time, EEST). In all nights the Sun was more than 18° below the horizon, i.e. the natural light was only available from the stars and the Moon. This limitation was caused by the fact that we only had daily weather data, altitudinal wind profiles including, for this period of night. Unfortunately, an important parameter horizontal visibility was not recorded. Using data only for this limited period of night, first, restricted our sample size, second, did not allow us to obtain comparable data for different periods of night, and third, did not make it possible to compare the data for the deep night with twilight periods in the beginning and end of the night.

#### 3.2. Data analysis

Wind direction and speed may directly influence flight tracks of the birds when they cross an illuminated area. Wind conditions are also known to be a most important factor that governs numbers aloft (Richardson 1978, 1990; Bolshakov 1981; Erni *et al.* 2002; Liechti 2006). Therefore, the analysis was performed separately for three functionally different wind conditions: still air (wind speed 0–2 m·s<sup>-1</sup>), favourable following and unfavourable opposing winds. In the latter two conditions wind speeds exceeded 2 m·s<sup>-1</sup>.

Wind direction and speed at altitudes 100–1000 m a.g.l. were estimated by weather balloons launched at the study site 3–4 times per night. We used a modified pilot balloon method, well known in meteorology (Bolshakov *et al.* 2010). In some

cases, wind direction and speed were estimated from radiosonde data at altitudes ca. 700 m. With radiosonde data included, high-altitude wind data were available for 33 observations nights in 2008, 27 nights in 2009 and 30 nights in 2010.

Preliminary analysis of linear tracks of birds crossing the light beam showed that the mean migratory direction of passerines in autumn in  $225^\circ$  (Bolshakov et al. in prep.). This direction closely fits the directions of ring recoveries of the most common songbird nocturnal migrants ringed on the Courish Spit, Song Thrushes *Turdus philomelos*, European Robins *Erithacus rubecula* and Goldcrests *Regulus regulus* (Payevsky 1973; Bolshakov et al. 2002a, b, c) and moon-watching data (Bolshakov 1981, Bolshakov et al. 2002d). We used  $225^\circ$  to identify winds with a tailwind component ( $45 \pm 90^\circ$ ) and with an opposing ( $225 \pm 90^\circ$ ) component.

Response of birds to the light beam was inferred from estimates of (1) numbers of birds per hour under following and opposing winds and in still air; (2) linearity of flight tracks. When estimating the flow of birds across of cone of light under the three wind categories, we estimated the mean hourly rate of traffic from estimates for the whole night. For the analysis of linearity of tracks, only the data collected during the two hours around midnight were used. We distinguished four types of tracks across the light beam: (1) linear tracks; (2) weakly curved tracks; (3) strongly curved tracks; (4) broken tracks, including apparent circling (these types of trajectories are illustrated in Fig. 9 in Bolshakov et al. 2010).

We tested for the effect of various predicting factors on flight tracks across the light beam under the three types of wind by Spearman's rank correlation. Response of birds to light was a categorical variable with a two-grade scale: 1 – straight, 2 – non-straight (i.e. weakly curved, strongly curved or circling). To determine combinations of factors and to test for their possible impact on the probability of response to light, we used a binary logistic regression. The presence of birds with straight vs. curved tracks (coded as 0 and 1, respectively) was used as the dependent variable. Both types of analysis were only performed for the data collected around midnight  $\pm 1$  hour.

The following factors were tested as explanatory variables:

1. *Linear size of birds.* We identified passerines from their typical silhouettes, wing-beat patterns, wing span and (or) body length. The parameter was scored as small and large passerines (coded as 1 and 2, respectively). The former group included songbirds with body length up to 0.18 m and/or wing span up to 0.28 m; the latter one was formed of birds with body length and/or with wing span exceeding 0.18 m and 0.28 m, respectively.

2. *Flight altitude.* We tested the hypothesis that response of birds to the light beam depends on their flight altitude above ground. It could be related both to the intensity of light at different distance from the source and to flight patterns at low and high altitude. To test this hypothesis, we distinguished three altitude types, below 200 m, 201–400 m, >400 m a.g.l. (codes 1, 2, 3, respectively).

