Avian Ecol. Behav. 18, 2010: 23–51

Application of the Optical-Electronic Device for the study of specific aspects of nocturnal passerine migration

Casimir V. Bolshakov, Michael V. Vorotkov,
Alexandra Sinelschikova, Victor N. Bulyuk & Martin Griffiths

Abstract: Bolshakov, C.V., Vorotkov, M.V., Sinelschikova, A., Bulyuk, V.N. & Griffiths, M. (2010): Application of the Optical-Electronic Device for study of specific aspects of nocturnal passerine migration. Avian Ecol. Behav. 18: 23–51.

This paper is dedicated to a new technique for advances in the study of the main parameters of migratory flight in passerine birds. In addition to a detailed technical description of the equipment it also addresses the limitations of the method and the opportunities it offers for studying the main parameters of nocturnal migratory flight in songbirds. Special attention is given to one of the major difficulties in research into bird migration – the potential for the identification of individual species of passerines flying in the night sky. This application is illustrated by different examples of characteristics of nocturnal flight during autumn passage at the Courish Spit of the Baltic Sea in 2008–2009. Primarily the equipment design is shown ideal for investigating in particular the mechanisms of adaptation of birds to flight in darkness under different wind conditions. It appears possible to study under natural conditions the following issues for individual species of passerines or groups of closely related species: 1) ground- and airspeed; 2) compensation for wind drift on the basis of direct measurements of headings and track directions of individual birds; 3) wing-beat pattern and its variation depending on wind direction and velocity.

Key words: optical-electronic device, nocturnal bird migration, passerines, ground speed, air speed, wind drift, wing-beat pattern

Addresses: C.V.B., A.S., V.N.B.: Biological Station "Rybachy", Zoological Institute, Russ. Acad. Sci. Rybachy 238535, Kaliningrad Region, Russia. E-mail: bolshakov@bioryb.koenig.ru; M.V.V.: Pulkovo Observatory, Russ. Acad. Sci., Pulkovskoye sh. 65/1, St. Petersburg 196140, Russia. E-mail: biser_gao@mail.ru ; M.G.: Durrell Institute of Conservation and Ecology, University of Kent, Canterbury, Kent, CT2 7NS, U.K. E-mail: martingrif@gmail.com

Received 23 October 2010 / Received in revised form 20 December 2010 / Accepted 21 December 2010

1. Introduction

The study of the nocturnal migration of birds under natural conditions is limited by the possibilities of the methods used for observation and identification of targets in the sky at different altitudes. Not all targets flying are birds but there may also be insects and bats which may be numerous in some regions (Gauthreaux & Livingston 2006). Historically, the best identification possibilities were offered by moon-watching, i.e. watching by telescope birds crossing the moon disc (Lowery 1951; Lowery & Newman 1955; Newman 1956; Nisbet 1959, 1963; Bolshakov 1981, 1985; Bolshakov et al. 1981; Liechti et al. 1995, 1996; Bruderer 2001; Liechti 2001), and by ceilometer, i.e. watching the birds crossing a narrow light beam by binocular or telescope (Gauthreaux 1969, Able & Gauthreaux 1975, Bolshakov et al. 1981). These methods are closely approached by image intensifiers and infrared devices (Gauthreaux 1979, Liechti et al. 1995, Zehnder et al 2001, Gauthreaux & Livingston 2006) and permit to obtain the thermal image of a bird as a chain of dots or silhouettes for low flying birds. One of the most enterprising early techniques was the use of radar to reveal wing-beat patterns of individual birds tracked across the night sky (Schaefer 1966, 1968; Griffiths 1969, 1970; Zaugg et al. 2008; Bruderer et al. 2010).

Moon-watching has been found to be preferable to the ceilometer technique for discriminating birds (Gauthreaux & Livingston 2006) because the dark silhouettes of the birds with the moon disc background are sharper than those illuminated from the ground. However, the narrow cone for scanning (especially as compared with the ceilometer) and high ground speed of birds (typical of favourable nights for migration with strong tailwinds) causes difficulties for even an experienced observer to identify birds, to distinguish them from other targets or to estimate their size and consequently altitude of flight. At lower velocity of tailwind typical silhouettes of at least 70% of birds may be easily identified to the order, family, or genus, but very seldom to species (Nisbet & Drury 1969, Bolshakov 1985). The main disadvantages of moon-watching are the limited duration of the lunar cycle, the movement of the moon in the course of the night and the changing proportion of the bright part of the disc, and the lack of observations for overcast nights. The ceilometer technique is usually limited to altitudes 200–700 m (Able & Gauthreaux 1975, Bolshakov et al. 1981) and the visibility of the vertical light beam may influence the flight behaviour of birds on nights with high atmospheric humidity (Bolshakov 1981, Bolshakov et al. 1981, Gauthreaux & Livingston 2006).

As a consequence both direct visual methods permit only limited research on some aspects of nocturnal migration of birds such as the number of birds, height distribution, direction, dispersion, as well as seasonal dynamics of these characteristics with some limited evidence of species composition. Flight parameters such as altitude of flight, track direction and heading, can be estimated by these methods only for some individuals in certain weather conditions and with variable degrees of accuracy (Bolshakov 1981, 1985). Quantitative estimates of such important parameters as ground and air speed, wingbeat frequency and pattern are not possible. No estimates of within and among-species variation in the main flight characteristics of nocturnal migrants are available.

Direct observations of flying birds through passive infrared cameras that became popular for a while (Gauthreaux 1979, Buurma 1988, Gauthreaux & Belser 2003) allow discrimination between birds, foraging bats, and insects, but the altitude of flight and size of an object cannot be accurately measured by this technique (Zehnder et al 2001, Gauthreaux & Livingston 2006).

Since 2003 the joint experimental research between the Biological Station “Rybachy” and the State Astronomical Observatory of Russian Academy of Sciences has culminated in the design and testing of a new optical-electronic device (OED) for the detection and recording of nocturnal aerial targets, tracking them up to 50 m and more, and receiving their images and practically all parameters of flight. The first testing of this technique was conducted in 2006 and 2007 (Vorotkov et al. 2009) with real-time monitoring in autumn season 2008–2009 and in spring 2009. Some preliminary results have been published as reports (Bolshakov et al. 2008, 2010; Sinelschikova et al. 2009).

This paper is a methodological one. Apart from the detailed technical description of the setup, it also provides an estimate of the method's limitations and the possibilities it suggests for studying the main parameters of the nocturnal migratory flight in passerines, with accuracy estimates. A special attention is paid to the possibility of obtaining estimates for individual species. The data refers to the results of observation of autumn nocturnal passage on the Courish Spit on the Baltic Sea in 2008–2009. Keeping in mind the present limitations of this method, we do not discuss the possibility of using the OED for standardised estimating of nocturnal passage, i.e. altitudinal distribution, flight direction and its variation, and hourly and daily variation of these characteristics.

2. Design solutions for the device

2.1. Main concerns taken into account

Our method is similar to the ceilometer technique to a considerable degree. The flying targets are illuminated from the ground by the searchlights and their images are received by the recording unit (Fig. 1). An important recent addition to the system, described here, is a device for wind direction and velocity measurement (see section 2.4.).

The main concern was to overcome the contradiction between the need for high angular resolution to receive a clear image of a target to ensure the required accuracy of measurements on the one hand, and the need for a wide field of vision, on the other, to achieve a statistically representative sample of targets and to achieve trajectory type information. It was also necessary to provide uninterrupted monitoring automatically throughout the night.

The detailed description of the device has already been published (Vorotkov et al. 2009). The principle of modular assembly underlying the device project since 2006 left room for potential improvements. The resulting device created was basic and was not changed significantly over subsequent years. Despite some further improvements to the system the data collected from different years are comparable.

Future improvements to the basic system are now desirable in several directions: 1) to receive more detailed and sharper images for increased accuracy of measurements; 2) increased altitude of detection of birds; 3) enabling observations in twilight; 4) minimizing the influence of light on the behaviour of flying birds; 5) simplification of the system operation and increasing its reliability; 6) development of dedicated software, methods of data storage of information and database management.

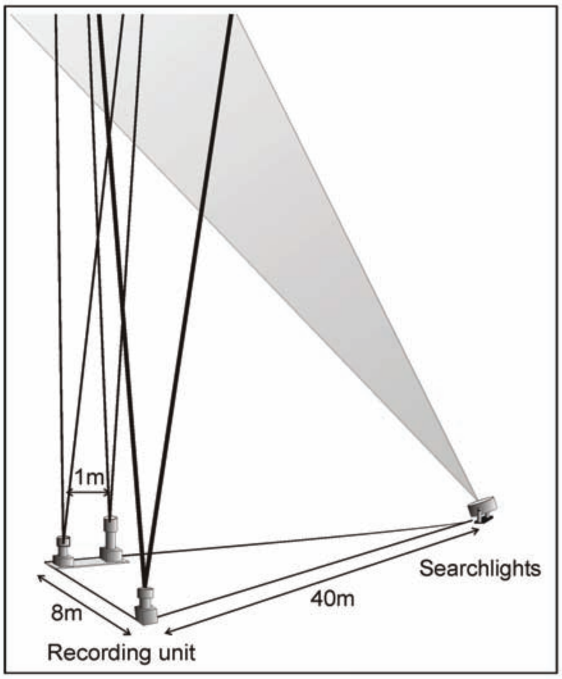

Figure 1. General scheme of the Optical-Electronic Device for the recording of nocturnally migrating birds.

One m and 8 m show the base between the channels of the recording unit. Forty m shows the base distance between the recording unit and the light source.

2.2. Recording unit

The image of an object, under artificial illumination by white light in the visible spectrum of wavelength, is received on high-sensitivity CCD matrices. The optical system is installed vertically and consists of three channels with parallel optical axes (Fig. 2). Each of the three channels includes a high-quality objective, a heating anti-condensation system, an image focusing unit, a CCD matrix and a video board (grabber). The objective lenses have different focal distances with the following parameters: the first channel F (focal length) = 86 mm (3.5°), S (focal length/aperture) = 1.5; the second channel F = 120 mm (2.5°), S = 1.8; the third channel F = 50 mm (6°), S = 1.7. At least two channels are required for parallactic computation of the altitude of the target. The separation between the first and the second channels is 1 metre. The third wide-angle channel is separated from the previous two channels at the locating distance of 8 metres perpendicular to their base.

The scales of the fields of vision differ by a factor of 1.5–2.5. Their centres are superimposed by the laser beam. During the exposure time (0.3–1.5 seconds) a target usually passes at an angular distance of 0°15´–5°. The long-focus channel is equipped with an obturator (rotating) shutter which chops the track of an object into 10–50 instantaneous and sequential images within one frame. The obturator shutter is servo controlled by an independent computer which allows the setting of an accurate speed of rotation and a required time interval between separate images with a duration of exposure of 36–12 milliseconds. The other channels (with wide fields of vision) work without shutter and form the image as a target track of variable width and brightness (Fig. 3).

