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An Assessment of the Annual Mortality Rate and Population Demographics Status in Birds Based on Ring-Recovery Data

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Abstract—A new method for assessing the annual mortality rate in bird populations is described. Ring recoveries from birds that died from various causes serve as the basis for such an assessment. The commonly accepted technique for such an assessment performed with the help of MARK software is laborious, yet fails to ensure a highly precise assessment. To calculate the mortality rate, we propose an exponential demographic model that is based on the geometric progression of a decrease in the annual numbers in some arbitrarily selected set of birds in a population. The equation of the model allows calculating the annual mortality rate of a bird population or even a species in a simple way, if the ringing data covers a vast area, for example, the territory of Russia. In addition, the proposed equation permits producing "a mortality pattern," namely, to present a chart of interrelations between the theoretical and real rates of the decrease in numbers in a given cohort of birds. The interrelations between the theoretical and real annual mortality rates allow understanding the status of a bird population each year during a period of ringing and recovery collecting: this makes it possible to reveal the population trend about whether the population is stable or decreasing or increasing in numbers.

Keywords: survival, mortality, population status assessment

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INTRODUCTION

The survival rate or survivability and the opposite value, the mortality rate or mortality, have always been considered as the most important population parameters in bird biology (Kharitonov, 2002; Paevskii, 2008). These parameters of exploited and protected species need to be known for adequate management of bioresources. The ring-recovery data are precisely the source of information on which the annual mortality of birds can be estimated. Extensive literature is devoted to this issue, and methodological recommendations have been developed, one of which is the publicly available MARK program (White and Burnham, 1999; www.cnr.colostate.edu/~gwhite/software.html).

SUBSTANTIATION OF THE METHOD

The results of ringing and repeated encounters with ringed birds are the main material for calculating the population parameters of different bird species. In addition to metal rings, other marks are used to mark birds. Nevertheless, the databases of the Ringing Centers of different countries contain mainly data on ring recoveries from dead birds, what is briefly called "dead recoveries." It is such recoveries that form the basis and databases of the Bird Ringing Centre of Russia of the Institute of Ecology and Evolution, Russian Academy of Sciences. A usual problem commonly arises in the course of work: in many cases a number of initially ringed birds for a considered sample of recoveries remains unknown. This happens for a number of reasons. In particular, in previous years, ringing reports arrived at the Ringing Center on paper carriers, and it was necessary to perform significant work to calculate the number of originally ringed birds. There are also situations when a marker does not send a report for a long time, but responds to requests, providing information about the details of the ringing of those birds, from which the recoveries have come. It is almost impossible to find out the number of ringed birds based on the number of recoveries of foreign rings on our territory, since the exchange of data between the ringing centers concerns only the recovery of the rings.

The method for calculating the survival and mortality rates based only on ring recoveries was developed long ago (Lack, 1954; Haldane, 1955; Paevskii, 1985). All that is required for this purpose is to know more precisely for each bird the time from the moment of ringing to the moment of its death. In modern conditions, a set of stochastic models is used to calculate the population parameters based on ring recoveries. A large number of such models are collected in the above-mentioned MARK program. To calculate the death rate based solely on ring recoveries, it is necessary to select the data type "BTO Ring Recoveries" in the program menu. After this, it is required to check which of the models corresponds to our data. For this purpose, it is necessary to use searching to obtain the results of calculations from link functions (in different versions of the MARK program), each of which has two variants of the evaluation path; i.e., it is necessary to choose one model from among 12 or 14 models. However, these are purely mathematical models without biological characteristics. We must interpret the latter ourselves. In addition, each of the models has seven options; the mathematical parameters in the models can also be fixed or arbitrarily variable. As a result, with the help of these models, the researcher receives a huge number of survival values, from which a correct value must be chosen. There are a number of criteria for selection. In particular, it is considered that a suitable model is one for which the Akaike criterion (AIC) (Burnham and Anderson, 1998) that is calculated by the MARK program takes the least value. However, there are a number of additional requirements. It is necessary that the value of the so-called deltaAIC be the smallest, and it is desirable to choose a model that also has the smallest number of parameters. The observance of all these requirements will mean that this model is consistent to the greatest degree with the original data (Burnham and Anderson, 1998). However, checking a large number of models is not only troublesome and difficult in practice, but also does not save us from a random choice of the best model. The fact is that one model can prove to be the best according to one criterion, another model can turn out to be the best according to a second criterion, and the third one can be the best according to a third criterion. This procedure can be mastered by few people. Most users will need not just the help of people who have mastered or written the MARK program themselves, but it will also be necessary for them to delegate completely all the work on calculating the mortality rate to just these few scientists-demographers. Not all versions of this program have a calculation of the average survival rate. If the version of the program nevertheless allows calculating this indicator, then it is necessary to use a more complex mathematical formula than in calculating the arithmetic mean in most statistical procedures. However, in most cases (it is recognized in the instructions to the program), this accuracy is not necessary, since the standard error of estimating the mean covers this difference between "more correct" and conventional methods of calculating the mean. Normally, the MARK program gives a whole series of survival values for each year for which recoveries were received. Sometimes it is necessary to import these data into the MS Excel program and to calculate the average survival rate only in this way. We should add to this that preparing an input file for the MARK program is also a difficult process. In my opinion, the MARK program is good for many other cases of calculating the survival rate (and, correspondingly, the mortality rate) in case of different ways of ringing birds. The process of calculating mortality on the basis of only ring recoveries is greatly overcomplicated in this program. One more complication is computer problems: different versions of the MARK program (which are developed once every few years) may give radically different results for the same data set and in the case of applying the same model.

