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Sexual selection, range size and population size

Anders Pape Møller[1] & László Zsolt Garamszegi[2]

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Abstract Sexual selection may impose fitness costs on both males and females due to the costs of developing and maintaining exaggerated sexual signals, reducing average fitness in strongly sexually selected species. Such reductions in average fitness could affect local extinction risk and hence distribution range. However, given that both sexually monochromatic and dichromatic species are common and widespread, benefits of sexual selection must be invoked to maintain equilibrium. We tested for differences in breeding range size and population size between monochromatic and dichromatic species of birds in a comparative analysis of species from the Western Palaearctic. In an analysis of standardized linear contrasts of the relationship between sexual dichromatism and range size and population size, respectively, that controlled for similarity among taxa due to common descent, we found no significant relationship. However, when we analyzed carotenoid-based sexual dichromatism sexually dichromatic species had larger distribution areas and higher northernmost distribution limits, but not southernmost distribution limits than sexually monochromatic species. In contrast, melanin-based sexual dichromatism was not significantly associated with range size or population size. Therefore, population density of sexually dichromatic species with carotenoid-based coloration was lower than that of monochromatic species, because dichromatic species had similar population sizes but larger ranges than monochromatic species. These findings suggest that the different physiological roles of pigments associated with sexual dichromatism have effects on total range size of birds.

Keywords: birds, carotenoids, melanin, sexual dichromatism, sexual selection

Összefoglalás Az ivari szelekció kihatással lehet az egyedi rátermettségre mind hímeknél, mind a tojóknál, mert a másodlagos nemi jellegek kifejlesztése és fenntartása bizonyos költségekkel terheltek, melyek visszahatnak a rátermettségre az erősen ivari szelekció alatt álló fajoknál. A rátermettségben megmutatkozó költségek további befolyással bírnak a helyi extinkciós rátára, és így az elterjedési területre. Ennek ellenére úgy tűnik, hogy az ivarilag monokromatikus és dikromatikus fajok gyakoriak és elterjedtek, így az ivari szelekció előnyei egyensúlyt teremtenek a költségekkel. Jelen komparatív vizsgálatban azt teszteltük a nyugati Palearktikus régióban költő madaraknál, hogy az ivarilag monokromatikus és az ivarilag dikromatikus fajok elterjedési területe és populációmérete is különbözik-e. A lineáris standardizált kontrasztok módszerét használva, amikor a fajok közötti rokonsági kapcsolatot is számításba vettük, nem találtunk összefüggést a vizsgált változók között. Amikor azonban csak a karotin alapú színezetre fókuszáltunk, kiderült, hogy a dikromatikus fajoknak nagyobb és északabbra nyúló elterjedési területe van, mint a monokromatikus fajoknak. Ezzel szemben, a melanin alapú színezetre nem találtunk ilyen összefüggést. Az eredményekből még arra is következtetünk, hogy a karotin alapon dikromatikus fajok populációs denzitása alacsonyabb, mint karotin alapon monokromatikus fajoké, mert a dikromatikus fajok hasonló populációmérettel bírnak, mint a monokromatikus fajok. Összegzésképpen elmondhatjuk, hogy valószínűleg a különböző pigmentekhez kapcsolódó fiziológiai mechanizmusok különböző szerepet játszanak az ivari dikromatizmus és az elterjedési területek kapcsolatának fenntartásában a madaraknál.

Kulcsszavak: madarak, karotinoidok, melanin, ivari dikromatizmus, ivari szelekció

[1] *Laboratoire d'Ecologie, Systematique et Evolution, Université Paris-Sud, Orsay France,* [2] *Department of Evolutionary Ecology, Estacion Biologica de Donana-CSIC, Seville, Spain, e-mail: laszlo.garamszegi@ebd.csic.es*

Introduction

Sexual selection arises from the fitness advantages of certain individuals over others in competition for mates, resulting in the evolution of exaggerated secondary sexual characters (Darwin 1871). While the variance in individual mating success increases as a consequence of sexual selection, this increase in variance may also have important implications for population processes. For example, an increase in the variance in reproductive success may increase demographic stochasticity with consequences for extinction risk (Sæther *et al.* 2004). Furthermore, average fitness of individuals of strongly sexually selected species may be reduced compared to species subject to less intense sexual selection, and such load due to sexual selection will invariably suppress population size relative to that expected in the absence of sexual selection (Tanaka 1996). However, the world is full of widespread and common monochromatic and dichromatic species, implying that sexual selection may also be advantageous. Given that the proportion of sexually dichromatic species is variable among taxa, and that dichromatism has evolved numerous times (Price & Birch 1996), we can assume that benefits as well as costs are present, maintaining the frequency of sexual dichromatism at an equilibrium level.

The effects of sexual selection on population processes should be visible at, at least, three different levels. First, individuals should differ in their ability to cope with the costs of sexual selection, with mating success, fecundity and viability being related to the expression of secondary sexual characters as predicted by models of condition-dependent secondary sexual characters (Andersson 1994). This should have consequences for the variance in individual contributions to populations. Second, populations consist of individuals that differ in their degree of sexual ornamentation, and this should have consequences for the local risk of extinction. Accordingly, Doherty *et al.* (2003) have shown for bird census data from North America that local extinction risk and local turnover rate are greater for sexually dichromatic than for monochromatic species. Therefore, it is not surprising that Doherty *et al.* (2003) for North American birds and Prinzing *et al.* (2002) for European birds did not find a relationship between sexual dichromatism and population trends because local extinctions would be expected to be balanced by a high local turnover rate. Third, given that species differ inherently in the costs and benefits of sexual selection, we should expect sexually dichromatic species to run greater risks of extinction than monochromatic species. Indeed, McLain *et al.* (1995, 1999) and Sorci *et al.* (1998) have shown for introduced birds to oceanic islands that the risk of immediate extinction is elevated for dichromatic compared to monochromatic species, even when controlling for potentially confounding variables such as inoculate size.

While numerous studies have investigated the effects of sexual selection on fitness components at the level of individuals, relatively few studies have investigated the effects of sexual selection at the population or species level. Here we test the prediction that population size, distribution range and northernmost and southernmost distribution limits differ between species that vary in the intensity of sexual selection. We used sexual dichromatism as a proxy for sexual selection, given that mating success (Gontard-Danek & Møller 1999) and fertilization success are positively related to sexual dichromatism within species (Møller & Ninni 1998). Similar patterns also occur among species (Andersson 1994, Møller & Birkhead 1994, Petrie *et al*. 1998). If sexual selection imposed significant average costs upon individuals of a species, we would expect population size more often to be suppressed in sexually dichromatic than in monochromatic species. Likewise, if such costs of sexual signals were present at the population level, we would expect marginal populations of sexually dichromatic species more often to go extinct (Doherty *et al*. 2003), resulting in a reduction in range size of sexually dichromatic species. We tested these predictions by analyzing range size and population size of the breeding birds of the Western Palaearctic because reliable information is readily available for the entire fauna. We have chosen range size and population as proxies of the effects of sexual selection at the species level, because these traits can be measured in a standard way in a large number of species We assume that interspecific differences in range size, distribution limits and population size reflect the outcome of population processes that occur due to local extinction risk and demographic stochasticity that may be affected by the interspecific variance in reproductive success.

Sexual coloration can be based on pigments or structural color, and pigment-based coloration can be due to carotenoids or melanins. Previous studies have implicated such pigments in various physiological functions such as free radical scavenging and immune function (e.g. McGinness *et al*. 1970, Krinsky 1989, 1998, Rózanowska *et al*. 1999, Møller *et al*. 2000, Moreno & Møller 2006), suggesting a trade-off between plumage coloration and physiological function. Therefore, we assessed sexual dichromatism for carotenoid and melanin based coloration to test explicitly if the population consequences of sexual selection differed between these two pigment categories.

Materials and methods

Study species

We included all bird species with a main breeding distribution within the Western Palaearctic (Cramp & Perrins 1977–1994) that resulted in a sample of 526 birds.

Sexual dichromatism

We scored the breeding plumage of all species as sexually monochromatic if males and females did not differ in coloration according to information provided by the descriptions in Cramp and Perrins (1977–1994), and otherwise as sexually dichromatic. This procedure was repeated separately for carotenoid- and melanin-based coloration. We distinguished carotenoid-based sexual monochromatism and dichromatism relying on colors that were yellow, orange and red as caused by carotenoids (see Tella *et al*. 2004, Olson & Owens 2005 for similar criteria). For melanin-based coloration we included all colors that were brown, black or reddish brown as typical for coloration based on phaeo- and eu-melanin (see also Gray 1996, Olson & Owens 2005).

Population size

Population sizes were obtained from Burfield and van Bommel (BirdLife International 2004), who reported the total number of breeding pairs in the Western Palaearctic west of the Ural Mountains, estimated in a consistent way from national bird census programs in all countries. We used the mean of the minimum and maximum estimates in that source.

Range size and distribution limits

We estimated total geographical breeding range size as the area of the shape bounded by the greatest span of latitude and longitude of each species' entire breeding range, as published in Cramp and Perrins (1977–1994). We extracted the northernmost, southernmost, easternmost and westernmost distribution limits for the entire breeding range to the nearest 0.1 degree from the distribution maps in Cramp and Perrins (1977–1994). To take into account the curvature of the earth (which was assumed to be spherical), this area was estimated by the equation $Area = R^2 \times (Longitude_1 - Longitude_2) \times (\sin(Latitude_1) - \sin(Latitude_2))$ where R is the radius of the earth (6366.2 km) and latitude and longitude are expressed in radians. We used the northernmost and the southernmost distribution limits as estimates of distribution limits.

In widespread species Old and New World ranges were calculated separately and subsequently summed in order to obtain more precise estimate on range sizes at the global level. The method over-estimates the real geographical range, but the error should be random with respect to the variables under test. Estimates of area were strongly positively correlated with geographical range size as calculated by counting one-degree grid cells overlain on published distribution maps for a sample of 20 Palaearctic and Nearctic bird species ($r = 0.87$, $P < 0.001$), and with range size as reported for a sample of 11 threatened species (Stattersfield & Capper 2000) ($r = 0.98$, $P < 0.001$, based on log-transformed data). Likewise, estimated range sizes based on the equation above were strongly positively correlated with estimates based on image analysis of breeding distributions of birds in the Western Palaearctic as reported in the electronic version of Cramp and Perrins (1977–1994) ($r = 0.52$, $N = 60$, $P < 0.001$, Møller *et al.* unpublished information).

The entire data set is provided in the appendix.

Comparative analyses

Analyses of comparative data based on species may provide misleading conclusions, if sister taxa are more similar with respect to the variables under investigation than randomly chosen species, and if species richness differs considerably between categories of species such as monochromatic and dichromatic species. We used statistically independent standardized linear contrasts (Felsenstein 1985), which controls for similarity among species due to common descent to test the predictions. Contrasts were calculated using the software of Purvis and Rambaut (1995), implemented in the computer program CAIC. Standardization of contrast values was checked by examination of absolute values of standardized contrasts versus their standard deviations (Garland 1992, Garland *et al.* 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses.

We $\log^{10}$-transformed distribution area and population size before analyses.

Given that sexual dichromatism was a dichotomous variable we used the Brunch procedure in CAIC to identify all independent contrasts for nodes where transitions occurred in sexual dichromatism. At these nodes positive contrasts in breeding distribution or population size imply that they vary in the same direction as sexual dichromatism. Using a t-test, we tested whether the mean of these contrasts differed from zero, as expected for correlated evolution of traits. To address problems of outlier contrasts, we analyzed the distribution of contrasts with a non-parametric test (Signed-rank test), which provided equivalent results to those obtained from parametric tests. As more breeding pairs may be present if the distribution range is larger, we also calculated population size while controlling for breeding distribution. We controlled statistically for this problem in a phylogenetically adjusted regression model of population size on breeding density. For this phylogenetically adjusted regression, using the Crunch procedure in CAIC, we regressed contrasts for the two continuous variables through the origin. Then, we fitted the slope to the raw species data, and calculated residuals from this regression line. These residuals, representing breeding density, were later analyzed by using the Brunch procedure to test for any effect of sexual dichromatism.

To determine the strength and direction of the relationship between dichromatism and distribution and population size, we estimated effect sizes (such as Cohen's sensu Cohen 1988), and the associated 95% confidence intervals (CI) for each particular phylogenetic relationship. We preferred reporting and focusing on effect sizes, instead of using Bonferroni correction and significance levels, because the latter approach has been criticized in the field of ecology and behavioural ecology due to mathematical and logical reasons (Perneger 1998, Moran 2003, Nakagawa 2004, Garamszegi 2006). Therefore, to balance between Type I and II errors, we followed the recent recommendations of Nakagawa (2004), who emphasized the importance of unbiased reports of effect sizes. We used the software Comprehensive Meta Analysis (BioStat, 2000, http://www.meta-analysis.com/) to calculate effect sizes and corresponding confidence intervals (CI).

Comparative analyses rely on a phylogenetic hypothesis for identifying independent contrasts due to a transition from one kind of sexual coloration to another. We used a composite phylogeny created by using information from Sibley and Ahlquist (1990). This phylogeny for higher taxa was supplemented with information from other sources to resolve relationships between species (Randi *et al.* 1991a, b, Sheldon *et al.* 1992, Seibold *et al.* 1993, Sheldon & Winkler 1993, Suhonen *et al.* 1994, Wittmann *et al.* 1995, Blondel *et al.* 1996, Badyaev 1997, Leisler *et al.* 1997, Slikas 1997, Cibois & Pasquet 1999, Kimball *et al.* 1999, Svensson & Hedenström 1999, Voelker 1999, Johnson & Clayton 2000, Kennedy *et al.* 2000, Sheldon *et al.* 2000, Geffen & Yom-Tov 2001, Johnson *et al.* 2001, Møller *et al.* 2001, Barker *et al.* 2002, Dimcheff *et al.* 2002, Donne-Goussé *et al.* 2002, Broders *et al.* 2003, Riesing *et al.* 2003, Cibois & Cracraft 2004, Kruckenhauser *et al.* 2004, Thomas *et al.* 2004, Voelker & Spellman 2004, Lerner & Mindell 2005, Webb & Moore 2005). We applied branch lengths from the phylogeny of Sibley and Ahlquist (1990) for higher taxonomic levels. Within families the distance between different genera was set to 3.4 $\Delta T_{50}H$ units, and between species within genera to 1.1 $\Delta T_{50}H$ units (Sibley & Ahlquist 1990, Bennett & Owens 2002). The phylogenetic hypothesis for the 526 species used in the comparative analyses is available in "nexus" format as supplementary material.

Availability of information for different variables varied, and hence sample sizes differed for the statistical tests. Although we had a huge sample size in terms of number of species, when using the Brunch procedure, contrasts could be calculated for nodes only, where transition (from 0 to 1 or from 1 to 0) occurred in sexual dichromatism. These transition events are the focus of the current study.

Results

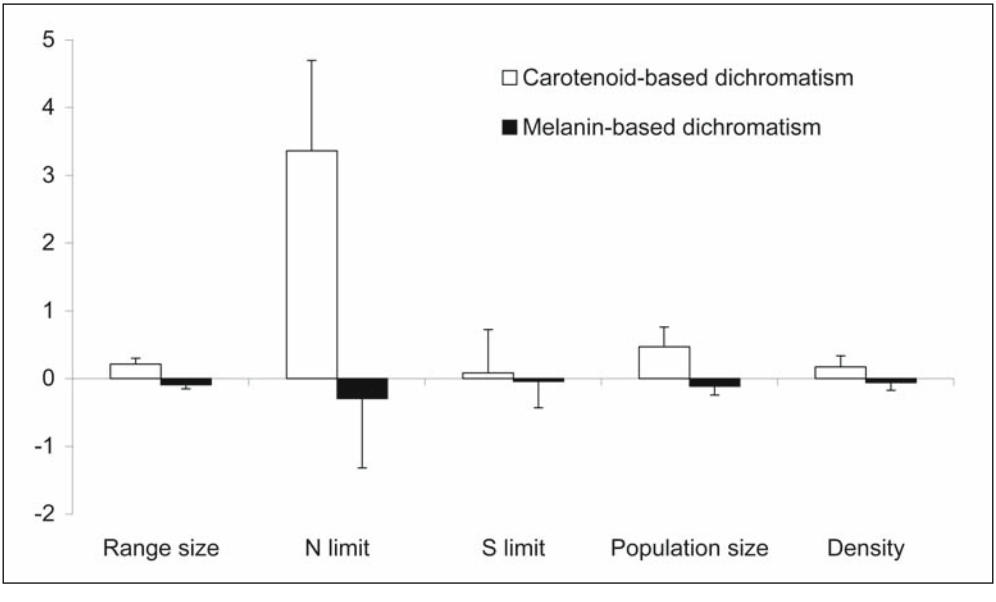
Analyzing transitions from monochromatic to dischromatic coloration, we failed to find strong effects for the relationship between range size and sexual dichromatism (Table 1). That was also the case when the analysis was restricted to melanin-based sexual dichromatism (Fig. 1, Table 1). In contrast, we detected strong effects for a phylogenetic pattern, with range size being larger for taxa with sexually dichromatic carotenoid-based coloration compared to taxa with monochromatic coloration (Fig. 1, Table 1).

The association between carotenoid-based sexual dichromatism and range size was due to an increase in the northernmost distribution limit, whereas the southernmost distribution limit did not show strong differences between monochromatic and dichromatic species (Fig. 1, Table 1). In contrast, there was no such effect at a robust magnitude for melanin-based sexual dichromatism or for overall sexual dichromatism (Fig. 1, Table 1).

Effect sizes corresponding to overall population size and density were generally small, indicating that these traits did not appear to differ considerably between mono-

Fig. 1. Mean (SE) contrasts associated with carotenoid-based and melanin-based sexual dichromatism and range size, northernmost and southernmost distribution limit, population size, and density. Numbers are sample sizes.

