

Estimating Survival of Thrushes: Statistical Model of Capture–Recapture Probabilities

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Abstract—Astochastic modeling technique provides for the correct partition of the “return rate” of marked animals into survival probability (ϕ) and capture probability (p). Application of this method is enhanced by the program MARK, available free of charge through the Internet (Cooch and White, 2009). The input data for the program are the capture histories of marked animals: strings of ones and zeros indicating the presence or absence of an individual among captures (or sightings) during subsequent recapture seasons. The probability of any history is a product of binomial probabilities ϕ , p , or their complements $(1 - \phi)$ and $(1 - p)$ for each year of observing the individual. Assigning certain values to the parameters ϕ and p , it is possible to predict the combination of histories of all marked individuals and to assess the prediction probability. The survival parameters for different years and cohorts of individuals can be set either identical or different, and the recapture parameters can be set in different ways. It is possible to constrain the parameters according to a tested hypothesis in the form of a specific model. Within the specified constraints, the program searches for parameter values that describe the observed composition of histories with the maximum likelihood. The program computes the estimates for each parameter, their confidence limits, and the overall model probability. A set of tools is provided for testing model goodness-of-fit under the assumption of independent fates of individuals and their equiprobable survival. Other tools aid in the proper selection of the model that provides for the best parity between detail and precision in describing reality. The method was applied to determine survival probabilities using 20-year capture, marking, and sighting data series for populations of four thrush species (genera *Turdus* and *Zoothera*) breeding in the middle taiga subzone of the Enisei River floodplain. The capture probabilities were almost independent of capture efforts but significantly differed among the species and sexes. The estimates for survival probabilities of Siberian migratory thrush populations were lower than those for the resident species from both the tropics and midlatitudes with a marine climate (data by Ricklefs, 1997). Two factors—the average annual temperature, which influences birds during their migrations, and climatic seasonality (temperature difference between summer and winter) in the breeding area—best fit the latitudinal pattern of survival ($R^2 = 0.90$). The final survival of migrants reflects an adaptive life cycle tradeoff of using superabundant summer resources in the breeding area at the cost of avoidance of severe winter conditions.

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The efforts of generations of zoologists have allowed the accumulation of a tremendous volume of long-term data on animal capture and marking. Population ecology as a science is currently transitioning from a purely descriptive stage of study to the investigation of the internal mechanisms explaining the structure and dynamics of wildlife populations (Paevskii, 1985, 2008). The regulatory mechanisms maintaining a certain population size in ecological time act on the demographic parameters, namely, fecundity, mortality, and immigration-to-emigration ratio. From the evolutionary perspective, selection leads these parameters to equilibrium with the other ecological, morphological, and physiological adaptations of a species to an environment (Ricklefs, 1980, 1983).

Comparative demographic studies provide for clarification of the adaptive essence in the strategies of individual species, which is reflected in the life history cycles (Shmal'gauzen, 1939; Stearns, 1976, 1980). A

study of the changes in demographic parameters caused by external factors opens up a more direct and, correspondingly, more efficient means of controlling population sizes (Paevskii, 2008).

However, the estimation of demographic parameters encounters several obstacles. First, this is feasible only for mass data. Second, there are a multitude of estimation methods, each based on a considerable number of assumptions. These assumptions, both explicit and implicit, are not always realistic, tested, or testable. This leads to diverse estimates that are “ready” to explain opposing phenomena yet lack sufficiently strict foundations (for a review, see Paevskii, 2008).

The survival of birds is easily and relatively precisely assessed by the life table method when a sufficient number of reported death events of ringed individuals is available. However, such data are as a rule sparse for nongame species and species inhabiting underpopulated regions. Then another method is

used; i.e., the “return rate” of ringed individuals marked a year before is calculated. Although this approach has been repeatedly criticized (for example, Clobert et al., 1987; Bardin, 1993), it still remains one of the main tools for Russian ornithologists in the estimation of both survival probability and breeding area fidelity (for example, Shitikov and Fedchuk, 2008).

On the other hand, the foundations for modeling the reencounter of marked animals were laid as early as the 1960s (Cormack, 1964; Jolly, 1965; Seber, 1965, cited according to Lebreton et al., 1992). By the early 1990s, there were over ten free-access computer programs that were able to perform different variants of such analysis with a user’s empirical data (Lebreton et al., 1992). Currently, the majority of these programs are united in the program MARK, which is freely distributed through the Internet (Cooch and White, 2009). Each year at least 100 scientific papers are published on the use and development of recapture modeling for the analysis of wildlife populations.

Isolated attempts of Russian researchers to apply the elements of this new approach have led to ambiguous results (Bardin, 1988; Titov and Chernetsov, 1999; Kharitonov, 2002; Vysotskii and Paevskii, 2002; Paevskii, 2008). Frequently, these works have lacked a necessary stepwise description of the procedures used, so that it is impossible to both repeat and interpret the author’s results.

The goal of this paper was to give to Russian-speaking users a brief presentation of the recapture modeling methodology and application of the MARK program by the example of original data on nesting passerine birds. During the breeding period (2 months or more), birds are confined to a certain area chosen by young individuals during the juvenile dispersion, as a rule, within a radius of several kilometers from the birth site. In subsequent years, birds return for nesting to the same or a neighboring site or, more rarely, move several hundred meters away. The majority of individuals display nesting area fidelity, and this trend becomes stronger with age (Greenwood and Harvey, 1982; Paradis et al., 1998). Thus, birds were and still are a traditional object for capture–recapture modeling. We have chosen four thrush species cobreeding in the Enisei River floodplain. This group of closely related species displays similar ecological requirements during reproduction, but they differ in their wintering areas. We have long-term data on the capture–recapture of the chosen species, and the literature provides data on other species for comparison.

Avoiding where possible excess technical detail, we try to trace the algorithm used in this analysis, interpret the statistical and biological meanings of the main parameters and procedures of the model, assess their fit to actual data, and obtain reasonable estimates for survival probabilities of the compared species. Correct estimates are necessary to confirm, expand, or revise the patterns discovered by other methods.

MATERIALS AND METHODS

Data Collection

The material was collected at the Enisei Ecological Station of the Severtsov Institute of Ecology and Evolution near the village of Mirnoe, Turukhansk raion, Krasnoyarsk krai. In 1989–2008, a model plot of 1000 × 500 m in the Enisei River floodplain was annually covered by marked bird surveys. Perpendicular to the river bank along its longer side, the plot comprised three main types of floodplain habitats:

- (1) Low floodplain covered by willow shrubs of various ages annually flooded until at least mid-June (18 ha);
- (2) Natural levee, usually not flooded, represented by a long-boled birch–willow stand with abundant bird cherry undergrowth and pieces of meadow vegetation (7 ha); and
- (3) High floodplain usually flooded to the beginning of June covered by a spruce–alder stand and alder undergrowth (25 ha).

Birds were captured using a mist net (10 × 3 m, 14–18 mm mesh) uniformly placed over the area with an interval of 50 m. The nets were kept open from 8:00 p.m. to 12:00 p.m. the next day on an area of 5–7 ha, so that 20–30 nets worked concurrently and the interval between the checks did not exceed 1 h. The next day, nets were opened on the neighboring lines of the plot and so on, until the control area was completely covered. The capturing procedure was repeated on the plot after 10 days in the same order. The adult birds were marked with standard rings and, as a rule, individual colored bands.

The capturing schedule was preserved in its full volume during the first years but was later reduced in both area and duration:

1989–1995: 50 ha, ten decades (first decade of June–first decade of September);

1996–1998: 50 ha, six decades (first decade of June–third decade of August);

1999: no regular capturing; and

2000–2008: 15 ha; six decades (first decade of June–third decade of July).

The reduced area included the entire natural levee (7 ha) and parts of low and high floodplains (4 ha each).

Four thrush species were selected for analysis, namely, the Siberian thrush (*Zoothera sibirica*), redwing (*Turdus iliacus*), fieldfare (*T. pilaris*), and dark-throated thrush (*T. ruficollis*). During the breeding period, these birds keep to areas with a diameter of 50–70 m but can fly over hundreds of meters for food, which is especially typical of the fieldfare. During the breeding period, the nests were searched for and marked birds were individually sighted over the entire control area. There were many factors hindering constant adherence to these conditions in every year and for every species. For example, marking of fieldfares failed to give the required effect and was stopped in

1996. On the other hand, an increase in observation efforts provided for a considerable increase in the resighting of redwings and Siberian thrushes.

Only the data on adult individuals (at an age of 1 year and older) were used for analysis. Since the accuracy of survival estimates is connected not only with the number of marked individuals, but also with the observation time for each individual, the sample volume can be represented as the sum of annual resighting events for all individuals after release or recapture. The number of such events for the Siberian thrush was 1314 (of these, 493 were more than 1 year after marking); for the dark-throated thrush, 836 (193); for the redwing, 649 (205); and for the fieldfare, 895 (237).

