Sex-biased Survival and Philopatry in Birds: do They interact?

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Abstract—A review of studies of sex-biased dispersal and philopatry and sex-biased survival in birds is presented. The comparison between sex-related mortality and natal and breeding dispersal at the species-level shows that dispersing birds (mainly females) suffer higher mortality, while philopatric birds (mainly males) have higher survival. The interaction between sex-biased survival and spatial behavior is a crucial component of avian vital strategy, which determine population dynamics and genetic structure.

Spatial structure of bird populations and their territorial behaviour are a large array of topics in avian research related to regulation of population density and numbers. Analyses of temporal and spatial distribution of sex and age groups and estimates of their survival rate are necessary prerequisites for theoretical and applied studies of population demography and community ecology.

Fidelity of birds and other animals to their natal areas, or to the areas of previous breeding, and movements towards novel territory, are studied under the umbrella of philopatry and dispersal. These aspects of spatial behaviour are discussed in numerous publications. The aim of this review is to discuss mainly the sex-related difference in spatial behaviour and the possible link to sex-specific survival. This supposed link draws interest, because some studies find a sex-related difference in fitness between dispersing and philopatric individuals (when higher fitness is understood as producing more numerous and more viable offspring). This review and analysis of relationships between philopatry and survival rate are based on quantitative data reported in wide range of publications.

History of Conflicting Views on Dispersal and Philopatry in Birds

Identifying the degree of territorial constancy and genetic isolation of within-species groups (local populations) is a topical direction of current biological studies with a rich history of research. Survival rates of birds and their site fidelity after returning from non-breeding areas have been studied since long ago (Howard, 1920; Nice, 1937).

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In his publication on conservative and dispersive types of evolution in birds A.S. Malchevsky (Malchevsky, 1968) forwarded the hypothesis on species-specific difference in the degrees of dispersal and philopatry. Even though the author did not use the term "philopatry" in his paper, but rather preferred to speak of "the phenomenon of breeding conservatism" and "urge to return to the birth place", he obviously meant philopatry, i.e. breeding or natal site tenacity. Prevailing settlement beyond the borders of their home area in some species and returning to the place of previous breeding in others have been treated as different evolutionary tendencies. In this paper, Malchevsky argued against the concept of H. Howard (Howard, 1920) who stated that in spring, all surviving birds return to their home population, and suggested that local populations of many avian species are support their numbers by recruiting immigrants. However, the views of Howard were supported by a number of authors who argued for the existence of "micropopulations" (local, or elementary populations), fine-tuned to very local environmental conditions (Isakov, 1949; Likhachev, 1955; etc.).

In the subsequent decades many ornithologists who worked at the northern edges of ranges of many bird species developed the view that, contrary to Howard, peripheral populations of all avian species suffer high mortality rates, their members show a high degree of dispersal, and existence of such populations is not possible without a constant influx of immigrants (Zimin, 1988, 2002; Ryabitsev, 1993; Hoffman and Blows, 1994; Ryzhanovsky, 1997; Thingstad et al., 2006; etc.). Gradually this view has been extended to many other avian populations, which caused a controversy. Some authors believed that the proportion of philopatric individuals did not exceed several percent, whereas others claimed that a significant proportion of

birds showed natal philopatry (return for breeding to their natal areas) and breeding philopatry (return to the area of previous breeding). The data and viewpoints available at that time have been summarised in the only monograph on philopatry and dispersal of birds (Sokolov, 1991). It is rather revealing that the basis of all controversies in philopatry research was actually the difference in interpretations of methods of estimating site fidelity (Sokolov, 1976, 1988, 1991, 1997; Sokolov et al., 1990; Bardin, 1990, 1993, 1996; Martin et al., 1995; Payevsky, 1992, 2009; Vysotsky, 2001; Catry et al., 2004; Artemyev, 2008).

The main source of these controversies is the assumption on the fate of birds marked but never re-encoutered. Capture-mark-recapture studies performed in a restricted area do not allow differential estimates of survival (or mortality) and return rate (or emigration). The birds that vanished include those that died or emigrated, but also the ones present in the population but evaded detection. The so-called "return rate", i.e. the proportion of individuals re-encountered from the number ringed, is often used in the discussions of philopatry, even though its inade-quacy for estimating territorial behaviour has been repeatedly shown (Bardin, 1990, 1993; Cooch, White, 2006; etc.). Moreover, this parameter is included in all models estimating local survival, known as "minimum number known alive" (Marshall et al., 1999). However, nearly all researchers realise that this proportion of re-encountered marked individuals depends on three main components: annual survival rate, probability of return of survivors and probability of their detection. The latter depends on the effort spent and on the size of the study area: detection efficiency by captures and observations declines with increasing radius of the area under control (Dolnik and Payevsky, 1982; Sokolov and Vysotsky, 1988; Hestbeck et al., 1991; Lebreton et al., 1992; Martin et al., 1995; Robertson and Cooke, 1999).

Because of all that, special stochastic demographic models have been developed to estimate survival rate and other parameters (Pollock et al., 1990; Lebreton et al., 1992; etc.), which are more biologically realistic than previously used so-called demographic tables ("Lack method"; Hickey, 1952). Growing development of software for analysing data on marked animals makes it possible to efficiently estimate demographic parameters from capture-mark-reencounter data (Anderson and Burnham, 1999; Cooch, 2001; Cooch and White, 2006). In the population studies, it is usu-ally not the true survival rate which is estimated, but rather the local, site-specific, or apparent survival rate (Vysotsky et al., 1998; Bardin, 1990). It includes the probability to survive and the probability to return rather than emigrate. The probability that dispersal results in survival or death is treated as a crucial parameter in the evolution of dispersal and related events, and a method of estimating survival rate of emigrants is suggested (Waser et al., 1994).