The MARK program may have a high-precision mathematical apparatus. However, whatever the mathematical accuracy, it cannot be higher than the accuracy of the incoming biological material. While it is impossible to do without the MARK program for many ringing cases, where a fairly large number of parameters are initially known (the number of originally ringed birds, etc.), there is no need to resort to excessive mathematical accuracy for the case when the number of input parameters is the smallest. This refers to the greatest mass material of any European ringing center, when only the number of recoveries from dead birds is known for the sample under consideration, but the total number of ringed birds is unknown. In addition, in these cases the main requirement of the MARK program for such recoveries is usually not fulfilled, namely the constancy of the share of recoveries for the entire territory surveyed. This requirement especially cannot be fulfilled for the entire vast territory of our country. Under these conditions, there is no guarantee that the survival and mortality values obtained with the help of the MARK program will be more accurate than the results obtained by simpler methods. Such a guarantee may exist, if the data received correspond strictly to the conditions of the model. In reality, it is possible to obtain a strict compliance with the conditions of the model only in very rare cases.

Since 1997 (Kharitonov, 1997, 1998) we have used a much simpler and mathematically obvious method for calculating the survival and mortality rates. The method proposed here is a simpler mathematical model than the models that are used in the MARK program. In addition, the method proposed by me makes it possible not only to calculate the required population parameters (the survival and mortality rates), but also to assess the status of the species or population under study during ringing and ring recovery. The MARK program does not support such an additional possibility.

DESCRIPTION OF THE METHOD

The proposed model is based on a well-known demographic regularity: the population of some initially selected group of birds (a set of individuals, from which we received ring recoveries) gradually decreases over the years, because a certain number of birds die each year. On average, the number of individuals that survive to each subsequent year after ringing decreases exponentially, or geometrically progressively. The first thing that must be taken into account is the size of the group, i.e., the number of birds from which recoveries have been received. The same value reflects the number of individuals that were alive at the very beginning of the study (let us designate this value as N). Second, we need to know the number of years over which all these birds have died (let us denote it as n). Next, we need to get a geometric progression: the number of birds that have remained alive from the first year of receiving recoveries to the last one. In the last year, there is often only one bird that remains alive. The last member of this progression, namely, the number of birds in year $n + 1$ after ringing must be a member showing that all the birds have already died. Mathematically, in this year there must be "less than one bird." Therefore, to make the calculations, it is assumed that 0.99 birds remained alive in year $n + 1$ and all other members of the progression will be greater than 1. In this case, the average survival rate (denoted as S) will be calculated as the denominator of this geometric progression (Kharitonov, 1998, 2002):

$$S = \sqrt[n]{\frac{0.99}{N}},$$

where S is the average annual survival rate for a group (cohort) of N birds for n years.

However, in the real situation it often turns out that, in the last year for which there is information about recoveries, there are not one but several birds alive. Therefore, further we derived a more universal formula:

$$S = \sqrt[n]{\frac{D - 0.001}{N}},$$

where the designations are the same as in the previous formula and D is the number of birds that have remained alive in the last year of receiving recoveries.