Data on the wintering area of the studied populations and dates of their migration in the overall species area were obtained from consolidated sources (*The Birds of the Soviet Union*, 1954; Rogacheva et al., 1991; Clement and Hathway, 2000). The highest winter concentration of the Siberian thrush was recorded in Thailand, and that of the dark-throated thrush, in Iran. According to individual returns of our rings, the redwing winters in central Italy and southern France, while the fieldfare winters from northern Italy to Poland. Despite the approximate nature of this information, it allows the species populations to be unambiguously ranked according to both the latitude of their locations during the year and the climatic zone of their wintering.

The data were processed using the CJS module (Cormack–Jolly–Seber model) with the MARK program. The main principles of its operation were obtained from basic developments (Clobert et al., 1987; Lebreton et al., 1992; Burnham and Anderson, 2002) and the user's guide (Cooch and White, 2009).

Basic Definitions

Anticipating ambiguity, we define the key terms. The *marked* birds are those individuals released at the capture site on the control plot with an individual label (numbered ring or combination of colored bands). *Survival* of an individual is the possibility of its presence in the control plot during a given season. This presence is possible if the bird did not die before the beginning of observation and did not move permanently to another place. This implies an *apparent* survival probability, which can be lower than the actual value. A *capture–recapture* is any recording (be it one or several recaptures, an accidental encounter, or a regular sighting near the nest) of an individually recognized marked bird on the control plot over the observation period. The reencounter of a surviving marked individual in the years after marking is frequently referred to as “return,” meaning the return of an individual label (ring).

Not all the individuals inhabiting the control plot were marked; however, to construct the model, we are interested exclusively in the marked individuals as a

representative sample of the population. Let the apparent survival probability, or *survival probability* (ϕ), be defined as the fraction of this sample that survived to the next season. Not all the marked individuals can be recaptured during the season. The *reencounter probability* (p) is defined as the expected rate of reencountered individuals relative to the total number of marked individuals actually present on the control plot in a given season. These two unknown probabilities, ϕ and p , are the key parameters in all the models described below. In several cases, the product of these two probabilities is used, i.e., the unpartitioned parameter $\beta = \phi p$, which can be interpreted as the “return rate.” We try to avoid using this term for the reasons considered in a special section.

It is necessary to keep in mind that the definitions introduced for this particular case are rather conditional. Their content may change in other modules of the MARK program. For example, it is possible to consider the animals with group labels or without any labels at all, survival may include moving to other territories, and reencounter can be confined to only recapture. The intervals between observations can also be different, including an unequal period; however, the observations in our case study are associated with the breeding season, with an interval of 1 year.

THE METHODOLOGY FOR MODEL CONSTRUCTION

It is evident that it is practically impossible to trace the fates of all labeled individuals in an animal population. Despite regular examinations, the moment of death for many individuals remains unknown, since the chance of recapture is determined by several random factors. In particular, we obtained by 1991 four variants of the capture “history” for 29 male Siberian thrushes marked in 1989 (Table 1). Here, ones denote the years when an individual was recaptured (whether once or several times), and zeros represent the years when it was not recaptured. For example, the history “101” denotes the individuals marked in the first year, not found in the second year, but recaptured in the third year. The total number of individuals with such a history in this example $x_{101} = 1$.

Stochastic Approach

The expected number of recaptured marked animals is determined by the probabilities of their survival (ϕ_t) and capture (p_t) in each year of observation. The individuals recaptured 1 year after marking (moment t_2) include only those that survived from the moment of release (t_1) and whose presence was recorded by recapture or resighting. Designating the number of marked animals as R_1 , survival probability as ϕ_1 , and recapture probability as p_2 , we can calculate the expected value $x_{11} = R_1\phi_1p_2$. In a similar manner, it is possible to express the expected number of animals with

Table 1. The capture–recapture histories for individuals of one cohort (all marked in the year t_1) during two control periods (t_1/t_2 and t_2/t_3)

Capture–recapture history			Number of individuals	Tree of possibilities			Expected number of individuals
1989	1990	1991		t_1	t_2	t_3	
1	1	1	4	$R_1 = 29$	$R_1\varphi_1p_2p_3$ $R_1\varphi_1p_2(1 - \varphi_2p_3)$ $R_1\varphi_1(1 - p_2)\varphi_2p_3$ $R_1[1 - \varphi_1p_2 - (1 - p_2)\varphi_2p_3]$		
1	1	0	5				
1	0	1	1				
1	0	0	19				
Studied parameters:			capture–recapture probability	p_1	p_2	p_3	To be estimated: φ_1, p_2 , and $\beta_3 = \varphi_2p_3$
			survival probability	φ_1	φ_2		

Note: the ascending branches of the tree of possibilities correspond to recaptured individuals; the descending, to unencountered individuals. The data on capture of male Siberian thrushes marked in 1989 are used.

any capture–recapture history using the corresponding set of parameters φ_t and p_t or their complements.

At the end of the second observation period (year), we have the frequencies of two alternative histories: $x_{11} = R_1\varphi_1p_2$ and $x_{10} = R_1(1 - \varphi_1p_2)$, which provides for obtaining the return rate: the unpartitioned product $\beta_2 = \varphi_1p_2$, but not φ_1 and p_2 separately. For separating the contributions of φ_1 and p_2 to the product, the next observation year is required to estimate the frequencies of histories x_{111} and x_{101} of the known surviving individuals, which are completely similar except that the former were recaptured during the second year and the latter were not. Their ratio allows p_2 to be estimated and $\varphi_1 = \beta_2/p_2$ to be calculated. Considering three years of observation, we can estimate three parameters— φ_1, p_2 , and β_3 (parameter p_1 is undeterminable since it is absent in the equation)—according to the number of individuals with four recapture histories using expressions from Table 1.

Let us return to the results of the second observation year (Table 1), i.e., to obtaining the frequencies $x_{11} = 9$ and $x_{10} = 20$ and estimating the parameter β_2 . The actual frequencies x_{11} and x_{10} are one of the possible events of a random binomial process, the result of which depends on a definite yet unknown value of parameter β_2 , the size of sample $R_1 = 29$, and a multitude of uncontrolled (random) impacts. The estimate $\beta_2 = 9/29 = 0.31$ seems evident but is in no way the only possible one. Frequencies 9 and 29 correspond to the result of the occurrence of a random binomially distributed variable $\{x_{11}; \beta_2; R_1\}$, i.e., the occurrence of x_{11} positive (and x_{10} negative) results of R_1 tests at a mathematical expectation of $\beta_2 = 9/29$. However, the probability that the result of 9 : 29 is determined by the value $\beta_2 = 9/29$ alone amounts to only 16%. The remaining 84% are accounted for by analogous binomial processes at $\beta_2 = 7/29, 8/29, 20/29$, etc. As we will see later, the probability of similar but not the “best” solutions of the problem allows the accuracy of the chosen solution to be statistically estimated.

Applying this reasoning to three observation periods (see Table 1), it is possible to derive the equations that will determine the three unknown parameters from the actual frequencies of four histories. The increase in the number of observation periods (years) to k does not fundamentally change the model: $k - 1$ parameter pairs φ_t and p_{t+1} ($t = 1, \dots, k - 1$) and unpartitioned parameter $\beta_k = \varphi_{k-1}p_k$ are to be estimated. The parameters φ_{k-1}, p_k , and p_1 are undeterminable. The frequencies of different capture histories are unambiguously specified by a multinomial distribution with a combination of the target parameters. Reverse reasoning makes it possible to find the most probable combination leading to the observed frequencies.

Model Assumptions

The model implies equality of the target parameters for all individuals in the studied population and independence of individual fates (recapture histories) of the marked birds. It should be taken into account that the equality of parameters may be disturbed by the capturing scheme; for example, the size of individuals may influence the capture probability. The capturing duration should be insignificant as compared with the periods used for assessing survival probability. These and other violations of the specified assumptions can be taken into account or reduced by a certain complication of the model, in particular, by dividing the animals into categories within which the assumptions are retained (as will be demonstrated by an example).

The correctness of extrapolation of the features of marked birds to the entire population should also be tested. In particular, it should be kept in mind that the obtained estimates can be of a local character and refer only to the particular habitats covered by the study.

Here and below, we consider “apparent” survival, which is indistinguishable from irreversible emigration in a limited area. Thus, it is assumed that the studied area is large enough to ignore individual cases of irreversible emigration. If this assumption appears

implausible, it is necessary to turn to other MARK modules, which take into account the exchange of individuals between control plots and introduce the estimate for emigration as an additional multiplicative parameter.