To provide uninterrupted monitoring the system usually works automatically throughout the night. Total data flux per night is about 25–30 Gb. The images are

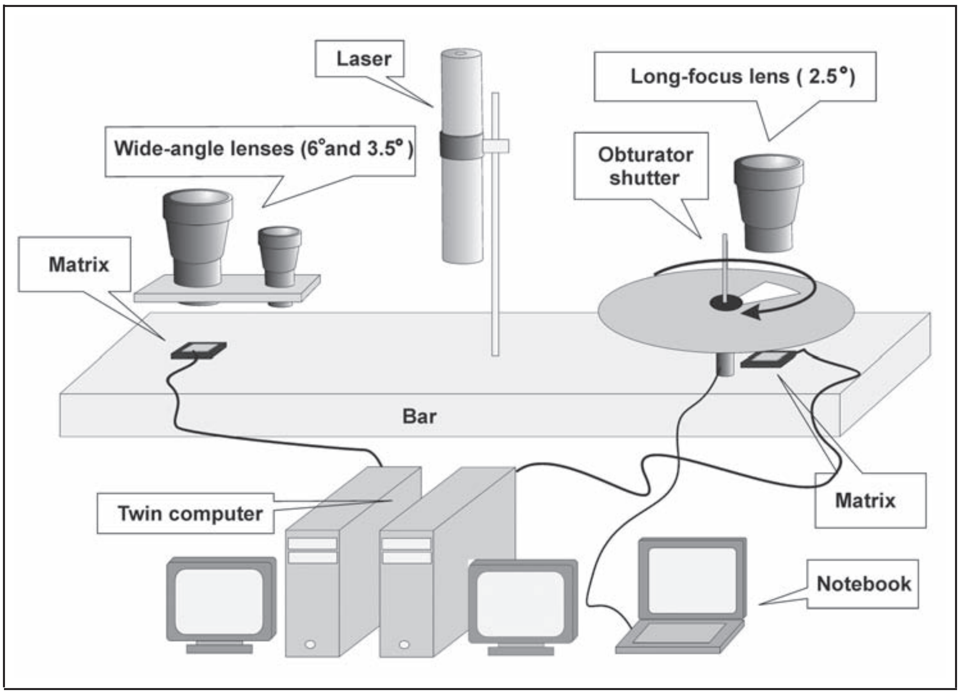

Figure 2. The optical-electronic recording unit (from Vorotkov et al. 2009).
The objective lenses of 2.5° and 3.5° are separated from each other at the locating distance by 1 m. The lens of 6° is separated from the previous two channels at the locating distance by 8 m perpendicular to their base (see Fig. 1).

written to the hard discs in a specific format. The system allows recording of flying objects of various types, and responds to cloud movement, radar, outer space and other disturbances. These disturbances are perceived by motion recording software. To identify bird tracks, complex visual recognition software is necessary. However, this software cannot perform the analysis in real time. The further bird track selection and data analyses are processed after the crude data collection.

2.3. Illumination system

The illumination system is installed 40m apart from the recording unit. This distance is the optimal one, because if the base is smaller, a spot on the clouds would be in the field of vision of the recording unit, and with greater base the zone of intersection of the light cone and the cone of vision would be too narrow. The zone of intersection of the cone of light and cone of vision has a lower and an upper boundary. Under perfect weather conditions, they are in the altitudinal range of 100–1000 m

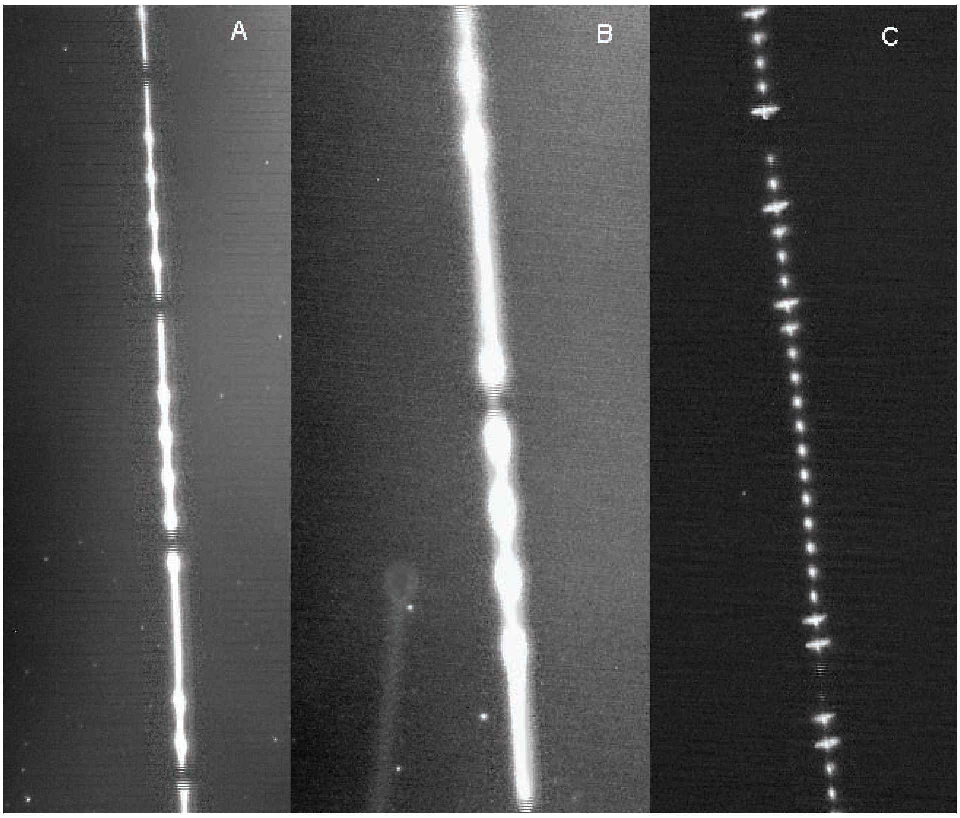

Figure 3. The images of the same bird received on three channels simultaneously.
A is the objective lens with the field of vision 6°; B is the objective lens with the field of vision 3.5°; C is the objective lens with the field of vision 2.5°.

where a uniform field of light is formed. The illumination system consists of three searchlights of differing luminance and angular size (Fig. 4). The OSRAM 250–400 W lamps were used in this project.

The parabolic mirrors installed in each searchlight permit the separate focusing of the light beams. The searchlight unit forms one combined beam with an open angle of 5°. Mutual alignment of the beams and their position relative to the optical axis of the recording unit can be adjusted depending on the altitude of the cloud canopy until the lowest and brightest part of the beam, and the spot of light on the clouds, appear to be out of the field of vision. Adjustment to the searchlights is a critical technique which requires preliminary computer simulation depending on the current weather conditions, primarily of the altitude of the lower boundary of cloud cover. To improve this procedure an additional adjusting searchlight was used. The parabolic mirror of the alignment searchlight has three incandescent bulbs that form a reference grid in the night sky using 3 needle shaped beams.

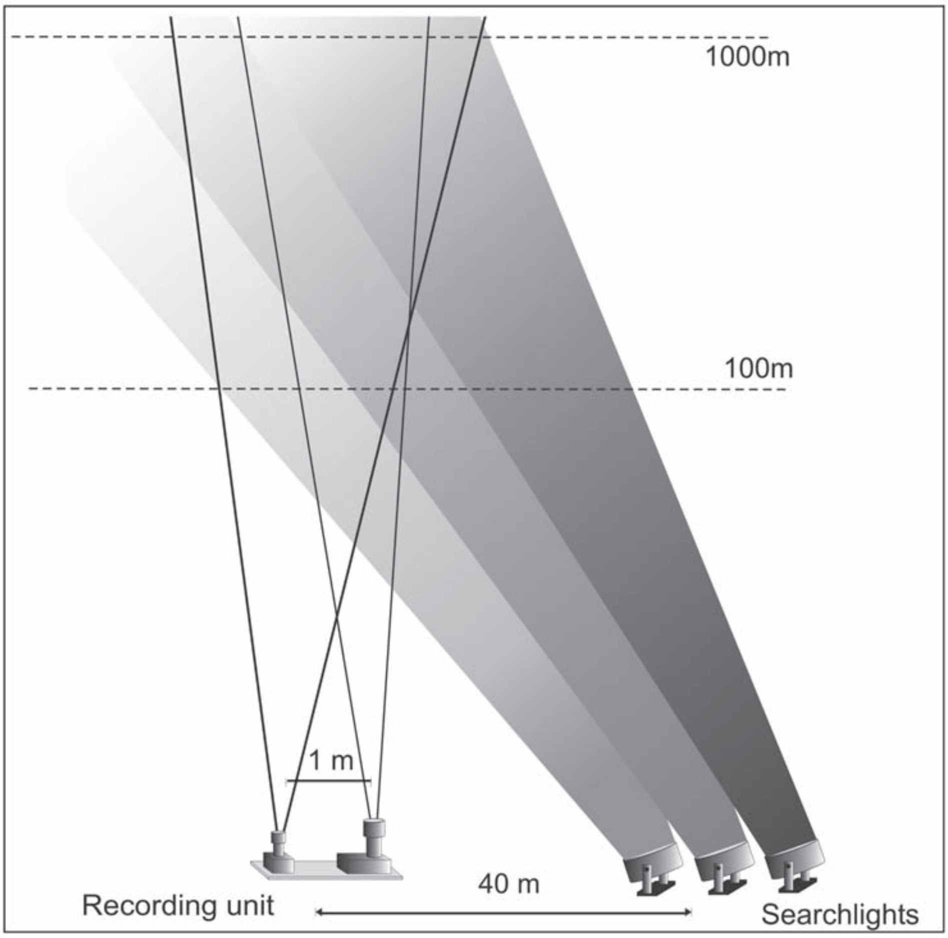

Figure 4. Illumination system (from Vorotkov et al. 2009).

2.4. Device for wind profiling

Night migration occurs under regularly changing wind conditions and accurate wind measurements are important for the investigation of the main characteristics of flight. The specially designed device for measuring wind direction and velocity has become an important addition to our system.