Estimates of natal dispersal distance and of recruit-ment of juveniles are strongly dependent on size and shape of areas in which dispersal takes place. A method of correcting estimates of dispersal and sur-vival rates, taking into account territory shape and number of habitats, has been proposed (Cooper et al., 2008). One factor that influences philopatry is latitu-dinal variation. In northern populations of pied fly-catchers (*Ficedula hypoleuca*)[1], a species with well studied spatial behaviour, return rates to natal area are significantly lower than in central and more south-western populations (Sokolov, 1991; Artemyev, 2008). These authors suggest that the reason for this variation may be in landscape features: in western Europe, iso-lated forest islands are more common, whereas north-eastern Europe still can boast large contiguous forests. Return rate is always higher in isolated forest frag-ments (Zubtsovsky et al., 1989; Sokolov, 1991; Artem-yev, 2008). Moreover, populations from the actual islands show the highest values of philopatry. In the population of linnets (*Linaria* (*Acanthis*) *cannabina*) from the island of Heligoland return rate of juveniles was 38%, which exactly fits their mean annual survival rate (Förschler et al., 2010). If we assume a reverse relationship for the birds in boreal forest, the opinion of some authors on prevailing dispersal and very rarely shown philopatry, based on the results from northern populations, can only be explained by local special conditions for the birds. Conflicting views on the exis-tence of mainly dispersive or mainly philopatric avian populations should take into account the fact that birds, like anadromous fish, sea turtles and other ani-mals, have sophisticated orientation and navigation mechanisms that make it possible for them to navigate towards their goal very exactly (Wiltschko and Wiltsc-hko, 2009). These features would have been utterly useless if philopatry were a rare random event.

BENEFITS OF PHILOPATRY AND OF DISPERSAL AND THEIR SEX-RELATED BIAS

First detailed reviews on mating systems, philo-patry and dispersal in birds and mammals (Green-wood, 1980) and on natal and breeding dispersal of birds (Greenwood and Harvey, 1982) showed on the basis of analysis of numerous data for different avian taxa that in most species, males are more philopatric than females, who are more prone to dispersal. There are few exceptions, but they included ducks (Anati-dae). It has been suggested (Greenwood, 1980) that sex-related bias in dispersal is primarily a result of a mating system, monogamy vs. polygyny. In the monogamic system, males monopolise and defend

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[1] Scientific names follow the latest recommended authorities: Dickinson and Remsen, 2013; Dickinson and Christidis, 2014. As some generic names are unwonted, in these cases the tradi-tional names of genera are given in parenthesis.

breeding territory, whereas territory and resources are necessary to attract a female for breeding. Therefore, the males gain benefits when they remain within their natal or previous breeding territory, where they are familiar with crucial resources and can defend them during competitive interactions. Females under such system enjoy benefits during dispersal, when they can evaluate and select the fittest and most successful male, and avoid the negative consequences of inbreeding. Unlike monogamy, under polygyny and polyandry males are more prone to dispersal, because they need to find additional female(s). As a development of this hypothesis, in the case of mammals it has been suggested (Dobson, 1982) that the gender which is more involved in competition, is also more dispersal-prone. In polygynous and promiscuous species these are males who compete most, therefore they are more likely to disperse; whereas in monogamous species competition levels within males and within females are comparable, and the proneness to disperse is similar between sexes. However, this assumption does not explain the facts in birds, because in monogamous species dispersal is significantly more pronounced in females. Knowledge of distribution of food and potential nesting sites is essential just because searching for them is energetically costly and exposes animals to predation risk (Bensch and Hasselquist, 1991). It has also been suggested that female-biased dispersal may also be explained by the lack of suitable nesting sites in a territory defended by a male (Arlt and Pärt, 2008). A spacious review of dispersal and philopatry theory (Johnson and Gaines, 1990) clearly demonstrated that the evolutionary origin of sex-biased dispersal remained debatable.

The cost of long-distance dispersal for an individual is reflected in energy and time expenditure and in the risk of death, which may happen immediately during movement or settlement, or be a delayed result of energy loss. Individual fitness makes it possible to rapidly adapt to a novel environment, and the advantage will be with the individuals that can adjust their behaviour, i.e. have a broad reaction norm. Individual cost : benefit ratios may result in a diversity of alternative strategies under different conditions. As costs depend on the environment, population density including, and on individual condition, a compromise between benefits and costs will result in dispersal strategies that reflect these relationships. Therefore both philopatry and dispersal may be optimal and evolutionary stable strategies, depending on cost/benefit ratio under different ecological and social conditions (Johnson and Gaines, 1990; Weatherland and Forbes, 1994; Dieckmann et al., 1999; Serrano and Tella, 2007; Ronce, 2007; Bonte et al., 2012).
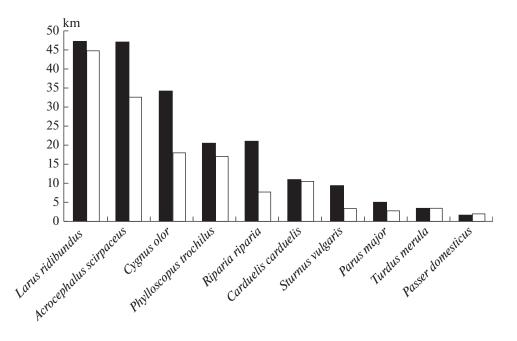
Benefits and costs of dispersal may vary depending on which factor is the main driving force of evolution. Various hypotheses on the components of fitness in dispersing and philopatric avian species have been suggested. The birds either produce viable, numerous and fecund offspring, or do not do that; and a trade-off between costs and benefits of dispersal and philopatry has been hypothesised (Johnson and Gaines, 1990; Bélichon et al., 1996). Components of fitness in philopatric and dispersive individuals varied, but dispersal in both species often carried both benefits and costs. In birds, sex-biased fitness between dispersing and philopatric individuals was demonstrated in 10 studies out of 16, and the difference in fitness trade-offs might have been due to varying evolutionary strategies (Bélichon et al., 1996). Dispersal behaviour may also be influenced by the unbalanced sex ratio, if mating is hindered by the lack of individuals of some sex.