3. *Angle between migratory direction ( $225^\circ$ ) and direction of following and opposing wind.* For tail and headwinds we calculated the angle between the migratory direction and wind direction. This angle varied between  $0^\circ$  and  $90^\circ$ .

4. *Velocity of following and opposing wind.* This parameter was calculated for every single bird flying between 100–1000 m a.g.l. on the basis of wind balloon data.

5. *Relative air humidity*. This parameter was measured at ground level every night at midnight EEST.

6, 7. *General cloud cover and cloud cover below 2 km a.g.l.* These parameters were recorded every night at midnight EEST. Cloud cover was recorded on a scale of 0–10 units, where 0 is clear and 10 overcast. To estimate the possible variation in response of flying birds towards light under weak and strong cloud cover, we used two categories: 1 (0–7 units) и 2 (8–10 units).

8. *Visible size of the disk of the Moon*. The size of the moon disk was estimated using a two-number scale: 0 when the moon was not visible or  $\leq 50\%$  of the moon disk; 1 when  $> 50\%$  of moon disk was visible.

Model selection was done by forward stepwise inclusion. We also ran backward selection procedures to examine consistency of variable selection. Statistical analyses were performed in the statistical package SPSS 16.0 for Windows (SPSS Inc. 2007).

## 4. Results

### 4.1. Wind conditions on the Courish Spit in autumn

As shown by estimates made between 100–700 m a.g.l. during 102 nights in 2008–2010 between 12 September–28 October, in autumn on the Courish Spit opposing winds in respect to the general migratory direction ( $225^\circ$ ) predominate. Their share was 61.8%. Nights with following winds occurred in 23.5% of cases, still air was recorded in 14.7% of nights. Opposing winds were most common every year, with their percentage reaching 75.8% in some years.

Duration of periods with sustained headwinds varied between one and 12 nights, in 43% of cases (six out of 14) it was 7–12 nights in succession. Still air conditions in six cases out of eight only lasted during a single night. In five out of 10 cases following winds only occurred during one night, in the remaining cases positive wind assistance could be enjoyed during 3–6 nights.

### 4.2. Numbers of birds crossing the light beam under varying wind conditions

Numbers of birds crossing the beam of light per hour under three different wind situations are given in Table 1.

Under opposing winds, no birds were recorded in the light beam in 10 nights out of 47 recorded ones. In 21 nights, numbers of passerines did not exceed 1 bird·night<sup>-1</sup>. In just three cases (invariably before the wind changed to the following one in the subsequent night) numbers of songbirds aloft reached 10, 13 and 20 birds·night<sup>-1</sup>, respectively. The mean headwind velocity in the nights when songbirds were recorded was  $4.4 \pm 2.7$  m·s<sup>-1</sup>.

Under following winds, passerines were recorded flying across the light beam during all 18 nights of observations, with variation between 4–134 birds·night<sup>-1</sup>. In eight out of 18 nights the flow exceeded 23 birds·night<sup>-1</sup>. The mean velocity of tailwinds in the nights with passage of songbirds was  $8.0 \pm 2.8$  m·s<sup>-1</sup>.

Table 1. Numbers of songbirds crossing the light beam in autumn on the Courish Spit under different wind conditions, as estimated by OED. Means and medians are given to the whole number.

Wind direction	Number of nights with observations	Number of nights with passage	Numbers of birds crossing the light beam for the nights with passage		
			Mean	Median	Maximum
Opposing*	47	37	2	1	20
Following	18	18	27	13	134
Still air	18	15	24	13	122

\* Mean and median bird numbers under opposing winds were 2.4 and 0.8 birds-night<sup>-1</sup>, respectively.

Very similar numbers of migrating passerines were recorded in the 15 nights with still air conditions. Passage across the light beam under wind speed  $<2 \text{ m}\cdot\text{s}^{-1}$  occurred in all nights with observations, with numbers varying between 4 and 122 birds-night<sup>-1</sup>. In six nights the numbers exceeded 21 birds-night<sup>-1</sup>.