The mortality rate (M) is calculated as $M = 1 - S$. The survival and mortality rates obviously cannot be more than one. Replacing the values of the average annual mortality rate for different species, which were calculated using the above formulas, into the demographic tables obtained by other authors (for example, Lack, 1954; Onno, 1967), we will see an even greater correspondence with the real results than the authors mentioned did.

While the average mortality rate is calculated only on the basis of the mathematical equation without the use of statistics, we use the conventional statistical formula for the standard error of the mortality rate (Haldane, 1955; Paevskii, 1985):

$$E_M = M\sqrt{\frac{1 - M}{N}},$$

where E_M is the standard error of the mortality rate, M is the average annual mortality rate, and N is the total number of birds from which recoveries have been received. The use of the standard error obtained by the statistical method is necessary so that the average mortality rate will more adequately correspond to the amount of available data (the size of the group of birds considered).

It is not necessary that recoveries be obtained from birds that were ringed in the same year. Birds can be born in different seasons, and in this case, they are considered as members of the same age cohort (Paevskii, 1985). The same principle was used by the developers in the MARK program.

ILLUSTRATION OF THE METHOD FOR CALCULATION OF THE MORTALITY RATE

In order to show the features and advantages of the method, several examples must be considered. For example, we will use ring recoveries for the pintail (*Anas acuta*) and Siberian eider (*Polysticta stelleri*) from the Ringing Center database. For the pintail, there are only 7183 ring recoveries in the database at the moment, the death of birds was recorded in 6728 cases, and the date of this death is known. Out of the 12 models proposed in the MARK program (we are still considering the version of the early 2000s, and the problems of later versions will be mentioned below), the smallest value of the AIC criterion with the smallest deltaAIC = 0 belongs to the model designated as Log 2ndPart. If we calculate the average survival rate based on this model, we get $S = 4.38613$, $M = -3.38613$. It turns out that the survival and mortality rates are more than one; moreover, the mortality rate is negative. It is quite obvious that the "best" model gives pure nonsense. Trying to eliminate this nonsense, we look in the results file of the program, in the "Real Function Parameters" column and see that the survival rate is 43.227799 during approximately two years out of the 23 years of life of the ducks considered. It is clear that these years cannot be used. Thus, we have to use an intentional trick; we remove these two values from the calculation of the average survival rate. The model also presents difficulties as regards the number of the parameters, but we will not consider them in detail, the difficulty mentioned is quite "sufficient." As soon as we remove these two values from the calculation of the mean, we get a quite acceptable value of the survival rate $S = 0.686923$ and mortality rate $M = 0.313077$, or 31.31%.

Now we calculate the mortality rate with the help of the above-presented formula of geometric progression. We get the result $M = 0.3184$, or 31.84%. In this case, we need to know only three values: the total number of recoveries, the number of years over which all the birds have died, and the number of birds that remained alive in the last year of receiving recoveries after ringing. There is no need for a complex input file, which is used in the MARK program; it is not necessary to apply any intentional tricks. The difference between the method proposed here and the "best" model from the MARK is somewhat more than half of a percent, 0.53%. Given the low accuracy of the original data, there is no way to understand what value reflects the most real mortality rate. Both values are very close, which means that the level of accuracy can be considered approximately equal. This comparison shows that there is no need to take the complex way of calculation through the MARK program; the geometric progression method is quite sufficient.

After the above example with the pintail, it can be decided that, in case of using the MARK program, it is sufficient to remove the obvious incorrect values and continue calculating the survival rate through the MARK program. Unfortunately, this is not the case. The following example with the recoveries of Siberian eider rings shows that we must use even more tricks. For the Siberian eider (431 recoveries from dead birds, but the date of death is known), the same Log 2nd Part model appears the best. The resulting model file gives 22 values of the survival rate, indicating that 20 values are used, but not saying which exactly. Let us try to guess. The survival rate in one of these 22 years (S = 432.67820) is obviously nonsense, and this value must be excluded from further calculations. To obtain the average survival rate, it is necessary to remove one more value, but it is not clear which value, since all other values do not exceed the unit. In the output file, one of the survival values is, on the contrary, too small to be real. Here we have to perform the second intentional action: to remove the value that is too small. Only after that do we get an acceptable value of the mortality rate: $M = 25.65\%$. The geometric progression method gives us $M = 25.09 \pm 1.05\%$ without any tricks. The difference in the mean values obtained is again small, 0.56%, and is within the standard error. The geometric progression method has made it possible to obtain the value of the average annual mortality rate in a simple way, without resorting to tricks.