The definition of natal and breeding dispersal as some members of a population quitting others (Greenwood and Harvey, 1982) stresses dispersal distance as its crucial parameter. Authors of another review (Liu and Zhang, 2008) proposed that that to identify the essence of dispersal, the concept of home range should be included into it, because an animal exists not just within its breeding area, but also in the territory where it forages, rests and performs mating demonstrations. These authors distinguish between several types of dispersal: from the natal site to the first home range, from the first home range to the first wintering area, from the first wintering area to the first breeding site, and finally, between subsequent breeding areas.

To understand the biological meaning of sex-related philopatry and dispersal, one should estimate both the probability of movement and the distance of movement. Dispersal distance may be very different, because it depends on the geographic position of the population and on type of breeding, solitary vs. colonial. It should be emphasized that natal philopatry must not be understood as fidelity to the exact place of birth, the territory of the parents. The analysis of numerous publications shows that most authors treat philopatry as faithfulness to a rather broad area, so that an apparently paradoxical opinion that philopatry is a special case of dispersal, makes sense. The distance from the site of birth of the site of first breeding may depend on the peculiarities of imprinting of the future breeding area by juvenile birds. Special experiments in which juveniles were maintained in different areas and released into the wild at different age showed that the bond to the future breeding area is established in migratory songbirds when 30–50 days old, and the degree of their philopatry depends on how far from the birthplace they are at that age (Sokolov, 1976, 1991). Natal dispersal distance of pied flycatchers exceeded the values for chaffinches (*Fringilla coelebs*), barred warblers (*Curruca* (*Sylvia*) *nisoria*) and willow warblers (*Phylloscopus trochilus*), because most pied flycatchers imprinted territory beyond their immediate natal site, up to 6 km from it (Sokolov et al., 1990). Controlling the birds in the areas of such size may yield basic data on the spatial behaviour of birds. Natal and breeding philopatry also depend on a multitude of factors,

Distance of natal (filled histogram) and breeding (open histogram) dispersal in kilometres in British birds from different taxa (data from Newton, 2008).

including hatching date (birds hatched early are more prone to come back), growing conditions, age, breeding performance, stability of habitats.

For an individual and for the population the optimal choice is dispersing for a moderate distance, because if distant populations exchange individuals on a large scale, all local adaptations would be useless. In colonial birds, philopatry and dispersal may only occur between discrete colonies, which forms a peculiar distribution pattern of breeding individuals. Greater Flamingos (*Phoenicopterus roseus*) in three colonies in the Mediterranean, located 600 − more than 1000 km one from another, mainly showed natal philopatry (>84%), and fidelity to colony increased with experience and age. However, breeding dispersal of adults was also non-negligible, up to 52%, but it is natal philopatry which was the driver of breeding dispersal (Balkiz et al., 2010). Mainly philopatric are also whooping cranes (*Grus americana*): 76% of juveniles return for breeding to their population, within 20 km of the natal site (mean 16 km), whereas breeding dispersal distance of adults was on average 1.4 km in females and 1.1 km in males. Neither juvenile nor adult whooping cranes showed a significantly sex-biased dispersal, unlike sandhill cranes (*Antigone* (*Grus*) *canadensis*), in which the natal dispersal distance was on average 12.6 km in females and just 3.9 km in males (Johns et al., 2005).

Comparisons of dispersal distances, both natal and breeding ones, in different species show that they show no taxonomic signal. The example of 10 species of British birds demonstrates that birds with very different systematic position and even ecological prefer-

ences may show similar dispersal distances (Newton, 2008; Figure). This fact agrees with the hypothesis of Greenwood (Greenwood, 1980) that mating system predicts sex bias in dispersal irrespectively of their taxonomic position. Natal dispersal distances in the vast majority of birds are much higher than the distance breeding dispersal: among 31 species, mostly passerines, the ratio of geometric means of natal to breeding dispersal varies between 0.17−6.17, on average 2.68 (Newton, 2008). Ecological features of foraging and breeding certainly influence dispersal distance. It is clearly shown mainly by the species whose primary food abundance varies broadly from year to year in different regions. Birds that depend on such sporadic resources are well known to move in different directions within their range in different years (Newton, 2006; see below for more details).

As already mentioned, longer dispersal distances in males are typical only of a number of duck species, some waders with reserved sexual roles, when males incubate the clutch and provide care to the brood (*Phalaropus* phalaropes and spotted sandpipers (*Actitis macularius*)), and of cooperative breeders white-throated magpie-jays (*Calocitta formosa*) (Langen, 1996). Female-biased dispersal, typical of most birds, is quantitatively pronounced to a very different degree. Characteristic is the considerable difference between the mean and maximum dispersal distance, which shows the potential for settling in novel areas. The maximum breeding dispersal distance in female house wrens (*Troglodytes aedon*) was 15000 m, mean distance 700 m; in males, the respective figures were 2100 and 432 m (Newton, 2008). In pied flycatchers on the Bal-

tic coast the respective figures for breeding dispersal were 23000 and 1500 m in females and 5970 and 500 m in males (Sokolov et al., 1989), in collared flycatchers (*Ficedula albicollis*) for natal dispersal they were 5500 and 840 m in females and 5500 and 518 m in males (Pärt, 1990), and in semipalmated plovers (*Charadrius semipalmatus*) 12700 and 800 m in females and 12600 and 4200 m in males (Nol et al., 2010). It should be particularly emphasized that in pied flycatchers ringed as nestlings on the Baltic coast the return rate for males was nearly twice as high as for females. The males dispersed on average 4300 m from their natal nest box, whereas the females dispersed 6600 m, and the difference was highly significant (Chernetsov et al., 2006).