1. ábra Az egyes változókra (elterjedési terület, legészakabb és legdélebb elterjedési határvonal, populációméret és denzitás) számolt átlagos (SE) standardizált kontrasztok eloszlása a különböző karotin és melanin alapú dikromatizmus csoportokban. A számok a mintaelemszámokat jelzik.



chromatic and dichromatic taxa, or between melanin-based and carotenoid-based sexual dichromatism (Fig. 1, Table 1).

Variable	Effect size Cohen's d	*Upper CI*	*Lower CI*	*t*	*P*
Sexual dichromatism					
Range size	–0.420	–1.051	0.174	$t_{46} = -1.43$	0.161
Northernmost distribution limit	0.020	–0.572	0.614	$t_{47} = 0.07$	0.941
Southernmost distribution limit	–0.020	–0.614	0.572	$t_{47} = -0.06$	0.955
Population size	0.000	–0.614	0.614	$t_{44} = -0.02$	0.986
Density	–0.120	–0.749	0.497	$t_{43} = -0.39$	0.697
Melanin-based sexual dichromatism					
Range size	–0.431	–1.063	0.164	$t_{46} = -1.46$	0.151
Northernmost distribution limit	–0.085	–0.689	0.511	$t_{46} = -0.28$	0.778
Southernmost distribution limit	–0.028	–0.629	0.570	$t_{46} = -0.11$	0.916
Population size	–0.275	–0.916	0.339	$t_{43} = -0.90$	0.371
Density	–0.153	–0.784	0.464	$t_{43} = -0.50$	0.618
Carotenoid-based sexual dichromatism					
Range size	1.077	0.132	2.244	$t_{21} = 2.47$	0.022
Northernmost distribution limit	1.072	0.150	2.203	$t_{22} = 2.51$	0.020
Southernmost distribution limit	0.057	–0.843	0.967	$t_{22} = 0.13$	0.899
Population size	0.720	–0.220	1.815	$t_{20} = 1.61$	0.123
Density	0.466	–0.494	1.532	$t_{19} = 1.02$	0.323

Table 1. Effect sizes and associated 95% confidence intervals (CI) for the relationship between sexual dichromatism and population size and range size, respectively. Effect sizes are calculated for statistical analyses of standardized linear contrasts. Effect size conventions: d = 0.20 small effect, d = 0.50 medium effect, d = 0.80 large effects (Cohen 1988). Signs of effects indicate whether the evolutionary changes in dichromatism and population parameters occurred in parallel (+) or in opposite directions (–)

1. táblázat A vizsgált kapcsolatokra számolt statisztikai összefüggések erőssége *(effect size)* és az azokhoz tartozó 95%-os konfidencia intervallum. Az *effect size* metrikák a standardizált lineáris kontrasztokon alapuló statisztikai analízisekből erednek. *Effect size* konvenciók: d = 0.20 gyenge hatás, d = 0.50 közepes hatás, d = 0.80 erős hatás (Cohen 1988). Az előjelek azt mutatják, hogy az adott evolúciós változások a dikromatizmus változásával párhuzamosan (+) vagy ellentétes (–) irányban történnek

Discussion

The present comparative study of sexual dichromatism in birds and population size and range size, respectively, did not show large differences between monochromatic and dichromatic species. However, when we distinguished between carotenoid- and melanin-based coloration, there was evidence of clear relationships for carotenoid-based color. Species that were sexually dichromatic for carotenoid-based coloration had larger distributions, particularly due to more northern distribution limits compared to sexually monochromatic species. In contrast, there was no significant difference between sexual monochromatism and dichromatism for melanin-based coloration. Population size and population densities were not found to differ significantly between sexual monochromatism and dichromatism, suggesting that species of birds with sexually dichromatic carotenoid-based coloration do not have significantly smaller population sizes or densities than sexually monochromatic species. These effects imply that species-specific effects of sexual coloration on range size depend on pigments involved in producing coloration.

Total breeding range size was larger when there was a transition from sexual monochromatism to sexual dichromatism for carotenoid-based coloration, but not when there was a similar transition for melanin-based coloration. This finding for carotenoid-based coloration was robust, as the corresponding effect size was larger than one (Table 1), indicating an explanatory power of 23% on the variance in carotenoid-based dichromatism (Table 1). This result is not consistent with the prediction that sexual selection imposes fitness costs on the average individual in a population (Andersson 1994) because that prediction should have produced a negative relationship. Given that the positive relationship only existed for species with sexual dichromatism for carotenoid-based coloration, but not for melanin-based coloration, it seems likely that the difference can be attributed to differences in the function of these two categories of pigments. Carotenoids play a major role in free-radical scavenging and immune regulation and stimulation (Ames 1983, Bendich 1989, Krinsky 1989, 1998, Chew 1996, Edge *et al*. 1997, Møller *et al*. 2001). Circulating levels of carotenoids in blood are positively related to the extent of sexual dichromatism in birds (Cassey *et al*. 2005, Tella *et al*. 2004), suggesting that the level of physiological function of carotenoids is directly reflected by the external phenotype. The effect of carotenoids as antioxidants is important, but less important than that of vitamins A and E (Hartley & Kennedy 2004), whereas it is likely that the role of carotenoids in immune function is particularly important. Melanins may also act as free radical scavengers (McGinness *et al*. 1970, Rózanowska *et al*. 1999, Moreno & Møller 2006). In addition, melanin-based coloration may also be indicative of overall antioxidant status of the underlying tissue because only high concentrations of antioxidants allow melanocytes to migrate to feathers and soft tissue before depositing melanin (Bowers *et al*. 1994, 1999). We hypothesize that the different relationships between sexual dichromatism and range size for carotenoid-based and melanin-based coloration depend on these differences in physiological functions of the two categories of pigments.

We found strong evidence for a positive relationship between sexually dichromatic carotenoid-based coloration and northernmost distribution limits, but not southernmost distribution limits. Northernmost limits in the northern hemisphere are assumed to be determined by abiotic factors such as climate (Grinnell 1917, Orton 1920, Setchell 1920, Root 1988a, b), while southernmost distributions presumably are regulated by biotic interactions such as competition and parasitism (Connell 1961, MacArthur 1972, Davis *et al*. 1998, Sax *et al*. 2002). The association between northernmost distribution and carotenoid-based sexual dichromatism suggests that carotenoids may play an important role in coping with extreme abiotic conditions as found in the North.

We found no evidence of a significant association between sexual dichromatism and population size. Given the association between carotenoid-based sexual dichromatism and range size, but the absence of an effect on population size, we would a priori expect a difference in population density between these two categories of species. However, that was not the case (Table 1), suggesting that density-dependent effects on competition, predation and parasitism would not differ between sexually dichromatic and monochromatic species with carotenoid-based coloration. Doherty *et al.* (2003) did not distinguish between carotenoid-based and melanin-based coloration in their analyses of sexual dichromatism and dynamics of bird populations in North America. It would be interesting to test if the population effects of sexual dichromatism differed between carotenoid-based and melanin-based sexual dichromatism as suggested by our study.

Given that the approach we used in this study is merely correlation, we cannot exclude that the results are due to some unmeasured variables. Several life history traits may affect both distribution ranges and the intensity of sexual selection, which would undermine the causal relationship between the traits under investigation in this study. Therefore, the proposed relationships as they stand here may not be robust to alternative explanations. In this respect, we regard our study as a pioneer effort, and subsequent research may further investigate alternative hypotheses and additional confounders under the framework we followed here.

In conclusion, range size was larger and northernmost distribution limits extended to higher latitudes of sexually dichromatic birds with carotenoid-based coloration in the Western Palaearctic compared to their monochromatic relatives. There was no similar difference present for melanin-based sexual coloration, suggesting that differences in the physiological functions of these two categories of pigments are involved in determining the range size of birds.

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Appendix

Breeding range, northernmost and southernmost distribution limits, population size, and carotenoid- and melanin-based sexual monochromatism (0) and dichromatism (1) of breeding birds from the Western Palaearctic. See Material and methods for sources.

Melléklet

Elterjedési terület, legészakabb és legdélebb elterjedési határvonal, populációméret, denzitás, karotin és melanin alapú ivari monokromatizmus (0) és dikromatizmus (1) a nyugati Palearktikus zónában költő madárfajoknál. Forrásokért lásd a módszertani részt.

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Accipiter brevipes	4986692	51.73	37.17	5150	1	0	1
Accipiter gentilis	85849275	70.31	35	185000	1	0	1
Accipiter nisus	59603419	70	35	395000	1	0	1
Acrocephalus agricola	15233035	56.36	35	675000	0	0	0
Acrocephalus arundinaceus	72532661	62.5	35	2200000	0	0	0
Acrocephalus brevipennis					0	0	0
Acrocephalus dumetorum	41083168	66.33	35	3500000	0	0	0
Acrocephalus melanopogon	20376220	49.8	35	225000	0	0	0
Acrocephalus paludicola	6111856	56.85	45.8	16000	0	0	0
Acrocephalus palustris	15087288	63.93	36.96	5000000	0	0	0
Acrocephalus schoenobaenus	22251413	70.63	37.17	5900000	0	0	0
Acrocephalus scirpaceus	28303507	64.64	35	3850000	0	0	0
Acrocephalus stentoreus	124263315	47.62	35		0	0	0
Aegithalos caudatus	58625883	70.33	35	8500000	0	0	0
Aegolius funereus	42058353	69	36.19	230000	0	0	0
Aegypius monachus	24840025	45.2	35	1850	0	0	0
Alaemon alaudipes	25932168	35.45	35		1	0	1
Alauda arvensis	52936591	71.16	35	60000000	0	0	0
Alca torda	22771938	76	42.38	600000	0	0	0
Alcedo atthis	129925253	60.71	35	119500	1	0	1
Alectoris barbara	6576177	41.17	35	13750	1	0	1
Alectoris chukar	20814845	50	35	1280000	1	0	1
Alectoris graeca	2380729	47.86	36.11	59000	1	0	1
Alectoris rufa	2543626	49.3	36.09	3250000	1	0	1
Alle alle	15305102	81.75	60	27500000	0	0	0
Ammomanes cincturus	21286928	35.46	35		0	0	0
Ammomanes deserti	31819081	36.81	35	0.165	0	0	0
Anas acuta	75773492	70.63	41.82	340000	1	0	1
Anas clypeata	69906543	68.17	36.96	190000	1	0	1
Anas crecca	80853819	70.31	35.83	1060000	1	0	1

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Anas penelope	25639400	70.63	50	330000	1	0	1
Anas platyrhynchos	118317547	71.09	35	4200000	1	0	1
Anas querquedula	35857348	65.67	36.96	490000	1	0	1
Anas strepera	62053837	66.33	36.22	78000	1	0	1
Anser albifrons	23552110	75.27	57.5	67000	0	0	0
Anser anser	51496171	71.11	35	155000	0	0	0
Anser brachyrhynchos	3111481	80.14	63.93	59500	0	0	0
Anser erythropus	3989674	70.48	65.33	0.345	0	0	0
Anser fabalis	21544124	73.39	50.91	140000	0	0	0
Anthreptes metallicus	6584564	35	35		1	0	1
Anthreptes platurus	12075301	35	35		1	0	1
Anthus berthelotii	277684	35	35	60000	0	0	0
Anthus campestris	55732972	59.64	35	1450000	0	0	0
Anthus cervinus	20597343	71.17	52	2000000	0	1	1
Anthus gustavi	29537788	72.73	41.81	5500	0	0	0
Anthus hodgsoni	46149324	66	35	37500	0	0	0
Anthus novaeseelandiae	175722189	63.64	35		0	0	0
Anthus pratensis	19961896	71.17	40.83	11500000	0	0	0
Anthus spinoletta	58944503	75	35	1520000	0	0	0
Anthus trivialis	43026566	70.5	35	34500000	0	0	0
Apus affinis	131610822	37.17	35	1700	0	0	0
Apus apus	44557537	70	35	11950000	0	0	0
Apus caffer	54478159	37.61	35	0.13	0	0	0
Apus melba	87114000	48	35	235000	0	0	0
Apus pallidus	22582503	45.6	35	99500	0	0	0
Apus unicolor	287145	35	35	6250	0	0	0
Aquila adalberti	231533	41.25	37.22	0.177	0	0	0
Aquila chrysaetos	125774721	70.16	35	9700	0	0	0
Aquila clanga	22871979	65.33	39.09	0.955	0	0	0
Aquila heliaca	18651961	58.18	35	1125	0	0	0
Aquila nipalensis	22944219	52.38	35	12500	0	0	0
Aquila pomarina	30050752	59.73	35	16500	0	0	0
Ardea cinerea	174570058	68.67	35	250000	0	0	0
Ardea purpurea	155278503	53.14	35	35500	0	0	0
Ardeola ralloides	74517607	49.8	35	22500	0	0	0
Arenaria interpres	3182088	83.33	54.42	57500	0	0	0
Asio flammeus	178060822	70.47	38.91	119000	0	0	0
Asio otus	135709736	67	35		0	0	0
Athene noctua	73165616	57.64	35	930000	0	0	0
Aythya ferina	30655029	66	36.33	325000	1	0	1
Aythya fuligula	42202535	70.16	39	805000	1	0	1
Aythya marila	47354956	70.63	48.42	185000	1	0	1

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Aythya nyroca	21338265	54.31	35	15000	1	0	1
Bombycilla garrulus	17809458	70.33	50.91	415000	1	1	1
Bonasa bonasia	35793103	69	38.18	2800000	1	0	1
Botaurus stellaris	145257380	61.73	35	44000	0	0	0
Branta bernicla	30327267	83.33	60	1650	0	0	0
Branta leucopsis	3110672	80	69.5	47500	0	0	0
Bubo bubo	94837463	69.67	35	28500	0	0	0
Bubulcus ibis	263346036	46.43	35	102000	0	0	0
Bucanetes githagineus	25504270	41.9	35	16000	0	1	1
Bucanetes mongolicus	16255585	50.9	35	2760	0	1	1
Bucephala clangula	48836042	70.31	44	540000	1	0	1
Bucephala islandica	27958081	66.32	39.26	0.55	1	0	1
Bulweria bulwerii	46406721	37.44	35	8000	0	0	0
Burhinus oedicnemus	62584206	54.31	35	62000	0	0	0
Buteo buteo	80859225	67.33	35	955000	0	0	0
Buteo lagopus	37620746	71.25	54.74	58500	0	0	0
Buteo rufinus	35371740	53.66	35	11850	0	0	0
Calandrella brachydactyla	33632687	52.69	35	10650000	1	0	1
Calandrella rufescens	31693703	50.96	35	2800000	0	0	0
Calcarius lapponicus	25955434	82	52.17	8400000	1	0	1
Calidris alba	19746119	83	62.86	37500	0	0	0
Calidris alpina	45810423	76.92	50.39	435000	0	0	0
Calidris canutus	8133350	83	61.82	22500	0	0	0
Calidris maritima	20683254	81.75	58.33	51500	0	0	0
Calidris minuta	4188252	76.41	67.27	253000	0	0	0
Calidris temminckii	10498393	71.25	60	252500	0	0	0
Calonectris diomedea	17232144	43.13	35	280000	0	0	0
Caprimulgus europaeus	39661425	63.93	35	735000	0	0	0
Caprimulgus ruficollis	2799658	42.92	35	65500	0	0	0
Carduelis cannabina	35387965	66	35	19000000	0	1	1
Carduelis carduelis	42127228	63.57	35	20500000	0	1	1
Carduelis chloris	33683563	70.31	35	23000000	1	1	1
Carduelis flammea	38772112	76	44.17	13900000	0	1	1
Carduelis flavirostris	42733807	71.25	35	465000	0	1	1
Carduelis hornemanni	39828582	82	56.36	132000	0	1	1
Carduelis spinus	48827224	70	35	14000000	1	1	1
Carpodacus erythrinus	56635635	67.67	35	4550000	0	1	1
Carpodacus rubicilla	13840898	51.82	35	7550	0	1	1
Carpodacus synoicus	8760831	38.1	35		0	1	1
Carpospiza brachydactyla	7427782	40	35		0	0	0
Catharacta skua	58138003	66.17	57.59	16000	0	0	0
Cepphus grylle	69606205	81.75	42.86	215000	0	0	0

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Cercomela melanura	4572806	35	35		0	0	0
Cercotrichas galactotes	42362514	47.62	35	64000	0	0	0
Certhia brachydactyla	11981649	55.74	35	6200000	0	0	0
Certhia familiaris	52296727	70.33	35	8350000	0	0	0
Cettia cetti	22945867	52.69	35	1100000	0	0	0
Charadrius alexandrinus	147247583	57.78	35	28500	0	0	0
Charadrius dubius	133225270	68.33	35	175000	1	0	1
Charadrius hiaticula	49403011	83.33	47.8	170000	1	0	1
Charadrius morinellus	39507955	73.28	42.08	26500	1	0	1
Chersophilus duponti	3171643	42.5	35	14000	0	0	0
Chlamydotis undulata	33255952	50.9	35	0.545	1	0	1
Chlidonias hybrida	153779188	51.92	35	64500	0	0	0
Chlidonias leucopterus	28419393	58.1	35	142000	0	0	0
Chlidonias niger	36059966	62.86	36.3	126500	0	0	0
Ciconia ciconia	38978214	59.73	35	200000	0	0	0
Ciconia nigra	156543483	63.08	35	9900	0	0	0
Cinclus cinclus	32649233	71.17	35.45	250000	0	0	0
Circaetus gallicus	51628656	60.36	35	10700	0	0	0
Circus aeruginosus	216191419	66	35	116500	1	0	1
Circus cyaneus	183998444	70.31	37.78	45500	1	0	1
Circus macrourus	9449299	55.91	39.39	0.755	1	0	1
Circus pygargus	24877885	60.71	35	50000	1	0	1
Cisticola juncidis	163848711	51.15	35	665000	0	0	0
Clamator glandarius	59374967	44.79	35	67500	0	0	0
Clangula hyemalis	49483737	82.22	51.71	720000	1	0	1
Coccothraustes coccothraustes	46328895	62.5	35	3300000	1	0	1
Columba bollii	19145	35	35	6250	0	0	0
Columba junionae	19145	35	35	1750	0	0	0
Columba livia	102111594	70	35	12150000	0	0	0
Columba oenas	31125952	65	35	625000	0	0	0
Columba palumbus	42222969	67.33	35	13000000	0	0	0
Columba trocaz	686	35	35	10550	0	0	0
Coracias garrulus	27947574	60.5	35	81500	0	0	0
Corvus corax	116351764	81	35	710000	0	0	0
Corvus corone	57070552	71.17	35	12000000	0	0	0
Corvus frugilegus	47448563	65.33	35	14000000	0	0	0
Corvus monedula	31652899	66.36	35	10100000	0	0	0
Corvus ruficollis	43735051	35.43	35		0	0	0
Coturnix coturnix	138134721	61.25	35	3750000	1	0	1
Crex crex	24591322	68	40.83	1650000	0	0	0
Cuculus canorus	79987916	70.47	35	6400000	0	0	0
Cuculus saturatus	82337843	50.45	35	375000	0	0	0

