

# Speed of Bird Migratory Movements as an Adaptive Behavior

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**Abstract**—The migration speed of 115 bird species from 35 families of 14 orders has been analyzed on the basis of ring recovery data from published sources. The results show that the average speed varies between 10 and 880 km/day and the maximum speed varies between 30 and 1392 km/day, but the respective values in the majority of species fall within the ranges of 20–100 and 40–360 km/day. There is a significant positive correlation between the average and maximum speed values. The ratio between them varies significantly between the species, with the overall average ratio being 4 : 1. On average, shorebirds migrate twice as rapidly as passerines, and the average migration speed in birds of prey is slightly higher than in shorebirds. Species of the family Turdidae migrate significantly faster than species of the family Fringillidae, and the latter migrate faster than the Paridae. No significant differences in migration speed have been revealed between the Sylviidae and Turdidae as well as between the Sylviidae and Motacillidae species. The average migration speed in shorebirds shows a significant negative correlation with body mass, but no such correlation is observed in the passerines. In many species, adult birds migrate significantly faster than juveniles, while male and female birds do not differ in this parameter. The average migration speed of passerines is significantly higher among long-distance early-departing nocturnal migrants than in short-distance late-departing diurnal migrants. In some species, the spring migration speed is much higher than the autumn speed. The behavior of migrants in flight and at stopovers is governed by complex interactions between their species-specific foraging habits, weather parameters, and habitat conditions.

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## INTRODUCTION

Seasonal migrations of birds inhabiting areas with regular changes in environmental conditions, i.e., their annual movements from breeding to wintering grounds and back, have been studied fairly well, and their adaptive nature is apparent (Dorst, 1962; Berthold, 1993; Alerstam et al., 2003). However, the distances and strategies of these seasonal movements widely vary among species and populations. The obvious advantage offered by migrations is that they improve chances for birds to survive between breeding seasons. It hence follows that the whole complex of migrational adaptations is aimed exactly at providing for the survival of birds under variable and often unpredictable conditions along their entire migration route. The set of characters and processes contributing to adaptation to migrations, also referred to as the migratory syndrome, includes modifications in bird morphology, orientation and navigation capacities, and regulation of behavior toward a wide range of ecological factors.

During migrations of most birds, the periods of flight alternate with stopovers, which the birds must make in order to rest and forage (except for swallows and swifts, which can forage while flying). The study of bird migrations has long history, but it is only in the past two decades that researchers have paid due attention to stopovers. Their role in migration success is

very important, considering that migrating birds spend much more time at stopover sites, where they restore their energy reserves, than in flight: the corresponding time ratio in passerine songbirds reaches 7 : 1 (Newton, 2008) or even 9 : 1 (Chernetsov, 2012). Both these mutually exclusive forms of behavior should be taken into account while evaluating migration speed and time. Flight over unfamiliar or altered areas is associated with energy expenditures and risks, which can be minimized if migration is accomplished within the shortest possible time. Moreover, the time spent for migration can restrict the periods of breeding and molting. Thus, the duration of the migration process is a factor that limits the distance of bird movement and, consequently, the geographic distribution of species (Newton, 2008).

Quantitative relationships between the parameters of migration having an energy component (e.g., the rates of accumulation and expenditure of body reserves, primarily subcutaneous fat, and the duration of stopovers) and the time expended to cover the entire migration route have provided a basis for the so-called optimal migration theory (Alerstam and Lindström, 1990). Its basic principle is that migratory habits of different species or groups of birds are adapted so as to minimize time and energy expenditures and the risk of mortality from predation during migration. As shown in recent studies, the speed of migration can indeed

have a major selective significance, because saving time on seasonal movements provides for optimization of the entire annual life cycle of birds (McNamara et al., 1998; Alerstam, 2003). On the whole, the optimal migration theory assumes minimization of time expenditures to be the general strategy of migration. In nature, the speed of migration (usually measured in kilometers per day) depends on a complex group of factors, including weather conditions, bird's position along the migration route, the possibility of selecting an adequate biotope for a stopover, the amount of food supply in this biotope, stopover duration, the rate of energy reserve accumulation, competition, and flight speed. Many of these aspects of migratory behavior are ignored in the optimal migration theory, which makes it at least incomplete for deriving actual quantitative relationships allowing a comprehensive analysis of migration adaptations (Chernetsov, 2012).

All the aforesaid shows that analysis of the speed of migratory movements is an essential aspect of research into details of seasonal bird migrations. Migration can be accelerated via an increase in flight speed, but the rate of energy expenditure also drastically increases in this case. This is why all more or less distant migrations typically proceed in several stages with stopovers between them.

Many publications on bird migrations contain factual data on the speed of migratory movements of individual species (Hilden and Saurola, 1982; Ellegren, 1993; Fransson, 1995; Hedenström and Alerstam, 1998; Shamoun-Baranes et al., 2003; Nowakowski and Chruściel, 2004; Payevsky et al., 2004; Newton, 2008; Hedenström, 2008; Bojarinova et al., 2008; Yohannes et al., 2009; Payevsky, 2010; etc.). Nevertheless, none of published studies, except one by Hilden and Saurola (1982) containing information on 51 bird species, provide factual data on the migration speeds of birds from different orders, families, genera, and species that have been compiled for comparative analysis. This has been the main reason to collect the maximum possible amount of reliable empirical data on the migration speed of different birds, to analyze them with regard to previous relevant publications, and, in this context, to discuss all aspects of differences in the speed of movement among seasonally migrating birds.

The main purpose of this study was to elucidate the adaptive significance of the behavior accounting for a certain speed of migratory movement. To this end, it was necessary to analyze differences in the migration speed among birds of various taxonomic groups differing in body size and ecological features, in particular, diurnal vs. nocturnal, long-distance vs. short-distance, and regular vs. irregular (invasive) migrants.

## MATERIALS AND METHODS

There are various methods for determining the speed of bird migration, from analysis of ring recovery data (Hilden and Saurola, 1982; Ellegren, 1993;

Fransson, 1995; etc.) to radar tracking and telemetry (Bloch and Bruderer, 1982; Sokolov, 2011). Some of these methods are empirical, while others are based on theoretical estimates, but any of them have problems with the accuracy of measurements and can be used if certain conditions are met (Newton, 2008).