Site fidelity in birds limits settling in novel areas and facilitates speciation (Mayr, 1963). At the same time, dispersal to new areas is mainly performed by young individuals. Novel areas are most commonly colonised along the routes of spring migration by "overshooting", each spring farther from the former range limit. The case of the serin (*Serinus* (*canaria*) *serinus*) is a good example. During the 170 years, the serin colonised *ca.* 2.5 million km^2, which is almost one-half of its current range. The birds settled an average of 14300 km^2 per year, and new records were reported 100−270 km from the previous ones. It shows that new areas were colonised by discrete long-distance hops. Long-distance recoveries of breeding birds and nestlings showed that of 80 records, 62 marked individuals were recovered within 10 of the site of ringing, whereas 5 birds were found 50 km from the ringing site, 7 birds within 51−100 km, 3 individuals within 101−200 km and one bird each at 323, 415 and 660 km (Payevsky, 2004). This means that just *ca.* 20% of the population consists of birds that participate in a rapid range expansion. Rapid northward expansion might be due to emergence of mutant individuals carrying the novel character of urge to disperse (Mayr, 1926). Taking into consideration the difference in fitness between philopatric and dispersing individuals, one may assume that some of dispersing birds are most fit, and they should be of both sexes to establish a novel population. Thus, movements of juveniles might be the crucial factor that governs the demographic features of a population (Bowler and Benton, 2005).

All kinds of movements during dispersal, in spite of the possible risks due to increased energy expenditure and predation exposure, as compared to philopatric individuals, are fundamental behavioural characteristics and may carry selective advantages. Advantages may include mating to a new better partner, acquiring a new better territory, but primarily it is avoiding inbreeding and its consequences, i.e. lower fitness of offspring and its increased mortality (Motro, 1991; Perrin and Mazalov, 2000; Keller and Waller, 2002). It should be however mentioned that in an insular population of great tits (*Parus major*), where the proportion of inbred pairs was 20−47%, no negative consequences in the fitness of offspring have been found (Noordwijk and Scharloo, 1981). Nevertheless, selection may support behaviour which results in dispersal or in recognition of a relative, which in its turn may also cause dispersal. Kin selection will favour long-distance dispersal, even if survival cost during dispersal is very high (Rousett and Gandon, 2002). For example, in Siberian jays (*Perisoreus infaustus*) conflicts between siblings in the natal territories result in eviction of subdominant individuals (Ekman et al., 2002). A follow-up study (Gienapp and Merilä, 2011) showed that subdominants left the family group immediately upon gaining independence, whereas dispersal of dominants was delayed. Natal dispersal distance was related to sex of the birds and timing of its beginning. Young females and early leaving juvenile male dispersed on average longer distances than the remaining males and individuals that left late. It was also found that dispersal distance and timing were inversely related to the number of recruits, produced in a lifetime in males but not in females. These results support the hypothesis that natal dispersal, which is more pronounced in females, mainly depends on reproductive success of philopatric males. In monogamous territorial species of birds the benefits or philopatry should be higher in males, because males gain territories, where knowledge of local resources is crucial.

Most publications on costs and benefits of philopatry and dispersal claim that natal philopatry is beneficial for birds (Pärt, 1994, 1995; Bensch et al., 1998; Wheelwright and Mauck, 1998; etc.). Philopatric birds are fitter than those dispersing, not just due to the advantage of knowledge of spatial distribution of food, but also because of their knowledge of how to avoid predators and find optimal breeding sites (local knowledge hypothesis). One reason to be philopatric may also be the successful breeding in the preceding season. It has been shown for a yellow wagtail (*Motacilla flava*) population in northern European Russia, where all birds recorded as successful breeders returned to their previous breeding site (Shitikov et al., 2012). Breeding philopatry of females in three duck species in Latvia − shoveler (*Spatula* (*Anas*) *clypeata*), pochard (*Aythya ferina*) and tufted duck (*A. fuligula*) was also high and reverse to many other species in respect to sex bias, as usually these are males who are more philopatric. In all these species site fidelity of females was 0.88−1.0, and emigration rate was only 0−0.12 (Blums et al., 2002). The authors concluded that such a high return rate to the site of previous breeding was due to successful reproduction. However, the local knowledge hypothesis is the most widely accepted one which explains the high breeding site tenacity in female waterfowl (Rohwer and Anderson, 1988).

Knowledge of ecological and evolutionary causes of dispersal may be crucial for understanding avian behaviour in spatially structured populations and predicting responses of animals to habitat change. As dis-

persal and philopatry may include inheritance of a certain type of behaviour by the offspring, it may have broad consequences for the genetic structure of populations and population and community dynamics (Bowler and Benton, 2005). If exchange of individuals between populations is small or constant, genetic structuring may increase or decrease (Chesser, 1991). The composition of the breeding pair, whether it consists of residents or immigrants, is also important in this respect. A comparison of philopatry levels between offspring of local resident and immigrant pied flycatchers in the eastern Baltic showed no significant difference. Moreover, even siblings demonstrated varying natal dispersal distances (Sokolov, 1991). However, in other pied flycatcher populations offspring of residents returned to their natal areas significantly more often than offspring of immigrants or of mixed resident x immigrant pairs. It has been reported from very different parts of that species' range (Berndt, 1960; Gashkov, 2003; Artemyev, 2008). It apparently suggests an inherited component in the spatial aspects of behaviour. In great tits between-brood variation in dispersal distance was greater than within-brood variation, which has also been tentatively explained by the genetic component controlling this behaviour (Vilbaste et al., 1988).

Even though philopatry and dispersal are sometimes presented as alternative reproductive tactics (Andersson, 1980), it should be emphasized that it is only correct at the level of an individual, and for all individuals in each age and sex group any behaviour is always a prevailing tendency, followed by less than 100% of birds. Theoretical models predicting spatial distribution during dispersal usually describe the events in respect to just one gender, commonly females. To overcome this limitation, a full equilibrium model has been developed which included both sexes. This model predicted that sex biased dispersal might considerably change recruitment rate, and it depended on the relative contribution of males and females in population growth (Miller et al., 2011).