Estimating Parameters

The parameters are estimated by the maximum likelihood method. This is a classical statistical method widely used in ecology for the comparison of stochastic models. In this case, the maximum likelihood method provides for a mere determination of the probability that an actually observed combination of different recapture histories of all the sets of marked individuals will accidentally occur. As we have seen, the probability of each history is unambiguously derived from the multinomial distribution of the frequencies at a given number of marked individuals and the combination of probabilities φ_i and p_i . The target likelihood value is the product of probabilities for the histories of all individuals. In practice, the logarithm of the likelihood function is calculated as the sum of the logarithms of probabilities for each history with the number of individuals displaying the same recapture history as a weight coefficient. As has been noted, the same combination of histories (for example, 9 recaptured and 20 nonrecaptured individuals of the 29 birds marked 1 year before) can appear with different parameter combinations. The model with the parameters that provide the maximum value of the likelihood function, i.e., the highest probability of occurrence of the observed data, is considered the best model.

The parameter estimates obtained by the maximum likelihood method display an asymptotically unbiased value and a normal distribution, as well as a minimum variance. These features determine the high robustness of estimates. The partial second derivatives of the likelihood function are the basis for calculating the variance for each parameter used to determine the standard error and confidence interval.

The necessary condition for applying this method is a normal distribution of the parameter, which can hardly be expected for the survival probability values falling into the range [0, 1]. To meet this requirement, survival probability is transformed with the logit function $\text{logit}(\varphi) = \log[\varphi/(1 - \varphi)]$. After all calculations are performed, the confidence interval is determined and transformed using the inverse function $\varphi = \{1 + \exp[-\text{logit}(\varphi)]\}^{-1}$.

When processing mass data, the probability of the frequencies of each history is unambiguously determined, and the parameters can be estimated by the maximum likelihood method in an explicit manner by solving equations analogous to those shown in Table 1. However, realistic estimates cannot be obtained for some parameters because of insufficient data. Then the problem is solved in an iterative manner by selecting the model parameters until the combination with a

maximum likelihood estimate is found. The development of modern programs is aimed at optimization of such solutions (Cooch and White, 2009).

General Model

As a rule, animals are marked under a long-term program, where a new cohort of marked individuals is added every year. Their history will start with zero: for example, "010" means that this individual was marked and released in the second year of observation and was not reencountered. Other conditions being equal, each new cohort consists of the animals that are younger by one year on average, although they experience the effect of the same survival and capture factors as the individuals marked earlier. The age difference between the cohorts can be a sufficient reason for assuming that their recapture and survival probabilities are also different. Nonetheless, all cohorts inhabit the same area, and the periods of their stay overlap; therefore, it is purposeful to consider their parameters as one general model. Table 2 gives an example of data representation and parameter designations in such a model.

Constraining Model Parameters

A complete general model describes the data in maximum detail. The obtained parameter estimates may be further used for comparing and averaging over cohorts, ages, and periods or their combinations (for example, over the years favorable or adverse for breeding). However, another approach is statistically more justified, namely, a group constraint on parameters via an equality before their estimation, i.e., construction of partial models with a limited number of parameters. The point is that it is practically unfeasible to provide actual data for the general model so that each parameter would be reliably estimated. In the case of a model, the data are correctly grouped and provide a more correct calculation of the mean estimates. However, the main advantage of the partial models is that they allow a diversity of hypotheses on the equality of parameters to be constructed and tested by their comparison with the complete model. Both statistical and software tools for testing have been well worked out.

Parameterization of partial models in the MARK program is specified by two triangular matrices (Table 3) analogous to those shown in Table 2. In these matrices, the parameters of a complete model (Fig. 3a) are replaced with unique index numbers (indices), and the same number is assigned to the hypothetically equal (constrained) parameters. The program finds the combination of values for the numbered parameters displaying a maximum likelihood estimate.

The model with a time dependence (Fig. 3b) is specified by a vertical constraint, i.e., by setting equal the survival and capture probabilities of different cohorts within one observation period. This model, known as the Cormack–Jolly–Seber model, gave the

Table 2. Representation of the capture–recapture data for male Siberian thrushes in 1989–1994 as an example of parameterization of the general model over $k = 6$ capture periods

C	History	R	Survival parameters between periods t						
C	t_1	t_2	t_3	t_4	t_5	t_6			
1	111000	4							
	110000	5		φ_{11}	φ_{12}	φ_{13}	φ_{14}	φ_{15}	
	101000	1			φ_{22}	φ_{23}	φ_{24}	φ_{25}	
	100000	19				φ_{33}	φ_{34}	φ_{35}	
	011000	3					φ_{44}	φ_{45}	
2	010100	1							
	010000	11							
	001111	1							
3	001110	1							
	001100	1							
	001000	29		p_{12}	p_{13}	p_{14}	p_{15}	p_{16}	
	000111	1			p_{23}	p_{24}	p_{25}	p_{26}	
4	000110	4				p_{34}	p_{35}	p_{36}	
	000101	1					p_{45}	p_{46}	
	000100	28						p_{56}	
5	000011	4							
	000010	7							
6	000001	27							

Note: the input data, namely, C , the year of marking (cohort), and R , number of marked individuals, are shown on the left, and the unique description of parameters (φ , survival probability, and p , capture probability) and their scope are on the right. The probability of capturing individuals alive at moment t belongs to the moment t . Survival probability for the individuals found to be alive at moment t belongs to the period between t and $t + 1$. The parameters listed in the last column can be determined only as the product $\beta_{ik} = \varphi_{ik} - 1p_{ik}$. Therefore, this model, formally comprising 30 parameters, actually contains only $(k - 1)^2 = 25$ determinable parameters (10 φ , 10 p , and 5 β).

name (CJS) to the overall methodology of collecting and processing data on marked animals that are released in order to record reencounters of live individuals. In other situations, the assumption that the changes in survival probability depend on the cohort (horizontal constraint, Table 3c) or age group (diagonal constraint, Table 3d) may be more effective.

The model with a mixed dependence on time and two age cohorts is of special interest (Table 3e). “Age” may have a conditional meaning as the time since marking. Then the “younger” group will comprise both the local individuals and the transiting ones never reencountered after marking, while the “older” group will contain only the residents, whose survival estimate is the goal of the study.

Further reduction in the number of parameters is intended to eliminate the insignificant differences, find the significant factors, and more precisely assess their role. This procedure can follow different paths. One is to set the p value constant. If the recapture effort changed insignificantly relative to the observation period, this assumption will elevate the significance of the test for the dependence of φ on other fac-

tors. However, if the capture effort was changed, it may be purposeful to assume the φ value constant and estimate it with an increased accuracy. Finally, reducing the diversity of parameters to constant φ and p , we can efficiently analyze comparatively small samples.

Another method to constrain parameters is to represent them not as equal but rather proportional to a certain external variable; for example, instead of a constant capture efficacy, one can represent it as a linear function of the number of working nets or observation time during each period. Survival probability can also be represented as a function of, for example, the degree of severity of external factors between the capture periods. This method is analogous to regression analysis.

By analogy with variance analysis, the parameters of a complete model can be grouped into classes according to the qualitatively different categories to which they belong, for example, juvenile, mature, and old individuals; “bad” and “good” conditions; and so on. To construct such models, the MARK program utilizes a matrix of dummy variables, which is a more flexible tool than the described triangular matrices.

Frequently, it is necessary to divide the studied animals into groups concurrently present in all observations, such as two morphs, males and females, or control and experimental animals. Indeed, it is possible to consider each group separately and then compare the resulting parameter estimates. However, it is rather likely that the parameters of different groups correlate relative to years and ages. Then it is more effectual to construct a general model with a separate pair of matrices for the parameters of each group. MARK makes it possible to constrain any parameters both within and between like matrices for different groups even to constant ϕ and p for all individuals.

Model Description

The diversity of model variants requires their brief description, i.e., representation of the factors responsible for the inhomogeneity of parameters and correlations between them. In the accepted nomenclature, a time-dependent model is designated as $\{\phi(t)p(t)\}$. After setting parameters constant, it forms the variants $\{\phi(t)p(\cdot)\}$, $\{\phi(\cdot)p(t)\}$, and $\{\phi(\cdot)p(\cdot)\}$. An age-dependent model corresponds to $\{\phi(a)p(a)\}$, and a completely parameterized model corresponds to $\{\phi(a^*t)p(a^*t)\}$. If group distinctions (for example, sex-related) are also considered, the model is designated as $\{\phi(s^*a^*t)p(s^*a^*t)\}$.

These designations assist in tracing the logic of parameter constraining. It is appropriate here to recall the symbolism of classical ANOVA, i.e., analysis of the observed variance in a variable by partitioning it into the additive components: random and factor-dependent. The latter component in a two-factor analysis was designated as $A^*B = A + B + A \cdot B$, as being composed of the additive components: the direct action of factors A and B and their interaction $A \cdot B$. If factors A and B can be regarded as independent, their interaction is negligible and the complete analysis of the effect of these factors (A^*B) is substituted by analysis of their direct effect ($A + B$).