For wind profiling at altitudes between 100 m and 1 km we have significantly advanced the technique used in meteorology for tracking pilot-balloons. The principle used here is a computation of 3D coordinates of the pilot-balloon at fixed instants during flight to estimate the distance from the device to the balloon. The distance can be calculated by from angular size of the balloon when its diameter is known. With known parameters of the optics used is it no problem to calculate the frame

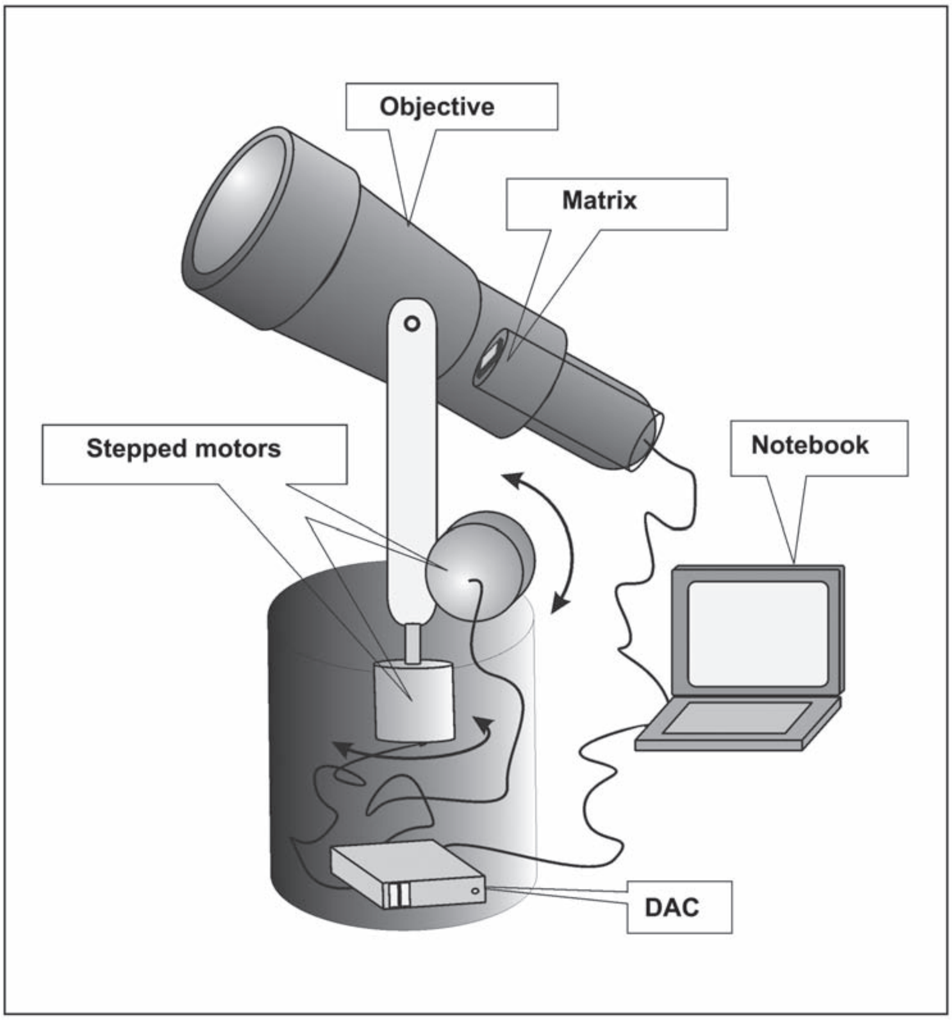

Figure 5. The scheme of the wind profiling device.

resolution in degrees/pixel. The determined elevation angle and distance permit calculation of the altitude of the target.

The device for wind profiling (Fig. 5) is installed in such a way that two rotation axes of the optical system coincide with the azimuthal coordinates and is equipped with vertical and horizontal stepping motors which permit the tracking of the balloon by the computer. The optical-electronic part of the device consists of one objective lens (5°), an image focusing unit and a CCD matrix; producing images that are written to the hard discs for the further analysis.

Translucent helium filled latex balloons of 40 cm diameter are used. To receive an image of the balloon on the CCD matrix in darkness a light-emitting diode (LED) with a tiny battery is installed inside the balloon. The total weight of such a balloon is 11 ± 0.5 g. LED with a battery have sufficient specific luminosity (Lm/g). This internal illumination provides a significant enough bright sharp image of the flying balloon to a distance of up to 2 to 2.5 km. The balloon is tracked for 2 to 10 minutes depending on the weather conditions while receiving an image array of 50 to 300 frames.

Computation of the wind profile is performed by unique dedicated software. As a result a dense data array with a height resolution of 50 to100 m is produced. The intermediate values are interpolated.

This technique permits wind profiling in the range of 100–1500 m above ground level (agl) when the average wind velocity does not exceed 7 to 8 $m \cdot s^{-1}$ and up to 800–900 m when the winds are stronger. The lowest boundary of cloud canopy restricts the altitude of the profiling. Under favourable weather conditions the balloons are launched 3 to 4 times a night.

3. Method advantages and limitations

3.1. At what time of night we may record birds?

Clear images of flying birds can be received in darkness between the nautical twilights (the sun 12° below the horizon), i.e. from the end of the 2nd to 3rd hour after sunset until the 3rd to 2nd hour before sunrise. The silhouettes are clear and sharp against the background of cloudless sky and complete or variable high overcast. In 2009 it became possible to record birds during twilights due to automatically controlled adjustment of the exposure depending on brightness of the sky. However, during the civil twilights the recording was impossible because the natural glow made artificial illumination useless.

3.2. Limitations due to precipitation, overcast and fog

The main limitations of the method are rain, fog and low overcast. On misty and foggy nights when atmospheric humidity is high a light area around of the search beams attracts and disorients birds. This phenomenon has been documented by numerous visual observations at lighthouses and other tall illuminated structures (Hansen 1954, Taylor 1972), when the ornithologists used ceilometer (Gauthreaux 1969, Bolshakov et al. 1981), horizontal light beams (Bolshakov & Bulyuk 1999, 2001), method of illuminated ground (Bolshakov & Bulyuk 1978) and by special research using mechanisms of bird attraction to artificial light (Gauthreaux & Belser 2006, Evans et al. 2007). This "light effect" results in the following behaviour of birds: 1) concentrating around the illuminated area and changing their uniform spatial distribution; 2) repeated entering into the light flow; 3) losing the direction of flight; 4) curved flight trajectories (see section 4.3.). The number of recorded birds is extremely high on such nights. Data collected during these nights cannot be used for any quantitative estimates or for the study of the natural migratory flight of birds. When skies are clear or high overcast is present such abnormal behaviour caused by artificial illumination is not observed (Bolshakov 1981, Bolshakov et al. 1981, Gauthreaux & Belser 2006).

Complete thin overcast illuminated by the full moon when it is over 30° above the horizon as well as low overcast below 800 m cause complete or partial flashing of the background of the frame (bright spots on the clouds). This degrades the quality of the images, so that contrast of many bird silhouettes is low and few details of their shape are discernible. The data for two autumns presented in Table 1 show what proportion of the observation period was (1) possible for observations and (2) was covered by weather limitations and problems arising which in practice prevented observations or the collection of high quality material.

3.3. Quality of images

The quality of target images is of great importance. High quality images permit the discrimination of birds from other flying objects. Only sharp images permit the measurement of the linear size of birds (i.e. wing span and body length). Such detailed images make taxonomic identification of birds possible.

The quality of received images depends on at least four factors:

1) The ground speed of a target. The edge sharpness of a silhouette depends to a great extent on the speed of rotation of shutter which is controlled manually. Usu-

Table 1. Real limitations of the method during autumn migration at the Courish Spit of the Baltic Sea in September–October 2008–2009. Percentage of the hours suitable and unsuitable for observation.

Condition of observation		2008 (19.09–25.10)		2009 (8.09–24.10)	
		N hours	% hours	N hours	% hours
Total possible hours of observation		478	100	586	100
Good conditions for receiving high quality material		200	42	290	49
Astronomic and weather factors preventing observation	Twilight	105	22	88	15
	Fog, mist	18	4	57	10
	Rain	71	15	83	14
	Moon around the full moon	12	3	18	3
	Low overcast	17	3	15	3
Technical problems		55	12	35	6

ally the time interval between sequential images is set up with a duration of exposure of 22 ms. In this mode birds flying at a speed of 8 to15 $m \cdot s^{-1}$ have sufficiently sharp silhouettes. If the ground speed is higher than 17 $m \cdot s^{-1}$ the image is blurred along the flight direction of bird. If a bird flies slower than 5 $m \cdot s^{-1}$ its sequential silhouettes are not sufficiently separate. The wings are clearly visible but the "tails and heads" on the neighbouring silhouettes may overlap. When the tail winds are strong the exposure is set at 12 ms. However, in this mode the silhouettes of birds flying slower than 8 $m \cdot s^{-1}$ overlap. An exposure of 36 ms provides sharpness of the silhouettes for slow flying birds under headwind conditions but the birds flying faster than 13–14 $m \cdot s^{-1}$ have blurred images.

2) The contrast of the image against the background. Light clouds reduce the contrast of silhouettes.

3) Altitude of flight. The sharpest images are received in the range between 200 and 500 m.

4) Atmospheric humidity and visibility.

We scored the quality of images following a six-grade scale (Fig. 6):

Score 1. The silhouettes are highly blurred with wing beats indistinguishable. For such tracks only altitude and direction are available.

Score 2. The track is not fragmented into separate silhouettes or they overlap. Seeing the wing beat pattern confirms a bird rather than a bat or other object. For such tracks altitude, direction, ground speed and wingspan are available (see section 4).

Score 3. The bird shape silhouette confirms a bird but it is blurred or not contrasting. All flight parameters are available but the error in wingspan and body length measurements is 10%–30%.

Score 4. The silhouettes are contrasting but the body length is slightly blurred. All parameters are reliable but an error of the body length is 10%–15% (see section 4).

Score 5. The silhouettes are detailed and sharp. All parameters are reliable.

Score 6. The silhouettes are outstanding.

The images of Classes 5 and 6 permit the most accurate linear size measurement. All other parameters (see section 4) are accurate for the images with quality score indexs, 4–6. The Table 2 shows the actual proportion of images of different quality we could achieve in different years.

3.4. Birds and other targets

Clear series of silhouettes in fragmented tracks (section 4.2.) with measurements of linear size allow reliable discrimination of birds from other targets (Table 3).

Insects differ from birds by the following characteristics: 1) small size (usually less than 10 cm), 2) faint tracks, 3) relatively low altitude of flight, usually up to 300 m under good weather conditions, and 4) low air speed (1–3 $m \cdot s^{-1}$). Due to the low flight velocity of insects their tracks are usually not fragmented. Wing beats are poorly distinguishable and wing-beat pattern has no pauses.

Bats are not numerous in the study area (the Courish Spit of the Baltic Sea) and during their feeding activity they fly at low altitudes. They do not have bird shape silhouettes (without a tail) and have sharply curved or zigzag tracks. Long-term

Table 2. Quality of images of the birds received by Electronic-Optical system in different years. Percentage of birds with different ratings of quality of images.