Unfortunately, these are not just problems for the MARK program. Not only the values of the AIC and deltaAIC criteria, but also the number of parameters in the used models in a number of cases depend on the order in which we test the models. Although this obvious programming problem has been overcome in the subsequent versions of the MARK program, it should be borne in mind that each version exists for several years, and the results of the analysis based on these versions are used in the articles published. So, is it inevitably necessary to review the previous calculations each time as new versions of the program appear? Nonetheless, the new versions of the program are not necessarily better than the old ones. The new versions can eliminate some problems, but often create new ones. For example, in version 8 of the MARK program (after 2008), the mortality rate that is obtained based on the same 6728 recoveries of pintail rings and using the same "best" model is not 31.31%, but 37.15%! The difference is very serious. A practicing ornithologist cannot figure this out in the overwhelming majority of cases. Therefore, he often has to delegate completely the work of calculating the mortality rate to a recognized narrowly focused specialist in this field, who, in addition to objective criteria, uses his subjective experience in choosing a suitable model. Then, of course, this specialist becomes a coauthor of the article, which we observe on a mass scale in the publications of American ornithologists.

To give more evidence for the suitability of our method, we will make one more comparison of the results from calculating the mortality rate in the MARK program and by the geometric progression method. We will not use the "best" model that requires intentional actions to remove invalid and other inconvenient values, but we will use the models that do not produce values, which require an exception from the calculations. Even in these cases, it turns out that the results from calculating the mortality rate by the geometric progression method are often very close to the results obtained using one of the MARK program models (Table 1). This means that among the MARK program models there is at least one model that produces almost the same result as our geometric progression method. As a result, we have gathered a lot of evidence showing that the geometric progression method is much easier to use to calculate the average mortality rate than the calculation using the MARK program. Moreover, the accuracy of the proposed method is no less than the accuracy of this program.

ASSESSMENT OF THE STATUS OF A POPULATION

The above-described method for calculating the average mortality rate for bird populations is not only easy to apply, but is also suitable for assessing the status or degree of success of a population. To carry out such an assessment, we must compare the theoretical and real mortality rates of any cohort of birds (species, population, group of birds of the same sex, group of birds that were ringed in a certain place, etc.) for different years, i.e., to estimate the variation of these values in time. A graphic representation of these changes will be called a mortality pattern.

Based on the average annual mortality rate calculated by the geometric progression method, we obtain the curve of the theoretical mortality rate for different years. This procedure allows one to obtain the number of birds that must theoretically remain alive in each particular year after ringing. The equation for this procedure is quite obvious:

$$Y = NS^x,$$

Table 1. Comparison of the average mortality values that were obtained by the geometric progression method and using the models that are proposed in the MARK program

Species	Number of used ring recoveries	Average mortality rate calculated by the geometric progression method ($X \pm SE$), %	Mortality value according to the MARK program that is the closest to the value obtained by the geometric progression method, %. The name of the model is indicated in parentheses	Difference between the mortality values according to the MARK program and the values obtained by the geometric progression method, %
Wigeon (*Anas penelope*)	3026	20.47 ± 0.33	20.93 (CLogLog_2ndPart)	0.46
Gadwall (*A. strepera*)	639	26.48 ± 0.90	26.41 (CLogLog_2ndPart)	0.07
Pintail (*A. acuta*)	6728	31.84 ± 0.32	30.20 (CLogLog_2ndPart)	1.64
Mallard (*A. platyrhynchos*)	6635	27.82 ± 0.29	28.35 (CLogLog 2ndPart)	0.54
Garganey (*A. querquedula*)	5010	30.44 ± 0.67	29.60 (Sin_2ndPart)	0.84
Common shoveler (*A. clypeata*)	1273	28.86 ± 0.68	29.39 (CLogLog_2ndPart)	0.53
Common pochard (*Aythya ferina*)	2358	29.74 ± 0.51	29.25 (CLogLog_2ndPart)	0.49
Tufted duck (*Ay. fuligula*)	3388	26.00 ± 0.38	26.77 (Sin_2ndPart)	0.77

where N is the number of birds in the cohort under consideration, S is the average annual survival rate, x is the number of years after ringing, and Y is the number of birds that are alive in the x-th year after ringing.