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Cursorius cursor	44734680	40	35	0.36	0	0	0
Cyanopica cyanus	1669659	53.91	35	360000	0	0	0
Cygnus columbianus	24434047	72.38	55.45	10000	0	0	0
Cygnus cygnus	32594300	70	45.58	18500	0	0	0
Cygnus olor	30854760	62.41	35.92	103000	0	1	1
Delichon urbica	86520645	70.33	35	16950000	0	0	0
Dendrocopos leucotos	62001980	64.82	35	365000	0	1	1
Dendrocopos major	79065128	68.67	35	15000000	0	1	1
Dendrocopos medius	14754778	58.7	35	225000	0	1	1
Dendrocopos minor	45996198	70.63	35	775000	0	1	1
Dendrocopos syriacus	9427112	51.54	35	815000	0	1	1
Dryocopus martius	54009695	69.33	35	1070000	0	1	1
Egretta alba	256307748	50	35	17500	0	0	0
Egretta garzetta	180897650	49.08	35	81000	0	0	0
Elanus caeruleus	137707888	40.73	35	1405	0	0	0
Emberiza aureola	29976359	68.17	40	60000	1	1	1
Emberiza brunciceps	8171900	49.4	35	0.625	1	0	1
Emberiza buchanani	14835912	51.82	35	13200	1	0	1
Emberiza caesia	1979136	41.04	35	185000	1	0	1
Emberiza cia	21375695	51.82	35	2700000	1	0	1
Emberiza cineracea	470123	39.35	36.74	5200	1	0	1
Emberiza cirlus	10526563	51.73	35	3600000	1	1	1
Emberiza citrinella	26826063	70.44	38.91	24500000	1	1	1
Emberiza hortulana	27681228	67.5	35	10600000	1	0	1
Emberiza leucocephalos	26353704	68.89	35	0.075	1	0	1
Emberiza melanocephala	10976526	47.8	35	6050000	1	1	1
Emberiza pallasi	17872157	71.43	45.22	115000	1	0	1
Emberiza pusilla	11732608	70.29	56.36	6500000	0	0	0
Emberiza rustica	19690540	68.67	50.9	8050000	1	0	1
Emberiza schoeniclus	55690608	71.18	35	6800000	1	0	1
Emberiza striolata	23851423	35.65	35		1	0	1
Eremalauda dunni	14348353	35	35		0	0	0
Eremophila alpestris	59723033	73.83	35	4400000	1	1	1
Eremophila bilopha	10175943	36.14	35		1	1	1
Eremopterix nigriceps	36523947	35	35		1	0	1
Erithacus rubecula	38251134	70	35	63000000	0	0	0
Falco biarmicus	61373886	44.38	35	0.69	1	0	1
Falco cherrug	28545648	59.09	35	0.45	1	0	1
Falco columbarius	60142061	71.09	42		1	0	1
Falco eleonorae	6491767	43.13	35	6050	1	0	1
Falco naumanni	30494411	57.27	35	33500	1	0	1
Falco peregrinus	414461752	75.37	35	18500	1	0	1

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Falco rusticolus	49680402	83.33	51.59	1800	1	0	1
Falco subbuteo	66368745	66.65	35	95500	1	0	1
Falco tinnunculus	202451931	70.63	35	415000	1	0	1
Falco vespertinus	16355333	64.11	42.92	32500	1	0	1
Ficedula albicollis	7661786	58.2	38.91	1900000	1	0	1
Ficedula hypoleuca	31222685	70.67	35	16000000	1	0	1
Ficedula parva	35801053	65	36.84	3900000	0	1	1
Ficedula semitorquata	3083761	45	36	34000	1	0	1
Francolinus francolinus	12586362	41.04	35	12000	1	0	1
Fratercula arctica	29362245	81	42.86	6500000	0	0	0
Fringilla coelebs	43879941	71.25	35	185000000	1	0	1
Fringilla montifringilla	21206352	71.25	50	17500000	1	0	1
Fringilla teydea	27935	35	35	1750	1	0	1
Fulica atra	236002248	66	35	1800000	0	0	0
Fulica cristata	47534848	37.17	35	0.08	0	0	0
Fulmarus glacialis	39811561	81.89	47.8	3600000	0	0	0
Galerida cristata	83319431	57.59	35	5600000	0	0	0
Galerida theklae	25706181	43.33	35	1800000	0	0	0
Gallinago gallinago	361621654	71.25	35	1415000	0	0	0
Gallinago media	12684637	70.63	47.27	116000	0	0	0
Gallinago stenura	13666038	71.43	50.91	1750	0	0	0
Gallinula chloropus	264037374	66		1300000	0	0	0
Garrulus glandarius	70688189	69.83	35	9500000	0	0	0
Gavia arctica	52965781	73.28	41.86	71500	0	0	0
Gavia immer	40351251	77.56	41.82	1500	0	0	0
Gavia stellata	66565237	82.19	44.39	62000	0	0	0
Geronticus eremita	3925676	37.07	35	15000	0	0	0
Glareola normanni	6039961	55.24	41.88	3800	0	0	0
Glareola pratincola	91406600	47.62	35	14000	0	0	0
Glaucidium passerinum	26060857	67.83	41.43	78500	0	0	0
Grus grus	34386572	69.67	36.52	92000	0	0	0
Grus virgo	13648596	52.73	36.36	22500	0	0	0
Gypaetus barbatus	105828315	49.09	35	0.805	0	0	0
Gyps fulvus	32363011	45.58	35	20000	0	0	0
Haematopus ostralegus	46951331	71.25	36.52	375000	0	0	0
Haliaetus albicilla	76333390	70.87	35	5800	0	0	0
Hieraaetus fasciatus	154645128	45	35	1010	0	0	0
Hieraaetus pennatus	32217377	56.2	35	6650	0	0	0
Himantopus himantopus	333140845	53.33	35	50500	0	0	0
Hippolais caligata	24195303	63.57	35	55000	0	0	0
Hippolais icterina	21131336	70	36.84	5300000	0	0	0
Hippolais languida	7199961	44.76	35	25500	0	0	0

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Hippolais olivetorum	1845761	44.17	35	17000	0	0	0
Hippolais pallid	34296106	48	35	5000000	0	0	0
Hippolais polyglotta	5102647	50.38	35	2000000	0	0	0
Hirundo daurica	123066917	55.45	35	265000	0	0	0
Hirundo rustica	79406477	70.38	35	26000000	1	0	1
Histrionicus histrionicus	62285997	72	36.3	7000	1	0	1
Hydrobates pelagicus	7903184	63.39	35.65	470000	0	0	0
Hypocolius ampelinus	2789769	36.36	35		1	0	1
Irania gutturalis	6786932	43.64	35	665000	1	0	1
Ixobrychus minutus	159527643	59.91	35	90000	0	0	0
Jynx torquilla	44408201	69.5	35	940000	0	0	0
Lagopus lagopus	30623543	70.95	46.82	2700000	1	1	1
Lagopus mutus	107664662	83.33	35	915000	1	1	1
Lanius collurio	10296961	66.33	35	9650000	1	0	1
Lanius excubitor	114718756	70.62	35	325000	0	0	0
Lanius isabellinus	4992568	35	35		1	0	1
Lanius minor	22100451	55	35	1060000	1	0	1
Lanius nubicus	4100048	42.5	35	67500	1	0	1
Lanius senator	16564816	53.85	35	840000	1	0	1
Larus argentatus	58999039	71.25	47.4	1525000	0	0	0
Larus armenicus	424761	41.67	38.04	18500	0	0	0
Larus audouinii	2975151	43.33	35	18500	0	0	0
Larus canus	41869022	71.25	47.27	1045000	0	0	0
Larus fuscus	30475763	71.25	39.35	325000	0	0	0
Larus genei	14672467	35	35	46500	0	0	0
Larus glaucoides	4004503	76	60	65000	0	0	0
Larus hyperboreus	30987298	83.33	55.81	93500	0	0	0
Larus ichthyaetus	13106511	54.88	35	21500	0	0	0
Larus marinus	39787926	79.31	35.24	145000	0	0	0
Larus melanocephalus	5495226	54.31	38.7	220000	0	0	0
Larus minutes	17595446	68.25	47.27	41000	0	0	0
Larus ridibundus	43657220	68	36.67	1850000	0	0	0
Limicola falcinellus	7777206	70.16	60.36	15600	0	0	0
Limosa lapponica	5950810	70.31	63.53	4400	0	0	0
Limosa limosa	35726624	69.33	42.86	119500	0	0	0
Locustella fluviatilis	9966148	63.92	42.92	3250000	0	0	0
Locustella lanceolata	23056193	68.89	40.9	75000	0	0	0
Locustella luscinioides	30803045	59.07	35	665000	0	0	0
Locustella naevia	24571177	66	37.14	1520000	0	0	0
Loxia curvirostra	69460520	69.17	35	9400000	0	1	1
Loxia leucoptera	23590629	69.09	41.82	1950000	0	1	1
Loxia pytyopsittacus	5803577	69.67	53.85	680000	0	1	1

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Loxia scotica	25456	57.96	56.67	0.775	0	1	1
Lullula arborea	17661277	62.14	35	2300000	0	0	0
Luscinia calliope	29042344	65.45	35	0.9	1	0	1
Luscinia luscinia	16872175	65	40	5300000	0	0	0
Luscinia megarhynchos	24692308	54.42	35	8100000	0	0	0
Luscinia svecica	63131559	71.17	35	6150000	1	0	1
Lymnocryptes minimus	12293323	70.31	55.56	44000	0	0	0
Marmaronetta angustirostris	14948033	46.67	35	0.695	1	0	1
Melanitta fusca	58407439	70.63	38.48	92500	1	0	1
Melanitta nigra	51699236	74.53	46.67	115000	1	0	1
Melanocorypha bimaculata	7727760	49.09	35	1600000	0	0	0
Melanocorypha calandra	23008892	51.9	35	17000000	0	0	0
Melanocorypha leucoptera	5775780	56	42.08	42500	1	0	1
Melanocorypha yeltoniensis	2256999	53.85	47.08	5500	1	0	1
Mergus albellus	23270884	69.67	47.04	6850	1	0	1
Mergus merganser	92714908	71.25	35	60500	1	0	1
Mergus serrator	77015015	73.2	40.91	96500	1	0	1
Merops apiaster	94226129	57.5	35	740000	0	0	0
Miliaria calandra	26299101	59.26	35	14950000	0	0	0
Milvus migrans	187366916	66.33	35	82000	0	0	0
Milvus milvus	27521009	59.44	35	22000	0	0	0
Monticola saxatilis	29812419	58.18	35	210000	1	0	1
Monticola solitarius	86047027	49.09	35	190000	1	0	1
Montifringilla nivalis	23133428	51.82	35	1060000	1	0	1
Motacilla alba	96194964	71.17	35	19500000	1	0	1
Motacilla cinerea	62906102	70.33	35	1170000	1	1	1
Motacilla citreola	38290500	76.36	35	365000	1	1	1
Motacilla flava	95983445	70.67	35	10950000	1	1	1
Muscicapa striata	39661505	70.5	35	18000000	0	0	0
Nectarinia osea	15450373	35	35		1	1	1
Neophron percnopterus	65013349	48.2	35	4550	0	0	0
Netta rufina	22710229	55	35	43000	1	0	1
Nucifraga caryocatactes	60803989	67.33	35	630000	0	0	0
Numenius arquata	25798929	70.63	42.71	290000	0	0	0
Numenius phaeopus	30525640	71.11	50	260000	0	0	0
Nyctea scandiaca	3804858	83.33	56.19	3450	1	0	1
Nycticorax nycticorax	285640786	51.92	35	75000	0	0	0
Oceanodroma castro	66294810	35	35	4250	0	0	0
Oceanodroma leucorrhoa	51639528	67.83	40.95		0	0	0
Oenanthe alboniger	5816897	37.27	35		1	0	1
Oenanthe deserti	38780022	51.82	35	0.605	1	0	1
Oenanthe finschii	5174727	46	35	205000	1	0	1

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Oenanthe hispanica	12349014	45.83	35	2350000	1	0	1
Oenanthe isabellina	21902794	51.15	35	4200000	1	0	1
Oenanthe leucopyga	17221802	36.36	35		1	0	1
Oenanthe leucura	6367277	42.92	35	10050	1	0	1
Oenanthe lugens	31194386	37.27	35		1	0	1
Oenanthe moesta	8121655	35.91	35		1	0	1
Oenanthe monacha	6365661	35.79	35		1	0	1
Oenanthe oenanthe	84869865	71.17	35	8800000	1	0	1
Oenanthe pleschanka	18344613	55	35	86000	1	0	1
Oenanthe xanthorprymna	5332285	41.25	35	4550	1	0	1
Oriolus oriolus	37953232	62.86	35	5250000	1	1	1
Otis tarda	23244921	55.37	35.22	33500	1	0	1
Otis tetrax	13465079	50.98	35	210000	1	0	1
Otus scops	31441098	58.89	35	325000	0	0	0
Oxyura leucocephala	22254147	53.02	35	0.975	1	0	1
Pandion haliaetus	267565189	70	35	9300	0	0	0
Panurus biarmicus	29551674	59.26	35	360000	1	0	1
Parus ater	67081983	67.33	35	20500000	0	0	0
Parus caeruleus	22374181	67.33	35	32000000	1	1	1
Parus cinctus	26772997	70.67	51.11	1285000	0	0	0
Parus cristatus	17444546	67	36.09	9050000	0	0	0
Parus cyaneus	22366148	61	35.24	6950	1	0	1
Parus lugubris	7964820	46.88	35	875000	0	0	0
Parus major	124262164	70.67	35	68500000	1	1	1
Parus montanus	57808042	70.67	35	33000000	0	0	0
Parus palustris	60477603	65	35	4500000	0	0	0
Passer domesticus	92054602	71.25	35	96500000	1	0	1
Passer hispaniolensis	36844162	45.78	35	4500000	1	0	1
Passer iagoensis	72905	35	35		1	0	1
Passer moabiticus	2361777	38.48	35	1950	1	0	1
Passer montanus	127746779	70.1	35	3.70E+10	0	0	0
Pelagodroma marina	24137770	35	35	61000	0	0	0
Pelecanus crispus	19199362	48.88	35	1800	0	0	0
Pelecanus onocrotalus	112271620	46.8	35	4600	0	0	0
Perdix perdix	22588135	65.67	36.96	2350000	1	0	1
Perisoreus infaustus	27954938	70.33	43.64	525000	0	0	0
Pernis apivorus	24169813	66.75	35	135000	0	0	0
Petronia brachydactyla				12500	0	1	1
Petronia petronia	32839062	52.73	35	2750000	0	1	1
Petronia xanthocollis	17106070	38.04	35	1250	0	1	1
Phalacrocorax aristotelis	22003193	71.27	35	92000	0	0	0
Phalacrocorax carbo	256994846	71.27	35	340000	0	0	0

