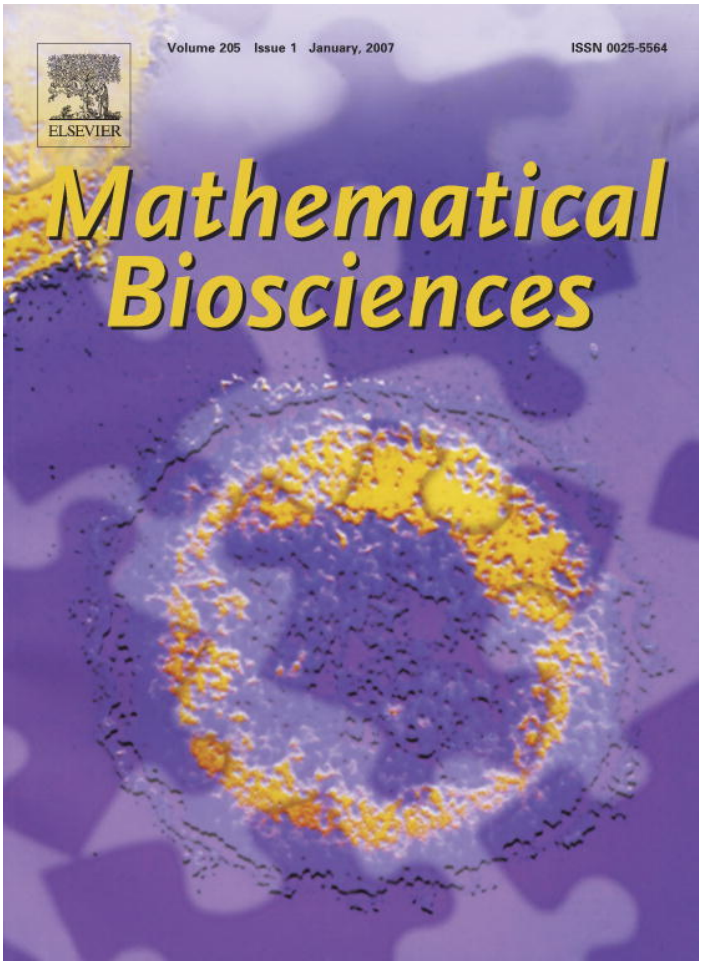
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On a probabilistic model for the numerical estimation of nocturnal migration of birds

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Abstract

The study of nocturnal bird migration by cone methods of observation has a century-long history but has continued to be used up to the present. To describe the flux and estimate the number of passing birds a probabilistic model is proposed. This model is based on the concept of dynamic Poisson ensemble of points in appropriate phase space and has two parameters. One is scalar and the other one is functional. We constructed consistent estimations of these parameters and discuss their use for the numerical estimation of the flux of birds observed in a narrow light cone generated by the bright lunar disk and formed by an open angle of telescope. Selection on the same type of birds was suggested as the necessary condition for the model application. Ground speed of each bird was introduced into the model as a new but obligatory value determining the quantification of the flux of bird.

Keywords: Bird migration; Intensity; Poisson ensemble of points

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1. Introduction

About 80% of bird species of North America, Europe and Asia, amounting to billions of individuals, demonstrate various forms of migratory behavior [1]. Twice a year they make journeys between their breeding grounds and winter quarters, covering a distance from a few hundred to tens of thousands of kilometers. Migration is one of the most complex phenomena in the avian life cycle and it has been actively addressed by ornithologists over the last 100 years [2,3]. The research work has focused on such key problems as orientation and navigation, energy expenditure and mechanics of flight, mechanisms of the period and pattern control of migration by internal and external factors. Many of these problems are of general biological significance since they not only concern birds but also other numerous living creatures which perform regular migrations. These questions could be tackled by observations in nature, laboratory experiments and theoretical elaboration.

A traditional branch of migratory behavior investigation is the direct observation of birds aloft. It deals with an estimation of species composition of migrants, their numbers, seasonal and daily temporal patterns of passage, height distribution of birds, flight direction and their probable association with weather and mainly wind conditions. An application of standardized quantitative methods for registration of flying birds has already enabled one to get a picture of the spatial and temporal distribution of migrants over the vast territories of North America, Asia and Europe [4–6], to detect funnels with high concentrations of birds and to determine what strategies the migrants use to overcome ecologically unfavorable extents such as seas, oceans, deserts and highlands [5,7,8].

More than half of the species nesting in North America and Europe migrate nocturnally [9,10]. Migration at night is typical for many waterfowl, waders, passerines and other groups of birds that use flapping flight and it has its special adaptive significance. Many radar surveys suggest that birds passing at night deviate to react to local terrain to a lesser extent, fly at high altitudes and are distributed in space more uniformly than the diurnal migrants [11–13]. Nocturnal migration is suggested to form from 63% to 85% of the total (day plus night) stream of passage [14].

Up to the present time the basic information about the structure of the nocturnal passage stream has been obtained by the cone methods, including optical observation of birds on the face of the lunar disc [15–17] and in light beam (ceilometer) [18,19], as well as infrared devices [20,21]. These methods differ mainly in the distance of detection of the birds, accuracy of their identification (identification to species or higher taxa) and weather-related limitations. One feature is common for all these methods: passing birds are recorded in the volume of air which represents the inverted cone formed by an open angle of the device. Thus, an obvious problem arises because of the cone effect – the different probability of getting the flying birds into the field of observation at different altitudes. If the density of birds is the same at all height levels we always record more birds in the upper air strata than in the lower ones. In this connection at least two main questions arise: (1) how to account for the effect of the cone; (2) how to find the relationship between the number of birds recorded and the general stream of birds aloft. In our work we discuss these questions on the basis of the moon-watching method.