One of the most widespread methods is based on recaptures of ringed birds during the migration season. A possible source of errors in this case is in the impossibility of precisely determining the response of each ringed and released bird to the very process of trapping and ringing, i.e., whether the speed of its movement is retarded, accelerated, or remains unchanged after release. Moreover, specialists often take into account the earliest recaptures (ring recoveries) indicative of the highest possible migration speed, e.g., recoveries on the second day after ringing, thereby ignoring the possible stopover time; as a result, the migration speed may be overestimated. Nevertheless, such estimates are more reliable than any others, provided the number of ring recoveries is sufficiently large and data used for calculations satisfy certain criteria (Hilden and Saurola, 1982), which are as follows: (1) the dates of ringing and recovery are within the normal migration period of a given species, (2) the time interval between ringing and recovery does not exceed 50 days, (3) the recovery site is located south of the west–east axis passing through the ringing site, (4) the distance between the ringing and recovery sites is greater than 50 km, (5) the circumstances of ring recovery indicate that the bird was living or had died very recently, and (6) the estimated migration speed exceeds 10 km/day.

The average migration speed can be estimated in two ways. The first way is to calculate its individual values by dividing the distance between the ringing and ring recovery sites ( $D$ , km) by the time elapsed after ringing ( $t$ , days) and then averaging the results by dividing their sum by the number of recoveries:  $(\Sigma D/t)/n$ . Thus, all ring recoveries are assigned equal weights, irrespective of the time interval between ringing and recovery, which may result in an overestimate if the number of recoveries after a minimum time interval is large. The second way is to sum up the distances covered by each bird and individual time intervals between ringing and ring recovery and to divide the first sum by the second:  $\Sigma D/\Sigma t$ . In this case, the estimated average speed depends more strongly on the proportion of ring recoveries after a long time interval and may be underestimated. However, the values calculated in the two ways may differ significantly only when there is a large proportion of birds that have managed to cover very long distances within a few days.

The speed of bird movement differs depending on the landscape below, and, theoretically, the average speed depends on how many and what kinds of landscapes the bird has crossed. However, it is impossible to take a detailed account of this parameter for different species, and records are usually made only of the

total distance covered by the birds. As for the maximum migration speed, it is considered to be equal to the highest speed ever demonstrated by a bird of a given species.

The speed of migration can also be estimated by comparing the times of bird arrival to different points on their migration route, i.e., the times when the birds of interest leave one region and appear in another region. The main problem here is uncertainty as to whether observations are performed on one and the same population. Moreover, young birds in autumn are always relatively more abundant than adults but migrate less rapidly; therefore, the calculated average speed is generally lower than the actual speed. Since individual departure and arrival dates are highly variable, the calculated average dates are not always reliable. Nevertheless, studies on migrations of the Bluethroat (*Luscinia svecica*) have shown that the above method is adequate for estimating the migration speed (Ellegren, 1990).

The most reliable data on the migration speed can be obtained by tagging the birds with transmitters of various types, from locally operating devices to satellite transmitters with a long service life. The results of telemetry (primarily of satellite telemetry) sometimes provide a basis for radically revising traditional views on the routes and speed of bird migration (Sokolov, 2011). It should be noted, however, that the their reliability is based on the assumption that transmitter tagging itself does not alter the migratory habits of the bird.

The above methods do not take into account the preparatory period when a migrant bird builds up its body energy reserves while still in the breeding range, which, strictly speaking, is also part of migration (Newton, 2008).

Theoretical approaches allowing the migration speed to be estimated are based on available data on flight speed and rates of energy reserve accumulation and expenditure. For a small-sized bird with flapping flight and an energy accumulation rate of  $1 \times \text{BMR}$  (basal metabolic rate, the daily amount of energy expended at rest in the thermoneutral zone, kcal/day), the average migration speed calculated in this way, taking into account both periods of active flight and stopovers, reached approximately 200 km/day (Hedenström and Ålerstam, 1998).

The factual data on the speeds of migratory movements, compiled from different published sources, are presented in the table. They are based mainly on ring recoveries during the migration season and calculated by the first method (see above). In cases when the data were taken from bird ringing reports (Payevsky, 1973; Noskov and Rezvyi, 1995; Bolshakov et al., 2001), calculations were made by the author. Data on bird body masses were taken from handbooks (Vinogradova et al., 1976; Dunning, 2008); when males and females significantly differed in this parameter, the average

value was taken. All data were processed statistically using the Statistica 8 program package.

## RESULTS AND DISCUSSION

### *Maximum and Average Migration Speeds*

As follows from the data on the speed of migratory movements of 115 bird species from 35 families and 14 orders (table), its maximum values vary from 30 km/day in the Squacco Heron (*Ardeola ralloides*) to 1392 km/day in the Common Sandpiper (*Actitis hypoleucos*), and average values vary from 10–28 km/day in two tit species, the Willow Tit (*Parus montanus*) and Blue Tit (*P. caeruleus*), to 880 km/day in the Gray-headed Albatross (*Thalassarche chrysostoma*).

The distributions of average and maximum speed values (Fig. 1) significantly differ from normal (Kolmogorov–Smirnov test,  $d = 0.215$ ,  $p < 0.01$  and  $d = 0.232$ ,  $p < 0.01$ ; chi-square test,  $\chi^2 = 44.6$ ,  $p < 0.01$  and  $\chi^2 = 115.6$ ,  $p < 0.01$ , respectively) and approach the Rayleigh distribution, which approximates moderately asymmetrical variation series. Such a distribution pattern is determined primarily by one of the criteria for the calculation method (Hilden and Saurola, 1982), namely, that only speeds over 10 km/day are included in analysis. Apparently, migration at a lower speed rarely or never takes place in the majority of bird species, because such a slow movement cannot ensure the timely arrival to the wintering grounds.

The histograms in Fig. 1 show that the average and maximum migration speeds in most species fall within the ranges of 20–100 and 40–360 km/day, respectively. The maximum-to-average speed ratio varies between the species from 1.3 : 1 in the Whinchat (*Saxicola rubetra*) to 12.5 : 1 in the Song Thrush (*Turdus philomelos*), averaging 4 : 1 in the total sample. The available data are indicative of a definite moderate correlation (determination coefficient  $R^2 = 0.43$ ) between the average and maximum speed values (Fig. 2), which is evidence for the reliability of the initial factual data on the speed of migratory movements.