As shown in Table 1, numbers of passerines crossing the vertical light beam were very low under headwinds and increased sharply in still air and under tailwind. However, these data need to be corrected. Even though the volume of the light cone was similar under different winds, two factors should be taken in consideration: ground speed of flying birds and their flight altitude.

As shown in Table 2, ground speed was the highest under following winds and the lowest in still air. Even under opposing winds with a mean velocity of ca.  $4.4 \text{ m}\cdot\text{s}^{-1}$  songbirds were flying quicker than in still air (wind speed  $<2 \text{ m}\cdot\text{s}^{-1}$ ). The highest flight altitudes were recorded under opposing winds, and on average 1.6 times lower in still air. With corrections for flight speed and altitude, the density of flow of passerines in the light beam peaked in still air, was two-fold lower under following winds and 21-fold lower under opposing winds (Table 2).

Table 2. Estimates of density of birds in the light cone in autumn on the Courish Spit with corrections for flight speed and altitude.

Wind direction	Mean ground speed, $\text{m}\cdot\text{s}^{-1}$ *	Mean flight altitude, $\text{m}$ *	Mean density of birds in the light cone, birds $\cdot\text{h}^{-1}$
Opposing	12.3	400	3
Following	18.6	335	32
Still air	11.1	250	64

\* Estimates for midnight  $\pm 1$  hour.

#### 4.3. Cloud cover, relative air humidity, Moon disk size and numbers of songbirds aloft

As shown in Table 3, under all kinds of wind in autumn the birds prefer to migrate under restricted cloud cover. However, the proportion of birds recorded in the vertical beam under strong cloud cover and overcast (score 8–10) peaked in still air conditions.

Proportions of songbirds recorded under low and high relative air humidity in still air conditions, from one hand, and under headwinds, on the other hand, did not differ significantly ( $\chi^2_1 = 1.8$ ,  $p > 0.05$ ). Proportion of passerines recorded under low and high relative air humidity in still air conditions and under headwinds, on one hand, and under tailwinds, on the other hand, showed a highly significant difference ( $\chi^2_1 > 305.8$ ,  $p < 0.0001$ ). In autumn passage in tailwinds occurred in dry air conditions.

Under head- and tailwinds roughly similar number of songbirds crossed the light beam when much and little of the Moon was visible. However, in still air 2.4 times more birds crossed the vertical beam when no or less than one-half of the Moon was visible than when >50% was visible (Table 3).

Table 3. Percentage of birds recorded in the light beam in autumn on the Courish Spit under different wind conditions (headwind, tailwind, still air) under varying cloud cover, relative air humidity and visible part of the Moon disk (estimates for midnight  $\pm 1$  h).

Wind direction	Cloud cover, score		Relative air humidity		Visible part of the Moon	
	0–7	8–10	low	high	0–50%	>50%
Headwind	94.0	6.0	36.3	63.7	56.9	43.1
Tailwind	82.8	17.2	89.1	10.9	41.4	58.6
Still air	74.7	25.3	30.9	69.1	70.6	29.4

#### 4.4. Proportion of straight and curvilinear flight tracks of songbirds across the vertical light beam

As apparent from Table 4, curvilinear flight tracks in the light beam occurred under all types of wind conditions, with its proportion the highest in still air (43%) and lowest under tailwinds (25%). The proportion of birds with complex flight tracks, circling including, was highest in still air (14.5%) but dramatically declines under following winds (5.6%).

Straight flight trajectories were most common under all wind conditions (Table 4). However, if in still air and under opposing winds the proportions of straight and curvilinear tracks were not significantly different ( $\chi^2_1 = 3.5$ ,  $p > 0.05$ ), under following winds significantly more curvilinear tracks were recorded (still air vs. following winds:  $\chi^2_1 = 30.4$ ,  $p < 0.0001$ ; opposing vs. following winds:  $\chi^2_1 = 9.7$ ,  $p < 0.01$ ).

Table 4. Numbers of straight and curvilinear tracks across the light beam in autumn on the Courish Spit under different wind conditions (data for midnight  $\pm$  1 h).