This method of surveying nocturnal migration is based on observation with a telescope of the silhouettes of migrating birds crossing the bright part of the moon disc and is over 100 years old [22]. The early work showed how to calculate the geographical direction of bird flight based on the trajectory of movement of its silhouette across the moon disc [23]. Then the parallax method was suggested to calculate the height of the bird flight above the ground but his method was not used in practice [24]. In the second half of the 20th century some approaches were developed which permitted to estimate the altitude of the flying bird and to use the moon method for quantification of nocturnal migration [15,25,26].

Moon-watching permits one to get quantitative estimation of nocturnal migration. For each observed bird one receives main parameters: taxa, direction and altitude of flight, and intensity of migration which is under consideration. These parameters are basic for the study of temporal and spatial distribution of birds during their nocturnal migration. The moon-watching method has important advantages which allows it to be useful in modern research work [26,34,35]: an observer is sure that he sees certain birds (but not dots or echoes of flying objects as on the radar or infrared devices screens). Moreover, based on the outlines of the silhouette, pattern of flight and the frequency of wing beating, an experienced bird-watcher is able to identify at least 70% of birds to the order, family, genus but very seldom to species [27,28]. Technical simplicity of this method and the possibility to use it in any field conditions is well known. The main disadvantages of the method are: the impossibility to observe on overcast nights; the movement of the moon in the course of the night; the changing size of the bright part of the disc. The moon-watching method may be used for quantitative estimates no more than 14 nights per moon cycle, when the visible part of its disc is at least 50%.

The first quantitative model establishing the relationship between observed number of silhouettes and the real bird stream was presented by Rense [29] and had a form of directly proportional dependence

$$\rho = \frac{C}{T} \cdot n, \tag{1}$$

where ρ is the number of birds crossing the line of 1 mile (or km) long per 1 h within the plane of the bird flight perpendicular to the flight direction; n is the true number of birds observed flying in the same direction and at the same altitude, T is the time of observation. The coefficient C depends on flight direction and geometric characteristics of the multitude gained by cross section of the cone of observation by the horizontal plane at the given altitude.

Rense has called ρ the density of bird migration in the given direction at the given altitude. To obtain more accurate estimates of actual numbers of flying birds the migration traffic rate (MTR) was brought into use (MTR – the index based on ρ) [30] where it was necessary to take into account the altitude of the flight of the bird. In the methods used earlier this demand was kept by convention. In the method elaborated by Nisbet [15] an assumption was accepted that the migration is absent lower than 290 m and higher than 3200 m and between these levels altitude distribution of migrants is uniform. Radar observations showed that the altitude of migration varies from night to night [31]. That is why the difference in estimates of numbers of flying birds by Nisbet's method may reach up to 2-fold if the most birds fly high or, conversely, low.

In 1967 Wolf suggested rather simple method of identifying the height of the flight based on estimating the visible size of the bird to the diameter of the moon crater Plato [32]. This made it possible to use MTR in subsequent studies by taking in account the flight altitude of each bird. Swiss ornithologists have suggested size classes of silhouettes and simplified the task methodologically [21]. Nevertheless, the form of expression of relationship between the observed and the real migration streams remained the same as the proportion (1). Index MTR is still the base for quantitative estimates of nocturnal migration done over recent years [6,20,21,26].

The model of MTR based on proportion (1) in our opinion has obvious deficiency: absence of a probabilistic approach. The model absolutely does not account for probability of the bird flight at the defined altitude and in defined direction.

The general assumption that birds, at least passerines, fly at night singly and are distributed in space uniformly is confirmed by radar observations [33]. Nevertheless, in the case of the moonwatching method this assumption is not concrete but abstract and does not permit one to judge the distance between birds.

(1) Ignoring of the ground speed of birds recorded, although the influence of this factor on MTR and real density of birds in the air has been discussed [27]. It is obvious that if the number of birds aloft is kept constant we always get higher value of MTR when the ground speed of birds is higher. It is worthy of note that this is essential for all types of cone observations both at night and day time.
(2) Problem of correct application of methods of circular statistics to the distributions gained on the basis of MTR model [17].

The aforementioned deficiencies of the model may cause either underestimation or overestimation of the migration stream. To avoid this it became necessary to create a stochastic model of the stream of migrating birds. It may serve as a basis for the statistically justified conclusions concerning the migration stream. This model is based on the Poisson ensemble of points in space.

2. Poisson ensembles of points

Let $(\Omega, \mathrm{E}, \mu)$ be a space with a positive measure μ. A family of random variables $\Pi = \{N(E); E \in \mathrm{E}\}$ defined on the same probability space is said to be *a Poisson ensemble of points in the space* Ω *with mean measure* (*measure of intensity*) μ if the following conditions are hold:

(1) for every $E \in \mathrm{E}$ satisfying $0 < \mu(E) < \infty$ the random variable $N(E)$ has Poisson distribution with the parameter $\mu(E)$, that is

$$\mathrm{Prob}\{N(E) = n\} = \frac{(\mu(E))^n}{n!} \cdot \mathrm{e}^{-(\mu(E))}, \quad n = 0, 1, \ldots;$$

(2) for non-intersecting sets E', $E \in \mathrm{E}$ the random variables $N(E')$, $N(E)$ are independent;
(3) for non-intersecting sets E', $E \in \mathrm{E}$ with probability one

$$N(E' \cup E) = N(E') + N(E).$$

Notice that the expectation and the variance of the random variable $N(E)$ in the case $0 < \mu(E) < \infty$ are equal; that is $\mathbf{E}(N(E)) = \mu(E)$, $\mathbf{D}(N(E)) = \mu(E)$.