### *Differences in Migration Speed between Taxonomic Groups of Birds*

To find out whether the daily speed of migratory movements differs between taxonomic groups of birds, analysis for this parameter was performed in three groups—birds of prey, shorebirds, and passerines—for which a sufficient amount of relevant data were available. The average migration speed was estimated at  $132.2 \pm 20.9$  km/day in birds of prey,  $116.5 \pm 15.5$  km/day in shorebirds, and  $56.4 \pm 3.0$  km/day in passerines, with the differences being statistically significant according to Kruskal–Wallis test ( $\chi^2 = 10.88$ ,  $df = 2$ ,  $p = 0.004$ ). Indeed, the migration speed of shorebirds proved to be twice higher than in passerines but slightly lower than in birds of prey. Previous estimates (Ålerstam and Lindström, 1990; Newton, 2008)

## Speed of bird migratory movements according to ring recovery data

Group, species	Average body mass, g	Season: (a) autumn, (s) spring	Speed, km/day		Source*
			limits or maximum value	average value ( <i>n</i> )	
Grebes					
<i>Podiceps nigricollis</i>	398	a	42		3
<i>P. auritus</i>	453	a	136	59 (7)	3
<i>P. cristatus</i>	674	a	69		7
Albatrosses, shearwaters					
<i>Diomedea nigripes</i>	3195	a	73		3
<i>Puffinus tenuirostris</i>	559	a	167		3
<i>Thalassarche chrysostoma</i>	3508			880	22
Hérons					
<i>Nycticorax nycticorax</i>	810	a	28–40		3
<i>Ardeola ralloides</i>	287	a	20–30		3
Storks					
<i>Ciconia ciconia</i>	3448	a	42–62	54	1, 4
<i>C. nigra</i>	2926	a	113		1
Ducks					
<i>Cygnus columbianus</i>	6750	s		26	21
<i>Anas platyrhynchos</i>	1082	a, s	27–123		1, 7, 23
<i>A. crecca</i>	306	a	26–120	62 (12)	7, 23
		s	37–77		7
<i>A. querquedula</i>	326	s	165–658	329	26
		a	33–120		7
<i>A. penelope</i>	772	a	58		7
<i>Aix galericulata</i>	570	a	901		24
<i>Ay thyaferina</i>	823	a	25		1
<i>A. fuligula</i>	702	a	31		1
Birds of prey					
<i>Pandion haliaetus</i>	1486	a	90, 150–746	59, 174	6, 27
<i>Pernis apivorus</i>	758	a	255	163	21, 23
<i>Aquila pomarina</i>	1370	a		133	21
<i>Circus macrourus</i>	389	s	134		6
<i>C. aeruginosus</i>	712		36–82		6
<i>Accipiter nisus</i>	238	a	20–224	48(19), 46(50)	6, 7, 23
<i>Buteo swainsoni</i>	959	a, s		188	21
<i>Falco columbarius</i>	191	a	70–177		14
<i>F. tinnunculus</i>	184	s	140–239		6
<i>F. peregrinus</i>	779	a		172	21
		s		198	21
Rails					
<i>Porzana porzana</i>	87		90		2
<i>Gallinula chloropus</i>	305	a	26–86		2
<i>Fulica atra</i>	836		59–263	150	1, 6
Shorebirds					
<i>Charadrius hiaticula</i>	64	a	80–459	102 (56)	2, 18, 23
<i>Ch. dubius</i>	39	a	83		2
<i>Vanellus vanellus</i>	219	a	23–173	70	2, 25
<i>Arenaria interpres</i>	136	a	913	103 (11)	2, 23
<i>Tringa glareola</i>	68	a	175–625	100 (50)	2, 23
<i>T. totanus</i>	129	a	215–362	94 (31)	23
<i>T. erythropus</i>	158	a	114–263	122 (6)	23
<i>Actitis hypoleucos</i>	48	a	51–1392	90 (15), 438	2, 19, 23
<i>Phalaropus lobatus</i>	37	a	122–355	201	2
<i>Philomachus pugnax</i>	136	s	160–757	71 (117)	23, 26
		a	16–64	32 (7)	7
<i>Calidris minuta</i>	21	a	400	137 (46)	23
<i>C. temminckii</i>	23	a	194		23
<i>C. ferruginea</i>	58	a	518	209 (9)	23
<i>C. alpina</i>	47	a	41–1023	115 (119), 209	23, 2
<i>C. canutus</i>	136	a	177	123 (6), 175	23, 21

Table. (Contd.)