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Phalacrocorax pygmaeus	8293493	46.8	35	33500	0	0	0
Phalaropus fulicarius	23272003	79.58	65	1045	1	0	1
Phalaropus lobatus	40516880	71.25	56.48	152500	1	0	1
Philomachus pugnax	21967652	71.25	50	355000	1	0	1
Phoenicopterus ruber	94427924	52.38	35	57000	0	0	0
Phoenicurus erythrogaster	18962799	58.18	35	4050	1	0	1
Phoenicurus erythronotus	5412343	53.04	36		1	0	1
Phoenicurus moussieri	1885549	37.17	35		1	0	1
Phoenicurus ochruros	35108160	60.36	35	6400000	1	0	1
Phoenicurus phoenicurus	39333278	70.5	35	11400000	1	0	1
Phylloscopus bonelli	11145975	51.92	35	2450000	0	0	0
Phylloscopus borealis	53980390	70.29	35	6250000	0	0	0
Phylloscopus canariensis				60000	0	0	0
Phylloscopus collybita	57078465	70.29	35	45445000	0	0	0
Phylloscopus inornatus	36998188	67.67	35	20000	0	0	0
Phylloscopus nitidus	9042071	45	35		0	0	0
Phylloscopus sibilatrix	20758794	68.33	38.91	18000000	0	0	0
Phylloscopus sindianus	5398213	43.54	35	195500	0	0	0
Phylloscopus trochiloides	33405236	65.33	35	13500000	0	0	0
Phylloscopus trochilus	34702775	71.18	43.13	78000000	0	0	0
Pica pica	125873841	71.25	35	13250000	0	0	0
Picoides tridactylus	71576575	60.63	35	725000	0	1	1
Picus canus	102686392	64.29	35	250000	0	1	1
Picus viridis	15764792	66	35	945000	0	1	1
Pinicola enucleator	46544352	70.31	35	200000	0	1	1
Platalea leucorodia	72330620	53.73	35	11950	0	0	0
Plectrophenax nivalis	25494753	83	53.64	1190000	1	0	1
Plegadis falcinellus	170666899	51.71	35	19000	0	0	0
Pluvialis apricaria	15646226	71.25	50.69	600000	0	0	0
Pluvialis squatarola	21151630	77.27	58.75	6550	0	0	0
Podiceps auritus	47747524	69.67	44.21	8650	0	0	0
Podiceps cristatus	216751787	66	35	375000	0	0	0
Podiceps griseigena	50645661	67.67	37.07	44000	0	0	0
Podiceps nigricollis	143944998	58.52	35	74500	0	0	0
Polysticta stelleri	7467798	72.73	59	7700	1	0	1
Porphyrio porphyrio	203357685	48	35	24000	0	0	0
Porzana parva	17089892	59.17	36.78	100500	0	0	0
Porzana porzana	30534300	65	35	190000	0	0	0
Porzana pusilla	209099178	57.87	35	1980	0	0	0
Prinia gracilis	26799729	37.39	35		0	0	0
Prunella atrogularis	7555104	66.17	38.88	2000	0	0	0
Prunella collaris	43136324	57.27	35	140000	0	0	0

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Prunella modularis	18168515	70.67	36.84	19000000	0	0	0
Prunella montanella	15909261	72.38	50.91	0.3	0	0	0
Prunella ocularis	4561671	43.54	35	22000	0	0	0
Pterocles alchata	16583502	48	35	15500	1	0	1
Pterocles orientalis	23634655	51	35	45000	1	0	1
Pterodroma feae				0.215	0	0	0
Pterodroma madeira				0.035	0	0	0
Ptyonoprogne rupestris	50741090	50	35	245000	0	0	0
Puffinus assimilis	10870919	38.04	35	6050	0	0	0
Puffinus mauretanicus	306058	40	35.43	1850	0	0	0
Puffinus puffinus	7809271	63.39	35	370000	0	0	0
Puffinus yelkouan	1757944	44.17	35.22	23000	0	0	0
Pycnonotus leucogenys	8950084	35.43	35		0	0	0
Pyrrhocorax graculus	25554494	51.82	35	220000	0	0	0
Pyrrhocorax pyrrhocorax	71209934	56.11	35	76500	0	0	0
Pyrrhula murina	0	38.44	38.4	0.24	0	0	0
Pyrrhula pyrrhula	48033841	70.31	35	10650000	0	1	1
Rallus aquaticus	61237985	66.17	35	250000	0	0	0
Recurvirostra avosetta		58.89	35	47500	0	0	0
Regulus ignicapillus	11619889	56.3	35	5000000	0	1	1
Regulus regulus	60111318	70.29	35	27000000	0	1	1
Regulus teneriffae				15000	0	1	1
Remiz pendulinus	34607944	60.36	35	315000	1	0	1
Rhamphocoris clotbey	7281554	35	35		1	0	1
Rhodopechys obsoleta	21566986	50	35	4500	0	1	1
Rhodopechys sanguinea	18028831	48.18	35	605000	0	1	1
Riparia riparia	71056288	70.5	35	7450000	0	0	0
Rissa tridactyla	87063032	82	39	2550000	0	0	0
Saxicola dacotiae	824	35	35	1300	1	0	1
Saxicola rubetra	23515354	70	37.17	7700000	1	0	1
Saxicola torquata	191983539	66.65	35	3300000	1	0	1
Scolopax rusticola	61514142	70.16	35	4200000	0	0	0
Scotocerca inquieta	30552038	45.71	35		0	0	0
Serinus canaria	1169421	39.2	35	60000	0	1	1
Serinus citronella	1979731	49.17	38.7	337000	0	1	1
Serinus pusillus	12794168	49.09	35	550000	0	1	1
Serinus serinus	17598255	59.81	35	14150000	0	1	1
Serinus syriacus	14323	35	35		0	0	1
Sitta europaea	95378950	67	35	13250000	1	0	1
Sitta krueperi	1668810	44.38	36.09	125000	1	0	1
Sitta ledanti	1310	36.74	36.3		1	0	1
Sitta neumayeri	9963123	45.6	35	4050000	0	0	0

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Sitta tephronota	7093661	42.73	35	61000	0	0	0
Sitta whiteheadi	3650	42.5	41.67	3000	1	0	1
Somateria mollissima	30201352	80.83	42.86	1020000	1	0	1
Somateria spectabilis	16888563	82.22	66.67	41500	1	0	1
Stercorarius longicaudus	39653124	78.89	51.58	45000	0	0	0
Stercorarius parasiticus	46690152	81.75	51.11	90000	0	0	0
Stercorarius pomarinus	17351156	77.03	65.45	35000	0	0	0
Sterna albifrons	206217797	65.94	35	45000	0	0	0
Sterna caspia	242849556	65.94	35	7000	0	0	0
Sterna dougallii	146908338	56.11	35	1850	0	0	0
Sterna hirundo	137032125	71.25	35	420000	0	0	0
Sterna nilotica	82533374	58.83	35	17000	0	0	0
Sterna paradisaea	66381992	81.75	50.59	700000	0	0	0
Sterna sandvichensis	55524756	59.26	39.5	106000	0	0	0
Streptopelia decaocto	84393908	69.67	35	7850000	0	0	0
Streptopelia senegalensis	97574458	45.37	35	135500	0	0	0
Streptopelia turtur	49092131	63.84	35	5350000	0	0	0
Strix aluco	55876079	65	35	740000	0	0	0
Strix nebulosa	41488904	68.83	45.5	4400	0	0	0
Strix uralensis	41750956	68.67	35	96500	0	0	0
Sturnus roseus	11585863	54.55	35.79	134000	1	1	1
Sturnus unicolor	3716312	43.75	35	2600000	1	0	1
Sturnus vulgaris	57229673	71.25	35	39500000	1	1	1
Sula bassana	15246153	70.78	46	305000	0	0	0
Surnia ulula	54632344	70	38.95	23600	0	0	0
Sylvia atricapilla	49004644	70.1	35	37000000	1	0	1
Sylvia borin	24656982	70.31	36.74	24000000	0	0	0
Sylvia cantillans	7240806	46	35	2300000	1	0	1
Sylvia communis	34153491	69.33	35	19500000	1	0	1
Sylvia conspicillata	20177769	46.2	35	310000	1	0	1
Sylvia curruca	44818321	69.67	35	6300000	0	0	0
Sylvia deserticola	1607574	37.61	35		1	0	1
Sylvia hortensis	16088720	47.4	35	325000	1	0	1
Sylvia leucomelaena	5398066	35	35		1	0	1
Sylvia melanocephala	12182597	46	35	5600000	1	0	1
Sylvia melanothorax	24440	35.65	35	105000	1	0	1
Sylvia mystacea	5804712	46.88	35	96500	1	0	1
Sylvia nana	42836194	49.17	35	3000	0	0	0
Sylvia nisoria	17364578	62.5	38.95	730000	1	0	1
Sylvia rueppelli	941133	41.04	35	405000	1	0	1
Sylvia sarda	674571	42.93	36.52	52000	1	0	1
Sylvia undata	4095075	51.35	35	2800000	1	0	1

Species	Breeding range (km^2)	N limit	S limit	Population size	Melanin	Carotenoid	Dichrom
Tachybaptus ruficollis	170152125	60.18	35	134500	0	0	0
Tadorna ferruginea	38145652	57.14	35	26000	1	1	1
Tadorna tadorna	38534754	66.17	35	53500	1	1	1
Tarsiger cyaneus	53194293	68	35	15500	1	0	1
Tetrao mlokosiewiczi	517607	45	38.78	84500	1	1	1
Tetrao tetrix	29140443	70	40.93	2850000	1	1	1
Tetrao urogallus	23208757	30.31	41.15	880000	1	1	1
Tetraogallus caspius	1994433	40.83	35	5750	1	0	1
Tetraogallus caucasicus	251888	43.75	40.52	49500	1	0	1
Tichodroma muraria	26203595	49.09	35	69000	1	1	1
Tringa cinereus	21277895	72.73	49	48000	0	0	0
Tringa erythropus	5342798	70.31	63.75	30500	0	0	0
Tringa glareola	22194411	70.78	50	775000	0	0	0
Tringa hypoleucos	56601323	71.25	35	1160000	0	0	0
Tringa nebularia	22863287	70.31	50	117500	0	0	0
Tringa ochropus	31097993	68.83	40	565000	0	0	0
Tringa stagnatilis	13130763	60.91	44.38	22000	0	0	0
Tringa totanus	52792516	71.09	35	445000	0	0	0
Troglodytes troglodytes	85810285	69.33	35	31500000	0	0	0
Turdoides altirostris	225670	35	35		0	0	0
Turdoides squamiceps	5803178	35	35		0	0	0
Turdus iliacus	25824771	71.17	49	18500000	0	0	0
Turdus merula	86850440	71.17	35	61000000	1	1	1
Turdus philomelos	30851069	70.33	36	28000000	0	0	0
Turdus pilaris	24506818	71.17	44.58	19000000	0	0	0
Turdus ruficollis	16765713	66.65	36	12500	1	0	1
Turdus torquatus	17793028	71.17	36.09	490000	1	0	1
Turdus viscivorus	33724781	69	35	5200000	0	0	0
Tyto alba	419862587	57.45	35	165000	0	0	0
Upupa epops	161518909	60	35	1295000	1	0	1
Uria aalge	54241213	78.89	39.35		0	0	0
Uria lomvia	52613330	81	46.83	2200000	0	0	0
Vanellus vanellus	37072931	70.16	35.79	2250000	1	0	1
Zoothera dauma	78736278	60.71	35	62500	0	0	0

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Sex ratio adjustment in birds

Eszter Szász[1], Dorottya Kiss[1] & Balázs Rosivall[1*]

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Abstract In a number of bird species, the sex ratio of the broods is not random, instead it is related to parental quality and environmental conditions. Several hypotheses have been proposed to explain this phenomenon, the so called sex ratio adjustment. According to these hypotheses, sex ratio adjustment is expected to evolve when the fitness benefit an offspring confers to the parents changes with ecological or social factors in a sex-specific way. Though many correlative and experimental studies support these hypotheses, there are still unresolved problems. In our paper, we provide details on the hypotheses related to sex ratio adjustment and explanations for the differences observed in sex ratio patterns between populations and years. Finally, we discuss the importance of sex ratio adjustment for species conservation.

Keywords: environmental effects, life-history, parental quality, sex allocation, sex ratio manipulation, species conservation

Összefoglalás Számos madárfajnál kimutatták, hogy a fészekaljak ivararánya nem véletlenszerű, hanem a szülői vagy környezeti tulajdonságok függvényében változik. Az ivararány-manipuláció néven ismert jelenség magyarázatára számos elméletet dolgoztak ki. Ezek szerint az ivararány-manipuláció azokban az esetekben alakulhat ki az evolúció során, amikor a hím és tojó utódok túlélése, várható szaporodási sikere vagy felnevelési költsége eltér. Bár számos korrelatív és kísérletes vizsgálat támogatja ezeket a hipotéziseket, vannak még az ivararány-manipulációval kapcsolatban megoldatlan kérdések. Cikkünkben részletesen tárgyaljuk az ivararány-manipulációt magyarázó elméleteket, valamint az ivararány-mintázatok populációk és vizsgálati évek közötti eltéréseinek lehetséges okait. Kitérünk a jelenség természetvédelmi jelentőségére is.

Kulcsszavak: életmenet, fajvédelem, ivararány-manipuláció, környezeti hatások, szülői minőség

[1]Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University,
1117 Budapest, Pázmány Péter sétány 1/c.
[*]corresponding author: rosi@ludens.elte.hu

Introduction

It has been revealed in a number of species that the sex ratio of the offspring is not random, instead it is related to parental quality and environmental conditions. These patterns are suggested to be adaptive, if the sex with the higher fitness potential is overproduced. This phenomenon is called sex ratio adjustment (or sex ratio manipulation), and it can evolve if the following conditions are met: (1) fitness benefit from male and female offspring varies with parental quality and environmental conditions in a predictable and sex-specific way; (2) the costs and benefits associated with the adjustment have a positive balance. As the predictability of and the difference in the fitness of male and female offspring increases, the selection for and the degree of sex ratio adjustment is also expected to increase (Oddie 1998, West & Sheldon 2002). Note that the net benefit of adjustment depends on the underlying mechanisms, thus more precise and less costly mechanisms are more likely to evolve and they are expected to result in more biased offspring sex ratios.

The exact mechanisms of sex ratio adjustment have been undetermined so far. However, it is possible that sex ratio adjustment has evolved multiple times during phylogeny, and thus different mechanisms are at work in different bird species. Nonetheless, in birds, females have been suggested to have more opportunity to adaptively bias the sex ratio of the offspring (Krackow 1995) for the following reasons. Female is the heterogametic sex (i.e. females possess two different, while males possess two similar sex chromosomes), and the sex of the offspring is determined just before ovulation during the first meiotic division. In addition, fertilisation and egg formation also take place inside the female's body. Manipulation at these early stages leads to biased "primary sex ratio" (i.e. biased sex ratio at egg laying). When sex ratio is altered after egg laying, the term "secondary sex ratio adjustment" is used. In the latter, fathers may also be involved (e.g. via sex-specific paternal provisioning). However, the adaptive value of secondary sex ratio adjustment is questionable, since it is achieved by differential mortality of the sexes, instead of differential production of the sexes, which may be beneficial under extreme conditions only (Clutton-Brock 1991).

After molecular sex determination techniques had been developed (Griffiths *et al.* 1998, Fridolfsson & Ellegren 1999), sexing the offspring at early stages and thus examining primary sex ratios became possible. The number of studies has been steadily and rapidly growing since then. Today, there is evidence for primary sex ratio adjustment in species from half of the avian orders (Pike & Petrie 2003), which suggests that this phenomenon is quite widespread in birds. Below, we review the hypotheses related to primary sex ratio adjustment, their implications for conservation biology, and discuss the potential problems arising in this research field.

Frequency-dependence and sex ratio

Early theories on sex ratios argued that the most common sex ratio, that is 0.5 (i.e. the proportion of males in the population is 0.5), is the result of frequency-dependent selection (Düsing 1884). Keeping in mind that in sexually reproducing populations, all the males taken together have exactly the same number of offspring as all the females taken together, it is easy to see that when one sex becomes less abundant it will have on average a greater number of offspring than the sex in majority. Consequently, as Düsing (1884) argued, it is adaptive to produce the rare sex, because this way parents can maximize their fitness. Such frequency-dependent sex ratio adjustment should lead to a population sex ratio of 0.5. However, as Fisher (1930) pointed out, in many species (e.g. in sexually size dimorphic species), the costs of producing or rearing male and female offspring differ. In these species, producing the more costly sex at a population sex ratio of 0.5 causes net fitness loss, because, despite the larger investment, the same fitness benefit is achieved as by producing the less costly sex. When less individual of the more costly sex is produced accordingly, its frequency in the population declines, hence its fitness potential increases. Finally, as a result of frequency-dependent sex ratio adjustment, the proportion of the sexes in the population will be the inverse of the proportion of the production and rearing costs of the sexes (e.g. if males cost 20% more, there will be 20% less males in the population). In other words, parents, on average, invest the same amount of energy into male and female offspring. This argument is called the "equal investment hypothesis" or the "Fisher-hypothesis" (Fisher 1930).

Individual variation in brood sex ratio

The theory of Düsing (1884) and Fisher (1930) does not take into account the individual variation in offspring sex ratio. However, such variation may be adaptive, because of individual variation in factors that may influence offspring fitness in a sex-specific way. Trivers and Willard (1973) were the first who gave prediction for individual offspring sex ratios. Their influential theory was developed for polygynous mating system.

The Trivers–Willard-hypothesis (TWH) has the following assumptions: (1) body condition of the offspring is correlated with body condition of the mother; (2) body condition of the offspring predicts their future reproductive success; (3) body condition has a disproportionately greater impact on the reproductive success of males, thus maternal body condition has a disproportionately greater impact on the future reproductive success of male offspring. The latter is a consequence of polygyny, since males in superior body condition are favoured both in male-male competition and during mate choice, resulting in a skewed genetic contribution to the next generation. It means that male reproductive success is highly variable, whereas female reproductive success is less variable. If the above assumptions are met, one may expect that mothers in better than average body condition overproduce sons, whereas mothers in poorer than average body condition overproduce daughters to maximize their net fitness return. This prediction not only holds for polygynous species, but also for many socially monogamous ones. Namely, in most bird species, extra-pair copulation and facultative polygyny occur (Griffith *et al.* 2002), thus the reproductive success of males may vary more than that of females. Indeed, in the Tree swallow *(Tachycineta bicolor)*, where extra-pair young add up to the 38-76% of all the offspring (Whittingham & Dunn 2000), a positive relationship has been found between maternal body condition and the proportion of sons in the brood.

The logic of the TWH can be extended to any parental or environmental attribute that may have sex-dependent relationship with offspring reproductive success. Parents of good quality, or in better breeding environment, should overproduce the sex that has a more variable reproductive success along the attribute of the parents or the breeding environment, whereas parents of poor quality, or in a poorer environment, should overproduce the sex that has a less variable reproductive success along the given attribute. Such attributes include maternal age, maternal mating status (i.e. primary or secondary female), paternal attractiveness (e.g. plumage colouration), parental social rank and parental genetic quality (manifested e.g. in body size or immune capacity), food availability, and also timing of breeding (for a review see Hasselquist & Kempenaers 2002). Note that the listed attributes are not independent from each other, making it hard to determine their relative importance in sex ratio adjustment. Below, we try to give an overview about the most significant hypotheses that follow the Trivers–Willard-logic.