On the other hand, the actual number of live birds for each year of the study can be obtained from the database. The mortality pattern can be visualized on the chart (the pintail as an example, Fig. 1).

The reliability of the differences between the theoretical and real values of the mortality rate for different years can be determined by the standard criterion χ^2. To compose the mortality pattern, the number of years of bird life is calculated as the number of years between the date of ringing and the date of bird death. Throughout the world, the ringing centers customarily estimate the bird life span in days (the elapsed time). Therefore, the number of years of bird life can easily be calculated by dividing the number of days of bird life by 365 (the number of days in a year). All this can easily be done in a computer program that builds the mortality pattern on a computer screen. The input file for this program is a text file, in which the columns contain the data on the life span for each bird in years. It is not difficult to get such a file by exporting from the database. This does not require special additional training, which is necessary for preparing the input file of the MARK program.

The mortality pattern obtained in this way also allows us to assess the status of a population. Comparison of the mortality patterns for different bird species with the information on the degree of success of a species or population, which was obtained in a different way (for example, during counting the abundance in nature), has made it possible to observe the following regularity. If it is known that the status of a species is good and that its population was stable during ringing and receiving recoveries, then the theoretical mortality curve will pass very close to the tops of the bars of the real mortality histogram. In this case, the difference between the real and theoretical number of surviving birds according to the criterion χ^2 will be insignificant, and in a number of clearer cases the theoretical and real mortality patterns will not significantly differ. An example is the status of the Atlantic population of the brent goose (*Branta bernicla bernicla*) (Fig. 2a). According to other studies, it is known that the status of this subspecies was stable while ring recoveries were collected to construct this mortality pattern (Fox et al., 2010). If the bars that reflect the real mortality rate in the chart are located above the theoretical mortality line, this means that the species or population under consideration is in a good state, and its abun-

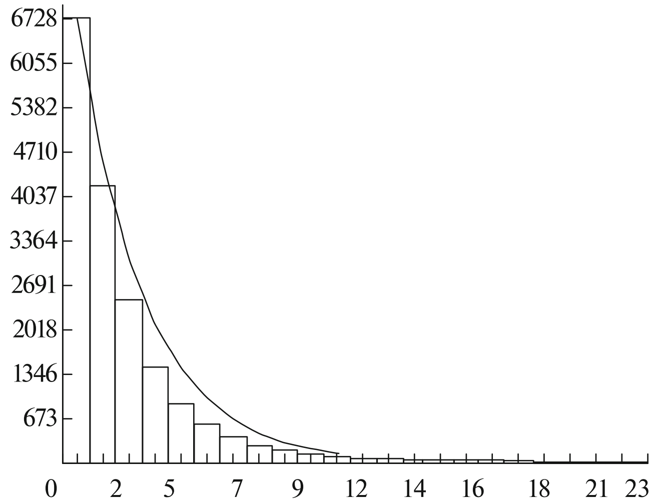

Fig. 1. Mortality pattern of the pintail according to the ring-recovery data. The number of birds that remained alive in different years after ringing is plotted on the *Y*-axis. The number of years that elapsed after ringing is plotted on the *X*-axis. The exponent line shows the theoretical number of surviving birds, which was calculated by the geometric progression method. The histogram shows the actual annual number of surviving birds.

dance is increasing. This is observed in the Pacific brent goose (*B. b. nigricans*) and barnacle goose (*B. leucopsis*) (Figs. 2b, 2c). According to the data for the Pacific brent goose, it is known that its abundance is actually growing (Dau and Ward, 2009; Christian Dau, personal communication). The population of the barnacle goose has grown from several tens of thousands in the middle of the 20th century to almost half a million and continues to grow (*Polevoi opredelitel' guseobraznykh*..., 2011).

It has turned out that the form of the mortality pattern sometimes makes it possible to understand the internal source of success of a population. If the bars reflecting the number of surviving birds in the first years after ringing are above the theoretical curve, this logically means that the population growth is due to the contribution of younger birds to productivity (the Pacific brent goose, Fig. 2b). If the actual number of surviving birds exceeds the corresponding values of the theoretical curve in later years after ringing, this means that the main contribution to success of the population is made by older birds (the barnacle goose, Fig. 2c). If the tops of the bars showing the actual number of surviving birds in a whole series of years after ringing are significantly below than the theoretical curve, especially if this "deflection" of the histogram is more pronounced for the first years after ringing (i.e., for younger birds), this indicates that the species or population under consideration is in a poor state and is decreasing in numbers.