Group, species	Average body mass, g	Season: (a) autumn, (s) spring	Speed, km/day		Source*
			limits or maximum value	average value (n)	
<i>Gallinago gallinago</i>	105	a	177	54 (16)	23
<i>Scolopax rusticola</i>	306	a	31–178	64 (6)	7, 14
<i>Numenius arquata</i>	806	a	119	46 (10)	23
Gulls					
<i>Larus fuscus</i>	715	a	102		23
<i>L. ridibundus</i>	284	a, s	26–277		7
<i>Sterna hirundo</i>	120	a	64		1
<i>S. paradisaea</i>	110	a	330	200	21, 32
		s	520		
Owls					
<i>Asio otus</i>	299	a	38–51		14
		s	58		14
<i>A. flammeus</i>	347	a	83		23
<i>Aegolius funereus</i>	134	a	199	31(22)	23
Pigeons, nightjars, swifts, rollers, and woodpeckers					
<i>Columba palumbus</i>	490	a	51		1
<i>Caprimulgus europaeus</i>	67		48		8
<i>Apus apus</i>	38	a		150	21
<i>Coracias garrulus</i>	146	a	96		1
<i>Merops apiaster</i>	57	s	520		16
<i>Upupa epops</i>	61	a	56		14
<i>Dendrocopos major</i>	82	a	13–53	25 (13)	23, 8, 14
Passerines					
<i>Hirundo rustica</i>	19	s	264		7
<i>Lullula arborea</i>	27	a	31–134	80 (5)	8, 14
<i>Anthus trivialis</i>	24	a	22–124, >200	79 (11), 71 (18), 57 (8)	20, 23, 15, 14
<i>A. pratensis</i>	17	a	27–177	60 (36), 71 (8), 57 (18)	8, 14, 23, 15
<i>Motacilla flava</i>	16	a	88–179	71 (11), 57 (101)	23, 15
		s	132		7
<i>M. alba</i>	20	a	62	42 (10)	15
<i>Lanius collurio</i>	29	a	74–303, >200	96 (6), 63 (25)	20, 23, 15
<i>L. excubitor</i>	67	a	97		23
<i>Sturnus vulgaris</i>	71	a	19–170	47 (31)	8, 14
<i>Garrulus glandarius</i>	156	a	19–649	61 (28)	14
<i>Nucifraga caryocatactes</i>	161	a	23–121	43 (12), 39 (9)	23, 14
<i>Bombycilla garrulus</i>	57	a	13–244	53 (62), 26 (15), 25 (6)	7, 23, 15, 14
<i>Troglodytes troglodytes</i>	9	a	49	29 (16)	15
<i>Prunella modularis</i>	18	a	49–72	52 (11), 35 (16)	7, 23, 15
<i>Acrocephalus scirpaceus</i>	12	a	45–142, >300	56 (10), 46 (383), 39 (85)	20, 23, 15, 12, 14
<i>A. schoenobaenus</i>	12	a	88–397	89 (8), 50 (114), 55 (31)	20, 23, 15, 12
<i>Sylvia nisoria</i>	24	a	144	92	15, 17
<i>S. atricapilla</i>	18	a	91	75 (6), 46 (32), 47 (38), 66 (54)	23, 15, 17
<i>S. borin</i>	19	a	65–330	102 (19), 58 (33), 62 (20), 93 (71)	7, 23, 15, 17, 14, 20
<i>S. communis</i>	14	a	153	55 (16), 58 (44), 75 (19)	23, 15, 17
<i>S. curruca</i>	12	a	84, >300	57 (12), 43 (16), 75 (10)	15, 17, 20
<i>Phylloscopus trochilus</i>	9	a	38–249, >300	84 (13), 85 (129), 62 (143), 71 (15)	23, 22, 5, 15, 14, 20
<i>Ph. collybita</i>	8	a	182	86 (14)	15
<i>Ph. sibilatrix</i>	9	a	82		14
		s	96		14
<i>Regulus regulus</i>	6	a	10–450	53 (61), 57 (154), 52 (279), 57	23, 15, 13, 21
<i>Ficedula hypoleuca</i>	12	a	141, >300	93 (12), 60 (19)	23, 15, 20
		s	32–148	80 (7)	14
<i>Muscicapa striata</i>	15	a	120	65 (20)	23, 15
<i>Phoenicurus phoenicurus</i>	14	a	141, >200	74 (35), 70 (50)	23, 15, 20
		s	162		8, 14

Table. (Contd.)

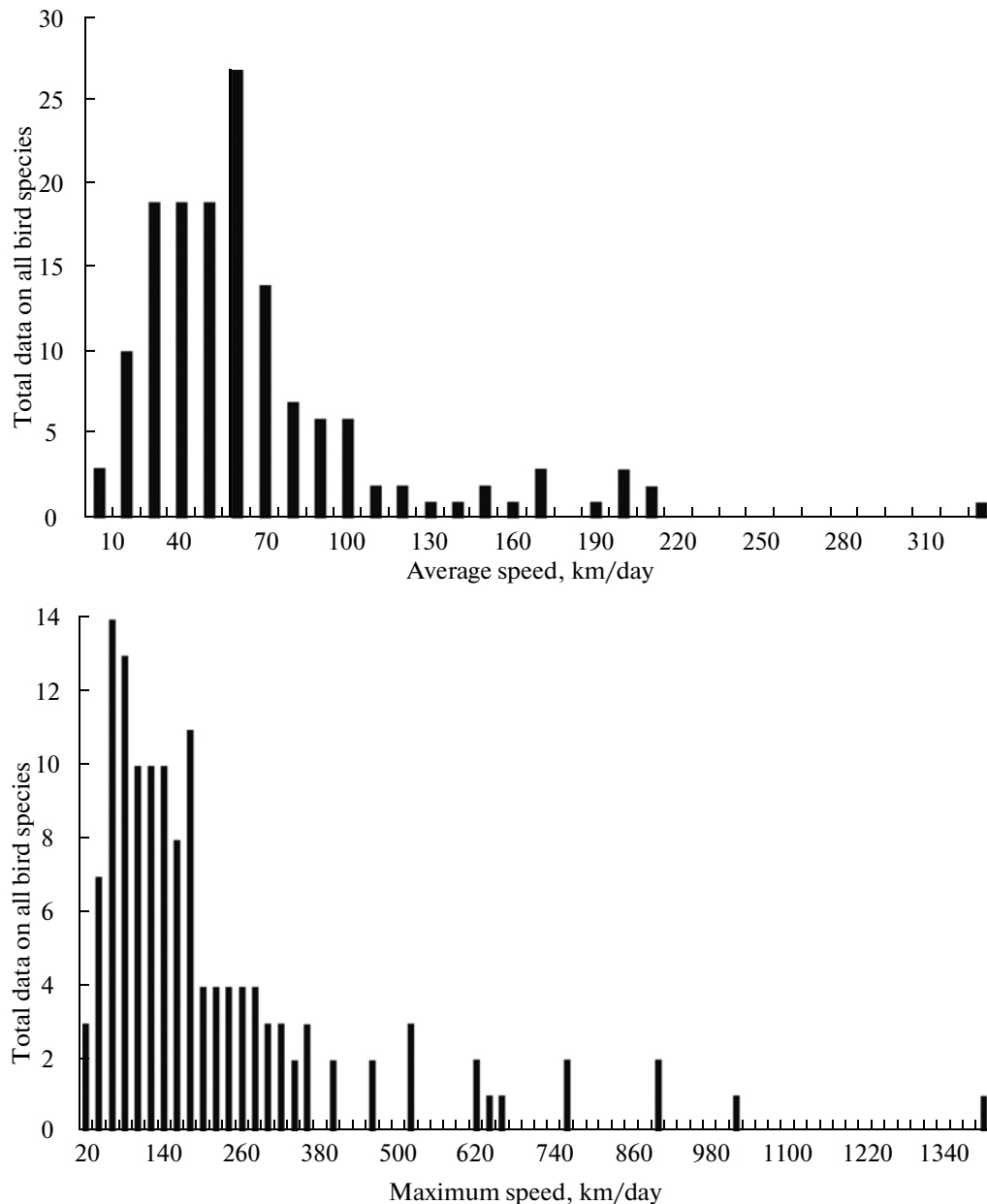
Group, species	Average body mass, g	Season: (a) autumn, (s) spring	Speed, km/day		Source*
			limits or maximum value	average value (n)	
<i>Erithacus rubecula</i>	16	a	5–168	60 (100), 56 (236), 58 (55)	23, 15, 10
		s	6–89	41 (21)	10
<i>Luscinia svecica</i>	16	a	161	41 (27)	15, 23
		s	89		7
<i>Saxicola rubetra</i>	15	a	103	81 (6)	23, 15, 7
<i>Oenanthe oenanthe</i>	22	a	263	110 (7)	23, 15
<i>Turdus pilaris</i>	96	a	23–55	33 (7)	9
<i>T. merula</i>	91	a	21–65	36 (5), 40 (22), 43 (18)	23, 15, 9
<i>T. philomelos</i>	65	a	23–762	67 (56), 61 (112), 69 (106)	23, 15, 9
<i>T. iliacus</i>	58	a	24–625	65 (41), 53 (41), 47 (31)	11, 23, 15, 9
<i>Aegithalos caudatus</i>	9	a	10–72	40 (28), 36 (33), 25 (80)	23, 7, 14
<i>Parus montanus</i>	11	a	14–34	10 (13), 23 (10)	23, 7
<i>P. ater</i>	9	a	10–122	33 (12), 31 (152)	23, 7, 14
<i>P. caeruleus</i>	11	a	11–122	12 (10), 17 (83), 28 (320), 27 (109)	23, 15, 29, 14
<i>P. major</i>	17	a	11–353	23 (20), 31 (31), 33 (981), 35 (215)	7, 28, 14
<i>Certhia familiaris</i>	9	a	100	32 (15)	23
<i>Fringilla coelebs</i>	22	a	20–285	63 (13), 54 (224)	23, 30
<i>F. montifringilla</i>	22	a	19–176	41 (9), 68 (7), 53 (43)	23, 7, 14
<i>Carduelis chloris</i>	30	a	24–110	29 (17), 45 (5)	15, 8, 14
<i>C. spinus</i>	13	a	20–145	59 (35), 40 (90), 52 (350)	23, 15, 14
		s	28–88		7
<i>C. carduelis</i>	17	a	25–66		14
<i>Acanthis flavirostris</i>	15	a	63	28 (10)	15
<i>A. flammea</i>	12	a	20–180	40 (27), 30 (23), 28 (9)	23, 15, 14
<i>Pyrrhula pyrrhula</i>	30	a	31–288	22 (12)	23, 7, 14
<i>Emberiza hortulana</i>	24	a	181, >200		23, 15, 20, 7, 14
<i>E. schoeniclus</i>	17	a	8–277	24, 59 (45), 34 (100)	31, 23, 15