Let now $\{\Pi_t; 0 \leqslant t < \infty\}$ be a family of Poisson ensembles of points in the same space Ω and $\{\mu_t; 0 \leqslant t < \infty\}$ be the corresponding family of the mean measures. The parameter t will be interpreted as time. The family $\{\Pi_t; 0 \leqslant t < \infty\}$ will be called *stationary* if for every $0 \leqslant t < \infty$ $\mu_t \equiv \mu_0$ on E.

In the sequel we will be interested in families $\{\Pi_t;\ 0 \leqslant t < \infty\}$ of Poisson ensembles of points of a special nature. For every $t \geqslant 0$ define a one-to-one transformation S_t of the space Ω on itself which satisfies the following conditions:

(1) $S_{t_1} * S_{t_2} = S_{t_1+t_2}$ for every $t_1, t_2 \geqslant 0$;
(2) for every measurable function $f : \Omega \to \mathbf{R}$ the function $g(\omega, t) = f(S_t(\omega))$ is measurable on Cartesian product $\Omega \times \mathbf{R}$.

Notice that here $*$ denotes the composition of transformations defined by the rule $S_1 * S_2(\omega) = S_1(S_2(\omega))$ and that a family of transformations satisfying (1) is called a *one-parameter semi-group of transformations*. The space $(\Omega, \mathrm{E}, \mu)$ with a given one-parameter semi-group of transformations on it satisfying (2) is said to be *a dynamic system with continuous time* or *a flow on the space* $(\Omega, \mathrm{E}, \mu)$.

A one-to-one transformation S of the space $(\Omega, \mathrm{E}, \mu)$ will be called *regular* if it is measurable and if for every $E \in \mathrm{E}$ the following condition holds:

$$0 < \mu(S^{-1}(E)) < \infty \text{ if and only if } 0 < \mu(E) < \infty. \tag{2}$$

A flow $\{S_t;\ 0 \leqslant t < \infty\}$ on the space $(\Omega, \mathrm{E}, \mu)$ will be called *regular* if for every $t \geqslant 0$ the transformation S_t is regular.

Assume there is a regular flow $\{S_t;\ 0 \leqslant t < \infty\}$ on the space $(\Omega, \mathrm{E}, \mu)$ and also it is given a Poisson ensemble of points $\Pi_0 = \{N(E);\ E \in \mathrm{E}\}$ in the space Ω with mean measure μ. Define for every $t > 0$ the family $\Pi_t = \{N_t(E);\ E \in \mathrm{E}\}$ of the random variables by the rule: $N_t(E) = N(S_t^{-1}(E))$, $E \in \mathrm{E}$. It is easily checked that the family Π_t is the Poisson ensemble of points in the space Ω with mean measure $\mu_t \equiv \mu S_t^{-1}$. The family of Poisson ensembles of points $\{\Pi_t;\ 0 \leqslant t < \infty\}$ will be called *a dynamic Poisson ensemble of points in the space Ω generated by flow* $\{S_t;\ 0 \leqslant t < \infty\}$. It is obvious that the dynamic Poisson ensemble of points $\{\Pi_t;\ 0 \leqslant t < \infty\}$ is stationary if and only if every transformation S_t preserves the measure μ.

3. Basic model

Suppose that an observer is connected the Cartesian system of coordinates $Oxyz$ in the space in such way that its center O coincides with the eye of the observer, the axis Oz is perpendicular to the surface of the Earth, and the axis Ox is directed to the North. Let the moments $t = 0$ and $t = T$ be the beginning and the end of some set of observations. To simplify the models introduced below we will suppose in the sequel that the movement of every bird during its flight satisfies some hypotheses usually accepted when one is interested in the numerical estimation of night migration. In particular:

(H1) Birds fly parallel to the surface of the Earth during the given set of observations;
(H2) The direction of a flight of every bird is constant during the given set of observations.

Under hypotheses (H1)–(H2) the direction of the bird's flight is uniquely defined by the angle Φ which is formed by the vector of the ground speed of the bird and by the axis $\boldsymbol{Ox}$. As is usually accepted in ornithology, we consider that the angles are counted from the axis ***Ox*** in the clockwise direction varying from 0 to 2π radians.

In relation to the bird's speed we additionally suppose the correctness of the following hypotheses.

- (H3) The value of the ground speed of every bird is constant during the given set of observations and is uniquely defined by the height of the flight and by the direction of the fly of the bird.
- (H4) The vector field of velocities of the flight continuously depends on the height of the flight and on the direction of the flight.

Remark 1. In hypotheses (H3)–(H4) by the velocity of bird's flight we understand its velocity in relation to the fixed system of coordinates $Oxyz$; that is, the velocity includes both the velocity of bird's movement and the velocity of the movement of air masses.