Wind conditions	Number of tracks recorded		
	total	straight	curvilinear
Headwind	267	173	94
Tailwind	801	598	203
Still air	269	153	116

#### 4.5. Relationship between flight trajectories and the factors studied

As apparent from Table 5, under all wind conditions curvilinear tracks in the light beam occurred significantly more often in small songbirds, under no or weak illumination by the Moon and in humid air. A significant trend for occurrence of curvilinear tracks was recorded with decreasing speed of opposing and especially of following winds. Under following winds flight tracks across the light beam were also significantly dependent on wind direction. The further wind was from the strictly following one, the more birds flew curvilinearly.

Increasing cloud cover (both general and low-altitude ones) was also directly related to increasing percentage of curvilinear tracks under opposing and following winds (Table 5). Forward stepwise inclusion of all variables in the multivariate logistic regression analysis, where “presence of straight flight track vs. presence

Table 5. Spearman’s correlation coefficients between flight track form of songbirds in autumn on the Courish Spit estimated on a 2-grade scale (1 – straight, 2 – curvilinear) with eight variables under different wind conditions (data for midnight  $\pm$  1 h).

Variable	Still air n = 269		Headwind n = 267		Tailwind n = 801	
	$r_s$	P	$r_s$	P	$r_s$	P
	Linear size of birds	-0.26	<0.0001	-0.19	<0.01	-0.29
Flight altitude	-0.01	n.s.	-0.05	n.s.	-0.03	n.s.
Angle between flight direction and the general direction of migration	–		0.01	n.s.	<b>0.25</b>	<b>&lt;0.0001</b>
Wind velocity	–		-0.17	<0.01	-0.30	<0.0001
Moon disk size	-0.23	<0.0001	-0.12	<0.05	-0.25	<0.0001
Relative air humidity	0.17	<0.01	0.25	<0.001	0.25	<0.0001
General cloud cover	-0.08	n.s.	<b>0.21</b>	<b>&lt;0.0001</b>	<b>0.21</b>	<b>&lt;0.0001</b>
Low-altitude cloud cover	-0.11	n.s.	<b>0.21</b>	<b>&lt;0.0001</b>	<b>0.21</b>	<b>&lt;0.0001</b>

Table 6. Final logistic regression models of the presence of straight vs. curvilinear tracks as the dependent variable under different wind conditions in autumn on the Courish Spit (data for midnight  $\pm$  1 h).

Model	Predictor	B-coefficient	P
Straight (n = 153) vs. curvilinear (n = 116) tracks, still air*	Linear size of birds	-0.97	<0.001
	Relative humidity	0.09	<0.05
	Moon disk size	-1.03	<0.01
	Constant	-5.09	<0.05
Straight (n = 173) vs. curvilinear (n = 94) tracks, opposing wind**	Linear size of birds	-0.71	<0.05
	Relative humidity	0.09	<0.001
	Moon disk size	-0.63	<0.05
	Total cloud cover	1.67	<0.01
	Constant	-8.2	<0.001
Straight (n = 598) vs. curvilinear (n = 203) tracks, following wind***	Linear size of birds	-1.26	<0.0001
	Relative humidity	0.02	<0.05
	Wind velocity	-0.14	<0.001
	Angle between flight direction and the general direction of migration	0.02	<0.0001
	Constant	-0.20	>0.05

Notes. \* Model  $\chi^2 = 35.0$ ; df = 3;  $P < 0.0001$ .  $-2 \log L = 332.8$ ; Cox and Snell  $R^2 = 0.122$ , Nagelkerke  $R^2 = 0.164$ . Goodness-of-fit test Hosmer and Lemeshow  $\chi^2 = 2.8$ ; df = 6,  $P > 0.05$ . \*\* Model  $\chi^2 = 40.7$ ; df = 4;  $P < 0.0001$ .  $-2 \log L = 305.8$ ; Cox and Snell  $R^2 = 0.141$ , Nagelkerke  $R^2 = 0.194$ . Goodness-of-fit test Hosmer and Lemeshow  $\chi^2 = 3.7$ ; df = 7,  $P > 0.05$ . \*\*\* Model  $\chi^2 = 150.0$ ; df = 4;  $P < 0.0001$ .  $-2 \log L = 756.9$ ; Cox and Snell  $R^2 = 0.171$ , Nagelkerke  $R^2 = 0.252$ . Goodness-of-fit test Hosmer and Lemeshow  $\chi^2 = 7.7$ ; df = 8,  $P > 0.05$ .

of non-straight flight track" was the dependent variable, yielded models with three predictors for flight in still air and with four predictors for opposing and following winds (Table 6).