In respect to genetic adaptation, i.e. contribution of alleles into the gene pool of future generations, many researchers concluded that dispersing individuals have lower fitness than philopatric ones. If dispersal-prone individuals produce offspring with similar qualities, fitness estimates based on local survival rate of adults and the number of recruits are likely to also be lower for dispersers. A review of studied on similarity between dispersal characteristics of parents and their offspring, and on individual lifetime proneness to dispersal, showed that the relationship was significant in 5 studies of 12, and only 3 reports confirmed individual consistency in dispersal (Doligez and Pärt, 2008). However, further studied in collared flycatchers showed a significant similarity between parents and offspring in this behaviour and thus proved the existence of an inherited component of dispersal probability between populations (Doligez et al., 2012). Evi-

dence for a genetic basis of typical dispersal-related behavioural features has been obtained also for individual consistency, and in different species of the same taxonomic family (Sinervo and Clobert, 2003). In spite of the great interest towards the possibility of estimating all aspects of adaptations in birds displaying different spatial strategies, the existing methods can result in significant errors. For instance, the proportion of recruits may be underestimated by 4–60%, especially in long-lived species (Doligez and Pärt, 2008).

FIDELITY TO NON-BREEDING TERRITORIES

As mentioned earlier, several hypotheses have been suggested to explain the adaptive significance of breeding philopatry (Greenwood, 1980; Johnson and Gaines, 1990; Doligez and Pärt, 2008; etc.). However, for better understanding of evolution of philopatry it is also necessary to study spatial behaviour during migration and wintering. Fidelity to wintering and moulting areas, and to migratory stopovers is often as pronounced as breeding site tenacity. This behaviour shows the same features as fidelity to breeding areas, i.e. gradually decreasing number of records of ringed individuals with increasing distance from the core part of the study area, and territorial behaviour in non-breeding areas. As reviewed by Sokolov (Sokolov, 1991), the tendency to return to non-breeding sites has been reported for more than 150 species of birds, with return rates to non-breeding areas as high as on average 20% in passerines (Passeriformes), 55% in geese and ducks (Anseriformes) and 60% in Charadriiformes. An extremely high winter site fidelity has been reported for whinchats (*Saxicola rubetra*) in Nigeria. In two years, 54% of birds returned and occupied the same territories they used in the preceding winters (Blackburn and Cresswell, 2016). These authors believe that this return rate is representative of the true survival between winters.

Many birds also show temporal consistency on passage and of arrival to wintering areas. A large dataset on recaptured in subsequent years has been collected at the site of mass passage on the Courish Spit in the Eastern Baltic. Of 265 recaptures of 9 species, *ca.* 70% occurred within 10 days of the calendar date of initial capture in previous years (Payevsky, 1985; Sokolov, 1991). Similar facts have been reported from Alaska (Bailey, 1974), Siberia (Yurlov, 1974) and the foothills of Tien Shan (Gistsov and Gavrilov, 1981). It suggests a tendency towards individual consistency of timing and routes of migratory movements. No sex-related bias has been reported in this trend, and age-related variation has only occurred in long-lived species: immature cranes and gulls were less prone to return to the previously used areas than adults.

A condition for constancy of timing, routes and migratory stopovers and wintering areas is obviously the stable food availability and predation risk. The

abundance of main food of some birds with specialised feeding habits varies broadly between the years and in different areas. Birds that depend on such sporadic resources have to migrate in different areas in different years, which sometimes may take the form of mass invasions, or irruptions. Most commonly irruptions occur in one part of the species' range, and usually not annually. To such irruptive, or nomadic, species, which often also show not breeding site fidelity, belong nutcrackers (*Nucifraga caryocatactes*, *N. columbiana*) and birds of prey and owls that forage on rodents with sharply varying numbers, especially Polar owls (*Bubo* (*Nyctea*) *scandiacus*). Among true finches (Fringillidae), nomadic species are first of all crossbills, especially common crossbill (*Loxia curvirostra*) and to a smaller extent parrot crossbill (*L. pytyopsittacus*) and two-barred crossbill (*L. leucoptera*), and also pine grosbeak (*Pinicola enucleator*), evening grosbeak (*Hesperiphona vespertina*), purple finch (*Haemorhous purpureus*), pine siskin (*Spinus pinus*), European siskin (*S. spinus*), common redpoll (*Acanthis flammea*) and Arctic redpoll (*A. hornemanni*), common bullfinch (*Pyrrhula pyrrhula*) and brambling (*Fringilla montifringilla*). Winter site fidelity could hardly be supported by selection in all nomadic finches due to unpredictable food availability in many continental areas of the temperate zone (Andersson, 1980; Yunick, 1983; Newton, 2006). The bulk of birds in most populations of these species do not return to their natal of previous breeding sites, even though some records to this effect are known (Vander et al., 1981). Dispersal distance in nomadic species may reach several thousand kilometres.

Waterfowl deserve a special discussion in respect to sex-biased spatial behaviour. As already mentioned, they show a reverse pattern of breeding philopatry, as females are more site faithful than males (Greenwood and Harvey, 1982; Rohwer and Anderson, 1988; Anderson et al., 1992; Clarke et al., 1997). This is of special importance because mating in many species takes place in winter quarters, unlike many other birds, and therefore, selection pressure for winter site tenacity will be different from the selection for breeding philopatry. As summarised in a review (Robertson and Cooke, 1999), winter site fidelity had been reported in 28 publications on 19 species of waterfowl belonging to tribes Anserini (geese and swans), Anatini (dabbling ducks), Aythyini (diving ducks) and Mergini (sea ducks). The highest return rates to relatively small, 1–10 km², winter territories, were shown by geese and swans (49–98, on average 71%) and sea ducks (5–77, on average 30%), whereas dabbling ducks showed much lower return rates: 0–10, on average 3%. However, philopatry of any of these species is not absolute, because some birds do switch population, which is sufficient to break the genetic isolation. As for the sex bias in winter site fidelity in waterfowl, it depends on the features of social relationships. Swans and geese migrate in family groups, in which the social status of

a pair, determined by the male, may influence the behaviour of juveniles. Defence of the family group and territory by a philopatric male causes preferential return of juveniles in the subsequent year, but in a sex-related way. Yearling male Bewick's swans (*Cygnus* (*bewickii*) *columbianus*) are more faithful to their previous winter territories than females (Rees, 1987). As many species mate in winter quarters, winter site fidelity may result in maintaining the pair bond, if the males abandon their mates in summer soon after laying the clutch. Between-year constancy of pair bonds has been reported in Barrow's goldeneyes (*Bucephala islandica*), buffleheads (*B. albeola*), long-tailed ducks (*Clangula hyemalis*), common eiders (*Somateria mollissima*), harlequin ducks (*Histrionicus histrionicus*) (Robertson and Cooke, 1999).