Taking into account a profound analogy in model construction, we can imagine that the modification of a complete model $\{\phi(s^*t)p(s^*t)\}$ into $\{\phi(s^*t)p(s^* + t)\}$ implies parallel changes in the time of recapture parameters related to groups of different sexes (Fig. 1). Comparison of such a hypothesis with the complete model is equivalent to the test for significance of parallelism. The independence of impacts of different factors on the survival parameters is tested in an analogous manner.

Comparison of Models

A descriptive model must have a sufficient number of parameters to take into account all the existing sources of data variation. The smaller the number of parameters, the farther from reality the description of the data structure. However, the larger the number of parameters is, the more likely are random deviations

Table 3. Widespread variants of model parameterization for $k = 6$ capture periods according to the designations used in the MARK program (ϕ , survival probability, and p , capture probability)

(a) Complete model																																																			
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in the estimates for each of them. The principle of *parsimony* postulates the need for an optimal balance between these two trends.

Selecting a model with a smaller number of parameters, we can ignore the change in survival probability with time, although we do not doubt its existence. Increasing the number of parameters, we will estimate these changes, but if their mean square error exceeds that for a single total estimate, such details in description are farther from reality rather than closer to it. The choice between a single estimate of ϕ and many estimates is determined by the balance between the

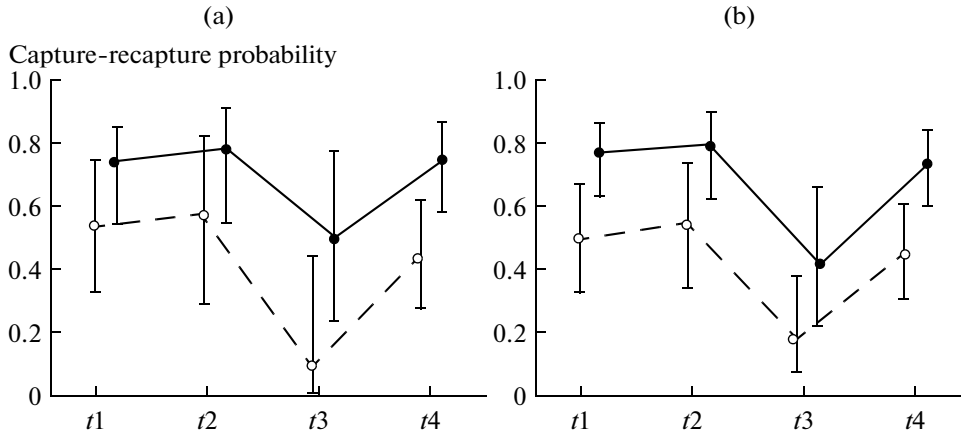


Fig. 1. Estimation of the capture probability (p) of old males (black circles) and females (white circles) of the Siberian thrush over four observation periods ($t_1 - t_4$) depending on the constraint of model parameters: (a) $\{\varphi(s \cdot t)p(s \cdot t)\}$ and (b) $\{\varphi(s \cdot t)p(s + t)\}$. The right plot takes into account only the direct effect ($s + t$) of sex and observation period on capture probability, whereas the interaction of the factors st is assumed random. A decrease in the confidence intervals of estimates confirms that this assumption is justified: the change in capture intensity in different years independently influences the capture–recapture probabilities for males and females.

variation range of a parameter and input data quality. This is the principle of parsimony.

Before the model is chosen, the problem is set to find the biologically meaningful model that explains the significant differences in data (for example, an age-dependent survival probability during the first two years of life) but, following the principle of Occam’s razor, concurrently sorts out the parameters whose importance is not suggested by the available data.

The main tool in selecting models is the likelihood ratio test (LRT). This test requires that one model be “nested” inside another, i.e., that it be part of a more

complete model and derived from it by constraining parameters. The complete model, as compared with a constrained one, formally describes the data more comprehensively, but numerous random deviations accompany a large number of parameters. The following reasoning is used to sort out the issues of a random nature. Starting from the most complete model (referred to as a saturated model), the constrained simplified models with a smaller number of param-

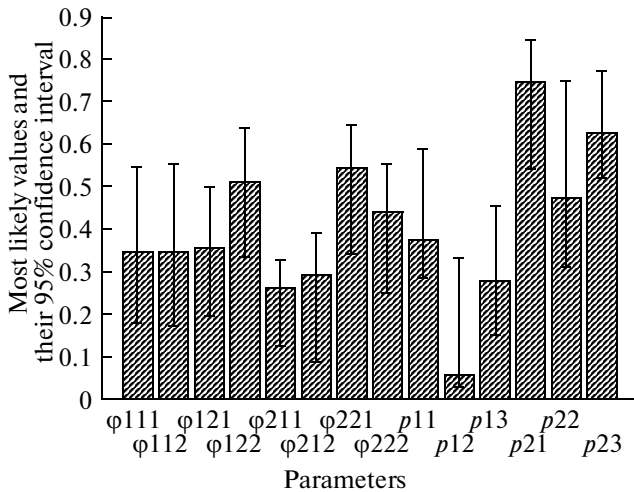


Fig. 2. Interactive parameter estimation by the example of the model $\{\varphi(2s \cdot 2m \cdot 2t)p(2s \cdot 3t)\}$: s , sex (1, female; 2, male); m , marking date (1, one year before; 2, over a year before); t , periods (for survival estimation: 1, 1989–1999; 2, 1999–2008 and for capture probability: 1, 1990–1998; 2, 1999; and 3, 2000–2008).

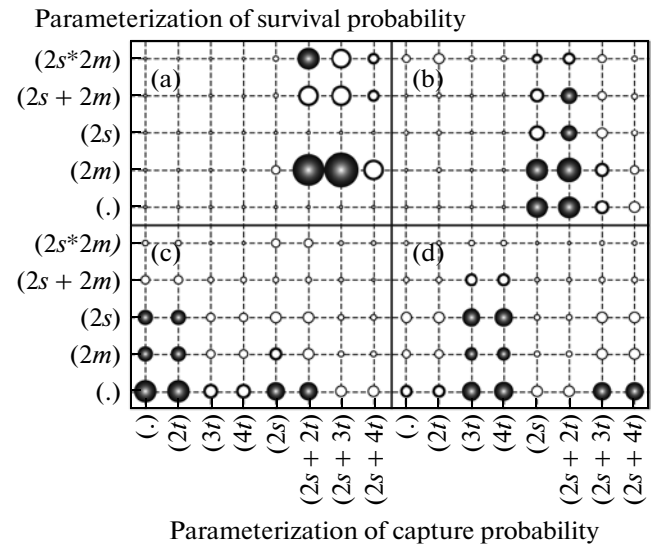


Fig. 3. Weight coefficients (according to AIC_c) in 40 models for four species: (a) Siberian thrush; (b) redwing; (c) fieldfare; and (d) dark-throated thrush. Dark circles denote the maximum parsimony models whose total weight exceeds 0.5. The models for dark-throated thrushes cover the observations to 1998. For comparability, they are set equal to $p(3t)$ and $p(4t)$ if they share the periods of 1990–1995 and 1996–1998, or $p(\cdot)$ and $p(2t)$ otherwise.

ters are constructed. Naturally, this reduces the verisimilitude of the model; however, as long as these losses are insignificant, simplification of the model is regarded as justified. To measure the losses, the deviance (doubled absolute value of the natural logarithm of model likelihood) is calculated; this is a sort of penalty for simplification. LRT compares the change in deviance with the change in the number of parameters. The difference between deviances (actually, this is $-\ln(L_1/L_0)$, where L_0 and L_1 are the likelihoods of saturated and constrained models) has a χ^2 distribution with the degrees of freedom equal to the number of reduced parameters. If this difference may be considered insignificant, i.e., when it is smaller than a standard χ^2 value, the parameter reduction increases the value of the model.

Testing the Goodness of Fit of Model and Data

Now let us return to the model assumptions. Do the data actually fit the applied methodology? Testing of the input data and their grouping at different stages of model construction provide the answer to this question. The embedded program RELEASE and independent program UCARE (Choquet et al., 2005) offer various tests. All of these tests are based on comparison of the actual with expected data if the assumptions are met. For example, one of the tests checks whether the cohort marked in the current year differs from the individuals marked earlier in the rate of future recaptures. The goodness-of-fit measure is the χ^2 test, the value of which should not considerably exceed the standard value, or, more precisely, the probability that this excess is random should be over 0.05 (or another accepted significance level). For the model selected as a starting point, the deviance divided by the number of parameters should be close to unity. A significant difference—data misfit—may mean that one of the assumptions was violated.

- (1) Any marked individual present in the studied area during the control period has an equal recapture probability.
- (2) Any marked individual recaptured during the control period has an equal probability of surviving to the next control period.
- (3) Labels cannot be lost and are read without mistakes.
- (4) The duration of the control period is sufficiently small, as compared with the interval between adjacent control periods.

In fact, all of these assumptions are violated to a certain degree. Testing enhances detection and reduction of some deviations or reconsideration of the model selection. Testing the data fit to the initial model is of special importance; it is the most complete and a starting point for further simplification. If this model is not saturated, there is a chance to overlook significant parameters.