Under hypotheses (H1)–(H4) the position and the direction of bird's flight at instant t may be represented by the point (X_t, Y_t, Z_t, Φ) in the phase space $\Omega = \mathbf{R}^2 \times \mathbf{R}_+ \times [0, 2\pi]$. We will consider the coordinates (X_t, Y_t, Z_t) and the angle Φ as random variables defined on some fixed probability space. Notice that there is some lack in such representation conditioned by the fact that the angles $\varphi = 0$ and $\varphi = 2\pi$ represent the same direction of the flight. After identification of the points $\varphi = 0$ and $\varphi = 2\pi$, the segment $[0, 2\pi]$ will transform into the unit circle. Under this transformation the Lebesgue measure on the segment $[0, 2\pi]$ will transform into the Lebesgue measure on the circle and for every $\varphi \in [0, 2\pi]$ there will be the corresponding point $p(\varphi)$ on the circle. We introduce the distance $a(p(\varphi), p(\varphi'))$ between the points $p(\varphi)$ and $p(\varphi')$ on the circle as the minimum of the lengths of two arcs having the points $p(\varphi)$ and $p(\varphi')$ as their ends. If we now define the distance $d(\omega, \omega')$ between the points $\omega = (x, y, z, \varphi)$ and $\omega' = (x', y', z', \varphi')$ of the space Ω by the rule (e.g., $d(\omega, \omega') = \max\{\sqrt{(x - x')^2 + (y - y')^2 + (z - z')^2}, a(p(\varphi), p(\varphi'))\}$), the space Ω will transform into a full separable metric space. In the sequel we will assume that the realization of this transformation takes place.

Our nearest goal consists in introducing the model of the flux of birds in some given domain D of the space as a realization of a suitable stationary Poisson ensemble of points in the space Ω. The next consideration concerns a specification of the corresponding mean measure M.

Let us consider the set $\Omega_D = \{\omega = (x, y, z, \varphi) | (x, y, z) \in D\}$. Suppose that set Ω_D has finite positive measure: $0 < M(\Omega_D) < \infty$. Then the conditional probability of the event that some point of the Poisson ensemble under consideration lies in some measurable set $E \subset \Omega_D$ under the condition that it lies in Ω_D is equal

$$p(E|\Omega_D) = \frac{M(E)}{M(\Omega_D)}. \tag{3}$$

Suppose that measure $p(E|\Omega_D)$ defined on measurable sets of the set Ω_D by (3) is absolutely continuous in relation to the Lebesgue measure $\mathrm{d}x \cdot \mathrm{d}y \cdot \mathrm{d}z \cdot \mathrm{d}\varphi$ on Ω_D. It means that there is measurable non-negative function $f : \Omega_D \to \mathbf{R}$ such that

$$p(E|\Omega_D) = \int_E f(x, y, z, \varphi)\, \mathrm{d}x\, \mathrm{d}y\, \mathrm{d}z\, \mathrm{d}\varphi. \tag{4}$$

Denoting $\mu = M(\Omega_D)$ we have from (3) and (4)

$$\mathrm{d}M = \mu \cdot f(x, y, z, \varphi)\,\mathrm{d}x\,\mathrm{d}y\,\mathrm{d}z\,\mathrm{d}\varphi. \tag{5}$$

The function $f(x, y, z, \varphi)$ may be considered as the conditional density of probability of finding a random point from the Poisson ensemble at the point (x, y, z, φ) of the phase space under the condition that it is situated in the set Ω_D. With respect to the structure of this function, an ornithologist often can accept some hypotheses which simplify its investigation. In particular, when studying night migration over a flat domain and considering as the domain D a cylinder whose axis coincides with the axis Oz, one can assume that

$$f(x, y, z, \varphi) = g(x, y)q(z, \varphi), \quad (x, y, z, \varphi) \in \Omega_D, \tag{6}$$

where $q(z, \varphi) \geqslant 0$, $\int_0^\infty \int_0^{2\pi} q(z, \varphi)\,\mathrm{d}z\,\mathrm{d}\varphi = 1$ and the function $g(x, y)$ is defined by the relation

$$g(x, y) = \begin{cases} \dfrac{1}{s(D^{xy})}, & (x, y) \in D^{xy}, \\ 0, & (x, y) \notin D^{xy}, \end{cases} \tag{7}$$

where D^{xy} denotes the projection of the domain D on the plane $Oxyz$ and $s(\Omega^{xy})$ denotes its square.

Remark 2. Our assumptions (6) and (7) are based on the fact that during a night migration a bird is not in touch with the Earth's surface (not busy finding food) and that the height of its flight is defined in general by the structure of air flows which is reflected in the distribution $H(\mathrm{d}z) = h(z)\,\mathrm{d}z$, where $h(z) = \int_0^{2\pi} q(z, \varphi)\,\mathrm{d}z\,\mathrm{d}\varphi$. Of course, this structure in reality is rather complicated but for simplicity we consider that the air space of the domain D is stratified into homogeneous flat layers. In addition as it was pointed out in the hypothesis (H1) we consider that a bird flies parallel to the surface of the Earth, and does not pass from one layer to another.

Under the assumptions (6) and (7) the relation (5) will reduce to the form

$$\mathrm{d}M = \lambda \cdot \mathrm{d}x\,\mathrm{d}y \cdot q(z, \varphi)\,\mathrm{d}z\,\mathrm{d}\varphi, \tag{8}$$

where $\lambda = \mu / s(D^{xy}) = M(\Omega_D)/s(D^{xy})$.

Now we can formulate the basic constructive assumptions of our model.

(H5) To the set of birds of given type situated in the domain D in arbitrary instant $t \in [0, T]$ corresponds a realization of the Poisson ensemble of points in the space Ω_D with mean measure M defined by (8).