In order to assess the status of a population more accurately, it is sometimes necessary to use the standard statistical method to remove strongly deviating variants. The fact is that in some species there are very long-lived individuals. Their age exceeds the maximum age of the majority of birds by many years. Therefore, when we are trying to make a conclusion about the status of a population on the basis of the mortality pattern, we require that these very long-liv-

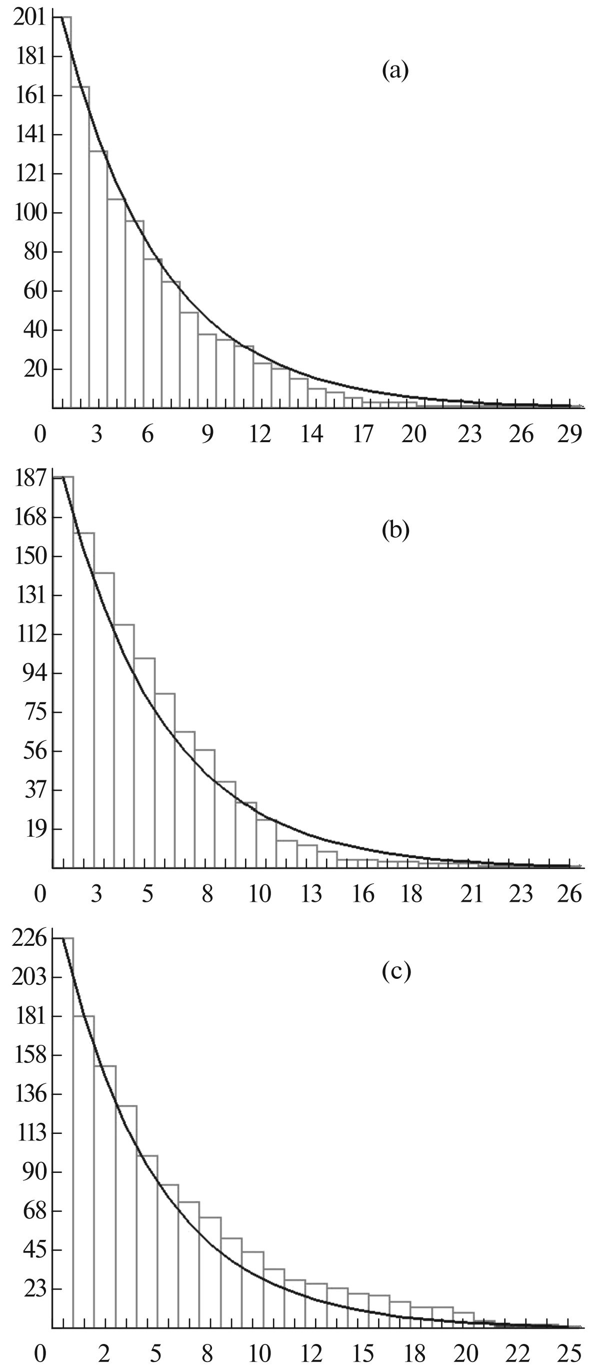

Fig. 2. Mortality patterns of the (a) Atlantic brent goose, (b) Pacific brent goose, and (c) Barnacle goose according to the ring-recovery data. The designations are the same as in Fig. 1.

Table 2. Population characteristics of spoonbills for decades

Decade	Total number of ring recoveries from dead spoonbills (*N*)	Average mortality rate for spoonbills ($X \pm SE$), %	Proportion of shot spoonbills in the total number of ring recoveries, %	Average age of all dead ($X \pm SE$), years
1950–1959	28	56.54 ± 7.05	82.1	0.48 ± 0.16
1960–1969	54	32.90 ± 3.67	87.0	1.15 ± 0.30
1970–1979	55	23.45 ± 2.77	52.7	1.03 ± 0.28
1980–1989	26	20.77 ± 3.63	30.8	3.46 ± 0.67

ing birds be temporarily excluded from the sample. An example is the famous oldest male tufted duck that lived 44 years. The closest oldest bird from the rest of the sample lived fewer than 27 years (the Ringing Center database). The second value is much closer to all the other ducks under consideration. If we leave this long-living individual in the sample, the mortality pattern will have a large deflection of the histogram, which will give a false conclusion about the catastrophic decrease in the abundance of tufted ducks. Excluding this deviating variant, we get a more realistic estimate: the status of the tufted duck population is fairly stable, which is more in line with reality (*Polevoi opredelitel' guseobraznykh*…., 2011).