Strategy for Model Selection

The likelihood ratio test makes it possible to notice a significant deterioration in the model with its gradual simplification, according to an increase in the deviance. Does this mean that a reduction in model parameters is always desirable? Akaike's information criterion gives the answer:

$$\text{AIC} = -2\ln(L) + 2K,$$

where $-2\ln(L)$ is the deviance for the model and K is the number of determinable parameters. (In practice, the criterion AIC_c is more frequently used, where K is corrected taking into account the sample size.) Akaike's criterion does not simply help find the optimal balance between the penalties and the number of parameters; it also indicates in a well-reasoned manner the model with the least AIC_c as the closest to reality, which controls the structure of actual data. Unlike the LRT, it is applicable to the comparison not only of the nested models, but also of the other object-based models. However, LRT remains a tool for assessing the significance of remote or additional parameters in nested models.

As is known, all models alter reality, but some do so to a lesser degree than others. There are situations when two or three models with approximately the same AIC_c values but different parameter estimates are found to be "the best." Evidently, the reality in this case is somewhere in between. In this case, the program utilizes AIC_c to compute the normalized weights for the models and the mean parameter estimates weighted proportionally to the qualities of selected models.

RESULTS AND DISCUSSION

Siberian Thrush

The sample of Siberian thrushes over 20 years of observation partitioned according to sex and comprising 90 various recapture histories was presented as a table of a specified format and tested for data goodness-of-fit. During these tests, several individuals with long-term capture histories displayed a high residual variance in addition to that explainable by the multinomial distribution underlying the model. This allowed us to detect and correct a mistake in the visual identification of a marked bird not confirmed by recapture. The histories of the remaining long-living individuals were true. Positive deviations in their variances are explainable by a uniqueness of history: the number of surviving individuals decreases with age, whereas the diversity of histories increases.

After correction, the data were tested using the embedded program RELEASE. According to the data presentation, the program fit the data to the model $\{\varphi(s \cdot t)p(s \cdot t)\}$ and did not detect any significant deviations according to the sum of the tests ($\chi_{77}^2 = 71.16$, $P_{\text{LRT}} = 0.666$). However, a partial test that compared further recapture histories of the birds captured for the first time and marked earlier detected a difference

Table 4. Changes in the properties of the model describing Siberian thrush recaptures with a reduction in parameters

no.	Model	<i>n</i>	<i>Dev</i>	AIC_c	<i>w</i>
1	$\{\varphi(2s \cdot 2m \cdot 19t) p(2s \cdot 19t)\}$	90	223.6	1602.0	0.000
2	$\{\varphi(2s \cdot 2m \cdot 7t) p(2s \cdot 7t)\}$	42	322.4	1593.6	0.000
3	$\{\varphi(2s \cdot 2m \cdot 2t) p(2s \cdot 3t)\}$	14	349.2	1561.7	0.009
4	$\{\varphi(2s \cdot 2m + 2t) p(2s + 3t)\}$	9	355.2	1557.6	0.073
5	$\{\varphi(2s \cdot 2m) p(2s + 3t)\}$	8	355.4	1555.7	0.186
6	$\{\varphi(2s + 2m) p(2s + 3t)\}$	7	357.3	1555.6	0.195
7	$\{\varphi(2m) p(2s + 3t)\}$	6	357.3	1553.6	0.536

Note: *n* is the number of parameters; *Dev*, deviance; AIC_c , Akaike's information criterion; and *w*, relative weight (contribution) of the model.

between them for males ($\chi_{18}^2 = 33.72$, $P_{LRT} = 0.014$). On this basis, we complicated the model to $\{\varphi(s \cdot m \cdot t)p(s \cdot t)\}$, where *m* is the factor partitioning the survival parameters into two groups, namely, the birds recaptured during the first period after marking and those recaptured in all the subsequent periods (see Table 3e). This factor was added only to the survival probability, since the time of marking could not influence the probability of bird recapture: the individuals passing through are never recaptured, while the local individuals are recaptured independently of the year of marking. In the case of such partitioning, the model fits according to all tests.

For convenience of description, we supplement the model with the number of levels (groups) of parameter classification for each factor: $\{\varphi(2s \cdot 2m \cdot 2t)(2s \cdot 19t)\}$. This model involves the maximal number of parameters and thus pretends to be a saturated model from which is it possible to begin the parameter reduction (Table 4). Below are the main stages in this procedure.

(1) The model $\{\varphi(2s \cdot 2m \cdot 19t)(2s \cdot 19t)\}$ contains 112 parameters (for each sex, 19 parameters for survival probability in the year after marking; 18, for survival probability in subsequent years; and 19, for capture probability). This provides for obtaining 110 estimates (except for two unpartitioned), but in fact only 90 parameters were estimated, since the data for the remaining ones were insufficient: either all of the individuals that survived this period were encountered, or, on the contrary, none of them were encountered. A degenerate estimate (0 or 1) was assigned to these parameters, and the corresponding observations were discarded. Thus, excess partitioning of parameters leads to the technical impossibility of estimating them and a partial loss of useful information.

(2) To avoid degenerate estimates, it is necessary to constrain those parameters, the differences between which are known to be accidental or insignificant from the standpoint of an object-based position. Trading the interannual differences, we pool the parameters of

three adjacent years and get six periods. As a separate period, we take the year 1999, since no captures were performed that year and all of the data are represented by resighting events. Reduction in parameters in the model $\{\varphi(2s \cdot 2m \cdot 7t)(2s \cdot 7t)\}$ leads to a considerable loss of information ($\chi_{48}^2 = 98.76$, $P_{LRT} < 0.0001$). However, each of the 42 parameters only now gets a nondegenerate estimate and can be used for further analysis. Therefore, we regard the model $\{\varphi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$ as a saturated model, assuming that each of its parameters can have a nonaccidental influence on the data structure.

(3) The capture efforts were relatively constant, at least during four periods (see Materials and Methods), so the capture parameters can be regarded as constant within each period. Almost no Siberian thrushes were recaptured in August; therefore, the years with and without capture efforts in August are equivalent for them and the differences in recapture probability before 1999 are of no interest. The survival probability for individual 3-year periods is also beyond our scope of interest, if it does not display a pronounced trend; thus, we consider its estimates equal up to (and including) 1999 and after. No significant information loss occurs when we consider three capture periods and two periods for estimating survival probability in the model $\{\varphi(2s \cdot 2m \cdot 2t)(2s \cdot 3t)\}$ ($\chi_{28}^2 = 26.78$, $P_{LRT} = 0.530$), which suggests that this step is appropriate. The program displays the current parameter estimates in an interactive mode (Fig. 2), providing for a purposeful selection of the further parameter constraint.

(4) There are good reasons for assuming that a change in the capture method during the considered periods influenced the results independently of bird sex and year of marking. Withdrawing the interaction with time from the model, $\{\varphi(2s \cdot 2m + 2t)(2s + 3t)\}$, we gain a simplicity in description without a significant increase in deviance ($\chi_5^2 = 6.05$, $P_{LRT} = 0.302$).

(5) Estimation of the survival parameters (see Fig. 2) demonstrates that they do not differ in individual capture periods, so that the dependence of φ on time can be excluded from the model, $\{\varphi(2s \cdot 2m)(2s + 3t)\}$, thereby simplifying the description ($\chi_1^2 = 0.143$, $P_{LRT} = 0.705$).

6) Is it also possible to assume that survival probability is independently determined by bird sex and year of marking? The model $\{\varphi(2s + 2m)p(2s + 3t)\}$ further simplifies the description ($\chi_1^2 = 1.93$, $P_{LRT} = 0.165$) with almost no effect on the quality (according to AIC_c). On the other hand, the confidence intervals for survival probabilities of the groups marked in different years do not overlap when using such estimation.