(H6) The Poisson ensembles corresponding to different types of birds are stochastically independent.

Notice that from hypothesis (H6) it follows that if one has some stationary families of Poisson ensembles which correspond to the flows of birds of different types then the common flow of birds will correspond to the stationary family of Poisson ensembles for which mean measure is equal to the sum of the mean measures corresponding to the component families of Poisson ensembles.

The scale factor λ in the definition (8) of the measure M will play an essential role in the consequent estimation of bird migration. In the sequel it will be called the *intensity of migration* of birds of given type in the domain D during the given time-segment $[0, T]$. If we consider an infinite cylinder C with a unit area for its base, then it follows from (8) that $\lambda = \mathbf{E}(N(C))$, where $N(C)$ is the number of birds situated in C in arbitrary instant $t \in [0, T]$. Notice that if the lengths are measured in meters then λ will have dimensionality $[\mathrm{m}^{-3}]$.

The last part of this point will deal with justification the consistency of our model; that is, with checking of compatibility of the requirement of stationarity of measure M postulated in (H5) and the hypotheses (H1)–(H4) about the dynamics of bird flight. For this goal we will construct the stationary dynamic Poisson ensemble of points in the space Ω with mean measure M which satisfy (8).

Let Π_0 be the Poisson ensemble of points in the space Ω at the instant $t = 0$ with mean measure M satisfying (8) and $\mathbf{v}(z, \varphi) = (v_x(z, \varphi), v_y(z, \varphi))$ be the vector of velocity at the height z and in the direction φ. For $t > 0$ define the transformation S_t of the space Ω by the rule: $S_t(x, y, z, \varphi) = (x + v_x(z, \varphi) \cdot t,\ y + v_y(z, \varphi) \cdot t, z, \varphi)$. The transformation S_t is one-to-one, continuous, and one has the relation: $S_{t_1+t_2} = S_{t_1} * S_{t_2}$ for $t_1, t_2 \geqslant 0$. In addition S_t depends on t in a continuous way. So, the family $\{S_t; 0 \leqslant t < \infty\}$ is a flow on the space (Ω, E, M). It is easily seen that this flow is regular. Therefore, for proof of the consistency of our model it is enough to check that transformation S_t preserves the measure M.

For arbitrary measurable set E and for fixed pair $(z, \varphi) \in \mathbf{R}_+ \times [0, 2\pi]$ consider the set $E(z, \varphi) = \{(x, y) | (x, y, z, \varphi) \in E\}$ on the plane Oxy and denote by $s(E(z, \varphi))$ its square. Introduce also the notation $E_{-t} = \{(x, y, z, \varphi) | (x + v_x(z, \varphi) \cdot t, y + v_y(z, \varphi) \cdot t, z, \varphi) \in E\}$. By the Fubini theorem and taking into account that Lebesgue measure is invariant with respect to shifts we have

$$M(S_t^{-1}(E)) = M(E_{-t}) = \lambda \int_0^\infty \int_0^{2\pi} q(z, \varphi)\,\mathrm{d}z\mathrm{d}\varphi \int \int_{E_{-t}(z,\varphi)} \mathrm{d}x\mathrm{d}y$$
$$= \lambda \int_0^\infty \int_0^{2\pi} s(E_{-t}(z, \varphi)) \cdot q(z, \varphi)\,\mathrm{d}z\mathrm{d}\varphi = \lambda \int_0^\infty \int_0^{2\pi} s(E(z, \varphi)) \cdot q(z, \varphi)\,\mathrm{d}z\mathrm{d}\varphi = M(E).$$

Ending with our proof notice that if one has a stationary family of Poisson ensembles of points $\{\Pi_t; 0 \leqslant t < \infty\}$ in the space (Ω, E) with mean measure M and where Ω_D is a measurable subset of Ω with positive measure, then the family $\{\Pi_t^D;\ 0 \leqslant t < \infty\}$ where $\Pi_t^D = \{N_t(E \cap D);\ E \in \mathrm{E}\}$ will be a stationary family of Poisson ensembles of points in the space $(\Omega_D, \mathrm{E} \cap \Omega_D)$ with mean measure $M_D(\cdot) = M(\cdot \cap \Omega_D)$.

4. A statistical estimation of the parameters of the model

Let $C \subset D$ be the light cone generated by the eye of an observer and by the lunar disk. Assume that the time-segment $[0, T]$ is small enough that the set C may be considered to fixed during it. Denote by $C(z)$ the section of the set C by the horizontal plane at the height z. Let $w(z, \varphi)$ be the width of the set $C(z)$ in the direction perpendicular to the direction defined by angle φ that is the distance between two supporting straight lines parallel to the direction defined by angle φ (see Fig. 1).

Notice that, if some bird intersects the cone of observations at a random height Z and in a random direction Φ then the width of the corresponding section, its square, and the value of the

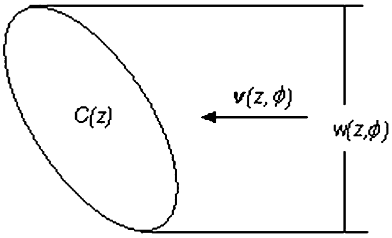

Fig. 1. The section of the light cone at the height Z.

velocity of the bird will be random variables: $W = w(Z, \Phi)$, $S = s(Z)$, $V = v(Z, \Phi)$. It is obvious that this bird will be registered on the time-segment $[0, T]$ if and only if at the instant $t = 0$ it was situated in the set $\widetilde{C}(Z, \Phi)$ which the set $C(Z)$ runs through under its movement in the opposite direction to the direction of the flight over the distance $v(Z, \Phi) \cdot T$ (see Fig. 2).