Quality of images	2006	2007	2008	2009
Low (classes 1–3)	80%	60%	42%	45%
Medium (class 4)	15%	25%	28%	40%
High (classes 5–6)	5%	15%	30%	15%

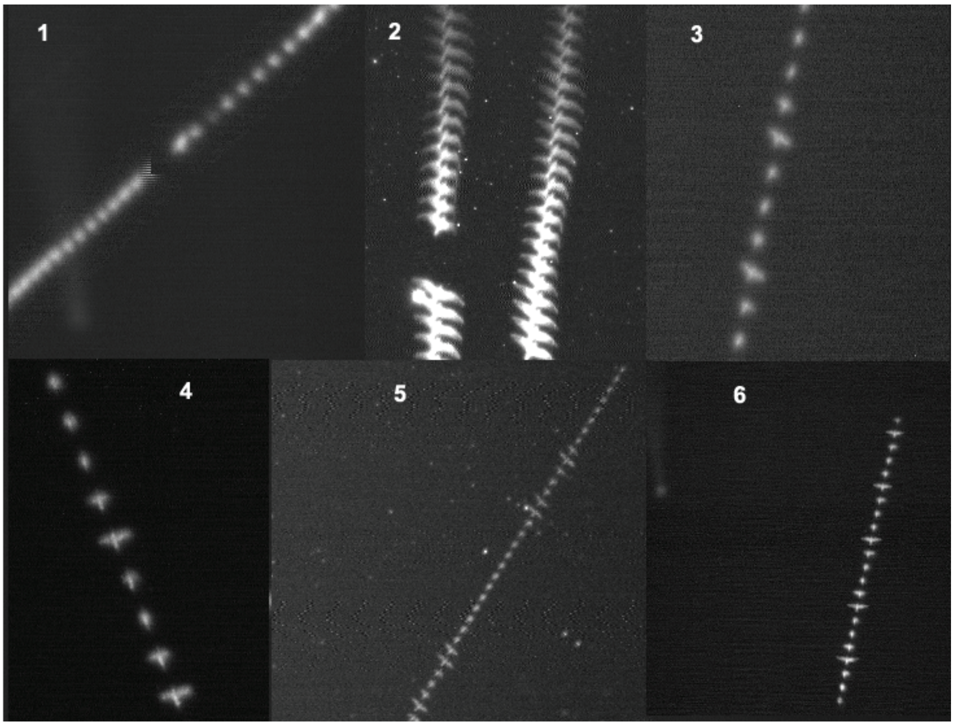

Figure 6. Quality scores of bird images obtained by OED. For further explanations see text.

moon-watching data suggests that no significant bat passage occurs in the study area (Bolshakov, unpublished data).

Satellites and artificial space debris are easily distinguishable. Their tracks are very bright and cannot be fragmented as their altitude is higher than 30 km.

3.5. The possibility for the identification of birds by the OED

Birds observed by an optical device when they cross the moon disc or the beam of the searchlight can be easily separated into particular groups of species by an ex-

Table 3. Quantitative ratio of the migrating birds and other nocturnal aerial targets at the Courish Spit of the Baltic Sea between the 14.09 and 11.10 (22 nights) in 2006 when all targets were recorded.

Type of target	Number	%
Birds	1284	83
Insects	47	3
Bats	3	<1
Satellites, space debris	34	2
Not identified	186	11

perienced observer under good weather condition by the following signs: type of silhouette, wing-beat pattern (Bolshakov 1985, Dolnik & Bolshakov 1985). Birds illuminated from the ground have indistinct silhouettes, their altitude of detection is restricted and the field of view is narrow. This method is inferior to moon-watching for the identification of birds by either type of evidence.

What difficulties for identification are there for the OED? There are at least three of them. 1) The proportion of high-quality images is relatively low (Table 2). 2) There is no actual movement of a bird but only sequential images. 3) Only high-flying birds have sufficiently long tracks to include their wing-beat pattern. On the positive side, this method allows the measurement of the bird's size and all data can be filed for future analysis.

High-quality images with long tracks make it possible to distinguish the group of passerine birds by their typical silhouettes, wing-beat pattern, size and proportion of the wing span to body length. As already shown by 2 years (2008–2009) of observations using this method, passerines form up to 93% of the total nocturnal bird passage (2748 passerine birds of 2945 recorded birds) at the Courish Spit in autumn. For sharp silhouettes it has been possible to divide all passerine birds into three size classes: small (Goldcrest *Regulus regulus* size), medium (European Robin *Erithacus rubecula* size) and large ones (thrush size). Until now the main problem has been that each size class is represented by several species with overlapping sizes.

However, the phenology of migration and number of particular bird species at their stopover sites reveals that during specific periods of autumn migration each size class, with high probability, is represented with a high probability by a single species clearly dominant in numbers. During the autumn season between September 10–November 1 (in 2008–2009) on the Courish Spit it was possible to distinguish several model species based on their trapping numbers at stopover (Table 4).

1. A group of small passerines (body length 0.08–0.12 m, wing span 0.15–0.20 m). This group is represented at the stopovers mainly by three species – the Goldcrest, Wren *Troglodytes troglodytes* and Chiffchaff *Phylloscopus collybita*. Goldcrests form ca. 87%–96% of birds of this size group during the most of autumn. The sizes of the Goldcrest and Wren nearly coincide but the Chiffchaff is about 2 cm larger. This makes it

Table 4. Quantitative and percentage ratio (% in brackets) of particular species of passerine birds of three size classes. Capture data at the stopover sites in “Rybachy Field site” in 2008–2009.

Groups and Species	Ten-day periods				
	Sept. II	Sept. III	Oct. I	Oct. II	Oct. III
Small passerine birds					
Regulus regulus	138 (66.0)	669 (87.0)	366 (87.6)	739 (90.7)	1321 (95.6)
Troglodytes troglodytes	57 (27.3)	78 (10.1)	32 (7.6)	48 (5.9)	58 (4.2)
Other species	14 (6.7)	22 (2.9)	20 (4.8)	28 (3.4)	3 (0.2)
Total number	209 (100)	769 (100)	418 (100)	815 (100)	1382 (100)
Medium size passerine birds					
Erithacus rubecula	1061 (81.2)	731 (74.9)	781 (91.0)	302 (82.1)	109 (86.5)
Sylvia atricapilla	75 (5.7)	84 (8.6)	56 (6.5)	21 (5.7)	10 (7.9)
Other species	171 (13.1)	161 (16.5)	21 (2.5)	45 (12.2)	7 (5.6)
Total number	1307 (100)	976 (100)	858 (100)	368 (100)	126 (100)
Large passerine birds					
Turdus philomelos	38 (100)	68 (100)	82 (96.4)	22 (52.4)	10 (76.9)
Turdus iliacus	0	0	3 (3.6)	20 (47.6)	3 (23.1)
Total number	38 (100)	68 (100)	85 (100)	42 (100)	13 (100)

possible to assume that birds with body length of 0.08–0.10 m and wing span of 0.15–0.17 m are mainly the Goldcrests even to a greater extent than shown in Table 4.

2. A group of medium sized passerines (body length 0.12–0.15 m, wing span 0.19–0.24 m) is represented at the stopover sites at this time by 22 species. At least 13 of these are uncommon (1.03% of total trapping figures), and 8 species form 22.8% of total number of birds of this size group (with 7.8% Blackcap *Sylvia atricapilla*) The most common species in this group is the European Robin. The proportion of European Robins in captures is 75%–91% of all birds of this size (Table 4).

3. A group of large passerine birds on the Courish Spit in autumn is mainly represented by thrushes and the Skylark *Alauda arvensis*. The sizes of the Song Thrush *Turdus philomelos* (body length 0.19–0.22 m, wing span 0.33–0.38 m) and the Redwing *Turdus iliacus* (body length 0.19–0.21 m, wing span 0.33–0.37 m) strongly overlap. Trapping data and phenology of nocturnal migration show that the passage

of the Redwings at the Courish Spit begins as late October 5 and even on October 15 in some years (Bolshakov et al. 2002). In September early October Song Thrushes make up to 100% and 91%–96% of this group, respectively (Table 4).

The passage of the Blackbird *Turdus merula* usually begins on October 5–10. This species is considerably larger than the Song Thrush and Redwing (body length 0.22–0.27 m, wing span 0.37–0.44 m). Blackbirds also have in good images a very specific silhouette of a bird in black.

In mid and late October the "large grey thrushes" migrate, not annually in considerable numbers. They are the Fieldfare *Turdus pilaris* (body length 0.22–0.26 m, wing span 0.40–0.46 m) and the less common Mistle Thrush *Turdus viscivorus* (body length 0.24–0.28 m, wing span 0.44–0.49 m).

A marked nocturnal passage of Skylarks occurs in October. These birds are a little smaller than Song Thrushes or Redwings (body length 0.15–0.19 m, wing-span 0.30–0.38 m). They can be determined by the proportion of their wing span to body length. For the Skylark this is about 2.0. In "small thrushes" (Song Thrushes and Redwings) it is ca. 1.6–1.7.

Therefore, it was possible to distinguish the following model species or groups of species during autumn migration at the Courish Spit 2008–2009: 1) The Goldcrest, 2) Robin, 3) Song Thrush, 4) Song Thrush and Redwing, 5) Blackbird, 6) Skylark, 7) Fieldfare and Mistle Thrush. The sizes of these groups with respect to their phenology practically do not overlap.

4. Measurements of different flight parameters in nocturnally migrating birds

4.1. Altitude of flight

The principle system design is a parallactic computation of a distance from the OED to the target. Simultaneous observation of a target from two points separated from each other at a fixed distance permits the calculation of the distance to a target by its angular displacement. A locating distance of 1 m provides an error of altitude measurement about ±50 m, while a locating distance of 8 m an error ca. ±10 m. The locating distance of 8 m is used since 2008.

In lowlands of Europe and North America passerine birds may fly at altitudes 2000–3000 and even 4000 m a.g.l. during their seasonal migrations. Nevertheless, the bulk of passerines (70%–80%) fly below 1000 m (Bruderer 1997, Gauthreaux & Livingston 2006). Moon-watching showed that the median altitude of thrushes the SE Baltic region is 700 m a.g.l. in spring and 500 m in autumn in. Under tail winds the thrushes fly about 150–200 m higher than in head winds (Bolshakov et al. 2002).

The illumination system of the OED allows the recording of targets within an altitudinal range of 100–1000 m. Birds flying higher have low quality silhouettes and an error of their size measurements is over 30%–40%.

The computations and testing have shown that under condition of high air visibility we can receive an image of a small passerine at a distance of 1 km. Brightness of an object does not depend on its size but depends only on luminance. Luminance is square-law dependent on the distance to the object in transparent air. Square-law dependence arises because OED, unlike radar, records a bird as an extended object, not as a dot. It means that from a particular altitude the probability of detection of an object declines exponentially and depends on the distinctness of the target amongst the noise of the background.