(7) Pooling of these two cohorts, $\{\varphi(2s)(2s + 3t)\}$, fails to lead to a statistically significant difference in

Table 5. Mean weighted estimates for parameters of four models describing Siberian thrush recaptures

Model parameters				Most likely estimates				
Type	Sex	TAM	Period, years	M	MSE	TSE	95%CL	95%CU
ϕ	f	1	1989–1999	0.302	0.040	0.053	0.209	0.415
ϕ	f	1	1999–2008	0.303	0.040	0.054	0.208	0.418
ϕ	f	2	1990–1999	0.467	0.036	0.043	0.385	0.551
ϕ	f	2	1999–2008	0.470	0.036	0.041	0.391	0.550
ϕ	m	1	1989–1999	0.280	0.025	0.026	0.232	0.334
ϕ	m	1	1999–2008	0.282	0.025	0.026	0.233	0.336
ϕ	m	2	1990–1999	0.483	0.033	0.034	0.416	0.550
ϕ	m	2	1999–2008	0.483	0.033	0.035	0.415	0.552
p	f		1990–1998	0.403	0.071	0.076	0.267	0.556
p	f		1999	0.134	0.058	0.060	0.054	0.298
p	f		2000–2008	0.314	0.057	0.060	0.210	0.441
p	m		1990–1998	0.738	0.051	0.051	0.627	0.825
p	m		1999	0.395	0.112	0.113	0.205	0.622
p	m		2000–2008	0.656	0.061	0.061	0.528	0.765

Note: Type includes ϕ , survival probability, and p , recapture probability; sex is denoted as f for female and m for male; TAM (time after marking) includes (1) first year and (2) subsequent years; period shows the years of interval (for survival) or estimation period (for recapture). The estimates (after inverse logit transformation) are M, mean value; MSE, mean square error; and 95%CL and 95%CU, lower and upper limits of 95% confidence interval including the model indeterminacy.

survival probabilities relative to sex but deteriorates the model in general. On the contrary, separate consideration of these cohorts and pooling of the sex groups, $\{\phi(2m)p(2s + 3t)\}$, gives the best model. As compared with the most complete model, $\{\phi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$, this variant does not lose significant features ($\chi_{36}^2 = 34.91$, $P_{LRT} = 0.521$) but is considerably simpler, complying with the parsimony principle.

Thus, the model $\{\phi(2m)p(2s + 3t)\}$ displayed the best quality of all the considered logically justified models. Three more models differing by 2–4 units according to AIC_c contribute considerably to the description. Using their relative weights (see Table 4), we obtain the average weighted estimates for the used parameters (Table 5).

Comparison of the mean estimates demonstrates that the change in capture schedule had a significant effect on the recapture probability when the capture was not performed and a weak effect when the control plot area and seasonal capture duration were reduced. However, these changes did not lead to a bias in the survival estimate. The probabilities for recapture of males and females differed twofold. However, the sex-related differences in survival probability were less than 2% and could not be confirmed. The survival probability during the first year after marking of both males and females was significantly lower. Such an estimate is explainable by the considerable number of individuals passing through among the marked birds, mainly during the end of spring migration.

The high adequacy of the “best” model allows the estimated parameters to be pooled and their error to be decreased. On the other hand, a single model does not guarantee the absence of a certain bias in this estimate. The use of several models corrects the possible bias, although the total error in this case increases. The increase in the error demonstrates the degree to which the reliability of estimates depends on the indeterminacy of models. The survival probability of local birds is estimated more stably independently of the model. The survival probability during the first year after marking displays a wider range, especially in females, which is associated with the phenology of migration.

Other Species

When testing the data on the redwing for goodness of fit, two mistakes in bird identification without confirmation by capture were detected and corrected. Neither partial tests nor the general test with the RELEASE program found any significant deviations from a multinomial distribution ($\chi_{46}^2 = 19.32$, $P_{LRT} = 0.999$). On the other hand, the testing cannot be considered efficient, since the larger part of the observation years had insufficient data for calculating χ^2 . For the same reasons, we succeeded in estimating only 62 parameters of the 110 potentially determinable ones for the redwing using the model $\{\phi(2s \cdot 2m \cdot 19t)(2s \cdot 19t)\}$. Therefore, the model $\{\phi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$ with 42 parameters, 38 of which had a nondegenerate

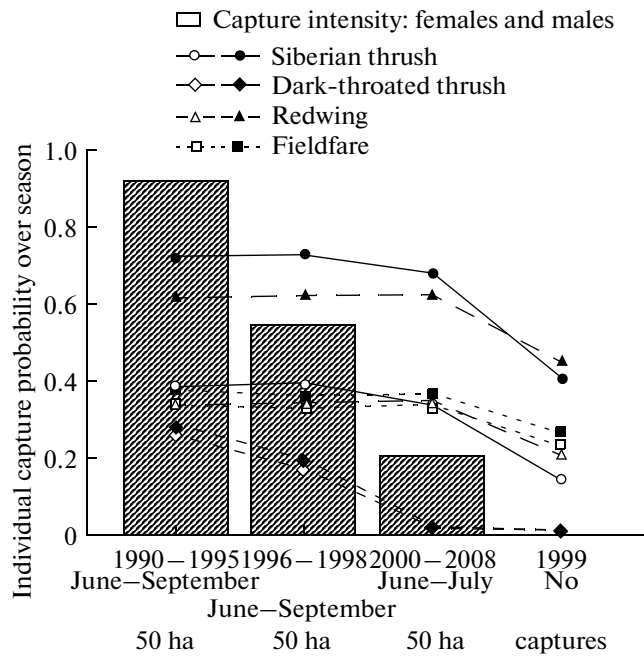


Fig. 4. Changes in the capture probability estimate with weakening of the control over population. For details of capture effort intensity, see Materials and Methods.

estimate, was taken as the main and logically saturated one. The fit of this model to the data was assessed using the interactive visual test, namely, a diagram of the residual deviances calculated for the frequency of each recapture history. The distribution of residual deviances is symmetric, close to normal, and displays no trend, while no more than 5% displayed significant deviations, thereby suggesting that the assumptions are met.

Using the logic applied to the analysis of the Siberian thrush, the model $\{\varphi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$ was simplified to $\{\varphi(2m)(2s + 2t)\}$ with an insignificant information loss ($\chi_{33}^2 = 34.31$, $P_{LRT} = 0.405$). In this case, AIC_c decreased from 716.4 to 679.8. A further reduction in parameters violated the parsimony principle. By analogy with the analysis of the data on redwings, the model $\{\varphi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$ was chosen for the fieldfare as a saturated model. It was simplified to $\{\varphi(\cdot)p(\cdot)\}$ with an insignificant information loss ($\chi_{37}^2 = 39.01$, $P_{LRT} = 0.379$). In this case, AIC_c decreased from 887.1 to 848.3.

The attempt to process the recapture histories of dark-throated thrushes according to the same scheme was unsatisfactory. The “saturated” model $\{\varphi(2s \cdot 2m \cdot 7t)p(2s \cdot 7t)\}$ processes only 23 of the total 42 parameters, while the remaining estimates are degenerated into 0 or 1. The parameter reduction led to the model $\{\varphi(2t)p(4t)\}$, which demonstrated that the recapture probability in the 2000s decreased to 0.017. During this period, the capture schedule was changed so that both

the favorable nesting habitats of this species and the season when the birds appear for molting were left out.

Correspondingly, the model was constructed for the data on the first 10 years of observation, where the year intervals were grouped in threes. Thus, we succeeded in estimating 17 determinable parameters of the 18 in the model $\{\varphi(2s \cdot 2m \cdot 3t)(2s \cdot 3t)\}$ ($AIC_c = 607.9$). According to the diagram of residual deviances, the distribution of recapture histories meets the assumptions. The model $\{\varphi(\cdot)p(2t)\}$, describing the data according to three parameters ($\chi_{14}^2 = 21.85$, $P_{LRT} = 0.081$), was regarded as satisfactory.

Comparison of Weighted Estimates

The goal of the study was to obtain comparable estimates for survival probabilities of species. The model best fitting the parsimony principle displayed a maximum contribution to the mean weighted estimates for parameters. However, depending on the way in which intermediate models were selected, the contributions of individual parameters to the final estimate can vary. The optimal way is still insufficiently elaborated (Burnham and Anderson, 2004; Link and Barker, 2006). Therefore, we used the same method for all species, namely, performing the calculations using 40 analogous models with a high parsimony. The relative weights of these models according to AIC_c were determined for each species (Fig. 3).

Graphical visualization gives another possibility to assess the order of model selection. In particular, the sex-related differences are significant for the Siberian thrush and redwing; without taking them into account, the model is far from reality. As for the dark-throated thrush, the estimate is better when the survival parameters are reduced, while a reduction in the total number of parameters gives better results for the fieldfare. Note that three models alone contribute over 50% of the weight to the optimal estimate in the case of the Siberian thrush; for the redwing, six models; and for the fieldfare and dark-throated thrush, eight models; i.e., the determinacy of the models decreases in this row.

The MARK program allows the weighted mean estimates for parameters to be calculated according to the data of all 40 models using the AIC_c weights (Figs. 4, 5). The mean weighted estimate comprises the variation of values both within an individual model and among the models. The error and confidence interval were obtained using logit-transformed data and were then expressed using an arithmetic scale by an inverse transformation.

Comparison of the capture probability estimates with the capture–recapture efforts (Fig. 4) discloses three facts that are not obvious. First, closely related species differ considerably in recapture probability. Second, two of these species (redwing and Siberian thrush) demonstrate significant sex-related differences in this parameter. Third, the parameters display a low sensitiv-

ity to changes in the data-collection schedule; moreover, it is different for species and similar for the same sex. Not only do these inferences give useful information for planning data collection, but they also expand our knowledge about the biology of these species, including the duration of stay, intensity of movements along the area, and sex-related task sharing.