Thus on the time-segment $[0, T]$ there will be registered those birds which at the instant $t = 0$ were situated in the set $C_T = \cup_{z=0}^{\infty} \cup_{\varphi=0}^{2\pi} \widetilde{C}(z, \varphi)$. To this set of birds in the phase space Ω corresponds the set $\Omega_T = \{(x, y, z, \varphi) | (x, y, z) \in C_T\}$. It is easy to see that the projection of the set $\widetilde{C}(z, \varphi)$ on the plane $Oxyz$ has square $s(z) + w(z, \varphi) \cdot v(z, \varphi) \cdot T$. Thus by the Fubini theorem we have

$$M(\Omega_T) = \lambda \cdot \int_0^{\infty} \int_0^{2\pi} (s(z) + w(z, \varphi) \cdot v(z, \varphi) \cdot T) \cdot q(z, \varphi) \, \mathrm{d}z \, \mathrm{d}\varphi = \lambda \cdot (\mathbf{E}S + T \cdot \mathbf{E}(WV)). \tag{9}$$

Denoting $\overline{U} = \mathbf{E}(WV)$, $\overline{S} = \mathbf{E}S$, we have from (9)

$$\lambda = \frac{M(\Omega_T)}{\overline{S} + T \cdot \overline{U}}. \tag{10}$$

It is easy to understand that in practice with T large enough we will have the relation $\overline{S} \ll T \cdot \overline{U}$. Thus from (10) follows the relation:

$$\lambda \approx \frac{M(\Omega_T)}{T \cdot \overline{U}}. \tag{11}$$

Consider also the set $C_T^0 = C_T \setminus C$ and corresponding set in the phase space $\Omega_T^0 = \{(x, y, z, \varphi) | (x, y, z) \in C_T^0\}$. Its measure is equal to $M(\Omega_T^0) = \lambda \cdot T \cdot \overline{U}$. Consequently, we also have the exact equality

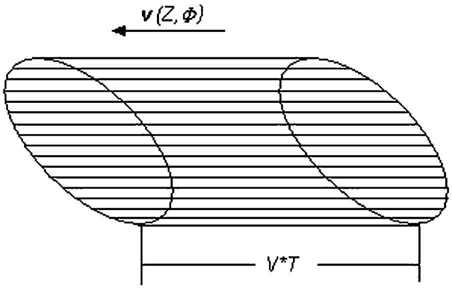

Fig. 2. The registration set at the height Z and in the direction Φ.

$$\lambda = \frac{M(\Omega_T^0)}{T \cdot \overline{U}}. \tag{12}$$

Let n_T be the number of the birds registered on the time-segment $[0, T]$. Then the random variable n_T is an unbiased estimator of the value $M(\Omega_T^0)$. Thus, under the condition that the value $\overline{U}$ is known we will get from (12) the unbiased estimator of λ:

$$\tilde{\lambda} = \frac{n_T}{T \cdot \overline{U}}. \tag{13}$$

The estimator (13) can also be derived in a different way. Assume that at the initial instant $t = 0$ there were no birds in the cone C and denote by $\eta(t)$ the number of birds registered on the time-segment $[0, t]$. Thus we have counting random process $\{\eta(t); 0 \leqslant t \leqslant T\}$. It is obvious that $\eta(0) = 0$ and that the random variable $\eta(t)$ has Poisson distribution with the parameter $M(\Omega_t^0) = \lambda \cdot \overline{U} \cdot t = \mu \cdot t$, where $\mu \equiv \lambda \cdot \overline{U}$. In addition increments of the process $\eta(t)$ corresponding to non-intersecting time-segments are independent. Therefore $\eta(t)$ is a homogeneous Poisson process with the parameter (intensity) μ. The maximum likelihood estimation of the parameter μ on the observed realization of the process on the segment $[0, T]$ is $\tilde{\mu} = n_T/T$ and we again derive the estimator (13) of the parameter λ. Notice also that if we are interested in the mean number $n(C)$ of the birds passing through a fixed infinite circle cylinder C of radius R during the time-segment $[0, T]$ then we will have the relation

$$n(C) = \lambda \cdot 2\pi R \cdot \overline{V} \cdot T \approx 2\pi R \cdot n_T \cdot \frac{\overline{V}}{\overline{U}}, \tag{14}$$

where $\overline{V} = \mathbf{E}\mathsf{V}$ is the mean value of the *value* of the velocity of a bird on the given time-segment. Thus the dependence of the value $n(C)$ on the radius of C is *linear*.