Theoretical computation, analysis of all our data under different weather conditions (2008–2009) and comparison with real moon watching data (1977–2003) resulted in a probability curve of detecting birds of different size depending on altitude of flight (Fig. 7). As shown in Fig. 7 the probability of detection of birds depends slightly on their size. These data should certainly be confirmed by synchronous moon-watching and OED observations.

The results of observations have shown that small objects (birds of wing span up to 0.2 m) are recorded regularly at the range of 650 m and large objects (birds with wing span of 0.3 m and more) – at 900 m (Fig. 8). The maximum altitudes of detection of these objects are higher. When quantitative estimates of the flow of migrants are made from OED data, it is certainly necessary to use correction factors for altitude-dependent detection probability of birds of different size.

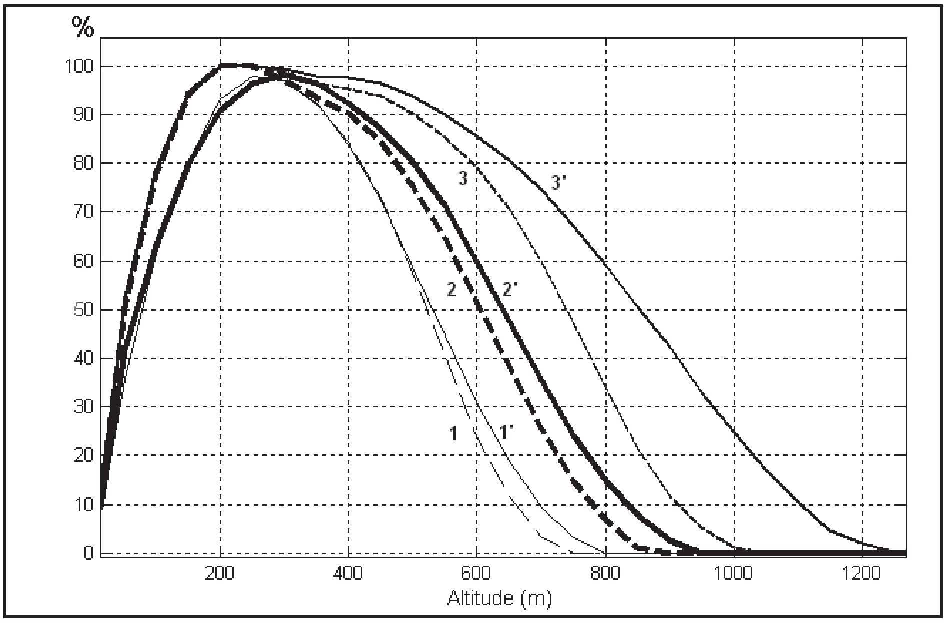

Figure 7. Probability of bird detection depending on its altitude of flight.

The curves 1, 2, 3 (dash lines) are the small targets (wing span 0.15 m). 1', 2', 3' (solid lines) are the large targets (wing span 0.35 m). 1, 1' (thin lines) – bad conditions of observation (low air transparency, light clouds). 3, 3' (normal lines) – perfect conditions. 2, 2' (bold lines) – averaged curves for the total sample.

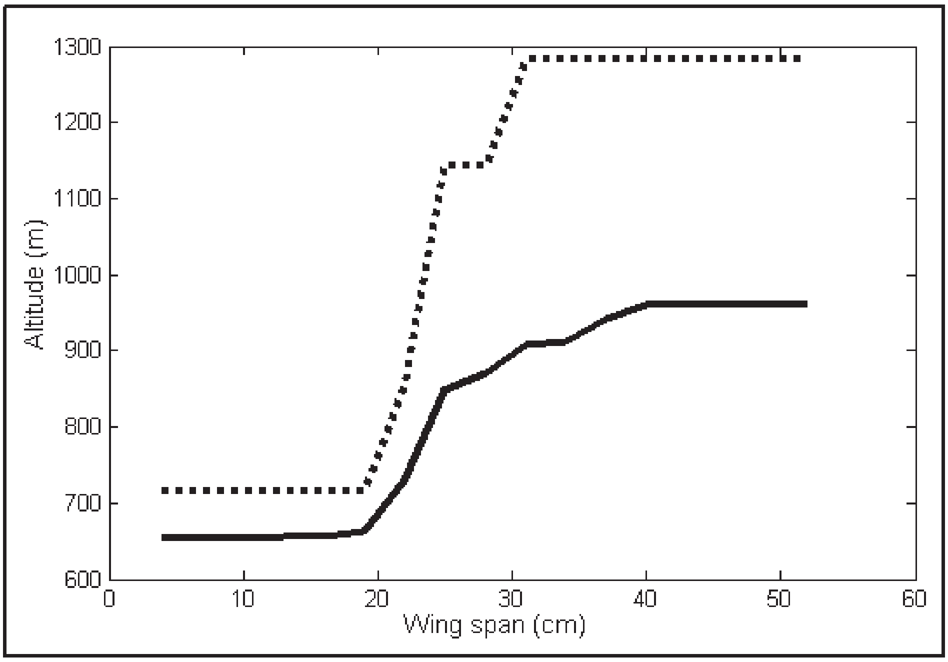

Figure 8. The highest possible altitude of detection of the birds of different sizes (wing span). Dashed line shows the maximum detection altitude of the birds with a given wing span. Solid line shows average altitude for 10 highest birds of corresponding wing span.

4.2. Linear size of birds

No technical system is currently available which allows measurement of the real size of birds flying at night. Radar systems also permit division of passerine birds into 3 size classes: small, medium and large ones. This division is based mainly on their wing-beat patterns (Gauthreaux 1970, Bruderer 1997). Infrared cameras permit silhouettes for low flying birds but their size cannot be accurately measured by this technique (Zehnder et al 2001, Gauthreaux & Livingston 2006).

In the method described here the linear size, i.e. wing span and body length, is measured on the basis of angular size and distance to a bird. An accuracy of measurement is strongly dependant on the sharpness of the silhouette and the altitude of the bird. The error of measurement of birds' linear size was calculated from measuring a sequence of silhouettes. For wing span measurements only silhouettes with most extended wings were used. The average error of size measurements of the silhouettes with score index of quality below 4 is 20%–30% and even more. The error of wing span for good silhouettes with score index of quality 4 and both measurements (wing span and body length) for high quality silhouettes (scores index 5 and 6) is 3%–10% depending on the altitude of bird. For these birds (scores index 4–6)

Table 5. Error of measurements of the linear size of images with the quality class (score index) of 4 (wing span) and 5–6 (wing span and body length) for the birds flying at different altitudes.

Type of the passerine bird	Error of linear size, cm					
	2006–2007			2008–2009		
	300m	500 m	700 m	300 m	500 m	700 m
The Thrush	3	4	5	1	2	3
The Robin	3	4	4	1	2	3
The Goldcrest	2	3	4	1	2	3

an error of measurements depending on an altitude of bird flight is presented in the Table 5. Additionally, benchtop measurements of stuffed specimens with extended wings were performed.

4.3. Flight direction of birds (track direction)

Visual observation of birds crossing the disc of the moon, the search beam or the illuminated background (Bolshakov & Bulyuk 1978; Bolshakov et al. 1981, 1985) have shown that the trajectories of their flight at low and high altitudes are usually straight. Arch-shape and zigzag tracks with deviation from the main course by 30–40 m are observed at low altitudes under conditions of strong opposing and side winds. This may be due to compensation for wind drift at low altitudes (Alerstam 1979, Cochran & Kjos 1985, Åkesson 1993). This behaviour may increase the spread of flight directions. The strong disruptions of flight orientation occur only under conditions of rain, fog and low overcast. The birds crossing the illuminated area have curved and zigzag trajectories of flight or they are simply circling (see 3.2.).

Through observing birds by the OED we have distinguished between 4 types of trajectory of flight (Fig. 9).

1. Straight shape trajectory over the whole visible length of track (in 2008–2009 – 60% of tracks).
2. Weakly curved arch (24% of tracks). It is possible that these tracks are typical for birds flying at low altitudes in gusty winds. Climbing or landing birds also show these types of track. This also may be a response of the birds to artificial light under conditions of fog and low overcast.
3. Strongly curved arch (13% of tracks).
4. Tracks of the complex shape, including loop-shaped (3% of tracks).

The strongly curved and loop-shaped tracks of flight across the light beam appear only during foggy nights or low overcast.

For estimating flight direction it is important to take into account the length of the track. The field of vision of the objective lenses determines the maximum pos-

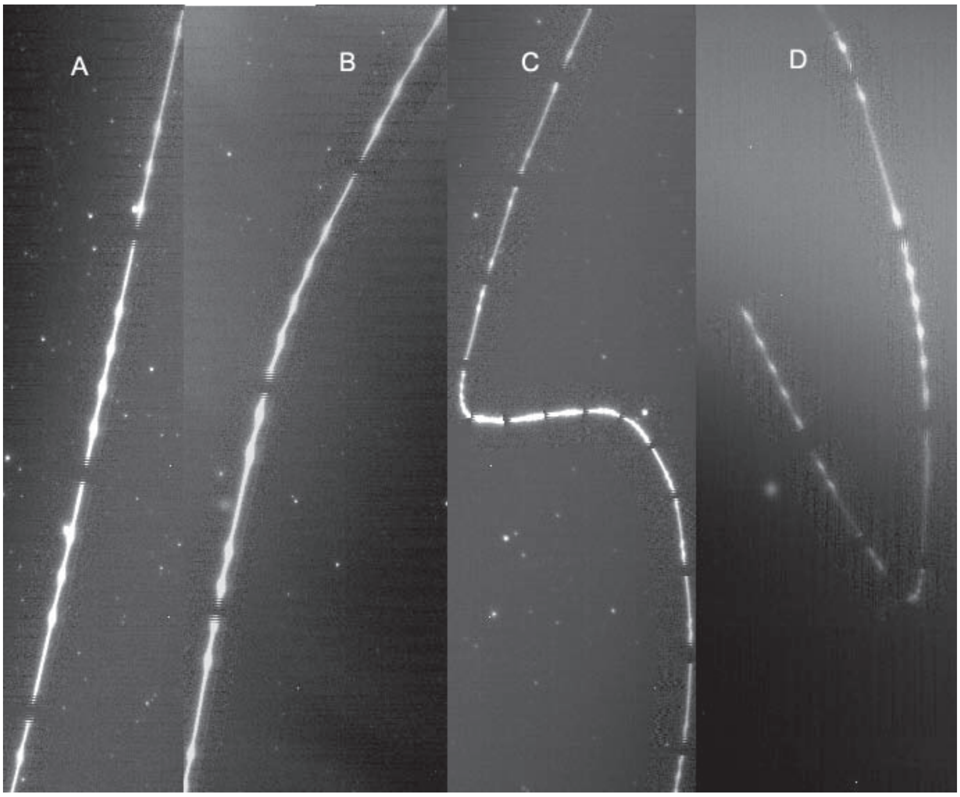

Figure 9. The samples of different types of trajectories of the recorded birds (objective lens 6°). A – straight shape trajectory; B – weakly curved arch; C – strongly curved arch; D – trajectory of flight during disorientation.

sible length of observed track (Table 6). It means that we may potentially track a bird over 90 m. In practice the longest recorded track was 86m. It was a thrush flying at an altitude of 940 m. Long tracks (>30 m) were recorded in 37% of birds.