The statistical significance of the conclusions is confirmed by the mean weighted error of individual estimates (not shown in Fig. 4 to avoid excess details). Critical pairwise comparisons may be performed in another way by constructing a joint model for two data series. For example, to clarify the differences between the Siberian thrush males and females, we compare the “best” model $\{\varphi(2m)p(2s + 3t)\}$ with the nested model not taking into account the sex-related differences in capture probability, $\{\varphi(2m)p(2s + 3t)\}$. LRT ($\chi_1^2 = 26.27$, $P_{\text{LRT}} < 0.0001$) confirms the doubtless significance of this parameter.

Finally, let us consider the mean weighted estimates for survival probability (Fig. 5). The estimates in the first year after marking of Siberian thrushes are significantly lower than in subsequent years (Student’s t -test, $P < 0.0001$). This decrease is explainable by the presence in the sample of individuals passing through (mainly, seasonal migrants). Therefore, the value obtained for the recaptures 2 years or more after marking should be regarded as a total estimate. In the redwing population, the estimates for the first year and subsequent years differ insignificantly: the models $\{\varphi(2m)p(2s + 2t)\}$ and $\{\varphi(\cdot)(2s + 2t)\}$ display marginal differences ($\chi_1^2 = 2.42$, $P_{\text{LRT}} < 0.12$). The same result is obtained by a direct comparison of the estimates with their errors (one-tailed Student’s t -test, $P = 0.14$). Other species display even lesser differences, suggesting the absence of a noticeable number of transit birds.

It seems as if the low numbers of migrants of the three last species allow the survival estimates to be united into a more accurate joint result independent of the period after marking (see Fig. 5). Nonetheless, the presence of even a low number of transit birds can lead to a bias toward underestimation in the joint estimates. Taking this fact into account, the total survival probability value was calculated separately for the lower and upper boundaries of the confidence levels in a logit scale. The upper boundary was determined over the entire sample, and the lower was determined only over the individuals marked more than 1 year before, which were sure to contain no transit birds. The median of the interval was assumed the total estimate; then all the values were transformed into an arithmetic scale (see Fig. 5).

According to the total survival probability estimates, the Siberian thrush as the only tropical migrant is considerably ahead of the remaining species. The dark-throated thrush, wintering considerably farther

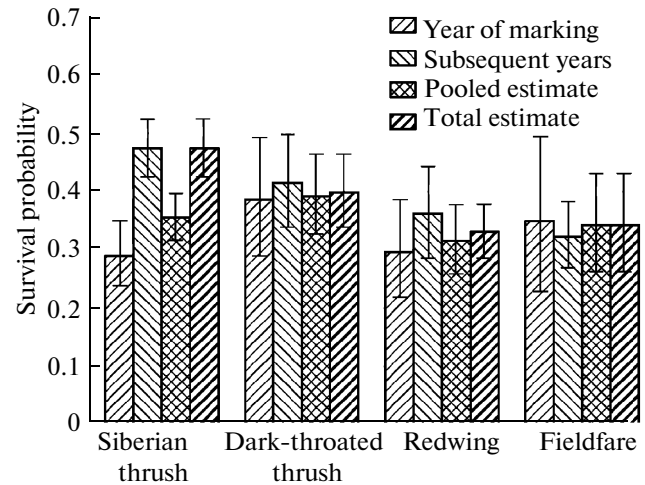


Fig. 5. Survival estimates obtained as weighted means of 40 analogous models with AIC_c weights. The total estimate was obtained from the previous ones depending on their balance (see text); 95% confidence intervals are shown.

to the south, significantly exceeds the redwing (one-tailed Student’s t -test, $P < 0.05$ for all comparisons).

“Return Rate”

After obtaining the correct estimates, it is necessary to discuss why and to what degree the traditional measure of “return rate” of the ringed birds differs from the survival probability. The return rate is defined as the fraction of ringed birds later returning to the area of release. It is evident that, the larger this fraction, the wider this “area” is considered and the higher are the capture efforts. If we standardize the estimation for return rate by considering a specified site (capture plot), effort (number of traps and duration of their operation), and time interval (year), other circumstances still remain, including the method used for calculation. Should we consider “returned” the birds that were not captured but whose survival is definitely known from recapture after two or three years? Should we include in the sample the returned ringed birds not met in the previous year? There can be different points of view, and we will consider two estimates: the minimal, in the case of negative answers to both questions, and the maximal, when both answers are affirmative (Fig. 6).

The diagram makes it evident that the minimal return rate reflects the product of survival and recapture probabilities; i.e., $\beta = \varphi \cdot p$. The maximal estimate is superficially close to survival probability, if it does not differ considerably from 0.5, as in this case. This should not encourage too much the apologists of “simple solutions”: it is rather easy to demonstrate that it asymptotically tends to $(\beta + 1 - p)/(2 - p)$. At real values of the recapture probability, such an estimate is always closer to 0.5 than to the survival proba-

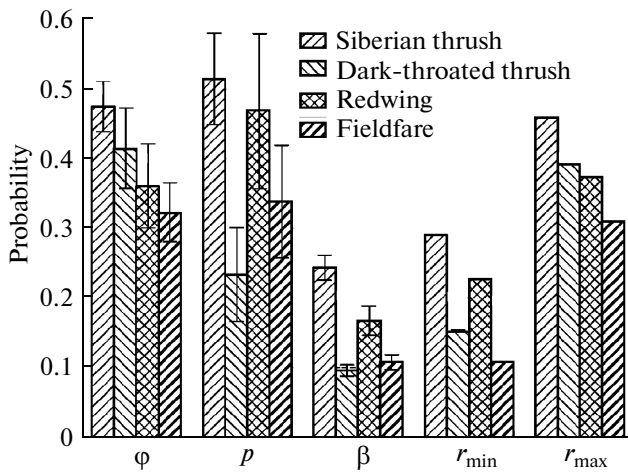


Fig. 6. Population estimates for the probabilities associated with recapture 2 years or more after marking: ϕ , survival probability; p , recapture probability; β , unpartitioned parameter, $\beta = \phi p$; r_{\min} , minimal return rate; and r_{\max} , maximal return rate.

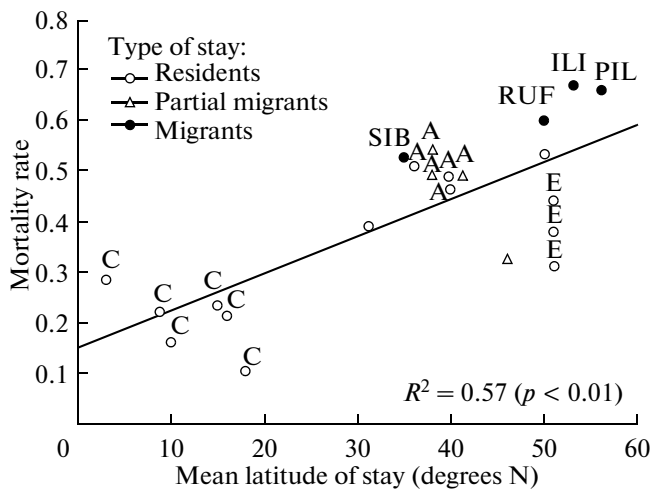


Fig. 7. Estimation of mortality rate in thrush populations of the northern hemisphere depending on geographic latitude. Nesting areas according to Ricklefs (1997): C, Central and South America; A, North America; and E, Europe. Central Siberia (our data): PIL, fieldfare; ILI, redwing; RUF, dark-throated thrush; and SIB, Siberian thrush.

bility. The limited series of observations further contributes to underestimation.

The return rate in any form prevents the comparison of heterogeneous groups (for example, different sexes of the same species), even with other conditions being equal. Nor does it take into account the survival variation according to observation periods. Thus, however “realistic” they may seem, the return rate estimates cannot adequately reflect the specific demographic features.

Mortality Gradients in Thrush Populations

According to the hypothesis of Ricklefs (1997), the mortality rate of adult thrushes in breeding populations increases with the geographic latitude of the area, which marks an increase in the climate seasonality. We assessed the average annual latitude for the studied populations, weighting it according to the duration of stay in the breeding area, on migratory paths, and in wintering sites. In general, the mortality rate in the populations of studied species also increases with the latitude of the area where they stay. The dependence becomes evident when we consolidate our data with the estimates for 18 resident and semiresident thrush populations described by Ricklefs. Its significance increases from 0.49 to 0.57 of explained variation, since our data cover the unstudied part of the gradient: they belong to higher latitudes and, in addition, to migrating populations (Fig. 7).

Ricklefs relates the effect of latitude to the climate seasonality, i.e., the average temperature difference over a year (between the warmest and coldest months) in the breeding area of populations. In the case of a pronounced seasonality, the abundance of adult birds is kept at a low level by mortality during the nonbreeding period due to a drastic deterioration in the physical conditions and reduction in food resources. Correspondingly, each surviving individual is provided with relatively rich resources during the breeding period. In low latitudes, where the biological production is relatively constant over the year, the population density is constantly close to saturation, whereas the resources (per individual) are considerably limited. Under these conditions, selection favors the adaptations directed at the survival of adult individuals rather than renewal of the population by reproduction (Ricklefs, 1980, 1997, 2000).