It is easy to check that the estimation $\tilde{\mu}$ of the parameter μ is unbiased and has a variance equal to μ/T, which vanishes when $T \to \infty$. Therefore the estimation $\tilde{\lambda}$ of the parameter λ is also consistent. If in addition we have any consistent estimation U_T of the value $\overline{U}$, we will get a consistent estimation of the parameter λ of the form

$$\lambda_T = \frac{n_T}{T \cdot U_T}. \tag{15}$$

Let us now suppose that the parameter λ of the model is known and consider the problem of estimation of the density $q(z, \varphi)$. Let the unit circle be partitioned into K arcs of the same length l_K. Denote by φ_k the polar angle of the middle point of the arc a_k, $k = 1, \ldots, K$. Let $Z_{\min}$ and $Z_{\max}$ be correspondingly the minimal and maximal height of the flight observed during the time-segment $[0, T]$. Divide the interval $[Z_{\min}, Z_{\max}]$ into R intervals $\{\Delta_1, \ldots, \Delta_R\}$ of the same length h_R. Denote by z_r the middle of interval Δ_r, $r = 1, \ldots, R$. Introduce the following notations: $v_{rk} = v(z_r, \varphi_k)$ – the velocity of a bird (its ground speed) at the height z_r and in the direction φ_k; $w_{rk} = w(z_r, \varphi_k)$ the width of the section of the light cone by the horizontal plane at the height z_r and in the direction φ_k; Ω_T^{rk} – the set of points of the phase space defined by the following condition: the bird which flies at the height $z \in \Delta_r$ and in the direction $\varphi \in a_k$ will be registered on the time-segment $[0, T]$ if and only if at the instant $t = 0$ its phase coordinates was situated in the Ω_T^{rk}. It is easy to see that under the conditions $h_R \to 0$, $l_K \to 0$ and supposing the continuity of the function $q(z, \varphi)$ we have

$$M(\Omega_T^{rk}) = \lambda \cdot (s(z_r) + w_{rk} \cdot v_{rk} \cdot T) \cdot q(z_r, \varphi_k) \cdot h_R l_K + \mathrm{o}(h_R l_K). \tag{16}$$

The relation (16) makes clear the following way of defining of the histogram $\hat{q}_T^{RK}(z,\varphi)$. Let $\pi_{rk} = \{(z,\varphi)|z \in \varDelta_r,\ \varphi \in a_k\}$, $\chi_{rk}(z,\varphi) = \begin{cases} 1, & (z,\varphi) \in \pi_{rk} \\ 0, & (z,\varphi) \notin \pi_{rk} \end{cases}$, $\delta_{RK} = h_R l_K$, n_T^{rk} – the number of birds registered in fact on the time-segment $[0,T]$ and having the height $z \in \varDelta_r$ and the direction $\varphi \in a_k$. Let

$$\hat{q}_T^{RK}(z,\varphi) = \frac{1}{\lambda\delta_{RK}} \sum_{r=1}^{R} \sum_{k=1}^{K} \frac{n_T^{rk}}{(s(z_r) + w_{rk}v_{rk}T)} \cdot \chi_{rk}(z,\varphi). \tag{17}$$

Notice, that from (16) we have the following relation:

$$q(z,\varphi) = \lim \frac{1}{\lambda\delta_{RK}} \sum_{r=1}^{R} \sum_{k=1}^{K} \frac{M(\Omega_T^{rk})}{(s(z_r) + w_{rk}v_{rk}T)} \cdot \chi_{rk}(z,\varphi) \tag{18}$$

for every fixed $T > 0$. So as we can suppose that for some constant C

$$\inf\{w(z,\varphi) \cdot v(z,\varphi)\} > C > 0 \tag{19}$$

and taking in account that $\mathbf{E}n_T^{rk} = M(\Omega_T^{rk})$, one can derive from the relations (17) and (18) that under the conditions $\delta_{RK} \to 0$, $T \to \infty$, $\delta_{RK} \cdot T \to \infty$

$$\mathbf{E}(\hat{q}_T^{RK}(z,\varphi) - q(z,\varphi))^2 \to 0. \tag{20}$$

However a proof of the relation (20) is rather cumbersome and is omitted here.

Operating with artificial model data we observed that for λ large enough the estimator (15) and (17) were rather likely in spite of the fact that in practice T is about 15 min and the condition $T \to \infty$ fails. Nowadays we have a technical opportunity to measure ground speed of birds and to accumulate complete data for using our model in real practice.

5. Application of the approach in ornithology

The following example of how this approach might be applied in ornithology concerns the influence of wind on numbers aloft in thrushes (*Turdus* spp.). The main point is the quantitative estimation of the bird flux in various wind conditions. What winds do birds prefer during migration and what winds do they have to use in real natural situation?

It is well known that wind is a weather factor, which is of great importance to the migratory activity of birds. Numerous radar studies of nocturnal migration showed that numbers aloft are strongly correlated with the following winds. However, the stream of nocturnal migrants usually consists of dozens of species which may differ by their migratory directions, flight abilities and migratory strategies. Therefore, it is relevant to study wind effect on migratory activity of particular species or groups of species similar in their taxonomy and ecology.

Thrush species (*Turdus iliacus*, *T. merula*, *T. pilaris*, *T. philomelos*) migrating at night have similar morphology and air speed; similar general migratory directions and they can be identified by their silhouettes and flight patterns by moon-watching.

Long-term moon-watching data at the Courish Spit, Eastern Baltic allowed an understanding of what the relationships are between the wind conditions and flight activity of birds and what strategies of migration they use in spring and in autumn as a response to the general wind patterns.

A total of 107 nights in spring and 95 nights in autumn have been covered by observations.

Using the model suggested above we calculated the intensity of migration of thrushes for each midnight of observations. The obtained values of intensities were ranged according to the angle of deviation of the wind in the particular night from the strict tail wind for spring and autumn (Fig. 3). We can see that:

- In spring, some 78% of thrushes migrate in winds with tailwind component. More than one-half of birds migrate when the wind does not deviate from a strict tail wind by more than 39°. In spring the western tail winds predominate in Europe.
- In autumn, only 68% of thrushes migrate in winds with tailwind component. For one-half of flying birds, deviation of the wind from the strict tail wind was significantly higher than in spring and was 69° (Mann–Whitney test for median values: $z = 405.3$, $P < 0.001$). Unlike spring, no strong relationship with strict tail wind was found. Most frequent winds are opposing in autumn.