Perhaps the "male attractiveness hypothesis" (Burley 1981, 1986) has the clearest theoretical background: (1) traits that determine sexual attractiveness of males are heritable; (2) females prefer the attractive males during mate choice; (3) attractivity thus influences the reproductive success of males disproportionately more than that of females. Consequently, one may expect that females mated to more attractive males overproduce sons, whereas females mated to less attractive males overproduce daughters. Quite a few studies showing a positive correlation between feather ornamentation and brood sex ratio support this hypothesis (correlative studies: Collared flycatcher, *Ficedula albicollis*, Ellegren *et al*. 1996, Blue tit, *Cyanistes caeruleus*, Griffith *et al*. 2003; experimental studies: Zebra finch, *Taeniopygia guttata*, Burley 1981, 1986, Blue tit, Sheldon *et al.* 1999, Peafowl, *Pavo cristatus*, Pike & Petrie 2005). In addition, in species, where offspring body size is correlated with paternal body size and large body size is preferred during mate choice, females mated to larger male often overproduced sons (Great tit, *Parus major,* Kölliker *et al.* 1999, Rhinoceros auklet, *Cerorhinca monocerata*, Addison *et al*. 2008).

The mating status of the mother and the sex ratio of the brood also correlated in some species: broods of primary females contained more sons than broods of secondary females (Yellow-headed blackbird, *Xanthocephalus xanthocephalus*, Patterson & Emlen 1980, Oriental reed warbler, *Acrocephalus orientalis*, Nishiumi 1998, Great reed warbler, *A. arundinaceus*, Westerdahl *et al*. 2000). Because males are predominantly feeding at the primary nests, and, as a result of the polygynous mating system, male offspring are likely to profit more from the extra paternal investment, the observed patterns seem to be adaptive.

Numerous studies provide evidence for the "maturation time hypothesis" (Daan *et al.* 1996), which suggests that in those species, where timing of the first breeding is sex-specifically related to the date of fledging, a shift in the brood sex ratio during the breeding season may be adaptive. Accordingly, in species where the timing of the first breeding is influenced by fledging date in males, but not in females (e.g. the Common kestrel, *Falco tinnunculus*, Dijkstra *et al.* 1990, the Lesser kestrel, *F. naumanni*, Tella *et al.* 1996, and the American kestrel, *F. sparverius*, Smallwood & Smallwood 1998), male offspring were overproduced early in the breeding season, and female offspring were overproduced late in the breeding season. A seasonal brood sex ratio shift in the opposite direction was found in species, where the age at first breeding is advanced by early fledging in females, but not in males (see e.g. the Marsh harrier, *Circus aeruginosus*, the Goshawk, *Accipiter gentilis*, the Sparrowhawk, *A. nisus*, Daan *et al*. 1996).

There are examples for seasonal brood sex ratio shift in passerines too, but in these cases the adaptive reason may be other than a sex-difference in maturation time. For example, in the Eastern kingbird *(Tyrannus tyrannus)*, the early broods contained disproportionately more sons, which can be explained by the decline in recruitment probability with fledging date in males and the lack of this relationship in females (Dolan *et al*. 2009). In the Brown songlark *(Cincloramphus cruralis)*, early broods contained a surplus of daughters (Isaksson *et al*. 2010). Although, the authors had no information on the effect of fledging date on recruitment probability, they argued that the pattern may be the result of male offspring being more sensitive to the environment or more costly to rear (see below).

The TWH and the other hypotheses discussed above are based on sex differences in the future reproductive success of the offspring. However, the net fitness benefit through male and female offspring may also be influenced by the sex-specific survivorship of the offspring. Therefore, under unfavourable conditions, it may be beneficial for the mothers to produce the less sensitive sex, when sensitivity to rearing environment differs between male and female offspring (Råberg *et al.* 2005). Hereafter, we refer to this argument as the "sensitivity hypothesis". It is supported, for example, by some studies on Zebra finches. Under poor food conditions, female offspring grew slower (Martins 2004) and, accordingly, mothers produced male-biased broods (Bradbury & Blakey 1998, Kilner 1998).

All the above hypotheses on brood sex ratio overlook the fact that birds usually breed multiple times during their lifetime, making the trade-off between the current and the future reproductive event another factor that may influence the manipulation of brood sex ratio. This is because, as we mentioned earlier, producing or rearing male and female offspring may impose different costs on the parents. The relative cost of the sexes is usually estimated by the difference in their body size or body weight (Dijkstra *et al.* 1998, Ewen *et al.* 2001), but egg size (Cordero *et al.* 2000, 2001), food provisioning rate (Suorsa *et al.* 2003) and maternal stress hormone level during rearing (Addison *et al.* 2008) has also been reported to vary with offspring sex or sex ratio. Whenever there is a difference in the amount of investment required by male and female offspring, mothers in poorer body condition may overproduce the less demanding sex to ensure their own survival and future breeding. This is the "cost of reproduction hypothesis" for sex ratio adjustment (Cockburn *et al.* 2002). In line with the hypothesis, the smaller sex was overproduced by mothers in poor body condition (Lesser black-backed gull, *Larus fuscus*, Nager *et al.* 1999, Great skua, *Stercorarius skua*, Kalmbach *et al.* 2001, Japanese quail, *Coturnix japonica,* Correa *et al.* 2011).

In some bird species, the net fitness benefit through male and female offspring is influenced not only by sex-specific survivorship and reproductive success but also by sex-specific difference in site fidelity (i.e. offspring of the "philopatric sex" remain on the natal territory, while offspring of the "dispersive sex" leave and breed further away). The "local resource competition hypothesis" (LRC, Cockburn *et al.* 2002) says that in case of competition for limited resources between family members, it is beneficial for the mothers to produce the dispersive sex. Indeed, such a pattern has been found in the Western bluebird (*Sialia mexicana*, Dickinson 2004) and in the Bell miner (*Manorina melanophrys*, Ewen *et al.* 2003). Theoretically, it is possible that the limited resource is one of the sexes. This special case is called the "local mate competition hypothesis" (Hamilton 1967). The other side of the coin is described by the "local resource enhancement hypothesis" (LRE, Cockburn *et al.* 2002). It can be applied to cooperative breeders, where offspring of the philopatric sex help their parents in rearing the subsequent broods. Accordingly, the LRE says that as long as the presence of the helpers provides fitness advantage for the parents, selection favours the production of the philopatric sex. However, the fitness benefit of the helpers is decreasing as their number is increasing, because resources may become limited and this means that the LRC comes into effect. The complementary nature of the LRC and LRE can be best illustrated by the classical study on the Seychelles warbler (*Acrocephalus sechellensis*, Komdeur *et al.* 1997). In this species, female offspring stay on the natal territory to help, while male offspring disperse. When parents bred on high quality territory and had few helpers, philopatric daughters, whereas when parents bred on low quality territory or had enough helpers, dispersive sons were produced.

Complications of studying sex ratio adjustment

Though each hypothesis is supported by a number of studies, there are unresolved problems concerning sex ratio adjustment. Apart from the lack of knowledge on the mechanism, these are: (1) several studies have not found any relationship between the examined factors and offspring sex ratio or found a relationship, which contradicts the predictions; (2) results often differ between populations of the same species or between study years of the same population. The reasons behind these two problems overlap. (i) Considering the complex physiology and life-history of birds, it is very likely that a number of factors are involved in sex ratio adjustment, which act simultaneously and sometimes antagonistically and thus may cancel each other's effect (Frank 1990, Cockburn *et al*. 2002). (ii) Sex ratio adjustment is often predicted without information on whether parental or environmental quality has a sex-dependent effect on offspring fitness in the given study population, though this would be a prerequisite for sex ratio adjustment (Hasselquist & Kempenaers 2002). (iii) It is also rarely investigated before the authors make predictions, whether offspring impose sex-dependent costs on the parents. (iv) The sample sizes are often too small to obtain results with sufficient power (Rosivall 2008). (v) In several cases, the applied methodology does not allow the correct examination of sex ratio adjustment, or differs between studies making comparisons difficult. (vi) The fitness benefit of sex ratio adjustment may significantly vary with ecological or social conditions, and thus the sex ratio patterns are expected to differ between years and populations.

Collared flycatchers provide a good example how sex ratio patterns may differ between populations. In a Swedish population, males with the larger forehead patch had male-biased broods (Ellegren *et al*. 1996). On the contrary, in a Hungarian population of the species, there was no such a relationship between male phenotype and brood sex ratio (Rosivall *et al*. 2004). A likely explanation for this pattern is that the information content of male plumage characteristics differs between the two populations. Specifically, the size of the forehead patch is condition-dependent in the Swedish population (Gustafsson *et al*. 1995, Ellegren *et al*. 1996), while it is not in the Hungarian population (Hegyi *et al*. 2002), even though it seems to be heritable at both locations (Qvarnström 1999, Hegyi *et al*. 2002). Taking together, forehead patch size related sex ratio adjustment may be beneficial for Collared flycatcher females in the Swedish population, but not or less beneficial in the Hungarian population.

Sex ratio patterns differed also between Blue tit populations. In a Swedish population of the species, males with more UV reflective crown had more sons, and the UV reflectance of the crown had a positive relationship with male viability (Sheldon *et al*. 1999, Griffith *et al*. 2003). Pairs of more viable male Blue tits biased their brood sex ratio towards sons in another Swedish population too (Svensson & Nilsson 1996). However, at other locations, neither male survival (United Kingdom, Leech *et al.* 2001) nor male crown colouration (France, Dreiss *et al.* 2006) showed relationship with brood sex ratio. More recent results suggest that the relationship between male crown colouration and brood sex ratio is even more complex than it had been thought before. In an Austrian Blue tit population, females biased their brood sex ratio towards sons when paired to juvenile male with more UV reflective crown or adult male with less UV reflective crown (Delhey *et al.* 2007). Delhey *et al.* (2007) argued that this pattern is consistent with the finding that the information content of male plumage characteristics may differ between age categories. UV reflectance correlated positively with testosterone level among juvenile males, while correlated negatively with testosterone level and success in siring extra-pair young among adult males. Because of methodological differences between the studies (i.e. interaction between crown colouration and age was apparently not examined in the former studies), we can only speculate about the generality of the more recent results. In addition, methodological differences make it difficult to interprete the lack of relationship between male crown colouration and brood sex ratio in the French population. In this population, UV colouration was measured on two superimposed feathers collected from the crown of each male (Dreiss *et al.* 2006), while the other studies measured colouration on the crown of the living birds (Sheldon *et al.* 1999, Delhey *et al.* 2007).

Studies on Great tit populations also yielded mixed results. In a Swiss population of the species, male body size had a positive relationship with the proportion of sons in the brood (Kölliker *et al.* 1999), while in a British population, using 5 years of data, no such a relationship was found (Radford & Blakey 2000). The latter study revealed some significant relationships when years were analysed separately, but strength and direction of the relationships did not show consistency across years (Radford & Blakey 2000). This can be either the result of the relatively low sample sizes per year or the yearly variation in the fitness benefits of sex ratio adjustment.

To resolve the contradictions and to improve our understanding of sex ratio adjustment, studies with larger sample sizes and consistent methods on multiple populations and multiple years are required. However, we have to note that even if we have such studies, our understanding of the evolution of sex ratio adjustment will be hampered by the difficulty to determine the real factors involved, because different hypotheses often give the same prediction. For instance, according to the "male attractiveness hypothesis", pairs of more attractive males rather produce sons, whereas pairs of less attractive males rather produce daughters. However, when attractivity is positively correlated with body condition or the quality of paternal care and male offspring are more sensitive to the environment or more costly to rear, the "sensitivity hypothesis" and the "cost of reproduction hypothesis" predict the same pattern, albeit the selective forces are different in each of the three scenarios.

Implications of sex ratio adjustment for species conservation

The survival chance of small populations of endangered species may be influenced by sex ratio adjustment. Therefore, the knowledge and application of the relevant theories may significantly contribute to the success of *in situ* and *ex situ* species conservation programs. The measures taken in the case of the Kakapo *(Strigops habroptilus)* provide an excellent example. The Kakapo is a sexually size dimorphic, lek polygynous, endemic parrot of New Zealand. The number of individuals had dropped dramatically by the 1990s, because this flightless, ground nesting species had been an easy prey to the introduced mammals. Moreover, predation rate was higher for females, because only females incubate and rear the nestlings. As a result, the population sex ratio became male-biased (Clout *et al*. 2002). In 1989, a recovery program was started. The females were provided with *ad libitum* supplementary food to increase their bodyweight above the threshold necessary for breeding. However, as a result of this food regime, the body condition of the females improved so much that it was accompanied with male-biased offspring sex ratios (Clout *et al*. 2002). Considering the larger size and the greater variance in the reproductive success of males in this lek polygynous species, this result perfectly fits to the prediction of the TWH, the "sensitivity hypothesis" and the "cost of reproduction hypothesis". The observed sex ratio bias was suggested to hinder population growth and increase the risk of extinction (Robertson *et al*. 2006). Based on these findings, a new food regime has been developed that keeps female body weight above the breeding threshold, but prevents unbalanced offspring sex ratios (Robertson *et al*. 2006).

The Eurasian treecreeper *(Certhia familiaris)* is not an endangered species, however, its case is very relevant because habitat destruction is one of the most important issues of conservation biology. It alters landscape structure, the proportion of open areas and edges, and also the composition of the community. Therefore, members of the community may have to breed under unfavourable conditions, and this may have an impact on offspring sex ratio. The Eurasian treecreeper, which prefers old, continuous and diverse forests, produced female-biased broods when breeding in edges (Suorsa *et al*. 2003). This pattern seems to be adaptive, because the main food item of the species was scarce in the edges of the forest fragments and male nestlings being larger and suffering higher mortality before fledging are likely to be more costly to rear and more sensitive to the poor environment (Suorsa *et al.* 2003). Similar offspring sex ratio biases in small habitat fragments, either due to sex-specific sensitivity or sex-specific site fidelity, would increase the extinction risk of an endangered species.

Concluding remarks

Despite the problems that have arisen concerning sex ratio adjustment, this phenomenon seems to be quite widespread in birds (West & Sheldon 2002). Though further studies with larger sample sizes and consistent methods on multiple populations and years are clearly needed, the knowledge that has accumulated up to present is already valuable. For example, the application of the related theories may help to design breeding programs and conservation measures which promote the survival of threatened species by optimizing offspring sex ratios (Wedekind 2002).

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Relationship between sexual signals and louse (Insecta: Phthiraptera) infestation of breeding and migrating Barn swallows *(Hirundo rustica)* in Hungary

Enikő Gál[1], Tibor Csörgő[2] & Zoltán Vas[3,4,5,*]

Enikő Gál, Tibor Csörgő & Zoltán Vas 2012. Relationship between sexual signals and louse (Insecta: Phthiraptera) infestation of breeding and migrating Barn swallows *(Hirundo rustica)* in Hungary. – Ornis Hungarica 20(1): 37–43.

Abstract Lice (Phthiraptera) chew characteristic holes on the remiges and rectrices of Barn swallows *(Hirundo rustica)*. The number of these holes correlate positively with the intensity of louse infestation, hence hole counts are useful to quantify lousiness. Several papers showed that lice affect both life expectancy and reproductive success of hosts. In male Barn swallows, the length of the outermost tail feathers act as a sexual signal. Females prefer long-tailed males, which have significantly fewer feather holes. In this study we sampled breeding and migrating Barn swallows and compared their louse burden, and the relationship between tail length and the number of feather holes. We found significant negative correlation between feather holes and tail length in breeding males; however, we found non-significant correlation in migrating males. We suggest that attractive males have more physical interactions (e.g. extra-pair copulation) during the breeding season, than less attractive males, hence they are more exposed to louse transmission, and therefore the difference in the infestation declines towards the end of the breeding season. However, given that migrating swallow groups include colonial and solitary breeding birds, it cannot be excluded that a potentially different louse distribution on solitary breeding birds may contribute to the results.

Keywords: ectoparasites, lice, feather holes, extra-pair copulation, sexual selection

Összefoglalás A füsti fecskék *(Hirundo rustica)* evező- és faroktollain a tolltetvek (Phthiraptera) karakterisztikus lyukakat rágnak. A toll-lyukak száma korrelál a tolltetű fertőzöttség intenzitásával, így a toll-lyukak megszámolásával a fertőzöttség jól becsülhető. A magasabb tolltetű fertőzöttségi intenzitás a füsti fecskék túlélési és szaporodási esélyeit is csökkenti. A hosszabb szélső faroktollú füsti fecske hímek kevésbé fertőzöttek, mint a rövidebb farkúak, így a szélső faroktollak hossza a fertőzöttség megbízható jelzéseként szolgálhat a tojók számára. Munkánkban vizsgáltuk, hogy a költési időszak során, a vonulási időszakra megváltozik-e a költő populációkban kimutatott negatív korreláció a szexuális szignálok és a tolltetű-fertőzöttség között. Költési időszakban és vonulási időszakban jelölt füsti fecskéken összehasonlítottuk a toll-lyukak gazdaegyedek közötti eloszlását, a fertőzöttség mérőszámait és összefüggését a szexuális szignálok kifejezettségével. A költő hímeknél negatív korrelációt találtunk a farokhossz és a toll-lyukak száma közt, a vonuló hímeknél azonban ez az összefüggés nem volt kimutatható. Hipotézisünk szerint a költési időszak során a „vonzóbb" hímek gyakrabban és több fajtárssal kerülnek fizikai kontaktusba, mint „kevésbé vonzó" társaik, így ezek során nagyobb esélyük van tolltetvekkel fertőződni, ezáltal a költési időszak elején lévő fertőzöttségbeli különbség a vonulási időszakra lecsökkenhet. Ugyanakkor a minták különböző összetétele (a vonuló csapatokhoz magányosan költő madarak is társulnak) is hozzájárulhat a kapott eredményhez.