Note: [1] Vaitkevicius and Skuodis, 1965; [2] Viksne and Mikhelson, 1985; [3] Kishchinskii, 1978; [4] Kishchinskii, 1979; [5] Lapshin, 1991; [6] Mikhelson and Viksne, 1982; [7] Noskov and Rezvyi, 1995; [8] Payevsky, 1973; [9] Payevsky et al., 2004; [10] Tsvei, 2008; [11] Barriety, 1966; [12] Bensch and Nielsen, 1999; [13] Bojarinova et al., 2008; [14] Bolshakov et al., 2001; [15] Ellegren, 1993; [16] Erard, 1968; [17] Fransson, 1995; [18] Glutz von Blotzheim et al., 1975; [19] Glutz von Blotzheim et al., 1977; [20] Hall-Karlsson and Fransson, 2008; [21] Hedenström, 2008; [22] Hedenström and Pettersson, 1987; [23] Hilden and Saurola, 1982; [24] Holgersen, 1963; [25] Imboden, 1974; [26] Jarry, 1970; [27] Kjellen et al., 2001; [28] Nowakowski, 2001; [29] Nowakowski and Chruściel, 2004; [30] Payevsky, 2010; [31] Stromar, 1971; [32] Egelvang et al., 2010.

also show that, on average, shorebirds migrate faster than passerines: a median of 79 km/day vs. 27–75 km/day in different groups. According to the above authors, the explanation to this difference is that, first, the flight of shorebirds is more rapid and, second, they fly at higher altitudes with a tailwind, which allows them to cover up to 1000 km within 1–2 days. In contrast, passerines fly lower and at a more even speed of up to 200–300 km/day. The results of our research generally agree with these data, but there are examples showing that passerines can also fly for several hundred kilometers per night. Thus, a phenomenally high migration speed was recorded for three Song Thrushes ringed in the Baltic region, which managed to cover 1861 km within

7 days, 2465 km within 8 days, and 1525 km within 2 days.

The most abundant data on the migration speeds of different species and populations of the same species are available for the order Passeriformes. Species-specific features in this respect have been revealed in each family of the order. Thus, the average migration speed is significantly higher in the Garden Warbler (*Sylvia borin*) than in the the Eurasian Reed Warbler (*Acrocephalus scirpaceus*),  $82 \pm 11$  vs.  $45 \pm 5$  km/day ( $t = 3.0$ ,  $df = 5$ ,  $p < 0.05$ ), and in the Song Thrush (*Turdus philomelos*) than in the Common Blackbird (*Turdus merula*),  $65 \pm 2$  vs.  $41 \pm 2$  km/day ( $t = 7.5$ ,  $df = 4$ ,  $p < 0.05$ ). The average values of migration speed estimated



**Fig. 1.** Frequency distributions of the average and maximum values of bird migration speed.

for individual families also differ significantly in some cases. Thus, the Turdidae (nine species,  $58 \pm 4$  km) were found to migrate significantly faster than the Fringillidae (seven species,  $43 \pm 4$  km) ( $t = 2.7$ ,  $df = 32$ ,  $p < 0.01$ ), with the latter migrating significantly faster than the Paridae (four species,  $24 \pm 2$  km) ( $t = 4.3$ ,  $df = 25$ ,  $p < 0.001$ ). On the other hand, no significant differences in the average migration speed were revealed between the Sylviidae (nine species,  $66 \pm 3$  km/day) and Motacillidae (four species,  $63 \pm 4$  km/day) or between the Sylviidae and Turdidae.