It is interesting to add that when birds fly in head winds most intensive migration is observed in the low strata (not higher than 100 m) [34]. At this level radar is powerless to detect birds. Thus, it was shown that in head winds migration is not so negligible as it had been considered before.

On the basis of the results obtained by application of the proposed model and already published data [34,35] it became possible to draw out the next main conclusions concerning the migration strategies of thrushes which are of certain interest for ornithologists.

1. Predominance of the tail winds in spring allows the birds to increase the speed of their migration with smaller energy costs of flight. The fact that in spring thrushes select tail winds which closely agree with their general migratory direction suggests that they avoid deviating from their migratory goal.
   In spring the main strategy of migration is the long nocturnal flights under tail winds with subsequent long stopovers.
2. In autumn, rare occurrence of favorable winds does not permit the birds to use advantages of tail wind. Thrushes have to migrate regularly with head winds, using the nights with weak winds.
3. In autumn, the duration of nocturnal flights of thrushes under head winds is much shorter than under the tail winds. In our opinion, it allows thrushes to use two alternative strategies of migration in autumn:
   - long nocturnal flights under tail winds with subsequent long stopovers;
   - short nocturnal flights under weak head winds with subsequent short stopovers.

For the example under consideration we used data obtained by moon-watching. Nevertheless, an application of the model for estimation of the intensity of bird migration is absolutely suitable when the researcher uses alternative types of the cone methods of observation such as ceilometer, pencil-beam radar, infrared devices or even binocular observation. When we analyze data obtained by these methods for solving the problems of temporal and spatial distribution of birds

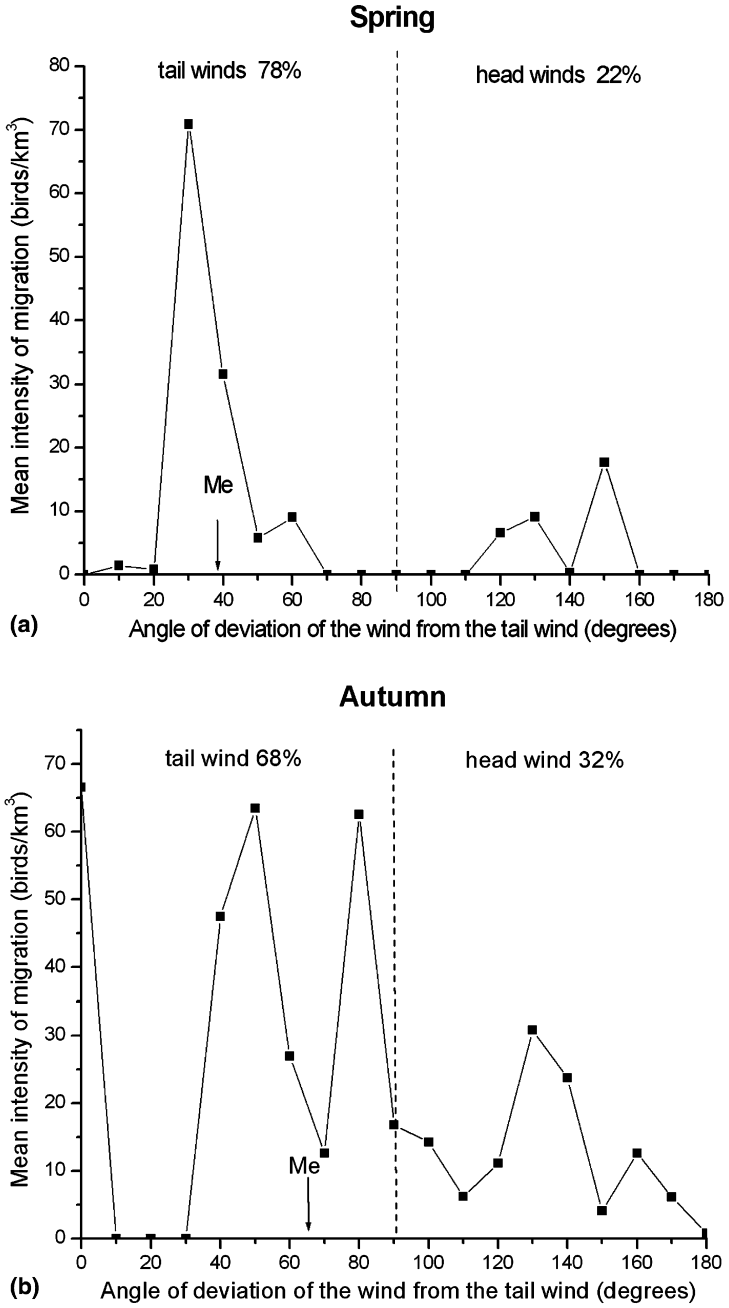

Fig. 3. Numbers of flying thrushes and the wind direction (moon-watching estimates for the period of mass migration): (a) spring migration and (b) autumn migration.

such as height distribution, phonological aspects and dependence of migration activity on external factors, we cannot use the real number of recorded birds (N). It is also incorrect to apply ‘migration traffic rate’ (MTR) used before. In this case we consider the proposed model to be the most correct one.

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