The most direct or accurate flight direction may be measured in straight and long tracks (Fig. 9).

4.4. Heading (axis of body, the line tail-head)

Direct visual observations of birds against the background of the moon disc and in the search beam have revealed that track directions and headings do not always coincide. Sharp silhouettes (score index 4–6) permit the measurement of heading as well as the angle between the track direction and heading with an accuracy of ±3°.

The headings are measured only in high quality images of birds with straight tracks. In the database of autumn migration 2008–2009 the heading measurements

Table 6. Size of the field of vision (m) of the objective lenses for three channels at different altitudes.

Altitude, m	Size of the field of vision, m		
	Objective lens 2.5°	Objective lens 3.5°	Objective lens 6°
300	12.3 × 15.6	16.5 × 21.2	27.5 × 35.7
500	21 × 36.7	28.2 × 36.1	47 × 60.8
700	30.8 × 39.2	41.4 × 53	69 × 89.3

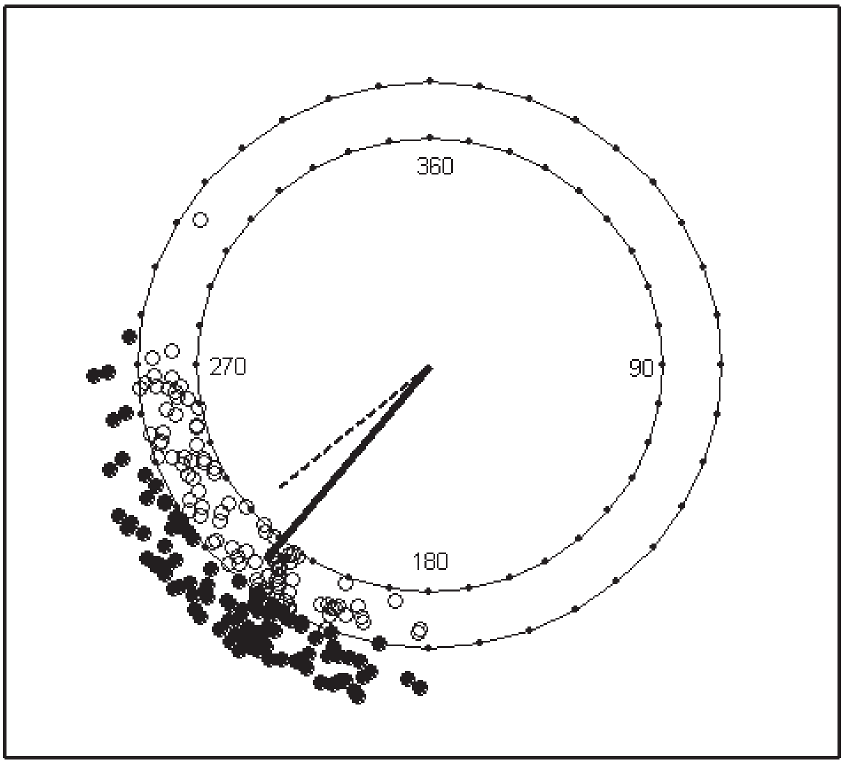

Figure 10. Distributions of the track directions and true headings in the Song Thrush during nocturnal autumn migration (8.09–10.10, 2008–2009) on the Courish Spit (data pooled for all wind conditions).

Distributions are plotted for 100 birds with the straight trajectory, track length of 30 m and longer, altitude > 300 m a.g.l., quality score indices 5–6. Black dots show tracks of individual birds. Black line is the mean track direction 219°, r = 0.89, P < 0.001. Circles – headings of the particular birds. Dash line – mean heading 229°, r = 0.84, P < 0.001.

were possible for 30% of birds. In most of these birds (75%) the headings and track directions deviated by more than 5° (Fig. 10). Pooled for all wind conditions, in 80% of birds the difference between the measured and the calculated heading did not exceed ±10°.

Measurement of the true heading, flight direction, ground speed, wind direction and speed at the altitudes of bird flight permit the following: 1) increase in accuracy of calculation of air speed, 2) the opportunity to investigate the problem of wind drift compensation.

4.5. Ground speed

Ground speed can be calculated by two methods:

Method 1. From the duration of the exposure of one frame at any channel. In each frame during exposure time a bird passes a certain path. The exposure duration is known. The path is calculated relative to the altitude of the bird. The ground speed of a bird is calculated on basis of the length of its path and duration of exposure.

Method 2. In some cases the beginning or the end of track are cut off by the edge of the screen. This is typical for the tracks of low flying birds. In these cases we can calculate the ground speed by the frequency of rotation of an obturator shutter on the channel with fragmented tracks. The frequency of rotation of the shutter is known and the time interval between the sequential silhouettes of a bird can be calculated. We mark each silhouette and like in previous case knowing the altitude of this bird easily can calculate the average ground speed for the whole marked part of the fragmented track.

The sample distributions (Fig. 11) show the ground speeds of three model species (the Goldcrest, European Robin and Song Thrush) under condition of weak wind (≤3 $m \cdot s^{-1}$). These data were collected during two autumn seasons 2008–2009.

4.6. Air speed

Obviously, the vector of ground speed of a bird is a sum of the vector of air speed and the vector of wind: $\vec{Vg} = \vec{Vw} + \vec{Va}$, where:

$\vec{Vg}$ is the vector of ground speed. Direction of this vector is track direction; its length is the ground speed value.

$\vec{Vw}$ is the vector of wind. Direction of this vector is wind direction; its length is wind velocity.

$\vec{Va}$ is the vector of air speed. Direction of this vector is heading; its length is the air speed value.

Air speed is $\vec{Va} = \vec{Vg} - \vec{Vw}$. If we know wind direction and velocity at the altitude of bird's flight, its ground speed and track direction there is no problem in calculating the air speed:

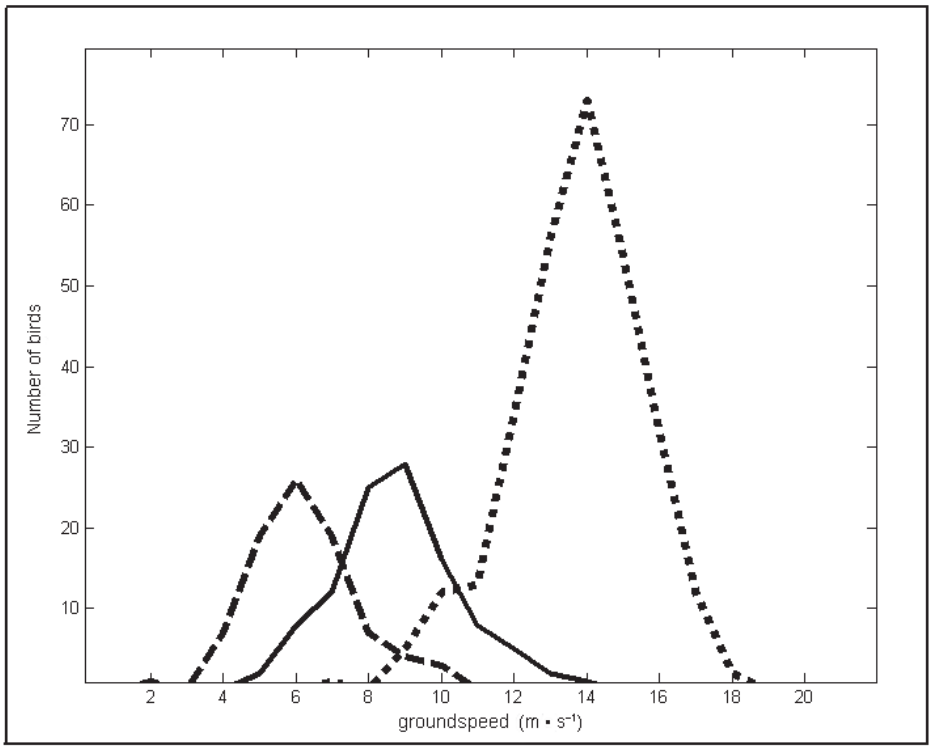

Figure 11. Ground speeds of the birds of three model species under weak winds (≤3 m·s^{-1}). Dashed line is the Goldcrest – 6.2 m·s^{-1}, SD = 1.5, n = 86. Solid line is the European Robin – 8.8 m·s^{-1}, SD = 1.7, n = 107. Dot line is the Song Thrush – 13.7 m·s^{-1}, SD = 1.8, n = 294.

$Va=\sqrt{(Vg \cos(\alpha) - Vw \cos(\gamma))^2 + (Vg \sin(\alpha) - Vw \sin(\gamma))^2}$, where:

Va is air speed (m·s^{-1}),

Vg is ground speed (m·s^{-1}),

Vw is wind velocity (m·s^{-1}),

α is track direction,

γ is wind direction.

As an example, distributions of the ground speed and air speed for the Song Thrush are presented at Fig. 12.

The OED permits to answer the following questions: (1) whether the nocturnally migrating birds are able to estimate and control their ground speed, depending on wind direction and velocity; (2) whether they can vary their air speed depending on the wind condition, i.e. to decrease it in the tailwinds and increase in headwinds; (3) what are the inter-species differences in wind selection that minimize the energy cost of flight.

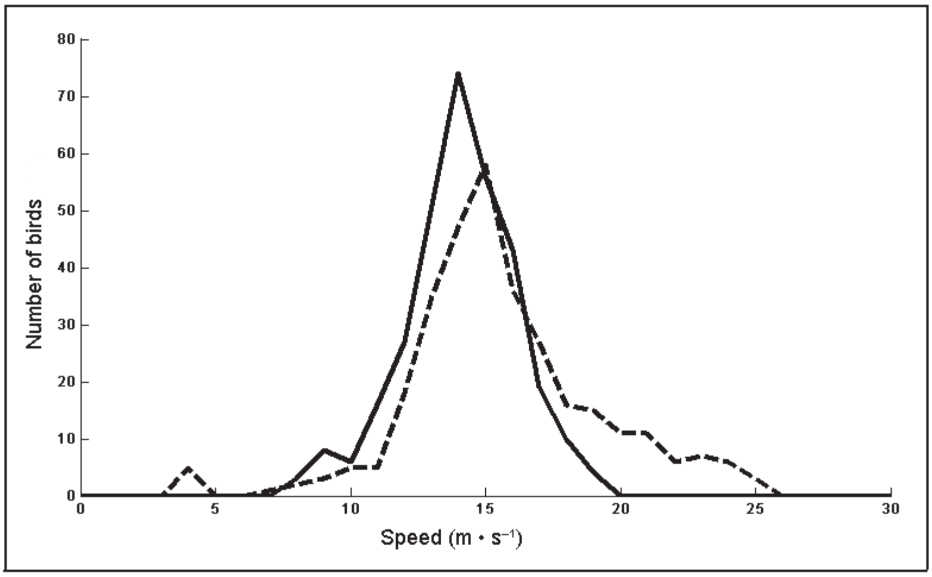

Figure12. Ground speed and air speed of Song Thrushes during autumn passage on the Courish Spit (8.09–10.10) (2008–2009).