However, comparisons between taxonomic groups of birds as such are poorly informative unless due

account is taken of differences in their body size, morphology, migration distance, locations of wintering grounds, and ecological features.

#### *Body Mass, Wing Shape, and Migration Speed*

Regarding the concept of minimization of time expenditures as a prerequisite for successful migration, attention should be paid to all major limiting factors that may have an effect on the corresponding behavior of birds (Hedenström, 2008). Body size (mass) is a potential limiting factor for many biological functions, including metabolic rate. It appears that the time

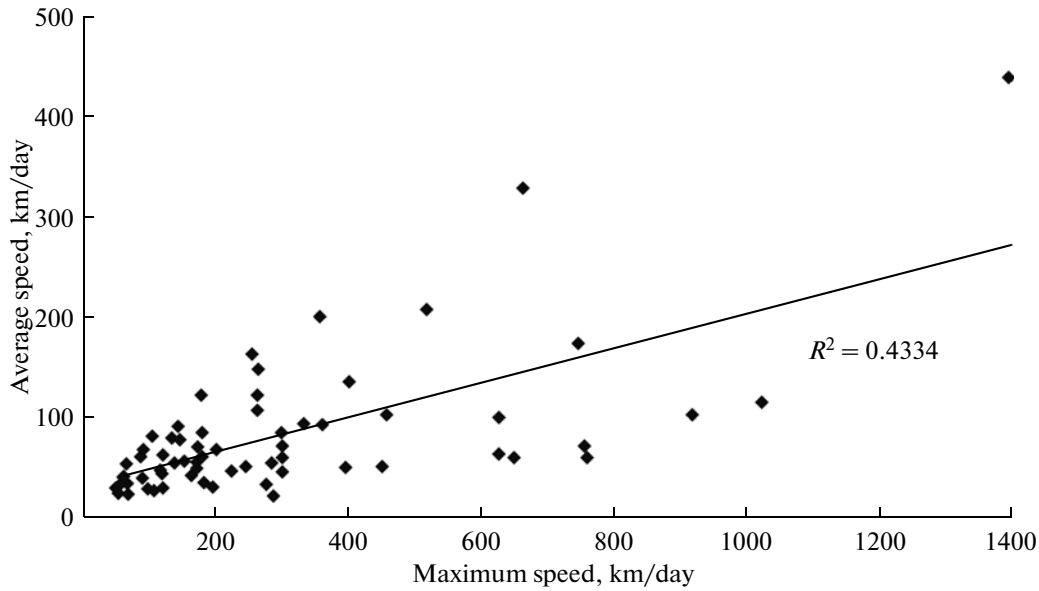


Fig. 2. Average-to-maximum migration speed ratio in 74 bird species from 24 families of 10 orders.

required for the basic activities in the life cycle of birds (breeding, molting, and migration) also depends on body mass. Rank correlations between migration speed and body mass in the pooled sample of all bird species were calculated for both daily average speed and maximum speed. It should be noted that calculations for the average speed were made excluding its values in the Gray-headed Albatross, White Stork (*Ciconia ciconia*), and Tundra Swan (*Cygnus columbianus*), which sharply differed in body mass from all other species in the sample (if several values of this parameter were available from different sources, the weighted average was calculated). The results confirmed a positive and statistically significant correlation between the daily average migration speed and body mass (Spearman's rank correlation test  $r_s = 0.426$ ,  $n = 77$ ,  $p < 0.001$ ), but no such correlation was

revealed for the maximum speed ( $r_s = -0.093$ ,  $n = 108$ ,  $p = 0.31$ ; n.s.).

Among individual taxonomic groups, a statistically significant correlation of the average migration speed with body mass was revealed in shorebirds, but this correlation was negative:  $r_s = -0.68$ ,  $n = 17$ ,  $p = 0.002$ ; i.e., the smaller the body mass, the higher the migration speed (Fig. 3). At the same time, passerine birds showed no correlation between these parameters ( $r_s = 0.075$ ,  $n = 47$ ,  $p = 0.615$ ; n.s.). Thus, the dependence of migration speed on body weight (if any) is ambiguous. Its analysis in the pooled sample has suggested that large-sized birds migrate more rapidly, but the result obtained in the group of shorebirds is opposite, and no definite relationship between these parameters is observed in passerine birds. Therefore, it appears that migration speed depends not so much on body weight as on morphological body features and ecological preferences of birds. A factor of major significance in this context is the type of bird flight, i.e., continuous flapping or soaring, gliding, etc. It is considered that a small body size in birds with flapping flight allows them to migrate more rapidly and that their flight speed decreases with an increase in body size (Hedenström and Ålerstam, 1998; Hedenström, 2006). In birds soaring and gliding with thermal air currents (e.g., large birds of prey), there is a certain critical body size at which this type of flight becomes the most expedient behavioral adaptation allowing them to minimize time and energy expenditures for migration and, hence, to restore their energy reserves more rapidly. Energy consumption for gliding flight is a constant multiple of BMR and does not depend on flight speed (Hedenström and Ålerstam, 1998; Newton, 2008).

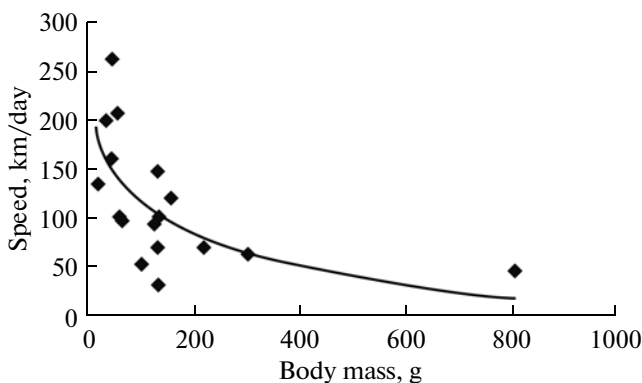


Fig. 3. Average migration speed as a function of body mass in shorebirds.



Since the speed of migratory movements apparently depends on flight speed, it is logical to consider the relationship between the latter parameter and body size in different species (groups) of birds. This problem has been discussed since the 19th century, but more or less distinct trends have been revealed only recently. It has been found that the above relationship is more complex than to be described by a simple exponential function (with flight speed increasing proportionally to body weight to the power of  $1/6$ ), as was considered previously (Tsvelykh, 1982). The flight speed increases proportionally to body mass (with the factor of proportionality differing between bird groups) only until the latter reaches 200–300 g, depending on the species or group. The point is that the power required for flight exceeds the critical level in birds with a smaller body mass, but this power reserve is reduced when the body mass increases above 200–300 g, because power scales to body mass with an exponent of  $3/4$ . Indeed, empirical data confirm that the fastest flyers among birds of prey, shorebirds, and ducks are the species in which body mass does not exceed 200–300 g.