Kulcsszavak: élősködés, ektoparazita, toll-lyuk, ivari szelekció

[1]H-1164 Budapest, Bóbitás str. 24., Hungary, [2]Eötvös Loránd University, Institute of Biology, Department of Anatomy, Cell and Developmental Biology, H-1117 Budapest, Pázmány str. 1/C, Hungary, [3]Szent István University, Faculty of Veterinary Science, Department of Biomathematics and Informatics, H-1078 Budapest, István str. 2., Hungary, [4]Hungarian Natural History Museum, Department of Zoology, H-1088 Budapest, Baross str. 13., Hungary, e-mail: vas.zoltan@gmail.com, [5]Ócsa Bird Ringing Station, H-2364 Ócsa, Némedi str. 592/1., Hungary, [*]corresponding author

Introduction

Lice (Insecta: Phthiraptera) are wingless, quite host-specific obligate ectoparasites of birds and mammals. They complete their entire life-cycle on the body surface of their hosts; hence their transmission requires direct physical contact among host individuals. Price *et al.* (2003) summarized their taxonomy, distribution and biology (for a Hungarian overview see Rózsa 2003).

Feather lice chew characteristic holes on the remiges and rectrices of Barn swallows *(Hirundo rustica)* as first described by Møller (1991) based on a strong positive correlation between the number of feather holes and the intensity of louse infestation. Møller (1991) suggested that the causative agent of feather holes is either *Machaerilaemus malleus* or *Myrsidea rustica* (Phthiraptera: Amblycera), however, a more recent study found that feather holes are more likely the chewing traces of *Brueelia domestica* (Phthiraptera: Ischnocera). Given that the diametrical size of these holes is about 0.5-1 mm, their count is highly repeatable, hence hole counts act as a proxy of the intensity of louse infestation (Møller 1991). In the recent years several important studies in parasite ecology were based on the feather holes of Barn swallows (Møller 1991, Saino *et al.* 1997, Kose *et al.* 1999, Kose & Møller 1999, Garamszegi *et al.* 2005, Pap *et al.* 2005).

The intensity of louse infestation affects both life expectancy and reproductive success in Barn swallows. Lice damage the structure of important flight feathers (and even cause feather breakage in extreme cases) by chewing feather holes. Hence, hosts with high louse intensity may have an aerodynamical disadvantage, causing higher mortality during migration (Kose & Møller 1999, Barbosa *et al.* 2003, Pap *et al.* 2005). Additionally, sexual selection may disfavour males with high louse burden, too. According to the theory of parasite-mediated sexual selection, females tend to choose uninfested males to ensure the parasite-resistant alleles for their offsprings and to avoid parasite transmission from the mates (Hamilton & Zuk 1982, Clayton 1991, Able 1996). In Barn swallow males, the length of the outermost tail feathers (and the size of white patches on the tail feathers) act as sexual signals for females, and – as expected – there is a significant negative correlation between the expression of sexual signals and the intensity of louse infestation (Møller 1991).

Several latter studies on Barn swallows confirmed the negative correlation between sexual signals and louse intensity, and provided further details such as males with longer tails arrive in better condition from spring migration, start the breeding earlier and have a greater chance for a second clutch during the breeding season than males with shorter tail feathers (Kose *et al.* 1999, Kose & Møller 1999, Garamszegi *et al.* 2005, Pap *et al.* 2005). Saino *et al.* (1997) showed that males with longer tails are more resistant against blood parasites, than males with shorter tails. Males with more expressed sexual signals may also be more frequently involved in extra-pair copulations (EPC), as there are significantly more nestlings from foreign males (i.e. EPC-nestlings) in the clutches of short-tailed males, than in the clutches of long-tailed ones (Møller *et al.* 2003).

However, all of the studies mentioned above were based on observations and experiments conducted in the breeding season. There is much less known about the relationship between sexual signals and louse infestation after breeding, during the dispersion and migration period. Nevertheless, there are hints that this co-variation may change over the breeding season. Barbosa *et al.* (2003) shoved that Barn swallow males with longer tail feathers suffer from more feather breakage until migration period, than males with shorter tails. Another hint that Burley *et al.* (1991) found a positive correlation between the expression male sexual signals and louse infestation after the breeding season in Zebra finches *(Taeniopygia guttata).*

In this study we examine the relationship between the expression of sexual signals (tail length) and the number of feather holes as proxy of the intensity of louse infestation, and compared it between breeding and migrating male Barn swallows to test whether there are any changes in this relationship over the breeding season and dispersion period. Our hypothesis was that the negative correlation found in the breeding season may disappear until migration, and even the direction of the relationship may turn to a positive correlation; due to males with more expressed sexual signals have more direct physical contact with other birds (e.g. EPC, fight), hence they are more exposed to horizontal louse transmission than less attractive males.

Materials and methods

Barn swallows are excellent candidates for ectoparasitological studies; due to semi-colonial breeding, complex social life and frequent body-to-body contacts the prevalence of their ectoparasites are usually high. Birds were ringed and sampled at Világospuszta Cattle Farm (Fejér County, Hungary) in the breeding season (May–July, 2006–2010) and at Ócsa Bird Ringing Station (Pest County, Hungary) in the migration period (15. August – 13. September, 2003). Swallows caught at Világospuszta were not separated by years in the analyses, rather were pooled together by representing each bird with its first caught.

Birds were caught with mist nets and marked individually with aluminium rings. We determined their sex and age according to Svensson (1995), and recorded their standard biometrical measures (3^{rd} primary length, wing length and tail length, all measured on the left side of the bird) and condition scores (Svensson 1995). Feather holes were counted on each remiges and rectrices, and summed thereafter in subsequent analyses. Adult females and young (i.e. first calendar year old) birds were omitted from the analyses.

Statistical analyses were carried out with Quantitative Parasitology 3.0 (Reiczigel & Rózsa 2005) and with R Commander (Fox *et al.* 2009) package in R 2.10.1 (R Development Core Team 2009). Prevalences were compared with Fisher's exact test, mean intensities with bootstrap-*t* test, and median intensities with Mood's median test (Rózsa *et al.* 2000, Rózsa 2003, 2005). We used Kendall's *tau* correlation as this non-parametric method is less sensible to the effect of outlier data points commonly present in aggregated distributions than Spearman's rank correlation (Reiczigel *et al.* 2007). All reported *P*-values are two-tailed.

Results

The distribution of the feather hole intensities among host individuals was aggregated in both samples (variance / mean abundance ratio > 1; Table 1), as it was expected from parasite distributions (Crofton 1971). We compared the prevalences, mean and me-

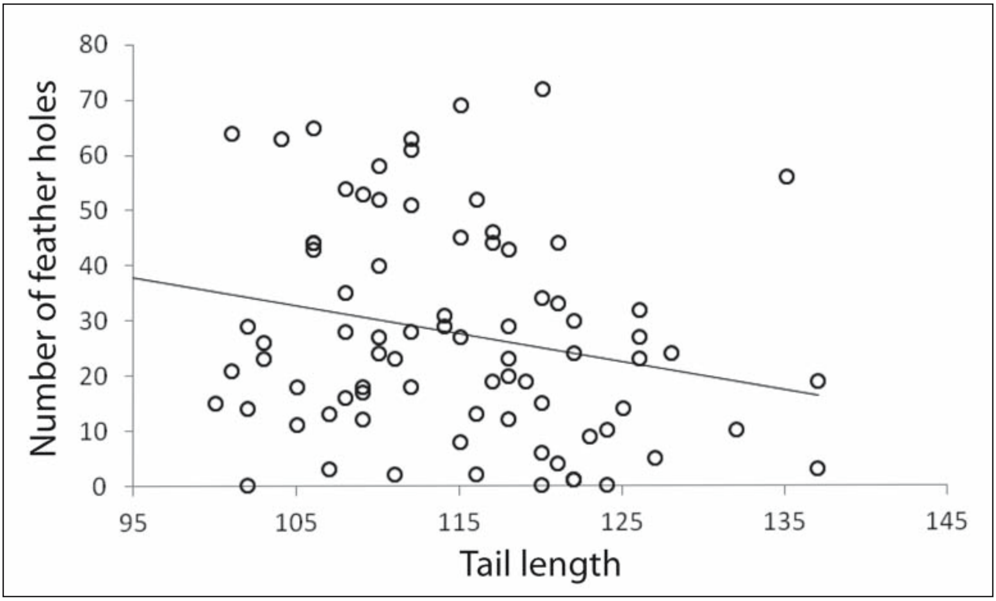
	breeding season	**migration period**
prevalence	0.97	0.98
95% confidence interval	0.91–0.99	0.91–1.00
mean intensity	26.5	24.0
95% confidence interval	22.9–30.2	19.6–28.8
median intensity	23.0	19.0
95% confidence interval	18–27	13–27
variance / mean abundance ratio	13.6	14.1

Table 1. Descriptive statistics of feather holes on Barn swallows in the samples from the breeding season (Világospuszta) and from the migration period (Ócsa)
1. táblázat A toll-lyukak statisztikái a fészkelési (Világospuszta) és vonulási időszakban (Ócsa)

dian intensities of feather holes between Barn swallow males caught in the breeding season (n = 97) at Világospuszta, and in the migration period (n = 60) at Ócsa; however, none of these measures differed significantly (P = 0.99, 0.39, 0.32, respectively) between the two samples.

We found a significant negative correlation between the number of feather holes and tail length in breeding males (tau = –0.16, P = 0.04; Fig. 1); however we found no significant correlation in the case of migrating males (tau = –0.15, P = 0.11; Fig. 2).

Figure 1. Relationship between tail length and the number of feather holes in breeding males
1. ábra A hímek farokhossza és a toll-lyukak száma közötti összefüggés a költési időszakban



Discussion

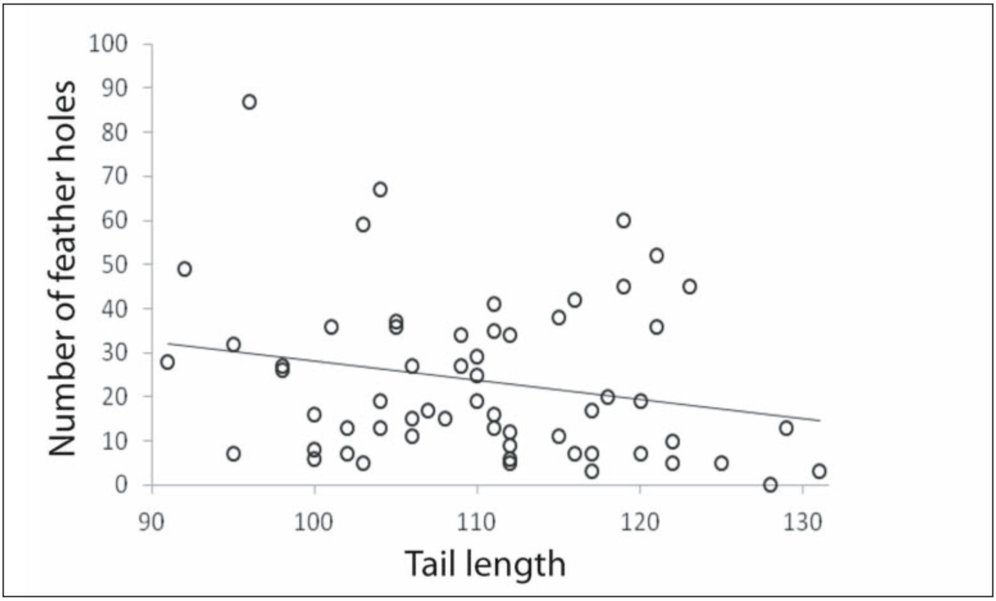
We found no significant differences in prevalence, mean and median intensity between the breeding and migrating males (see above). Prevalence was quite high in both samples (Table 1), probably due to the semi-colonial breeding of the host. Rózsa *et al.* (1996) showed that colonial birds are characterised by higher ectoparasite prevalence and less aggregated parasite distribution among host individuals than territorial birds.

In the case of breeding males, we found a significant negative correlation between tail length and the number of feather holes (Fig. 1), confirming the results of previous studies carried out in the breeding season (see e.g. Møller 1991, Kose *et al.* 1999, Kose & Møller 1999, Pap *et al.* 2005). These results suggest that the length of the outermost tail feather indeed act as an honest sexual signal of parasite load in the breeding season. However, according to our hypothesis, this relationship seems to change during the late breeding season and dispersion period, as the same correlation was not significant in the sample of migrating males (Fig. 2). This result is in concordance with the findings of Burley *et al.* (1991) and Barbosa *et al.* (2003); however, we could not prove a turn in the direction of the relationship.

There are at least two, mutually not exclusive hypotheses to explain the disappearance of the significant negative relationship between the expression of sexual signals (tail length) and intensity of louse infestation (feather holes).

We suggested that more attractive males (i.e. with more expressed sexual signals) are more exposed to louse transmission due to more frequent body-to-body contacts with conspecifics, such as more frequent EPC (Møller *et al.* 2003) or fights with other males. Recent studies showed that the number

Figure 2. Relationship between tail length and the number of feather holes in migrating males
2. ábra A hímek farokhossza és a toll-lyukak száma közötti összefüggés a diszperziós és vonulási időszakban



of feather holes increased significantly during the breeding season in adult Barn swallows (Vas *et al.* 2008, Vas & Fuisz 2010). Hence we suggest this increase is higher in attractive males during the breeding season than in less attractive ones. At beginning of the breeding season, attractive males harbour fewer lice; however, due to frequent horizontal louse transmission, the difference in louse infestation sinks toward migration period.

The benefit of attractiveness in the sexual selection may result a handicap in natural selection. Barbosa *et al.* (2003) found a significant positive correlation between Barn swallows' tail length and the amount of damaged tail feathers in the end of the breeding season. The authors of this study did not consider louse infestation; however, Kose and Møller (1999) previously showed that lice can cause feather breakage by chewing holes. Given that Barn swallows are long-term migrants (Szép 2009), the aerodynamical disadvantage caused by damaged or broken tail feathers may results higher mortality during migration (Pap *et al.* 2005).

Nevertheless, we cannot exclude an alternative hypothesis, based on the fact that the sampled populations differed both spatially and temporally. However, sampling the same birds in breeding season and in the migration period has serious methodological limits. Once the nestlings fledged, Barn swallows spread in the ca. 5 km area of the nesting site and do not return to the nest even for nights (Szép 2009), hence their recapture is almost impossible. Additionally, according to (Szép 2009), migrating groups gather from quite huge area, and consist of both colonially and solitarily breeding birds. Hence, the difference we found may be explained by the different compound of the samples. The breeding sample contained only colonial swallows, while it is very likely that some solitary birds were represented in the migrating sample. Until now, no study examined the louse infestation of solitarily breeding Barn swallows. Given the fact that that in the case of solitary males the body-to-body contact with conspecific birds is very limited, arguably their louse load may differ from colonial ones. We cannot exclude that this phenomenon may contribute to our results. Future studies should consider the solitarily breeding Barn swallow pairs as well to understand the complex system built by this species and their ectoparasitic lice.

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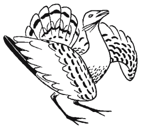
New species and host association records for the Hungarian avian louse fauna (Insecta: Phthiraptera)

ZOLTÁN VAS[1,2,3], CSABA PRIVIGYEI[3], VIOLA JUDIT PROHÁSZKA[4], TIBOR CSÖRGŐ[5] & LAJOS RÓZSA[6]



Zoltán Vas, Csaba Privigyei, Viola Judit Prohászka, Tibor Csörgő & Lajos Rózsa 2012. New species and host association records for the Hungarian avian louse fauna (Insecta: Phthiraptera). – Ornis Hungarica 20(1): 44–49.

Abstract A recently published checklist of Hungarian louse fauna (Insecta: Phthiraptera) listed 279 species and subspecies which have been recorded in Hungary. According to that checklist several louse species still await detection in Hungary, and many of the previously reported louse species have not been found on all expected host species yet. Our faunistical survey on avian lice started in 2005 at Ócsa Bird Ringing Station, resulting hundreds of ectoparasite samples collected from over 70 bird species. Additionally, our louse collection has grown by collecting samples in other research projects focusing on various bird species, and by sampling cadavers before taxidermy in the Bird Collection of the Hungarian Natural History Museum. As the results of a preliminary exploration of this collection, we list 20 louse species which are new to the Hungarian fauna, as well as the first Hungarian records of 17 host-parasite associations. We also found 3 louse-bird association records new for the World fauna.

Keywords: faunistics, ectoparasite, parasitism, lice, bird

Összefoglalás A tetvek rendjének (Insecta: Phthiraptera) hazai faunalistája 279 tetűfaj és alfaj előfordulásáról számol be. A faunalista szerint számos további tetűfaj fordul elő nagy valószínűséggel Magyarországon, és a már megtalált tetűfajok jelentős része sem került még elő valamennyi várható gazdafajáról. A madarakon élősködő tetvek faunisztikai kutatását 2005-ben az Ócsai Madárvártán kezdtük, ahol több mint 70 madárfaj ektoparazitáit mintavételeztük. A több száz, Ócsán gyűjtött minta mellett más madártani kutatások keretében is gyűjtöttünk külső élősködőket, illetve a Magyar Természettudományi Múzeum Madárgyűjteményében is vettünk mintákat a preparálásra előkészített madártetemekről. A gyűjtött minták előzetes feldolgozása során magyar faunára új 20 tetűfajt, és Magyarországon eddig nem jegyzett 17 gazda-parazita kapcsolatot dokumentáltunk. Eredményeink közt további 3, a nemzetközi irodalomból eddig ismeretlen gazda-parazita kapcsolatról is beszámolunk.