However, when discussing the permanency of pair bonds, and sex-related winter site fidelity, the so-called differential migration should be taken into account. This is the different proportion of birds in each age and sex group which perform migration, varying timing of migratory departure and arrival, and different migratory distance. This phenomenon is common among passerines, waders, ducks, birds of prey, herons and others, in a total of *ca*. 150 avian species. In some species this difference is rather substantial, in others means differ, but the ranges of values overlap broadly. Several reviews on this topic have been published (Payevsky, 1976, 1990; Gauthreaux, 1982; Ketterson and Nolan, 1983, 1985; Cristol et al., 1999; Newton, 2008), and it has been discussed in several papers and chapters in monographs (Payevsky, 1969, 1985, 2009; Myers, 1981; Spina et al., 1994; Rubolini et al., 2004; Kokko et al., 2006; etc.). Three main mutually non-exclusive hypotheses (Myers, 1981; Gauthreaux, 1982; Ketterson and Nolan, 1983) have been proposed to explain differential migration: 1) arrival time hypothesis; 2) social dominance hypothesis; 3) body size hypothesis, also known as winter cold hypothesis. These hypotheses are based on interpretations of a number of aspects of avian biology: social dominance among individuals of different age and sex groups, roles of sexes in reproduction and differential resistance to cold.

As in most species males compete in spring for breeding territories, selection should favour their wintering closer to that territory, i.e. making to possible to arrival earlier (arrival time hypothesis). Observations and trapping data show that at a given site on the migratory route the proportion of males decreases, and the proportion of females increased throughout the period of spring passage (Payevsky, 1985). Earlier spring arrival of males, known as protandry, is common, but sex-related difference in the mean arrival dates varies from several days to several weeks, depending on species and the features of the year. In some species, age and sex sequence is rather detailed: adult males are the first to arrive in spring, followed by yearling males and adult females; young females are

the last ones to arrive. It is typical of both Nearctic and Palaearctic songbirds, as shown in a review (Payevsky, 1976). Many ducks in spring migrate in pairs, after mating in winter quarters, so that sex bias is only due the behaviour of immature individuals. Experimental work has shown that sex-related difference in the onset of spring migratory activity is due to variation in circannual rhythmicity and sensitivity to photoperiod (Coppack and Pulido, 2009).

It is believed that in most birds males can survive winter in colder areas, located closer to their breeding sites, i.e. further north, because they are larger and stronger than females (body size hypothesis). Larger individuals have a smaller body surface : body volume ratio, therefore they lose thermal energy at a slower rate and can survive longer with the same feeding rate. Difference in migratory distance between sexes may be rather significant. For instance, most male ruffs (*Calidris* (*Philomachus*) *pugnax*) spend their winter within Europe, whereas reeves (females of the species) migrate to Africa. A reverse pattern is observed in birds of prey, whose females are much larger than males. After ringing on the Courish Spit in the Baltics, male sparrowhawks (*Accipiter nisus*) cover on average 1413 km, whereas females just 932 km. Females of peregrine falcons (*Falco peregrinus*) from Greenland winter around the Gulf of Mexico, and males migrate further 4000 km. These hypotheses support both the dominance hypothesis and body size hypothesis, but do not fit the predictions of arrival time hypothesis (Newton, 2008).

The difference in migratory distance of four age and sex groups of chaffinches, bramblings and European siskins in the Baltic area was only significant in chaffinches and bramblings (Payevsky, 2009). Females of these two species, both first-year and adults, spent their winter on average further south than males, among which adults wintered on average further south than juveniles. Adult male American goldfinches (*Spinus tristis*) also winter further south than first-year birds (Prescott and Middleton, 1990). As adult males spend their winter under milder conditions than juveniles but still north of females of any age, this pattern, on one hand, supports the social dominance hypothesis, but on the other hand, fits the predictions of the arrival time hypothesis.

The patterns mentioned show that benefits and costs of philopatry and dispersal in respect to wintering areas may differ for sexes due to varying selection pressures and ecological demands of males and females wintering under different conditions. Even small benefits of philopatry for one sex may exist alongside with benefits of dispersal for the other sex.

SEX-SPECIFIC SURVIVAL IN BIRDS: MALES LIVE LONGER THAN FEMALES

Sex structure of animal populations and its impact on birth rate, mortality and dispersal occupy an important place in the study of the regulation of numbers. When discussing sex-related mortality rates many authors claimed that in most animals from different taxa, humans including, males show an increased mortality as compared to females and thus a shorter lifespan (Comfort, 1964; Trivers, Willard, 1973; Geodakian, 1974; Clutton-Brock et al., 1985; Smith, 1989; Promislow et al., 1992). It was sometimes interpreted as a compensation for the male-biased sex ratio at birth, and sometimes as a consequence of inadequate energy input when raising male offspring which grows quicker. However, subsequent publications questioned the universality of this claim, first on the basis of data on birds (Payevsky, 1985; Curio, 1989) and later on some other animals as well (Gavrilov and Gavrilova, 1991). Among mammals, survival rate of males is higher than of females in a number of species of rodents, carnivors, bats and insectivors (Bolshakov and Kubantsev, 1984).