Apparently, long-distance migratory species with a small body weight have experiences especially intense natural selection for energy-efficient type of migratory movements, with a major role being played by evolutionary changes in the shape of feathers and the wing as a whole (for example, the notch in the inner vane of primaries has gradually decreased in length). The well-known Seebohm rule postulates that migratory bird species and populations differ from resident ones in having much more pointed wings. Despite differences in the indices proposed to determine the degree of wing pointedness (Tsvelykh, 1983), this rule has been confirmed for very many species from different taxonomic groups. It manifests itself especially when comparison is made between closely related species differing in the type of migratory behavior and the distance of migration (Potapov, 1967; Lockwood et al., 1998). Thus, comparisons between medium-sized birds migrating over different distances show that the highest migration speed is achieved by long-distance migrants with a body mass of no more than 350 g, such as the Garganey (*Anas querquedula*) among ducks (the maximum and average migration speeds of 658 and 329 km/day) and the Common Sandpiper (*Actitis hypoleucos*) among shorebirds (1392 and 438 km/day, respectively). Differences in migration speed among representatives of the best studied order Passeriformes are also accounted for by several other factors (see below).

*Relationships between the Speed of Migration  
and Its Timing, Distance, Time of Day,  
and Bird Age and Sex*

As early as in the first analytical paper dealing with the speed of bird migration (Hilden and Saurola, 1982), the authors provided evidence that, on average,

this speed is higher in nocturnal than in diurnal migrants and in adult than in young birds, being the lowest in partial and irregular migrants. All this has been confirmed in subsequent studies on different passerine species (Ellegren, 1990, 1993; Fransson, 1995; Nowakowski and Chruściel, 2004; Payevsky, 2010) and in reviews (Alerstam, 2003; Newton, 2008). A relationship has been revealed between the speed and dates of autumn migration, but its pattern has proved to differ between individual studies. Alerstam and Lindström (1990) found that the later the onset date of migration in a certain species, the slower its advance along the migration route. They attributed this phenomenon to the shortening of the daylight period and consequent reduction in the rate of energy reserve accumulation in the body. However, studies on passerines ringed in autumn in Sweden showed that, conversely, late-migrating birds moved at a higher speed than early migrating conspecific individuals (Ellegren, 1993). This trend has been confirmed in studies on *Sylvia* warblers (Fransson, 1995), the Goldcrest (*Regulus regulus*) (Bojarinova et al., 2008) and Willow Warbler (*Phylloscopus trochilus*) but not on reed warblers of the genus *Acrocephalus* (Hall-Karlsson and Fransson, 2008), although it was described in these species previously (Bensch and Nielsen, 1999). Neither was such a trend observed in our studies of the Chaffinch (*Fringilla coelebs*) (Payevsky, 2010).

It was also found that the longer the migration distance, the higher the migration speed (Ellegren, 1990, 1993). Analysis of data on *Sylvia* warblers ringed in Scandinavia and Britain (Fransson, 1995) showed that British birds moved relatively slowly, compared to Scandinavian birds, probably because they had to travel a shorter distance to their wintering grounds in Africa. Therefore, the expected duration and speed of migration may be important indicators for predicting the number and duration of stopovers on the migration routes of different populations (Alerstam, 2003).

Early departing passerine species are long-distance nocturnal migrants wintering in the tropics, and their migration speed is considered to be significantly higher than that of short-distance and diurnal migrants. Thus, according to the extensive review by Newton (2008), their median migration speed is 75 km/day (data from 13 sources), compared to 53 km/day for short-distance migrants wintering in the temperate zone and departing on later dates (data from 19 sources). It is important for long-distance migrants to tropical Africa to depart early and travel fast, because they have to cross the Sahara Desert in August to September, before the onset of the dry season in the Sahel zone. Therefore, the migration speed positively correlates with the migration route length, increasing from 80 km/day in birds migrating for 1000 km to about 140 km/day in birds migrating for 5000–6000 km. Moreover, the migration speed of some species is accelerated along the route. Thus, the speed of migratory movements in the Willow Warbler

(*Phylloscopus trochilus*) on the route from Europe to Africa averaged 41 km/day at distances of 400 to 1000 km, increased to 54–59 km/day at distances of 1000 to 3000 km, and reached 85 km/day at distances over 3000 km (Hedenström and Pettersson, 1987).

The above data are valid and sufficiently representative. Comparative analysis based on a significantly greater amount of material (table) confirmed the previous conclusions. The weighted average speed of early departing nocturnal migrants in the pooled sample of 19 passerine species from different families (Sylviidae, Muscicapidae, Laniidae, and Turdidae) proved to be significantly higher than that of early departing diurnal migrants (14 species from the families Sturnidae, Fringillidae, and Paridae):  $66.9 \pm 3.7$  vs.  $35.1 \pm 3.4$  km/day ( $t = 6.5$ ,  $df = 31$ ,  $p < 0.001$ ). Nocturnal migrants have most progressed in minimizing the time allotted for migration in their annual cycle. They migrate during the time free from foraging activity (except for some shorebirds that can forage at night on marine shoals).

Irregular migrants or invasive species from different passerine families, such as the Spotted Nutcracker (*Nucifraga caryocatactes*), Coal Tit (*Parus ater*), Long-tailed Tit (*Aegithalos caudatus*), Bohemian Waxwing (*Bombycilla garrulus*), and Eurasian Bullfinch (*Pyrrhula pyrrhula*), migrate very slowly as compared to regular diurnal migrants such as the Common Starling (*Sturnus vulgaris*), Common Chaffinch (*Fringilla coelebs*), and Brambling (*F. montifringilla*):  $34.2 \pm 4.2$  vs.  $51.3 \pm 2.2$  km/day ( $t = 22.8$ ,  $df = 74$ ,  $p < 0.001$ ). According to estimates compiled by Newton (2008), the median migration speed of invasive species and partial migrants is even lower, 27 km/day. The abundance of such migrants increases in invasive years, and so does the speed of their movements: in the Coal Tit, for example, from 30–40 to 40–80 km/day (Rute, 1976). On the whole, these data confirm the conclusion that species wintering and moving within Europe have no natural tendency (acquired via selection) to depart from territories that remain quite habitable for them. They usually move for relatively short distances, in the absence of significant body energy reserves. The term “roving” was proposed for a special form of migratory behavior where the annual life cycle of birds lacks the migration stage and the birds move only when the food supply becomes insufficient (Noskov and Rymkevich, 2008).