Dashed line is ground speed: Vg =15.6 m·s^{-1}, SD = 4.2; n = 317. Solid line is air speed: Va =13.6 m·s^{-1}, SD = 3.2; n = 317.

4.7. Wing beat pattern (WBP) and its characteristics

The OED allows the investigation of a very important element of migratory behaviour, the wing beat pattern (WBP). WBP coupled with the silhouette shape helps to discriminate the group of passerines among other migrants (Fig. 13). It makes it possible to investigate the flight characteristics in selected passerine birds under different wind conditions (Fig. 14).

WBP assumes the following characteristics:

1. Wing beat frequency within wing cycles of beats (beats·s^{-1} or Hz). In passerines the cycles are usually separated by the pauses. In literature this characteristic may be called the wing beat frequency or actual wing beat frequency (Cochran et al. 2008 and references within).
2. Effective wing beat frequency (beats·s^{-1} or Hz; Bruderer et al. 2001) – an average frequency during the whole track including cycles of beats and pauses.
3. Pause duration between the cycles of beats (s) in passerine birds.
4. Proportion of pauses (%) during the whole track.
5. Number of beats in each cycle.

Most of these characteristics (2–5) are reasonable only for long tracks (at least 30 m) with several wing beat cycles and pauses (Fig. 13, 14). The proportion of such tracks in the 2008–2009 database is 30%.

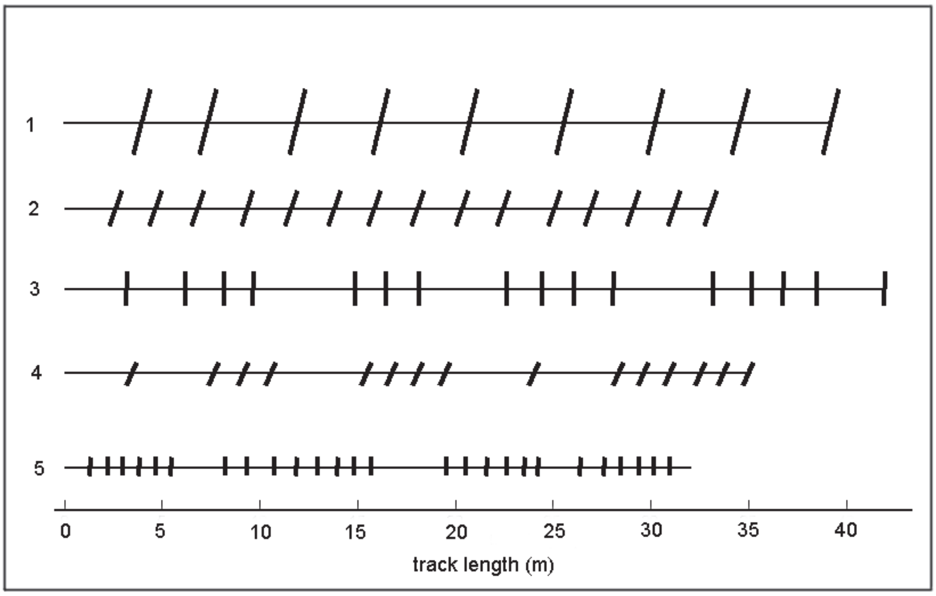

Figure 13. Wing beat pattern in different groups of birds.

The oblique stokes indicate the wing positions at the moment of wing flap. The tilting of the lines corresponds to wing position relatively the track direction of bird. 1 – large non-passerine, wing span 1.01 m. 2 – small non-passerine bird, wing span 0.41 m. 3 – Song Thrush, wing span 0.35 m. 4 – European Robin, wing span 0.22 m. 5 – Goldcrest, wing span 0.15 m.

To compute these characteristics, first we select the part of track at any channel where the WBP is clearly distinguished. The measurement of all wing beat parameters is accomplished semi-manually by draft designation of the graphics primitives which mark the control points of wing beats on the track.

WBP of the Song thrush under different wind conditions in graphical form is presented in Fig. 14. One might deduce from the results that nocturnally migrating passerine birds control their speed mainly by varying the pause duration rather than wing beat frequency per unit of sequential beats of the wing.

5. Appropriate software

Basically the method supposes three steps: night monitoring, computation and database management.

Monitoring provides a huge flux of crude data (the total volume per season of migration is up to 5 million frames, 1500–2000 Gb). Multistep processing of raw data consists of several steps as follows:

1) General data analyses. Cataloguing of the time schedule of observations, weather conditions, overcast, wind direction at the altitude of clouds.

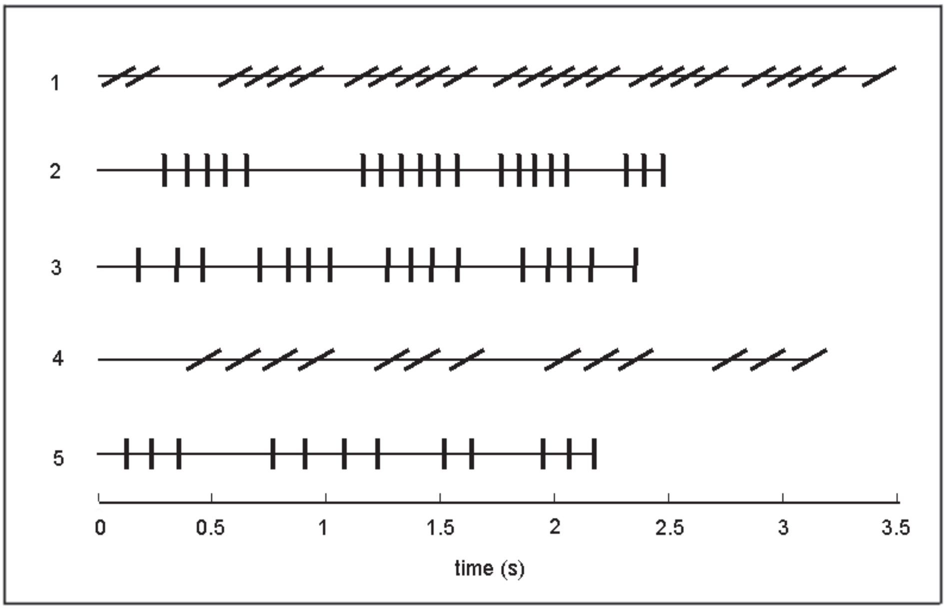

Figure 14. Samples of the wing beat patterns of the Song Thrush under different wind conditions. The oblique stokes indicate the wing positions at the moment of wing flap. The tilting of the lines corresponds to wing position about the track direction of bird. 1 – strong side wind 295° 10.7 m·s^{-1}; ground speed 10.2 m·s^{-1}, air speed 5.6 m·s^{-1}, track direction 215°, heading 256°. 2 – weak head wind 230° 4.3 m·s^{-1}; ground speed 12.3 m·s^{-1}, air speed 15.7 m·s^{-1}, track direction 217°, heading 220°. 3 – calm conditions 305° 1.3 m·s^{-1}; ground speed 13.8 m·s^{-1}, air speed 14.1 m·s^{-1}, track direction 222°, heading 225°. 4 – strong tail wind with side component 332° 12.3 m·s^{-1}; ground speed 16.7 m·s^{-1}, air speed 13.8 m·s^{-1}, track direction 210°, heading 255°. 5 – moderate tail wind 031° 9 m·s^{-1}; ground speed 19.7 m·s^{-1}, air speed 10.2 m·s^{-1}, track direction 218°, heading 223°.

2) Selecting of the frames which contain target tracks (about 2%–4% of total volume of crude data).

3) Association of the selected frames in groups (each target may be recorded by 3–20 frames). For each target the frames relating to the corresponding channel are pasted together. As a result the graphical constituent of the database is presented by the associated images where each target has 3 images (*.bmp files) of its track (one for each channel).

4) The selected material is subsequently displayed appropriately for measurements. The images of three channels are superimposed and the measurement of all target parameters is accomplished semi-manually by draft designation of the graphics primitives which mark the control points of the image. As a result the calculation of the required target parameters is achieved.

The basis of our database is formed by the frames with applied graphics primitives. On the one hand, the frames may be opened by any standard viewer as a *.bmp file. On the other hand, it contains all numerical information (parameter calculations) concerning the referred target. On the basis of this information it is possible to form the numerical database with an appropriate interface. This enables easy navigation through the database. An installed statistics module permits a direct initial summary of results in the form of diagrams and histograms.

This approach allows for re-measurement and recalculation of the data, adding new parameters and characteristics. It is "transparent" and hence resistant to the accidental errors which are inevitable in huge flux of data.

It is possible to export over 30 parameters to the text or MS Excel sheet. The main ones are the time of recording of a bird, altitude, wing span and body length, groundspeed, airspeed, characteristics of wing beat pattern, quality and accuracy.

The specially designed data management system provides easy control of the database. The program package of data management system permits recording and systematisation of the work, replenishment by new functions for calculation and means of display and easy return to the measurements and calculations to repeat, change or add new parameters.

6. Conclusions

The progress in the study of nocturnal migration under natural conditions is impossible without our understanding of differences in this phenomenon for particular species or narrow taxonomic groups. The methods used up to now have not allowed the comprehensive identification of species. We believe that new high tech instruments such as fluorescence lidar for example (Brydegaard et al. 2010) may contribute to species identification of birds flying at night in nearest future.

The original OED presented here may be a potential advance in technique for bird migration research. It permits the recording of birds at altitudes up to 1 km, receiving their images, measuring size, tracking wing beat pattern along up to 90 m. It also allows the measurement or calculation of main flight characteristics as follows: altitude of flight, flight direction, heading, ground and air speed, wing beat frequency and pause duration. The wind profiling device became an important supplement to the system by providing the regular data input on wind direction and velocity during the night.

Over 90% of images received, judging by the silhouette sharpness, size and wing beat pattern are passerine birds. Synchronous data on phenology of migration, and number of birds of particular species at their stopover sites, revealed that during specific periods of autumn passage each size class of passerine birds is represented by one or in some cases two clearly dominant species. It was possible to distinguish 7 well identifiable species or groups consisting of two species during autumn migration at the Courish Spit. The main criteria for this separation are the body length, wing span, proportion of the span to length. In the case of the Blackbird it is also feather coloration.