According to the models for still air conditions and opposing winds, the probability of recording curvilinear tracks was higher for small songbirds, no or limited part of the Moon visible and high air humidity. Under opposing winds, the probability of occurrence of curvilinear tracks also increased with cloud cover.

Regression model for following winds shows that the probability of occurrence of songbirds flying curvilinear tracks increased with the proportion of flying small birds, with growing air humidity, with weaker winds and with wind direction being

further from the strictly following one. Unlike the two other models, it did not include the visible size of the Moon.

All three models had small predictive power: with following winds 25.2%, with opposing winds 19.4%, in still air 16.4% (Nagelkerke rho-squared; Table 6).

## 5. Preliminary conclusions

### 5.1. Wind conditions, accompanying weather conditions and the brightness of light cone

In addition to the limitations of the present study (section 3.1), it is necessary to point to another important issue, that the brightness of the light cone is not considered. Visual ceilometer studies show that visibility of the standard light beam varies under natural nocturnal illumination conditions from nearly invisible and transparent beam to the bright cone well visible from the distance (Bolshakov 1981). Moon light, especially when a large part of the disk is visible and when the Moon is high above the horizon, decreases the perceived brightness of the light cone. This effect is weakened under cloud cover, especially when its multi-layered. Unfortunately, during the automated monitoring of birds aloft the brightness of the light cone was not recorded. Therefore we only can emphasize the general pattern, which may help better understand the significant effects recorded.

Following winds in autumn emerge in the certain zones of the highs, of which low cloud cover, low relative air humidity and good horizontal visibility are typical. Rather strong winds (in our study on average  $8.0 \pm 2.8 \text{ m}\cdot\text{s}^{-1}$ ) prevented fog formation at different altitudes. As shown by visual observations (Bolshakov 1981, 1987), vertical light cone under such conditions is least obvious from the side for humans and probably also for flying birds.

Passage under headwinds that dominate on the Courish Spit in autumn is usually associated with lows or cold fronts, of which low clouds, precipitation and, as a result, high air humidity are typical. Under such conditions, the artificial light beam often forms a spot on the lower edge of clouds, but the brightness of the light cone itself is not affected. For technical reasons, OED was nearly always switched off under low clouds and in precipitation. Therefore we can only assume that in the nights with opposing winds available for analysis the brightness of the beam was in the same order of magnitude as under following winds. Rather high speeds of opposing winds in the nights when passage was recorded (in our study on average  $4.4 \pm 2.7 \text{ m}\cdot\text{s}^{-1}$ ) prevented fog formation.

Passage in still air (wind velocity  $<2 \text{ m}\cdot\text{s}^{-1}$ ) usually occurred in the central part of a high, of which still air across a large range of altitude (our measurements covered the range between 100–700 m a.g.l.), low nocturnal air temperatures at ground level, development of fog and the resulting high air humidity. Under such conditions the light cone brightness is sharply increased, especially at low altitude. Light propagation is hampered by water vapor.

In spite of these limitations, our results make it possible to conclude that even a narrow vertical light beam with the angular size of  $5^\circ$  influences the recorded flow of

flying birds, and impacts flight tracks across the beam in some birds. We were able to record some significant effects of the cone of white light on the birds flying at night that deserve conclusions. It should be once again emphasized that these effects were recorded in the areas far from strong anthropogenic light pollution.