Studies of sex ratio in avian populations show that numbers of males and females in broods are usually equal. Among adults, however, sex ratio is usually male-biased, with an exception of a number of game species, where females outnumber males due to hunting pressure on the latter sex (Breitwitsch, 1989; Payevsky, 1993, 2009; Donald, 2007). Sex and age structure of a population is best considered during the breeding period, starting from the nestling stage. In chaffinches on the Courish Spit on the Baltic coast, sex ratio among 93 nestlings taken into captivity for hand-raising for subsequent experimental work was equal (47 males and 46 females). Among first-year birds males comprised in captures from 53−55% in early July to 56−61% in late August, and among adults, the overall mean was 55.9%, i.e. males consistently outnumbers females, starting from the age of one month. At the beginning of a breeding season, yearlings of both sexes made 51.1% of that population, two-year-old birds 22.4%, three-year-olds 11.6%, four-year-olds 6.5%, five-years-olds 3.9%, six-year-olds 2.6%, and 1.9% of birds were 7−11 years old (Payevsky, 1982).

A similar sex ratio has been reported for another finch, the palila (*Loxioides bailleui*), a Hawaiian honeycreeper (Lindsey et al., 1995). Sex ratio in nestlings was also equal, but males outnumbered females in first-years birds and in adults, comprising 57−69% in the latter group. A similar pattern has been found in Aleutian grey-crowned rosy finches (*Leucosticte tephrocotis griseonucha*). Among nestlings, the number of males and females was equal, whereas numbers of mature individuals always were male-biased (Schreeve, 1980). Thus, the equal sex ratio in nestlings in monogamous finches and other birds is replaced by a male-biased ratio. This pattern is common for many studied species in various families and orders (Payevsky, 1993; Donald, 2007). Apparently, a some point after gaining independence the mechanism of differential mortality is switched on, so that juvenile females, being less adapted, die more often than males. The increased mortality of females

might be caused by being less able to withstand the challenges due to females being the heterogametic sex in birds (see below). One review (Breitwitsch, 1989) discussed in what exactly age females are subject to increased mortality – as juveniles or adults from breeding-unrelated causes, or as adults due to the increased breeding effort. It is believed that as young females typically disperse farther than males after fledging, they are subject to increased mortality because of that (Greenwood, 1980). Even though no convincing evidence is available for any of these causes of increased mortality of females, many authors tend to believe that females are under much greater risk of death than males just during the breeding season.

In spite of seasonal and local variation of sex ratio, the mean annual values were very similar within species, and in many cases also between different species. It allows us to treat the increased proportion of males as a stable tendency. To test the hypothesis that male birds show higher survival rate than females, we estimated true survival and local survival of both sexes in 9 species of birds from the eastern Baltic from dead recoveries and from recaptures, and compared our results with numerous published data (Payevsky et al., 1997). True survival was estimated by ESTIMATE software (Brownie et al., 1985), and local survival rate by JOLLY software (Pollock et al., 1990). The results showed that survival of males was higher than in females in all species analysed, except of the great tit, which showed a sex-independent survival rate. However, sex-related difference in survival rate was significant only in pied flycatchers and willow warblers. Not a single species had a higher survival rate in females. This study also reviewed the data on the mean annual survival of males and females in 31 avian species from 12 orders, for many species from multiple populations (a total of 109 pairwise comparisons). In 80 cases annual survival was higher in males, and in 19 cases in females. Similar data have been obtained for passerines from Britain (Siriwardena et al., 1998), where the survival of males was higher than in females or did not differ from it in 10 species out of the 15 studied, and in just one species females survived better than males. However, exactly like in our study, the difference was significant in only two species.

Thus, one can safely say that the widely accepted concept of the increased mortality of males in all animals is not supported by the data on birds. Several hypotheses tried to explain the increased mortality of males in mammals (Trivers and Willard, 1973; Clutton-Brock et al., 1985; Clutton-Brock, 1986; Dobson, 1990). One of them is the lower resistance of the gender carrying the Y chromosome. Another hypothesis is that parents invest more energy in raising daughters rather than sons. A third explanation is the sex dimorphism in size and greater vulnerability of the larger sex to food shortages. Finally, sex-biased natal dispersal has been implicated. These hypotheses are not mutually exclusive, and unequal mortality rate might be due to a combination of factors. The causes of the increased survival of males in birds, unlike other animals, may also be discussed from the same perspectives: differential parental investment in daughters and sons when raising the young, differential natal dispersal of females and males, smaller tolerance of one of the sexes to food shortage. The hypothesis of sex-dependent cost of breeding, i.e. competition between males for females and territories and costs of egg formation and incubation for females, may also be discussed. Testing this hypothesis in a comparative analysis of sex-specific mortality in different families of birds showed that both competition between males and parental care by females may result in increased mortality, but in the evolutionary perspective increased costs of breeding should not cause higher mortality rates (Liker and Szekely, 2005). However, the genetic aspect of sex-specific survival may be most important. Different animals have several ways of chromosomal sex determination: either sex may be heterogametic or homogametic. Female birds are heterogametic (XZ), like male mammals (XY). As Y chromosome (analogous to Z) is believed to be responsible for the increased mortality, the same pattern might be expected to occur in birds. The aforementioned data agree with this hypothesis, which is probably most likely, given the rather shaky evidence in favour of the alternative explanations.

RELATIONSHIP BETWEEN SEX-SPECIFIC SURVIVAL RATES AND PHILOPATRY

Our review shows that sex and age-related dispersal and survival rates belong to the crucial components of avian life strategies, which govern population dynamics and their genetic structure. Moreover, this review strongly suggests that different levels of dispersal and different levels of survival are linked, and this relationship is reflected in sex bias in these parameters. In most bird species females perform dispersal for longer distances and suffer greater mortality, whereas males are more philopatric and survive better. Many publications that touch upon the topics of dispersal and survival, mention this relationship. For example, a study of survival rates of 14 adult songbirds in boreal forests of Canada suggested that higher site fidelity of males resulted in their higher survival rates and male-biased sex ratio in populations (Whitaker et al., 2008). A reverse sex bias is well illustrated by the case of Alaskan king eiders (*Somateria spectabilis*), where high degree of philopatry in females and a high rate of dispersal in males may result in greater survival rates in the former sex, which is also confirmed in other sea duck species (Oppel and Powell, 2010). Survival rate greatly influences population growth rate, and environmental factors may act on survival directly through mortality and indirectly via the tendency towards long-distance dispersal, where predation risk is a function of movement (Yoder et al., 2004).