The mortality rate in the studied populations also fits to a high degree to the climate seasonality in the breeding area (Fig. 8). However, the Siberian populations (and, most likely, part of the North American ones) winter far from their breeding areas. Presumably, the severe winter conditions and scarcity of resources in the breeding areas only indirectly influence the mortality rate. The mortality level is one of the demographic consequences of the life cycle adaptation to certain bioclimatic conditions. A set of such adaptations distributes the individual time and energy expenditures for reproduction and self-maintenance so that the population size varies around a long-term constant level (Ricklefs, 2000). The emergence of migratory populations could be initially adaptive only in the case where this balance was minimally changed (Salewski and Bruderer, 2007); thus, the dependence of mortality level on seasonality can be regarded as a characteristic inherited from the resident ancestors.

On the other hand, the line of regression constructed only according to the data of resident populations (dashed line in Fig. 8) has a steeper slope and demonstrates that the mortality rate for all migrants is

lower than the predicted value. Taking into account the fact that the migratory features appear and strengthen under the conditions with a more pronounced seasonality, we can expect that migrations contributed to a decrease in the mortality rate during colonization of the territories with such conditions. The migration distance, which was used as the second factor in the regression analysis, increases the fraction of explained differences in the mortality rate to 0.86, which is 3% higher than that obtained for the seasonality alone. Consequently, migration to a region more favorable for wintering can constrain the decrease in population size, as compared with that expected for a breeding area. However, the 3% contribution of migrations has only a marginal significance ($t_{19} = 1.91$, $P = 0.07$). It is important that the Siberian populations that are similar in both the breeding region and migration distance (4000 to 6000 km) differ considerably in their mortality rates. These differences correspond better to the degree of favorable conditions in the wintering areas assessed according to the temperature of the coldest month.

Both Siberian and European populations deviate from the general pattern of increase in the mortality rate with an increase in climate seasonality, since their mortality rate is in general higher than the norm (Fig. 8). The environmental conditions in a marine climate approach tropical conditions in a smooth seasonality but not in the sum of temperatures, which determines the productivity of ecosystems. Indeed, an increase in seasonality with latitude is, as a rule, accompanied by a decrease in the average annual temperature. However, it would be strange to expect that the temperature per se has no effect on survival probability. The sample represented by populations from the Western European regions with a marine climate and Central Siberian regions with a continental climate makes it possible to estimate the separate effects of these factors. The heat availability (as a sum of average temperatures of July and January in the population area) explains 70% of the variation in mortality rate and 90% together with seasonality (Fig. 9). In this pair, its unique contribution is about 7% ($t_{19} = 3.32$, $P = 0.003$), the contribution of seasonality is about 20%, and their joint impact associated with an increase in the geographic latitude amounts to 63%.

After taking into account the variation in mortality rate determined by seasonality and deficiency in heat, the migration distance has no significant effect on the mortality rate ($t_{18} = 1.10$, $P = 0.29$). Thus, the favorable conditions for wintering not only completely compensate for the expenditures on the migratory flight but also additionally decrease the mortality rate.

The climatic conditions that influence populations may be expressed via three variables: the temperatures of January and July in the breeding area and the temperature of January in the wintering area. This set of factors explains 91% of the variation in mortality rate in the considered sample, although the unique contri-

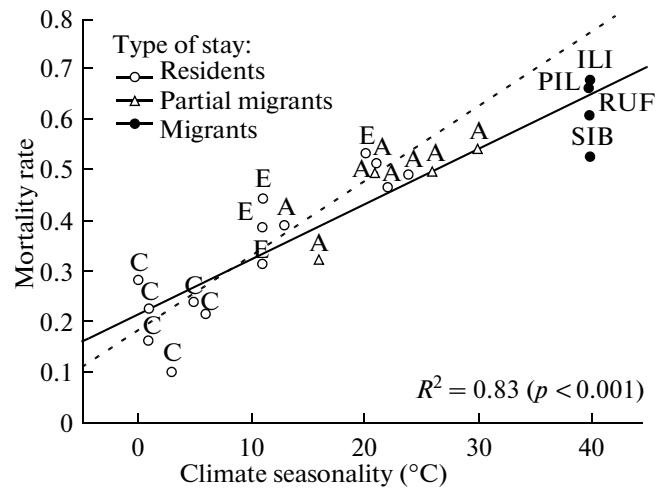


Fig. 8. Dependence of mortality rate in thrush populations of the northern hemisphere on climate seasonality expressed as the difference between average temperatures of the warmest and coldest months in the breeding areas of these populations (dashed line denotes the data for resident populations). See Fig. 7 for designations.

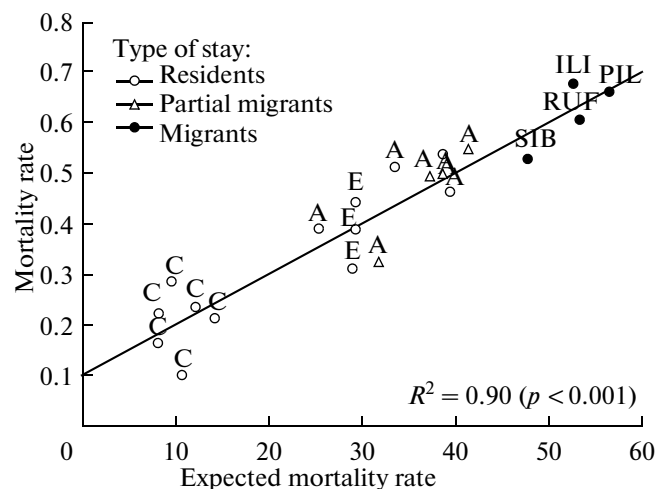


Fig. 9. The effect of climate on the mortality rate in thrush populations of the northern hemisphere. The abscissa shows the mortality rate expected according to the regression equation $y = 0.41 + (7.7x_1 - 4.4x_2) \times 10^{-3}$, where x_1 is seasonality (the difference between average temperatures of the warmest and coldest months in the nesting area) and x_2 is heat availability (the sum of the average temperatures of the warmest and coldest months in the population habitat). See Fig. 7 for designations.

bution of summer conditions is insignificant (2%; $t_{18} = 2.09$, $P = 0.052$). It would seem that this is an argument in favor of a winter constraint on the population size. This is actually so, since winter is a more severe season by definition. However, we should not disregard the fact that 63% of the variation in mortality rate is explainable by a joint action of all three factors, determining the major part of the spatial and temporal

contrasts on the planet. The balance between mortality and fecundity is also determined by adaptations to reproduction, which cannot but depend on the summer conditions and resources.

The final survival probability of migrants reflects a tradeoff of the utilization of superabundant resources in the breeding area in summer at the expense of adaptation to severe winter conditions. A decrease in the survival probability of resident species in the temperate latitudes can be regarded as a cost of the substitution of the competitive environment of tropical communities with physical constraints. In both cases, the mortality level is more tightly associated with the period of minimal temperatures, when physical stress becomes more probable, the amount of resources per individual decreases, and the temperature contrast between geographic regions increases.

The causes and mechanisms underlying the evolution of avian life histories are still vague. On the other hand, the clarified patterns make it possible to predict the population survival probability and fecundity as evolutionarily determined traits of the phenotype adapted to particular climatic conditions. This creates the possibility to detect the deviations in demographic characteristics from the norm caused by ecological disturbances in the breeding, migration, or wintering areas. The detection of critical deviations is the goal for ecologists trying to discover the causes of changes in population sizes.

CONCLUSIONS

Survival probability modeling according to capture–recapture data is an adequate and efficient method of estimation, and modern software tools enhance its application. The conclusions made earlier according to the return rate should be supported by a correct analysis.

The survival probability estimates for the Siberian populations of thrushes obtained by this modeling agree with the available data for other populations. The addition of new survival probability estimates allows the known patterns to be expanded to a wider range of objects and essential updates to be added.

The principles for processing data on live bird recaptures used in this work can be easily applied to other intervals and animal groups for comparative estimation of survival probability depending on time, age, sex, and other group characteristics of organisms. Other modules of the MARK program are able to expand the range of application of the same methodology to processing data on dead individuals, animal tracking, survival of nests, exchange of individuals between populations, and so on (Burnham and Anderson, 2002; Williams et al., 2002; Amstrup et al., 2006).

The successful application of modeling depends completely on the quality of input data and their compliance with the specified assumptions. Well-organized studies applying survival probability estimation

will provide the possibility to separate the parameters and factors of an object-specific interest from the inevitable noise, disturbances, and technical errors. This allows the survival probabilities of the control and experimental animal cohorts to be compared and the effects of selected factors or specially created situations on these rates to be estimated. Thanks to all of these possibilities, routine work on animal marking acquires the traits of an experimental study.

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