## 5.2. Numbers aloft in the zone of the vertical beam

1. Based on estimates of numbers aloft by OED during the whole night, with corrections for ground speed and mean altitude of migration at different altitudes, the actual density of the flow of migrants in the light beam peaks in still air conditions, is halved under the tailwinds, optimal for passage, and decreased 21-fold under unfavourable opposing winds. This ratio of numbers under opposing and following winds is in agreement with the long-term moon-watching data (Bolshakov 1981, Bolshakov *et al.* 2002). There are reasons to believe that very high numbers recorded in the light beam under still air conditions, together with very low flight altitude (on average 250 m a.g.l.) and low ground speed ( $12.3 \pm 3.7 \text{ m}\cdot\text{s}^{-1}$ ) resulted from attraction of birds by light and their concentration around the OED. Numbers of birds recorded in still air may be even higher than our estimates, because our OED practically does not record targets flying below 100 m (Bolshakov *et al.* 2010). Special visual observations under conditions of strong illumination of the ground and the lowest layer of air by white light confirm mass concentrations of birds below 100 m under still air conditions (Bolshakov & Bulyuk 1978, Bolshakov 1981).

2. Estimates made by OED at midnight ( $\pm 1$  hour), under all winder the birds prefer to migrate with weak cloud cover, but the proportion of birds recorded under cloud cover scored as 8–10 was the higher in still air. In still air 2.4 times more birds cross the beam when no Moon or just a small part of its disk is visible than when  $>50\%$  of the Moon is visible. These facts further support the idea of attraction of flying migrants to the light cone in still air when background illumination in the middle of the night gets weaker and the perceived light beam becomes brighter (section 5.1).

3. OED estimates at midnight ( $\pm 1$  hour) show that in autumn under following winds nearly 90% of birds migrate at nights when relative air humidity is low. The proportion of birds crossing the beam in high relative air humidity is similar in still air (69%) and under opposing winds (64%). These figures are difficult to interpret without the data on the brightness of the light beam.

## 5.3. Flight tracks when crossing the light beam

OED estimates at midnight ( $\pm 1$  hour) show that response of the flying birds to the vertical light beam by flying in curves occurs under all wind conditions, but is most pronounced in still air, with the proportion of non-linear tracks reaching 43% and the proportion of complex tracks (circling) 14.5%. There are good reasons to believe that in still air some flying migrants are not just attracted to the brightly lit beam at low altitude, but, apart from slowing down their ground speed, they change their flight tracks, including flying in circles.

#### 5.4. Correlations with external factors

1. OED estimates at midnight ( $\pm 1$  hour) suggest that under all types of wind conditions, the proportion of non-linear tracks across the light beam was inversely related to body size of migrants. The increased proportion of non-linear tracks in small birds (size of European Robins and Goldcrests) under all winds may be related to their undulating flight pattern. Another possibility may be their relatively low airspeed as compared to larger songbirds, e.g. thrushes. The increased proportion of non-linear tracks in weaker following and opposing winds may, in our opinion, be due to two reasons: (i) response to the light beam – the cases of ‘arrested’ flight or other flight interruptions when entering a light beam were often recorded visually (Bolshakov 1981); (ii) larger amplitude of undulating flight in weaker wind.

2. Around midnight, the proportion of non-linear tracks significantly increases when no or a small part of the Moon is visible, and in humid air. This phenomenon, and also the effect of increasing general and low-altitude cloud cover, is probably explained by the decreasing background nocturnal illumination, weakening visual control of the horizon and thus a stronger response to the light flash. The same effect is probably in place under high air humidity accompanied by fog which impedes horizontal visibility and increases the perceived brightness of the light cone.

#### 5.5. Final logistic models

1. The final logistic models for still air conditions and opposing winds show that the probability of appearance of non-linear flight tracks is higher for small birds flying under no or a small part of the Moon disk visible and in humid air. When flying with headwind, non-linear tracks also occur more frequently under strong general cloud cover.

2. For following winds, the probability of flying non-linearly increased with stronger passage of small passerines, in more humid air under weaker winds that were not strictly following. The visible part of the Moon disk, unlike in other conditions, was not a significant explanatory variable. Frequent occurrence of non-linear flight tracks under significant lateral wind components was probably due to problems of compensating strong side winds, especially by smaller birds with lower airspeed.

3. All three models calculated for the middle of the night ( $\pm 1$  hour) had a low predictive power, varying between 16.4–25.2% (Nagelkerke rho-squared). It was probably due to omitting a number of important predictors, primarily variation of the perceived brightness of the light cone under different weather conditions.

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