A good example of applying this method to determine the average mortality rate and assess the status of a population is the results from processing the ring-recovery data for the spoonbill (*Platalea leucorodia*). This method has made it possible to assess the status of the spoonbill population within territory of the former Soviet Union for a number of decades of the 20th century and also to explain the causes of the past poor and present relatively good status of the population of this species. It is known that in the middle of the last century the number of spoonbills decreased everywhere, but since 1980 it began to grow slightly in Europe, including Ukraine, the Trans-Volga region, as well as the Trans-Urals region (Belik, 2011). The real reason for the change in the abundance dynamics of populations remained unknown. Possible causes were supposedly mentioned for explanation: bird protection and warming and humidification of the climate, which improved the forage base, prolonged the nesting period, and increased reproductive success due to repeated breeding attempts (Belik, 2011). However, this growth did not cover all regions of Russia and nearby countries. The abundance of spoonbills in Dagestan, Kazakhstan, and Uzbekistan continued to decline. However, the reasons were not analyzed. The construction of mortality patterns of spoonbills for different periods of the 20th century on the basis of the geometric progression method proposed here has made it possible to assess the status of the spoonbill population and to answer the question about the causes of the improvement of this status more definitively.

In total, the Ringing Center database contains data on 189 ring recoveries from spoonbills, 168 of them were received from dead birds. Meanwhile, 163 recoveries fall on the period 1950–1989. This concentration of recoveries allows us to divide the data into four decades. Due to the fact that the last year of a relatively mass recovery is 1989, and the next recovery was only in 2014, we will divide the years by decades not in the traditional way, i.e., from the 1st year to the 10th one, but from the zero year to the 9th year.

The average annual mortality of all spoonbills during the entire ringing period was 22.60 ± 1.53%. However, the difference over decades is very significant (Table 2). In addition, while for the first three decades the difference in theoretical and real mortality rates is significant, for the period 1980–1989 both mortality values almost coincide: $p = 0.91$, which is very close to the conclusion "they are significantly not different" (Fig. 3).

The mortality patterns of spoonbills for decades that are given in Fig. 3 show the following. In the 1950s, the state of the species was bad; this ratio of real and theoretical mortality rates indicates a decrease in abundance of the species. In the 1960s, the state of the species was also bad, although the maximum life span increased. In the 1970s, the state of the species was also not very good, although the maximum life span had become even greater. Finally, in the 1980s, the mortality pattern began to show that the state of the species had become stable. We emphasize once again that, although in some populations there was still a tendency towards a decrease in abundance, it is only in the 1980s when growth began for the greater part of the population in Russia and adjacent territories, which is indicated, in particular, by the mortality pattern. Since growth did not begin for all species populations, the mortality pattern shows only "stability."

The reason for the change in the status of the population is easy to understand if we compare the finding conditions for birds for decades. In the 1950s and 1960s, more than 80% of spoonbills were shot by people (Table 2). In the 1970s, the percentage of shot birds decreased, and the 1980s, it fell even more (Table 2). Obviously, the spoonbill has long been considered a "harmful" bird that eats fish. When public opinion