Migration strategies differ not only among species and their groups but also within the species. Moreover, intraspecific differences are observed not only between populations, as in the aforementioned case of British and Scandinavian warblers, but also between age groups. Adult birds usually migrate faster than juveniles, as follows from observations on different species such as the Dunlin (*Calidris alpina*) (Hilden and Saurola, 1982), Bluethroat (*Luscinia svecica*) (Ellegren, 1990), Sedge Warbler (*Acrocephalus schoenobaenus*), Eurasian Reed Warbler (*A. scirpaceus*), Common Redpoll (*Carduelis flammea*) (Ellegren, 1993),

Chaffinch (Payevsky, 2010), *Sylvia* warblers (Fransson, 1995), and some other long-distance nocturnal migrants (Hall-Karlsson and Fransson, 2008). On the other hand, no age related differences in the migration speed have been revealed in the Great Tit (*Parus major*) and Blue Tit (*P. caeruleus*) (Nowakowski, 2001; Nowakowski and Chruściel, 2004). The existence of such differences may be regarded as evidence that the degree of adaptation to migration in birds increases in the course of individual life. As for sex-related differences in the migration speed, they have not been confirmed statistically in the Bluethroat, Great Tit, Blue Tit, and Chaffinch (Ellegren, 1990; Nowakowski and Chruściel, 2004; Payevsky, 2010).

The majority of data on the migration speed are based on ring recoveries during autumn migrations. Spring recoveries are much less numerous, but they provide evidence for a higher migration speed, compared to that in autumn. The data on spring migrations collected for this study (table) are insufficient for comparative analysis. Relevant published examples concern mainly passerine species. In particular, more rapid migration in spring than in autumn was observed in three out of four studied species of *Sylvia* warblers (Fransson, 1995) and also in the Barn Swallow (*Hirundo rustica*) and Aquatic Warbler (*Acrocephalus paludicola*) (Newton, 2008). This may be explained by the effort to arrive earlier in order to occupy the best nesting sites as well as by the increasing duration of the daylight period, compared to that in autumn.

#### *Selective Significance of the Speed and Dates of Migratory Movements*

Regardless of high variation in the migration speed and migratory habits among different conspecific populations and even individuals, the principle of minimization of the migration time is applicable to all species of the class Aves, providing for the optimal timing of the entire annual life cycle. This principle holds even in cases of species that migrate during the greater part of the year. In particular, the migration time accounts for about 59% of the annual life cycle in storks and cranes, up to 42% in some birds of prey, and up to 31% in the Barn Swallow, which migrates from Europe to southern Africa (Newton, 2008). Large birds with flapping flight require very much time for replenishing their energy reserves during stopovers, which may prevent the possibility for them to breed, molt, and migrate for a long distance during the same year. Therefore, the time available for migration is a factor limiting its possible distance and, in general, the size of the species range (Hedenström and Alerstam, 1998; Alerstam, 2003).

In addition to environmental conditions, the speed and dates of migration are regulated by an endogenous timing program that operates in accordance with external signals, primarily the photoperiod. However, global climate change in the recent period has caused

shifts in the timing of migration. During the past three decades, the arrival of birds to their breeding grounds has shifted to significantly earlier dates because of climate warming in the Northern Hemisphere (although not in all species and not in all regions). The speed of spring migrations has also increased, providing in particular for a more rapid passage of long-distance migrants across arid zones in northern Africa. Thus, ecological conditions in wintering areas and along the migration route have a significant effect on both dates and speed of migratory movements. However, since the birds may be incapable of increasing the migration speed over a certain threshold due to physiological limitations, changes will probably take place mainly in the dates of migration (Hedenström, 2008; Sokolov, 2010).

Among probable factors accounting for the selective significance of the migration speed, a major role is played by the risk of mortality along the migration route: the shorter the duration of migration, the higher the potential survival rate of migrants (Alerstam, 2003). Some ornithologists consider that mortality among migrants due to bad weather, collisions with tall buildings, and oil spills in the seas exceeds that in other periods of the annual life cycle and reaches 85% (Silett and Holmes, 2002; Newton, 2007). Moreover, the impact of environmental factors on migrating birds may strongly limit the abundance of bird populations (Newton, 2004, 2008). Thus, the essential stage in the bird life cycle appears to be a dangerous period of high risk for mass mortality. Is it really so?

In a previous study (Payevsky, 1999), ring recovery data were used to analyze between-month differences in the level of mortality in ten bird species, including four passerines and the Mallard (*Anas platyrhynchos*), Osprey (*Pandion haliaetus*), Northern Sparrowhawk (*Accipiter nisus*), Eurasian Coot (*Fulica atra*), Northern Lapwing (*Vanellus vanellus*), and Black-headed Gull (*Larus ridibundus*). This analysis in eight out of ten species was performed for males and females and for different age groups separately; thus, 18 comparisons were made. It was found that mortality during winter exceeded that during migrations in 10 out of 18 cases, while the inverse situation was observed in 3 out of 18 cases; mortality during migrations was higher than that during the breeding season in 12 out of 18 cases; on the whole, mortality during migrations and during wintering accounted for 36% and 45% of the annual average mortality, respectively, with the difference being statistically significant ( $p < 0.01$ ). These results show that the periods of seasonal migrations are no more hazardous to birds than any other periods of their annual life cycle. The survival of individuals exposed to powerful weather effects depends on random factors. Direct selection does not operate in such situations, and cases of mass death during migrations have no selective significance (Payevsky, 2009). At the same time, the behavior of birds both in flight and during stopovers is adaptive and dependent on complex

interrelations of species-specific foraging habits, weather factors, and biotopic conditions (Chernetsov, 2012).

However, specific relationships between the external and internal factors and their relative roles in the regulation and evolution of the speed of bird migratory movements have not yet been studied in detail (Alerstam, 2003).

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