Kulcsszavak: faunisztika, ektoparazita, élősködés, tetű, madár

[1]Hungarian Natural History Museum, Department of Zoology, H-1088 Budapest, Baross str. 13., Hungary, e-mail: vas.zoltan@gmail.com, [2]Szent István University, Faculty of Veterinary Science, Department of Biomathematics and Informatics, H-1078 Budapest, István str. 2., Hungary, [3]Ócsa Bird Ringing Station, H-2364 Ócsa, Némedi str. 592/1., Hungary, [4]Szent István University, Faculty of Agricultural and Environmental Sciences, H-2100 Gödöllő, Páter Károly str. 1., Hungary, [5]Eötvös Loránd University, Faculty of Science, Institute of Biology, Department of Anatomy, Cell and Developmental Biology, H-1117 Budapest, Pázmány str. 1/C., Hungary, [6]MTA-ELTE-MTM Ecology Research Group, H-1117 Budapest, Pázmány str. 1/C., Hungary

Introduction

Avian lice (Insecta: Phthiraptera) are wingless obligate ectoparasites that complete their entire life-cycle on the body surface of their hosts. They feed mainly on feathers and dead skin parts and are often highly specific to their hosts (Johnson & Clayton 2003). A recent world checklist of avian lice by Price *et al*. (2003) critically reviewed their nomenclature, taxonomy and host-parasite associations. They list 3910 louse species infesting 3248 bird species. Most probably a large number of louse species still await description (see e.g. Palma & Price 2010, Sychra *et al*. 2010, Valim & Weckstein 2012).

According to a recently published checklist, 279 louse species (and subspecies) have been recorded in Hungary (Vas *et al*. 2012). Additionally, this paper also list over 550 louse species, subspecies, and host associations which have not been detected in Hungary yet; however, their occurrence may seem to be likely as judged from host distribution. Further research shall reveal several louse species new for the Hungarian fauna, as well as new host records. These are new, formerly undocumented associations between host and louse species.

In this paper we report the results of a recent faunistical survey on the Hungarian louse fauna. We identified louse samples from various bird species collected at different locations between 1998–2012. Below we provide a list of louse species new to the Hungarian fauna (as compared to Vas *et al*. 2012). Furthermore, we also list host association records that are new either as compared to the Hungarian checklist or new as compared to the world checklist of Price *et al*. (2003).

Materials and methods

Our faunistical survey of avian lice (Insecta: Phthiraptera) started in 2005 at Ócsa Bird Ringing Station, resulting hundreds of ectoparasite samples collected from over 70 bird species. Other research projects on various bird species (e.g. Barn swallows *(Hirundo rustica)*, European bee-eaters *(Merops apiaster)*, and Red-footed falcons *(Falco vespertinus)*) provided further hundreds of louse samples. Additionally, a few samples were collected from bird cadavers before taxidermy in the Bird Collection of the Hungarian Natural History Museum (HNHM). All investigated cadavers were known to originate from Hungarian wild populations. Furthermore, many colleagues studying birds collected and sent us samples to help our work.

Lice sampled in focused ectoparasitological research projects (see e.g. Vas *et al*. (2008) on Barn swallows) were collected with pyrethroid insecticide in a standardised way to allow further quantitative analyses (Johnson & Clayton 2003, Rózsa 2003). However, some samples we obtained were collected by visual examination without following any standard; hence they satisfy faunistical purposes only. The samples were stored in 70% ethanol. The identification of louse species was made by the first author using a stereoscopic microscope. The samples are presently held by the last author for further research, and will be deposited in the Department of Zoology of HNHM in the future.

Our lists follows the nomenclature and host-parasite associations of the world checklists of chewing lice (Price *et al*. 2003) with a few complements based on Sychra and Literák (2008), and Sychra *et al*. (2008). Bird taxonomy follows Dickinson (2003).

Asterisk (*) marks the type host-parasite relationship. We also report the locality, date, and collector(s) for each louse sample in brackets. In the case of multiple samples from the same louse species the earliest one's data is given.

Results

New species for the Hungarian louse fauna

Amblycera: Menoponidae

Actornithophilus piceus piceus (DENNY, 1842)
Sterna hirundo LINNAEUS, 1758 [Nagybivalyos lake, Várpalota, 2012.06.08., Árpád Ferincz, Tibor István Fuisz, Bálint Preiszner, Szandra Sütő, Zoltán Vas]

Austromenopon atrofulvum (PIAGET, 1880)
Sterna hirundo LINNAEUS, 1758 [Nagybivalyos lake, Várpalota, 2012.06.08., Árpád Ferincz, Tibor István Fuisz, Bálint Preiszner, Szandra Sütő, Zoltán Vas]

Colpocephalum subzerafae TENDEIRO, 1988
Falco vespertinus LINNAEUS, 1766 [Kardoskút, 2012.07.07., Péter Fehérvári, Éva Horváth, Szabolcs Solt, Zoltán Vas]

Menacanthus camelinus (NITZSCH, 1874)
Lanius collurio LINNAEUS, 1758 [Máriahalom, 2006.07.28., Bálint Preiszner, Zoltán Vas]

Menacanthus fertilis (NITZSCH, 1866)
Upupa epops LINNAEUS, 1758* [Áporkai tanya, Bugyi, 2012.06.09., Lajos Rózsa]

Menacanthus obrteli BALÁT, 1981
Locustella luscinioides (SAVI, 1824)* [ringing station, Ócsa, 2007.06.20., Csaba Privigyei, Viola Judit Prohászka]

Myrsidea latifrons (CARRIKER & SHULL, 1910)
Riparia riparia (LINNAEUS, 1758)* [sandmine lake, Ócsa, 2008.07., Lajos Tóth, ZoltánVas]

Myrsidea sylviae SYCHRA & LITERÁK, 2008
Sylvia atricapilla (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.08.22., Zoltán Vas]

Nosopon clayae PRICE & BEER, 1963
Pernis apivorus (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.09.14., Zoltán Vas]

Ischnocera: Philopteridae

Aegypoecus trigonoceps (GIEBEL, 1874)
Gyps fulvus (HABLIZL, 1783)* [Egyed, 2005.09.05., Viktor Molnár]

Brueelia glizi BALÁT, 1955
Fringilla montifringilla LINNAEUS, 1758* [ringing station, Ócsa, 2006.03.11., Zoltán Vas]

Craspedorrhynchus dilatatus (RUDOW, 1869)
Buteo lagopus (PONTOPPIDAN, 1763)* [Bugyi, 2010.12.29., Zoltán Vas]

Degeeriella vagans (GIEBEL, 1874)
Accipiter gentilis (LINNAEUS, 1758)* [ringing station, Ócsa, 2005.07.15., Lajos Rózsa, Zoltán Vas]

Falcolipeurus quadripustulatus (BURMEISTER, 1838)
Gyps fulvus (HABLIZL, 1783) [Egyed, 2005.09.05., Viktor Molnár]

Falcolipeurus sulcifrons (DENNY, 1842)
Haliaeetus albicilla (LINNAEUS, 1758)* [HNHM Bird Collection, 2010.05.20., Zoltán Vas]

Philopterus modularis (DENNY, 1842)
Prunella modularis (LINNAEUS, 1758)* [ringing station, Ócsa, 2008.10.11., Csaba Privigyei, Viola Judit Prohászka]

Philopterus rapax (ZLOTORZYCKA, 1964)
Fringilla montifringilla LINNAEUS, 1758* [ringing station, Ócsa, 2008.01., Zoltán Vas]

Rallicola minutus (NITZSCH, 1866)
Gallinula chloropus (LINNAEUS, 1758)* [ringing station, Ócsa, 2005.09.01., Zoltán Vas]

Strigiphilus goniodicerus EICHLER, 1949
Bubo bubo (LINNAEUS, 1758)* [HNHM Bird Collection, 2010.10.08., Zoltán Vas]

Strigiphilus heterocerus (GRUBE, 1851)
Strix uralensis PALLAS, 1771* [Arka, 1998.10.05., Márton Horváth]

Host association records new for the Hungarian fauna

AMBLYCERA: MENOPONIDAE

Ciconiphilus decimfasciatus (BOISDUVAL & LACORDAIRE, 1835)
Ardea cinerea LINNAEUS, 1758* [Petőháza, 2006.02., Lajos Rózsa]

Colpocephalum subzerafae TENDEIRO, 1988
Falco tinnunculus LINNAEUS, 1758 [Kardoskút, 2012.07.07., Péter Fehérvári, Éva Horváth, Szabolcs Solt, Zoltán Vas]

Menacanthus alaudae (SCHRANK, 1776)
Emberiza citrinella LINNAEUS, 1758 [ringing station, Ócsa, 2008.11.11., Csaba Privigyei, Viola Judit Prohászka]

Menacanthus curuccae (SCHRANK, 1776)
Acrocephalus schoenobaenus (LINNAEUS, 1758) [ringing station, Ócsa, 2008.09.29., Csaba Privigyei, Viola Judit Prohászka]
Acrocephalus scirpaceus (HERMANN, 1804) [ringing station, Ócsa, 2008.08.01., Csaba Privigyei, Viola Judit Prohászka]

Menacanthus eurysternus (BURMEISTER, 1838)
Garrulus glandarius (LINNAEUS, 1758) [ringing station, Ócsa, 2007, Zoltán Vas]
Lanius collurio LINNAEUS, 1758 [ringing station, Ócsa, 2007.08.11., Csaba Privigyei, Viola Judit Prohászka]
Turdus merula LINNAEUS, 1758 [ringing station, Ócsa, 2006.02.11., Zoltán Vas]
Turdus philomelos BREHM, 1831 [ringing station, Ócsa, 2008.04.03., Zoltán Vas]
Fringilla coelebs LINNAEUS, 1758 [ringing station, Ócsa, 2008.11.30., Csaba Privigyei, Viola Judit Prohászka]

Menacanthus sinuatus (BURMEISTER, 1838)
Parus caeruleus LINNAEUS, 1758 [ringing station, Ócsa, 2006.11.04., Zoltán Vas]

Nosopon lucidum (RUDOW, 1869)
Circus aeruginosus (LINNAEUS, 1758) [HNHM Bird Collection, 2009.07.20., Zoltán Vas]
Accipiter nisus (LINNAEUS, 1758) [ringing station, Ócsa, 2011.03.21., Csaba Privigyei, Viola Judit Prohászka]
Pseudomenopon pilosum (SCOPOLI, 1763)
Gallinula chloropus (LINNAEUS, 1758) [ringing station, Ócsa, 2005.09.01., Zoltán Vas]

Trinoton anserinum (FABRICIUS, 1805)
Anser albifrons (SCOPOLI, 1769) [HNHM Bird Collection, 2004.01., Lajos Rózsa]

AMBLYCERA: RICINIDAE
Ricinus fringillae DE GEER, 1778
Emberiza schoeniclus (LINNAEUS, 1758) [ringing station, Ócsa, 2008.03.15., Zoltán Vas]

ISCHNOCERA: PHILOPTERIDAE
Degeeriella fusca (DENNY, 1842)
Circus pygargus (LINNAEUS, 1758) [HNHM Bird Collection, 2009.07.20., Zoltán Vas]

Host association records new for the World fauna (ordered by birds, alphabetically)

Acrocephalus melanopogon (TEMMINCK, 1823)
Philopterus sp. [ringing station, Ócsa, 2006.07.21., Zoltán Vas]

Carduelis spinus (LINNAEUS, 1758)
Philopterus sp. [ringing station, Ócsa, 2008.12.06., Csaba Privigyei, Viola Judit Prohászka]

Emberiza schoeniclus (LINNAEUS, 1758)
Menacanthus sp. [ringing station, Ócsa, 2008.05.03., Csaba Privigyei, Viola Judit Prohászka]

Discussion

The most recent checklist (Vas *et al.* 2012) reported 279 louse species and subspecies infesting 156 bird species in Hungary. The present study increases theses numbers to 299 louse species and subspecies infesting 170 bird species in Hungary. The species-level identification of the host records new for the world fauna requires further sampling and investigation as the specimens we found were almost exclusively nymphs. Future research will reveal whether these lice are accidentally "stragglers" from other host species or yet unknown host associations. As the louse list is still far from complete further updates to the Hungarian louse fauna are expected, contributing to the understanding of parasite biogeography.

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Local abundance and spatial distribution of some migratory birds during post-breeding period

József Gyurácz[1], Sándor Kalmár[1] & Réka Baráth[2]

József Gyurácz, Sándor Kalmár & Réka Baráth 2012. Local abundance and spatial distribution of some migratory birds during post-breeding period. – Ornis Hungarica 20(1): 50–58.

Abstract The local abundance and spatial distribution of the short- to medium-distance migratory and daytime stopover passerines (Robin *Erithacus rubecula*, Blackcap *Sylvia atricapilla,* Chiffchaff *Phylloscopus collybita,* Blue tit *Parus caeruleus*, Great tit *P. major*) were studied in a West Hungarian stopover ground during post-breeding season. The dispergation index of all migratory bird species revealed clumped distribution both in „smallest annual capture year" (abb. SACY) and the „largest annual capture year" (abb. LACY). According to the PCA the spatial occurrences of Blackcap, Blue tit and Great tit captured in LACY showed significantly higher concentration than of those migrating in SACY. The studied species appeared in all four habitats (bushy, forest, grassland, marsh) of the study stopover area, but their clumped spatial distribution showed habitat preference. The abundance-dependent shift of habitat selection was found only in Great tit, the most of them captured in SACY concentrated in grassland with bushy, while the ones captured in LACY grouped in forest habitat type. Blackcaps were grouped the grassland with bushes habitat type where many Dwarf elder *(Sambucus ebulus)* bushes were available during autumn migration.

Keywords: stopover birds, annual capture, habitat selection

Összefoglalás Jelen tanulmány öt rövid- és középtávú vonuló, vonulását napközben megszakító énekesmadár faj (vörösbegy *Erithacus rubecula*, barátposzáta *Sylvia atricapilla*, csilpcsalpfüzike *Phylloscopus collybita*, kék cinege *Parus caeruleus*, széncinege *P. major*) egyedszáma (éves fogás) és térbeli eloszlása közötti kapcsolatot vizsgálja az őszi vonulási időszakban, nyugat-magyarországi élőhelyen. A diszpergáltsági index értékei alapján a madarak csoportos eloszlást mutattak a legkisebb (SACY) és a legnagyobb (LACY) fogásszámú évben is. A PCA eredményei alapján a barátposzáták, a kék cinegék és a széncinegék csoportosulásának mértéke lényegesen nagyobb volt a nagy fogásszámú években. A vizsgált fajok megjelentek mind a négy élőhelyen (bokros terület, erdő, gyep, mocsár) a vizsgálati területen, de az egyedek csoportosulása élőhelypreferenciát mutatott. Az élőhelyválasztásban megmutatkozó denzitásfüggő eltolódást csak a széncinegék esetében sikerült kimutatnunk: a legkisebb fogásszámú évben az egyedek többsége a füves-bokros élőhelyeken koncentrálódott, míg a legnagyobb fogásszámú évben az erdei élőhelyen csoportosultak a madarak. A barátposzáták a füves-bokros élőhelyen koncentrálódtak, ahol a táplálékul szolgáló földi bodza nagy mennyiségben állt rendelkezésükre.

Kulcsszavak: vonuló madarak, éves fogás, élőhely-választás

[1]Institute of Biology, Faculty of Sciences, University of West Hungary, Szombathely, Károlyi Gáspár tér 4. H-9700, Hungary, e-mail: gyjozsi@ttk.nyme.hu, [2]István Chernel Ornithological and Nature Conservation Society, Szombathely, Károlyi Gáspár tér 4. H-9700, Hungary

Introduction

The spatial distribution of migrants is an important population factor in their stopover (Chernetsov 2002). Understanding the distribution and abundance of migratory birds is critical for the effective conservation strategy and comprises the core of bird ecology (Caughley & Sinclair 1994, Krebs 1994, Johnson & Sherry 2001). The distribution of birds among habitat types is particularly important because the conservation of migratory populations is usually realized by management of their habitats (Morrison *et al*. 1998).

Migratory birds move among habitats more than residents and are frequent subjects for stopover studies (Cody 1985). Although most studies of migratory bird habitat selection has focused on breeding populations, a simpler situation exists with birds during migration period, when they are free from bothering factors connected with nesting (Hutto 1985). The spatial distribution of migrants could be determined by vegetation structure (Preiszner & Csörgő 2008), prey availability (Levey & Stiles 1992, Sherry & Holmes 1996), predation risks (Rappole *et al*. 1989), habitat preferences from the breeding period (Morse 1971, Hutto 1980), evolutionary responses to paleoecological circumstances (Johnson & Sherry 2001), competition and population abundance (Greenberg 1986, Leisler 1992, Marra 2000). Density of intra- and interspecific competitors may effect habitat quality and thus the pattern of spatial distribution and habitat selection by stopover birds (Moore & Yong 1991). Most of the passerine migrants use stopover sites in a clearly non-random manner, even if many species have broader habitat preference during migration than during breeding (Chernetsov 2006). For example the stopover Robins establish small home ranges and do not move randomly across a large area during their autumn migration (Titov 1999a).

We studied the local abundance and spatial distribution of the short- to medium-distance migratory and daytime stopover passerines (Robin *Erithacus rubecula* abb. ERIRUB, Blackcap *Sylvia atricapilla* abb. SYLATR, Chiffchaff *Phylloscopus collybita* abb. PHYCOL, Blue tit *Parus caeruleus* abb. PARCAE, Great tit *P. major* abb. PARMAJ) in a stopover ground during post-breeding season. Our expectation was that the pattern of spatial distribution of bird species would differ between years when bird abundance was different.