Sex-related bias in the levels of dispersal and mortality

Species	ND		BD		Source*	1−S	Source*
	RR	DR	RR	DR			
Cygnus olor	M	M			5	MF	7
Anas platyrhynchos	F		F		14	F	6, 14
Anas acuta	M				5	F	6
Tetrao urogallus		F			11	F	6
Falcipennis canadensis	F	F			5	M	6
Otis tarda		M			5	M	12
Phoebastria (*Diomedea*) *immutabilis*	F	F		F	2, 5	MF	6
Phalacrocorax aristotelis	F		MF		5	F	6
Calidris alpina		F		F	5	MF	8
Calidris mauri			F	F	5, 17	F	17
Calidris pusilla				F	9	F	9
Stercorarius (*Catharacta*) *maccormicki*				F	5	MF	6
Chroicocephalus (*Larus*) *novaehollandiae*	F				5	M	6
Rissa tridactyla	F				5	M	6
Accipiter nisus	F	F	FM	F	5	F	6
Aegolius funereus		F	F	F	5	F	6
Picoides borealis	F	F	F	F	5	F	6
Falco tinnunculus				F	18	F	6
Anthus trivialis		F		F	2, 13	F	6
Fringilla coelebs	F		F		6, 13	F	6, 10
Fringilla montifringilla			MF		5	F	6
Erythrina erythrina			F		1	F	1, 6
Chloris chloris		MF		MF	5	F	10
Schoeniclus (*Emberiza*) *schoeniclus*			F	F	2, 5	F	6, 10
Melospiza melodia	MF	MF			5	F	6
Melospiza lincolnii	FM				15	F	15
Zonotrichia albicollis	M				15	F	15
Setophaga (*Dendroica*) *striata*	F				15	F	15
Setophaga (*Dendroica*) *coronata*	FM				15	F	15
Passerina cyanea		MF	F	M	5	F	6
Cyanistes (*Parus*) *caeruleus*	F				5	F	6, 10
Parus major		F		F	4, 5	F	6
Delichon urbicum		F			2	F	6
Hirundo rustica		F	F	F	5	F	6, 10
Riparia riparia	F		F		2	F	6
Phylloscopus trochilus	F		F		2	F	6
Curruca (*Sylvia*) *nisoria*	F		F		2	F	6
Curruca (*Sylvia*) *curruca*	F		F		2	F	3

Table. (Contd.)

Species	ND		BD		Source*	1−S	Source*
	RR	DR	RR	DR			
Regulus calendula	F				15	MF	15
Ficedula hypoleuca	F	F	F	F	2, 16	F	6
Turdus merula				F	5	F	6, 10
Catharus guttatus	F				15	F	15

(ND − natal dispersal, BD − breeding dispersal, RR − from return rate or the proportion of transients in captures, DR − from dispersal distance, 1−S − mortality, M − value male-biased, F − value female-biased, MF − no sex-related bias).
* 1 − Payevsky, 1981; 2 − Sokolov, 1991; 3 − Payevsky, 1992; 4 − Delestrade et al., 1996; 5 − Clarke et al., 1997, 6 − Payevsky et al., 1997; 7 − Brown, 1997; 8 − Warnock et al., 1997; 9 − Sandercock, Gratto-Trevor, 1997; 10 − Siriwardena et al., 1998; 11 − Moss et al., 2006; 12 − Martin et al., 2007; 13 − Newton, 2008; 14 − Gunnarsson et al., 2008 ; 15 − Whitaker et al., 2008; 16 − Artemyev, 2008; 17 − Johnson et al., 2010; 18 − Vasko et al., 2011

Sex-specific survival and philopatry rates are convenient to compare on the basis of the published data through the reverse parameters, dispersal and mortality, because most publications report dispersal rates, both natal and breeding. These data are compared in the table. The criterion for inclusion of a dataset was reporting quantitative data, for dispersal − either distance, or the proportion or recaptures; for mortality − the rate inverse to survival rate (1−S). In many cases the data are taken from reviews (Sokolov, 1991; Clarke et al., 1997; Payevsky et al., 1997; Newton, 2008). Certainly, in the best-case scenario, mortality data, like the data on any other demographic parameter, should be available for the same population for which the dispersal data are used. However, such publications are very rare, and the comparison is made on the specific level. It should also be kept in mind that sex-related dispersal and mortality data based on the proportion of recaptures in the same population, basically are using the same dataset. Mortality estimates from dead recoveries would have been more reliable, because it would have been an independent estimate. However, our comparison is not aimed at obtaining unbiased estimates, but to show sex-related tendencies.

To test for the significance of sex bias in the relationship between dispersal and mortality on the specific level, the sign test was used. As shown in the Table, the most common situation was F−F (25 cases), i.e. when female-biased dispersal was accompanied by female-biased mortality. The M−M situation was very rare (1 case), and M−F, MF−F and MF−M relationships were neutral, that is zero (16 cases). The sign test suggests that the birds more prone to dispersal (females), suffer significantly (<0.01) higher mortality, and conversely, philopatric birds (mainly males) survive better.

Whatever the mechanism of emigration of juvenile and adult individuals, the recruitment into a novel population should be supported by positive demographic and genetic results. The same is true of philopatry. How does the relationship between survival and spatial behaviour work? On one hand, philopatric individuals exist in a familiar environment, which secures their physical and physiological well-being and leads to longer lifespan and higher breeding performance. On the other hand, dispersal events support genetic polymorphism and this accelerate microevolutionary processes, which is essential for the ecological plasticity of populations. Higher resistance to the environmental challenges of the homogametic sex (in birds these are males) enables maintenance of stable population parameters, and enhanced sensitivity to the environment of the heterogametic sex (in birds these are females) leads to acquiring novel characters, which occurs during dispersal.

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