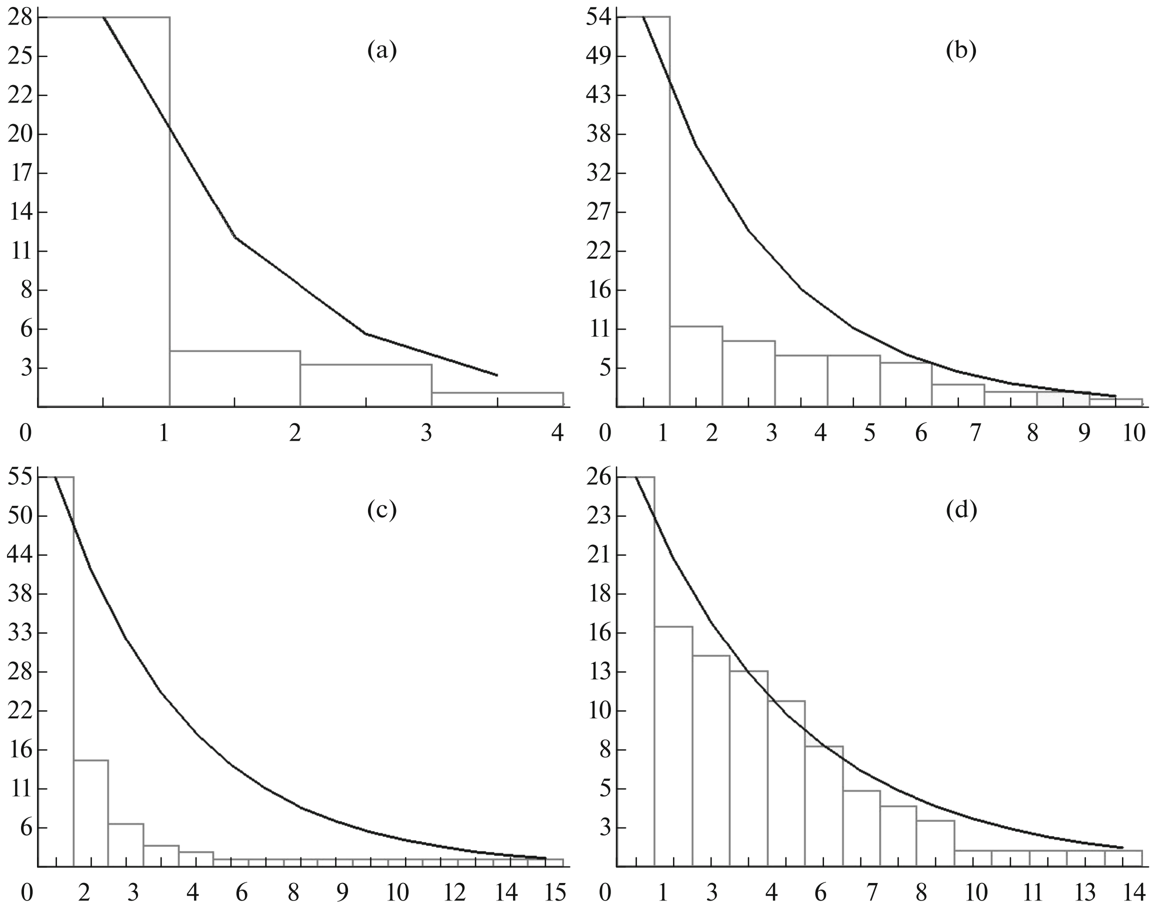

Fig. 3. Mortality patterns of the spoonbill for decades: (a) 1950–1959; (b) 1960–1969; (c) 1970–1979; (d) 1980–1989 according to the ring-recovery data. The designations are the same as in Fig. 1.

began to change, and, accordingly, shooting was reduced, the number of spoonbills began to grow. For the most part, the birds shot were young. While the average age of dead spoonbills in the 1950s was about half a year and in the 1960s and 1970s it barely exceeded a year, in the 1980s it sharply increased to three and a half years (Table 2) and, according to the Bailey criterion (Plokhinskii), 1978), it began to differ from the indicator of the previous decade with a high reliability ($p = 0.002$). The increase in life span led, in particular, to the spoonbills "obtaining" a larger number of breeding individuals, and their abundance went up.

THE AREA OF APPLICATION OF THE GEOMETRICAL PROGRESSION METHOD

In summarizing the proposed approach for estimating mortality, it is necessary to emphasize the following: if we use only ring-recovery data for this estimate, then the recovery rate in different regions of Russia and in other countries fluctuates to a large extent (the data of the Ringing Center). For the MARK program, this proportion is assumed to be constant, whereas in the geometric progression method the constancy of this value does not matter. Therefore, it makes no sense to use more complex models, if we can get almost the same result with a simpler model. It also makes no sense to use complicated models for another reason: in real natural conditions, we cannot assess a number of important factors affecting the ring recovery from birds. Therefore, the process of choosing a suitable model in many cases looks like "looks like gambling" (Rinne et al., 1999).

For the case when we are forced to rely only on ring recoveries, the model constructed on the basis of geometric progression is much simpler than the totality of the stochastic models that are presented in the MARK program. Moreover, the model proposed here not only allows calculating the survival and mortality rates, but also gives an idea of the degree of success of a population. There is no guarantee that the generally accepted more complex method yields more accurate results than the simpler method. Based on the arguments presented here, we suggest that the geometric progression method should be widely used in studies based on ring recoveries.

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