Material and methods

Study site

The study was carried out at Tömörd Bird Ringing Station in West Hungary (47°21’23”N 16°40’04”E), located 15 kilometres from Szombathely. There were four natural habitat types around the station *(Figure 1).* These habitats were characterized according to the SE European Bird Migration Network (Busse 2000) (see below) as follows.

Bushes: Bushes and herbs were made up a compact, dense vegetation, which were dissected by small grass patches. Its characteristic plants were: Blackthorn *(Prunus spinosa)*, Common hawthorn *(Crataegus monogyna)*, Wild pear *(Pyrus pyraster)*, Wild rose *(Rosa canina).* There were great variety of crops but there was not management in the bushes. The height of vegetation was 2-3 meters.

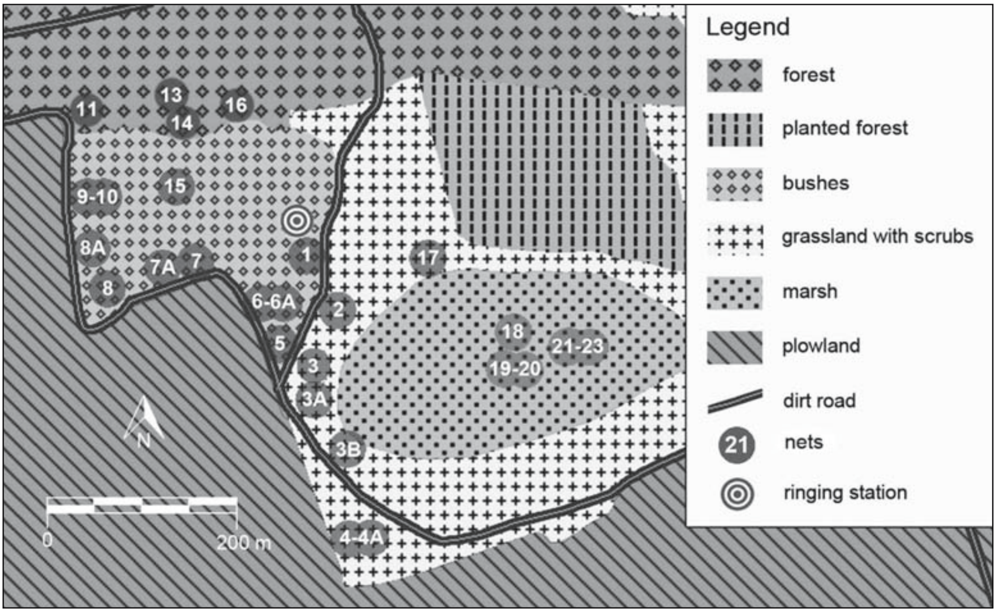

Figure 1. Habitat map of the study area with the locations of nets
1. ábra A vizsgálati terület élőhely-térképe hálóhelyekkel

Forest: Broadleaf trees and bushes show a compact, dense edge vegetation, forming an ecoton community with Turkey oak *(Quercus cerris)*, Blackthorn, Common hawthorn, Wild pear as characteristic plants. There were plenty of crops and normal forestry management in the forest. The height of vegetation was 6-7 meters.

Grassland with scrubs: This habitat type made a transition between the wet habitats of the swamp and the steppe communities that used to cover the croplands around the marsh. There were a few bushes in the grassland, with two small patches of Dwarf elder *(Sambucus ebulus)*. There grassland was not managed.

Marsh: It was a small (6 ha) permanent and an isolated wetland. Characteristic plants were Reedmace *(Typha latifolia)* and Rush *(Schoenoplactus lacustris)* in the marsh. The height of vegetation was 1-2 meters. Water was supplied to the marsh only by precipitation. The marsh dried out and marsh vegetation was degraded because of scarce rainfall in 2000 and 2001.

Field work

The birds were captured and ringed at the Tömörd Bird Ringing Station between 1998 and 2011. Bird ringing took place during the post-breeding period (dispersion and autumn migration), from the third decade of July to the first decade of November, 95-100 ringing days each year. For catching the birds we used 28 numbered mist-nets (12 meter long and 2.5 meter high with 5 shelves and a mesh size of 16 mm). There was a line of six nets in the deepest part of the marsh. Four nets were in the forest, eleven in the bushes and seven in the grassland. Birds had been captured from dawn to dusk, except on rainy and stormy days. All birds were ringed and aged according to Svensson (1992). The birds

	ERIRUB		SYLATR		PHYCOL		PARCAE		PARMAJ	
Year	2003	2007	2002	2009	2002	2004	2003	2004	2006	2010
AC	565	911	393	1132	237	558	119	1040	141	958
D	19.48	31.41	13.55	39.03	8.17	19.24	4.10	35.86	4.86	33.03
V	312.62	402.25	136.54	1753.53	59.08	235.90	29.81	5477.91	26.55	2055.82
SD	17.68	20.06	11.69	41.88	7.69	15.36	5.46	74.01	5.15	45.34
DI	16.05	12.81	10.08	44.92	7.23	12.26	7.26	152.75	5.46	62.23
X^2-test	205.09	230.26	26.32	712.26	59.71	81.09	25.37	1344.00	43.97	306.62
P	<0.001									

Table 1. Annual captures (AC), density (D), variance (V), standard deviation (SD) and dispergation index (DI) of bird species. (See the introduction for species abbreviations.) The results of X^2-test and significance level (P) relate to the dispergation index (DI)

1. táblázat A madárfajok évi fogása (AC), denzitása (D), varianciája (V), szórása (SD), és diszpergáltsági indexe (DI). (A fajnevek rövidítését ld. a bevezetésben.) A X^2-teszt és a szignifikanciaszint (P) értékei a diszpergáltsági indexre vonatkoznak

were weighed to the nearest 0.1 g (using a spring balance) and the fat reserves (fat index, condition) were estimated visually according to SE European Bird Migration Network protocol (Busse 2000) – ranging from 0 (no fat) to 8 (bulging fat).

Data processing and statistical analysis

From the 13 study years we selected the „smallest annual capture year” (abb. SACY) and the „largest annual capture year” (abb. LACY) for all the five selected bird species. Table 1 shows the annual captures of the selected years. We used the number of caught birds (only birds with net number) per year and per net of five bird species. The first-year and adult birds were not separated in the statistical analysis. To determine the spatial distribution of bird population in SACY and LACY we used the dispergation index. It was calculated as $DI = s^2/d$, where s^2 is variance of number of caught/net/year, d is density, average number of caught/net/year. We tested the spatial distribution *(DI)* of birds caught by nets were standing in different habitat types with *X^2-test*. Chi square supplies us with a method for determining if a sample variance is significantly greater than or less than the average (Fowler & Cohen 1991, Moskát *et al.* 1992). We compared the mean body mass and condition of birds in SACY and LACY by *Student t-test* (Fowler & Cohen 1991).

We used *principal component analysis (PCA)* on number of caught birds in the four habitat types in SACY and LACY, to examine correlations among spatial distribution of birds and habitat types (Podani 1997). Statistical analyses were carried out by the PAST software version 1.38 (Hammer *et al.* 2006).

Results

The dispergation index of all migratory bird species revealed clumped distribution *(DI>1)* in both SACY and LACY *(Table 1),* but according to the PCA the spatial occurrences of Blackcap, Blue tit and Great tit captured in LACY showed significantly higher concentration than of those migrating in SACY *(Figure 2).* The most Blackcaps

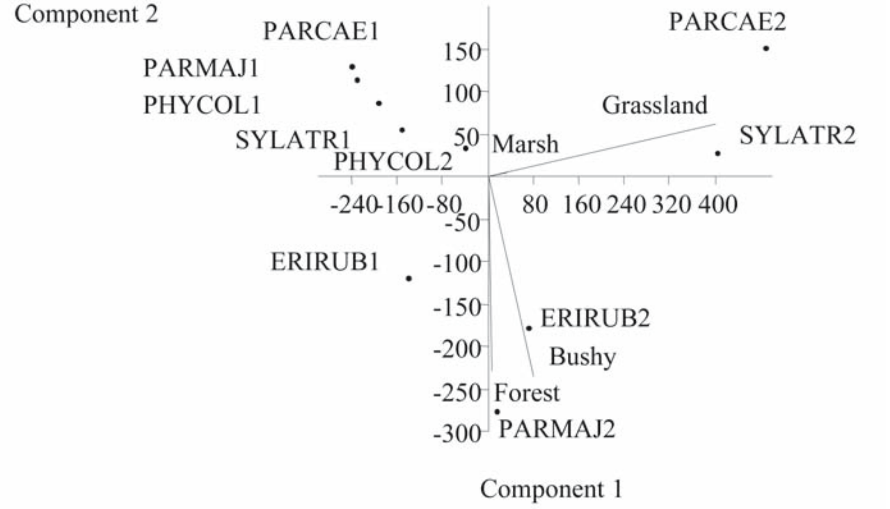

Figure 2. Principal component analysis ordination of bird distribution pattern in SACY (1) and LACY (2) over four habitat types: forest, bushy, grassland with scrubs, marsh. The first component explains 72.33% of the data variability, the second component 22.47%, the third component 4.58 % and the fourth component only 0.61%

2. ábra A madárfajok főkomponens-analízis ordinációja a kis (SACY=1) és nagy fogású (LACY=2) évek és élőhely-típusok (erdő, bokros, bokros-gyep, mocsár) alapján. Az első főkomponens az adatok varianciájának 72,33, a második 22,47, a harmadik 4,58, a negyedik mindössze 0,61 százalékára ad magyarázatot

and Blue tits clumped in grassland habitat type both in SACY and LACY, but the most Great tits were captured in grassland during SACY and most of them were captured in forest during LACY *(Figure 3).*

The average fat index and body mass of Robins caught in LACY was significantly smaller than of those migrating in SACY. The average fat index of Blackcaps, Blue tits and Great tits caught in LACY were significantly larger than of those migrating in SACY. The mean condition and body mass of Chiffchaffs, as well as mean body mass of Blue tits migrating in SACY and LACY did not differ significantly. The average body mass of Blackcaps and Great tits caught in LACY were significantly larger than of those migrating in SACY *(t-test, Table 2).*

Discussion

The spatial distribution of all five species showed clumped distribution at the study stopover site during post-breeding period. The spatial concentration of individuals could be explained by unequal food resource and refuge site distribution because the habitat selection during stopovers should be aimed achieving the two of the most important goals: to maximize the fuel deposition rate and to minimize the risk of predation (Alerstam & Lindström 1990). Another factor that can strongly effect spatial distribution and habitat selection of stopover birds is prey-based intraspecific competition (Moor & Yong 1991), which depends on the abundance of birds. Our results sup-

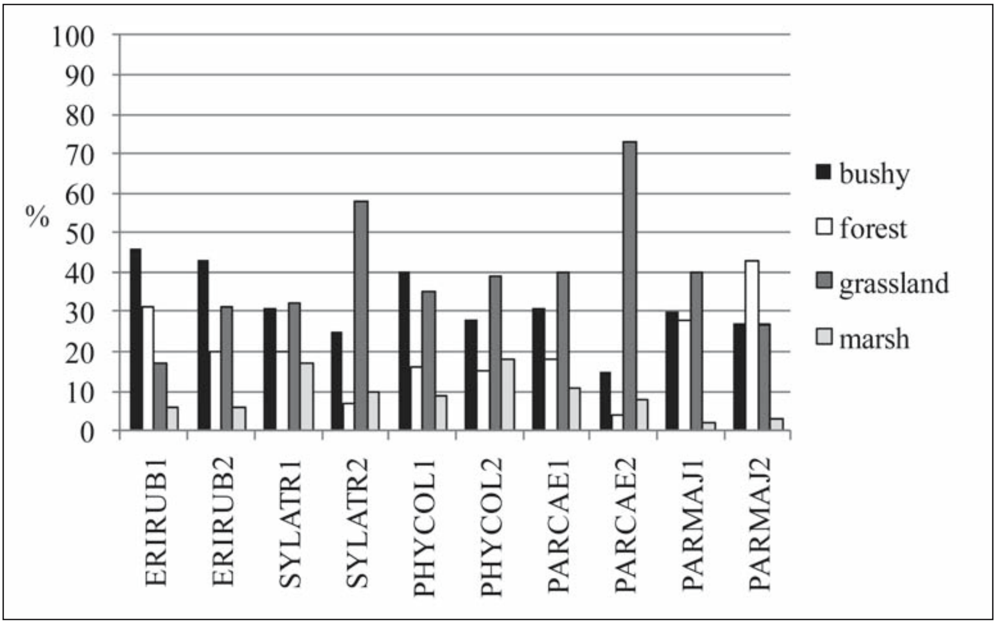

Figure 3. Distribution of the percentages (%) of annual captures in SACY and LACY according to habitat types

3. ábra A befogott madarak százalékos aránya élőhely-típusok szerint a legkisebb (SACY) és legnagyobb (LACY) fogásszámú években

	Mean±S.D.		**t-test**	**df**	**P**
fat	**SACY**	**LACY**			
ERIRUB	1.80±1.41	1.40±1.23	5.61	1476	<0.01
SYLATR	1.44±0.50	1.50±0.75	–2.1	1326	<0.05
PHYCOL	1.32±1.39	1.51±1.21	–1.84	790	NS
PARCAE	0.93±0.79	1.45±1.25	–6.25	1154	<0.01
PARMAJ	1.16±0.72	2.83±1.19	–23.10	1097	<0.001
body mass					
ERIRUB	16.47±1.39	16.19±1.25	3.99	1466	<0.01
SYLATR	18.00±1.38	18.26±1.48	–3.12	1499	<0.01
PHYCOL	7.45±0.67	7.40±0.76	0.83	770	NS
PARCAE	10.82±0.66	10.88±0.67	–0.92	1065	NS
PARMAJ	17.40±1.12	18.03±1.24	–6.07	1082	<0.01

Table 2. Mean fat index (condition) and body mass of bird species in SACY and LACY

2. táblázat A madárfajok átlagos vonulási zsírtartaléka (kondíció) és testtömege a legkisebb (SACY) és legnagyobb fogásszámú (LACY) években port the strong influence of local abundance on the spatial distribution of Blackcap, Blue tit and Great tit migratory populations, which stopovered at the study site during post-breeding period. Higher proportion of stopover Blackcaps, Blue tits and Great tits were captured in LACY by nets in grassland as well as forest habitat type than of those captured in SACY. The recapture rates showed that most migratory Blackcaps, Blue tits and Great tits captured stopover only 1-2 days at the study area in September and October (Gyurácz & Bánhidi 2008). The most migratory individuals with larger fat reserve and body mass in LACY could continue their autumn migration after short stopover. The Robin, Chiffchaff and Blackcap were dominant and regular migrant and stopover species during autumn at the study area. By contrast, the Blue tit and Great tit had intensive migration in 2004 or 2010. The bulk migration of the tits could be in relation with less beech crop and the number of tits breeding in Alps and Carpathians as well as areas north from Hungary (Smith & Nilsson 1987, Nowakowski & Vähätalo 2003, Nyquist 2007*)*. Flocking behaviour of the wintering birds was expected to relate inversely to food supply of habitat (Grubb 1987, Székely & Juhász 1993). Although the most Blue tits were captured in grassland with scrub, the forest and the bushy habitat types were better habitats in terms of feeding and fat accumulation, than the grassland with scrub and the marsh (Gyurácz *et al.* 2011). Some migrant species were known to establish defined home range or temporary territory within the suitable habitat during stopover (Chernetsov 2005). We suggest the territorial spacing of Blue tits may prevent the formation of large flocks during their stopover time in the local forest and bushy. Significantly more tits were displaced to poorer grassland with scrub during the intensive migration (2004) than during the weak migration (2003).

The spatial distribution of Blackcaps was related to the patchy distribution of the preferred berries. Blackcaps were grouped in the grassland with bushes habitat type where many Ground elder bushes were available during autumn migration. It previously was shown in Robins and other migratory passerines that the pattern of spatial distribution was related to the distribution of their prey (Titov 1999a, 1999b, Chernetsov & Titov 2001). The most Robins captured in LACY were leaner because of their fat reserve exhausted during nocturnal migration (Gyimóthy *et al.* 2011b). The more even distribution of Robins in SACY and LACY compared to distribution of other species could be due to the bulk of the migratory Robins remained within 350 m during their stopovers in autumn migration (Chernetsov 2005). Titov (1999b) shown that stopover Robins did not start the fat accumulation until they established a small defined stopover home range. These patterns probably also true for Chiffchaffs during stopover.

Habitat selection during post-breeding period varies among species and habitat change after breeding and dispersion is a frequent phenomenon for migrating birds. Usually the migratory passerines seem to use wider habitat during stopovers compared to breeding period, behaving as generalists in the habitat selection (Barlein 1983, Vega Rivera *et al.* 2003, Chernetsov 2006, Preiszner & Csörgő 2008). This behaviour reduces intra- and interspecific competition (Berthold 1993). The studied species occurred in all four habitats of the study stopover area, but their clumped spatial distribution showed habitat preference. The Robins were captured in many habitat types in Hungary during autumn migration but the most Robins occurred in stopover sites surrounding forest and bushy areas (Gyimóthy *et al.* 2011a). The abundance – dependent shift of habitat selection was found only in Great tit. The most of them captured in SACY concentrated in grassland with bushy, while the ones captured in LACY grouped in forest habitat type. The bushy and forest habitats were supposed primarily refuges for Great tits because the fat reserves of the recaptured tits did not change significantly during their stopovers.

According to the above mentioned results we assumed that local abundance of stopover passerines can be one of the major causes for the observed spatial distribution and habitat shifts beside the interspecific competition and other ecological factors.

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