Primarily the described technique is valid for the investigation of the problems concerning mechanisms of adaptation of different avian species to flight in darkness under different wind conditions. We believe that it has become possible to study flight behaviour in model species or narrow groups of close species under natural conditions. The primary problems which could be addressed are as follows: 1) ground- and airspeed, 2) wind drift and its compensation, 3) wing beat pattern and its variation depending on wind condition.

The OED is used for monitoring autumn migration at the Courish Spit on the Baltic Sea. Improvements of the technique are possible in several directions: 1) technical improvement of the system; 2) obtaining more detailed and sharper images to decrease any error in measurements of the linear and dynamic parameters; 3) increasing the altitude of detection of birds; 4) improvements in observations in twilight; 5) minimisation of the influence of light on the behaviour of flying birds; 6) simplification of the system of operation and increasing its reliability; 6) development of dedicated software, modes of storage of information and database management; 8) integration of the statistics module for prompt data analysis.

Acknowledgements

The authors are grateful to Dr. Felix Liechti for his careful reviewing of the manuscript. His suggestions helped much to improve the paper. This study was supported by the Russian Foundation for Basic Research (grant to C.V.B. no. 08-04-01658).

References

Able, K.P. & Gauthreaux, S.A. Jr. 1975. Quantification of nocturnal passerine migration with a portable ceilometer. Condor 77: 92–96.

Åkesson, S. 1993. Coastal migration and wind drift compensation in nocturnal passerine migrants. Ornis Scand. 24: 87–94.

Alerstam, T. 1979. Optimal use of wind by migrating birds combined drift and overcompensation. J. Theor. Biol. 79: 341–353.

Bolshakov, C.V. 1981. Reconstruction of the total picture of nocturnal passage and effectiveness of several methods of its estimation. In: Dolnik, V.R. (ed.) Methods of bird migration discovery and estimation, Proceed. Zool. Inst. Russ. Acad. Sci. 104: 95–123 (in Russian with English summary).

Bolshakov, C.V. 1985. Moon-watch method for quantitative studying of nocturnal passage (collection, calculation and analysis of data). In: Dolnik, V.R. (ed.) Spring nocturnal bird passage over arid and mountain areas of middle Asia and Kazakhstan. Leningrad: 14–36 (in Russian with English summary).

Bolshakov, C.V. & Bulyuk, V.N. 1978. The method of illuminated area and its possibilities for the study of nocturnal bird migration. Abstr. II All-Union Ornithol. Confer. Study Bird Migration. Alma-Ata: 177–179 (in Russian).

Bolshakov, C.V. & Bulyuk, V.N. 1999. Time of nocturnal flight initiation (take-off activity) in the European Robin (*Erithacus rubecula)* during spring migration: direct observations between sunset and sunrise. Avian Ecol. Behav. 2: 51–74.

Bolshakov, C.V. & Bulyuk, V.N. 2001. New comprehensive systematic data concerning the time of nocturnal departure in some passerine migrants in autumn. Ring 23: 131–137.

Bolshakov, C.V., Bulyuk, V.N., Žalakevicius, M., Rezvyi, S.P. & Yakovlev, V.V. 1981. A comparison of results of nocturnal migration counts by seven methods of observations at the Kurische Nehrung during autumn 1977. In: Dolnik, V.R. (ed.) Methods of bird migration discovery and estimation. Proceed. Zool. Inst. Russ. Acad. Sci. 104: 79–94 (in Russian with English summary).

Bolshakov, C., Žalakevičius, M. & Švažas, S. 2002. Nocturnal migration of thrushes in the Eastern Baltic region. Vilnius.

Bolshakov, C.V., Sinelschikova, A. & Vorotkov, M.V. 2008. Electronic-optical system for the recording of nocturnally migrating birds. In: Noskov, G.A. & Gaginskaya, A.R. (eds.). Study of the migration and stopovers. Saint-Petersburg, CSR Press, p. 34 (in Russian with English summary).

Bolshakov, C.V., Sinelschikova, A., Vorotkov, M.V. & Bulyuk, V.N. 2010. Intra- and inter- specific variation of flight speed in migrating nocturnally passerine birds. In: Ornithology in Northern Eurasia. The XIII Intern. Ornith. Conf. of North Eurasia. Orenburg. Orenburg Pedagogical State University: 66–67 (in Russian).

Bruderer, B. 1997. The study of bird migration by radar. Part 1: the technical basis. Naturwissenschaften 84: 1–8.

Bruderer, B. 2001. Recent studies modifying current views of nocturnal bird migration in the Mediterranean. Avian Ecol. Behav. 7: 11–25.

Bruderer, B., Liechti, F. & Bilo, D. 2001. Flexibility in flight behaviour of Barn Swallows (Hirundo rustica) and House Martins (Delichon urbica) tested in a wind tunnel. J. Exp. Biol. 204: 1473–1484.

Bruderer, B., Peter, D., Boldt, A., & Liechti, F. 2010. Wing-beat characteristics of birds recorded with tracking radar and cine camera. Ibis, 152, 2: 272–91.

Brydegaard, M., Lundin, P., Guan, Z., Runemark, A., Åkesson, S. & Svanberg, S. 2010. Feasibility study: fluorescence lidar for remote bird classification. Applied Optics, 49: 4531–4544.

Buurma, L.S. 1988. Thermal imaging, a new remote sensing technique for nocturnal wildlife studies. Proceed. Bird Strike Committee Eorope 19, Madrid, Spain.

Cochran, W.W., Bowlin, M.S. & Wikelski, M. 2008. Wingbeat frequency and flap-pause ratio during natural migratory flight in thrushes. Integrative and Comparative Biology 48: 134–151.

Cochran, W.W. & Kjos, C.G. 1985. Wind drift and migration of thrushes: a telemetry study. Illinois Nat. Hist. Survey Bull. 33: 297–330.

Dolnik, V.R. & Bolshakov, C.V. 1985. Preliminary results of vernal nocturnal bird passage study over arid and mountain areas of central Asia: latitudal crossing. In: Dolnik, V.R. (ed.) Spring nocturnal bird passage over arid and mountain areas of middle Asia and Kazakhstan. Leningrad: 260–294 (in Russian with English summary).

Evans, W.R., Akashi, Y., Altman, N.S. & Manville, A.M. 2007. Response of night-migrating songbirds in cloud to colored and flashing light. North American Birds 604: 476–488.

Hansen, L. 1954. Birds killed at lights in Denmark 1886–1939. Vid. Medd. Dansk Naturhist. Foren. 116: 269–368.

Gauthreaux, S.A. Jr. 1969. A portable ceilometer technique for studying low-level nocturnal migration. Bird-Banding 40: 309–320.

Gauthreaux, S.A. Jr. 1979. Image intensification: a new method of studying nocturnal bird migration. Proceedings Bird Strike Committee Europe 14, The Hague, Netherlands.

Gauthreaux, S.A. Jr. & Belser, C.G. 2003. Radar ornithology and biological conservation. The Auk 120: 266–277.

Gauthreaux, S.A. Jr. & Belser, C.G. 2006. Effects of artificial night lighting on migrating birds. In Rich, C. & Longcore, T. (eds.) Ecological consequences of artificial night lighting. Island Press, Washington, Covelo, London: 67–93.

Gauthreaux, S.A., Jr. & Livingston, J.W. 2006. Monitoring bird migration with a fixed-beam radar and a thermal-imaging camera. J. Field Ornithol. 77: 319–328.

Griffiths, M.E. 1969. The variation in the wingbeat pattern of the Starling (*Sturnus vulgaris*) and the Wood-Pigeon (*Columba palumbus*). Report No. 4 for the Ministry of Technology. London.

Griffiths, M.E. 1970. Wingbeat frequencies and flight patterns of the more common migrant birds of the British Isles and Europe. Report No. 9 for the Ministry of Technology. London.

Liechti, F. 2001. Calibration of moon-watching method – chances and limits. Avian Ecol. Behav. 7: 27–40.

Liechti, F. & Bruderer, B.1995. Direction, speed, and composition of nocturnal bird migration in the south Israel. Israel J. Zool. 41: 501–515.

Liechti, F., Bruderer, B. & Paproth, H. 1995. Quantification of nocturnal bird migration by moon-watching: comparison with radar and infrared observations. J. Field Ornithol. 66: 457–468.

Liechti, F., Peter, D., Lardelli, R. & Bruderer, B. 1996. Herbstlicher Vogelzug im Alpenraum nach Mondbeobachtungen – Topographie und Wind beeinflussen den Zugverlauf. Orn. Beob. 93: 131–152.

Lowery, G.H. 1951. A quantitative study of the nocturnal migration of birds. Univ. of Kansas Publ. 3: 361–472.

Lowery, G.H. & Newman, R.J. 1955. Direct studies of nocturnal bird migration. In*:* Wolfson, A. (ed.) Recent Studies in Avian Biology, Univ. Illinois Press, Urbana: 238–263.

Newman, R.J. 1956. Hour to hour variation in the volume of nocturnal migration in autumn. Ph.D. dissertation. Louisiana State University, Baton Rouge. LA.

Nisbet, I.C.T. 1959. Calculation of flight directions of birds observed crossing the face of the moon. Wilson Bull. 71: 237–243.

Nisbet, I.C.T. 1963. Quantitative study of migration with 23-centimeter radar. Ibis 105: 435–460.

Nisbet, I.C.T. & Drury, W.H.Jr. 1969. A migration wave observed by moon-watching and at banding stations. Bird Banding 40: 243–254.

Schaefer, G.W. 1966. The study of bird echoes using tracking radar. In: Eastwood, E. (ed.) Radar Ornithology. Proceed. of the 14th Int. Ornith. Congress: 85–87.

Schaefer, G.W. 1968. Bird Recognition by Radar. In: Murton, R.K & Wright, E.N. (eds.) A Study in Quantitative Radar Ornithology. Methuen, London: 53–86.

Sinelschikova, A., Vorotkov, M., Bulyuk, V., Bolshakov, C.V. & Griffiths, M.E. 2009. Electronic-optical system and its application for the study of nocturnal migration of birds. Abstracts of the 7th Conference of the European Ornithologists' Union 21–26 August 2009, University of Zurich, Switzerland, p. 78.

Taylor, W.K. 1972. Analysis of Ovenbirds killed in central Florida. Bird-Banding 43: 15–19.

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. J. Nav. 62: 1–9.

Zaugg, S., Sapporta, G., van Loon, E., Schmaljohann, H., & Liechti, F. 2008. Automatic identification of bird targets with radar via patterns produced by wing flapping. Journal of The Royal Society Interface 5: 1041–1053.

Zehnder, S., Åkesson, S., Liechti, F. & Bruderer, B. 2001. Nocturnal autumn bird migration at Falsterbo, South Sweden. J. of Avian Biol. 32: 239–248.