Ornis Fennica 91:187–194. 2014

Lack of polygyny in Central European populations of Reed Warblers *Acrocephalus scirpaceus*

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Received 17 August 2013, accepted 4 June 2014

So far discussions on the occurrence of polygyny have been conducted on an inter-specific or individual level. In this paper we analyse differences in polygyny rate between different populations of Eurasian Reed Warblers. We provide evidence that our study population in SW Poland, and also the nearby Slovak population, are purely monogamous in contrast to those from western Europe, and we discuss hypotheses regarding the occurrence of polygyny. We suggest that birds breeding in different parts of Europe may exhibit different strategies for optimising reproductive success. In richer habitats of western Europe, where solitary females are able to successfully rear their young, polygyny is more frequent and extra-pair copulations relatively rare. In contrast, in central Europe, where costs of rearing young unaided are high, males do not try to attract second females but engage more often in extra-pair copulations.

1. Introduction

Almost half a century ago Lack (1968) noted that monogamy occurred in more than 90% of families of passerine birds. He suggested that both parents were needed to raise the young successfully and, therefore, monogamy was generally advantageous for both females and males. Trivers (1972) was the first to suggest that each sex maximizes its reproductive success, which results in a conflict between the sexes over parental investment and development of alternative mating strategies and mating systems.

Smaller investment per gamete in offspring by males predisposes them to abandon parental responsibility more readily than females (Bateman 1948, Trivers 1972), and Emlen & Oring (1977) pointed out that social polygyny may develop when one sex is freed from parental duties, e.g. when abundant food resources enable a single parent to provide full parental care. According to this hypothesis polygyny should occur more often in habitats with more abundant food resources compared to places with poorer rearing conditions. In contrast, Shuster & Wade (2003) argued that a crucial factor responsible for the development of

polygyny is the distribution of receptive females in space and time, and not environmental resources. They predicted that if receptive females are dispersed in time and clumped in space, then males can be attached to a particular site and attempt to attract multiple mates. Therefore, according to this hypothesis, polygyny should occur in places with a higher density of breeding birds, or in areas with less synchronised breeding. It should be noted, however, that a high density of nesting females may be associated with some environmental factors (e.g. abundant food resources) and hence affect the environment's polygyny potential, as proposed by Emlen & Oring (1977). Such a density could also reflect female-female interactions (Shuster & Wade 2003), or both factors may operate simultaneously.

It is important to emphasise that even socially monogamous individuals can be genetically polygynous due to engagement in extra-pair copulations, and that hypotheses regarding genetic mating systems, based on similar assumptions, have been formulated (Møller & Birkhead 1993, Stutchbury & Morton 1995).

To date, the occurrence of social polygyny has been analysed at the inter-specific level (why some species are polygynous and others monogamous among closely related taxa, e.g. Leisler & Catchpole 1992), or the individual level (why some individuals are able to attract extra females and become polygynous, e.g. Westerdahl *et al.* 2000) but not at the intra-specific label (why polygyny occurs in some populations of a species while not in others).

The Reed Warbler is a common breeding bird of Eurasian reed beds *Phragmites* spp. (Schulze-Hagen 1991, Cramp 1992), and has been the subject of many papers, mostly considering migration and survival (e.g. Jakubas & Wojczulanis-Jakubas 2010) but also breeding ecology (e.g. Calvert 2005). However, data from individually marked populations are extremely limited. The species was previously considered to be socially monogamous (Schulze-Hagen 1991, Leisler & Catchpole 1992), but according to more recent classifications (Owens & Hartley 1998) it should be regarded as facultatively polygynous, with polygyny being regular in the studied colour-ringed populations (0–6.7%).

In this paper we compare differences in the polygyny rate between different populations of Eurasian Reed Warbler *Acrocephalus scirpaceus* (hereafter Reed Warbler), including new data from our study population in SW Poland. We use current hypotheses to discuss factors that may be responsible for intraspecific variation in the occurrence of polygyny in this species.

2. Material and methods

2.1. Study species

The Reed Warbler is a small (11 g) passerine, breeding in the Palearctic and wintering in sub-Saharan Africa. In spring, males settle in territories and commence singing, but this ceases after pairing and they begin mate-guarding their females as they build the nest. Breeding territories are very small and much of the food is collected in non-defended areas outside territories, often in bushes or small trees (Bibby & Thomas 1985, Duckworth 1990, Calvert 2005). Therefore, breeding densities can exceed 200 pairs / 10 ha (Schulze-Hagen 1991). On the breeding grounds the food of the Reed Warbler consists mostly of insects and spiders. However, the species is able to take advantage of local, variable and short-lived sources of abundant prey, so diet composition changes throughout the breeding period and between seasons (Henry 1978, Dyrcz & Zdunek 1996). The small, cup-shaped nests are generally attached to reed stems and contain 2–6 eggs (Med = 4). The species has a relatively long breeding period (May–August), but suffers high nest losses (55.1% on average in Europe; Schulze-Hagen *et al.* 1996) and frequently re-nests, laying up to five clutches per season. In general, pairs remain together throughout the whole breeding season (Duckworth 1990, Davies *et al.* 2003), and both parents are engaged in incubation and feeding of the young.

2.2. Study population at Milicz fish-ponds

We studied Reed Warblers during 14 years (1980–83, 1994, 2005–2013) in the Stawy Milickie (Milicz fish-ponds) nature reserve (SW Poland).

Each year we monitored the 3 ha study plot

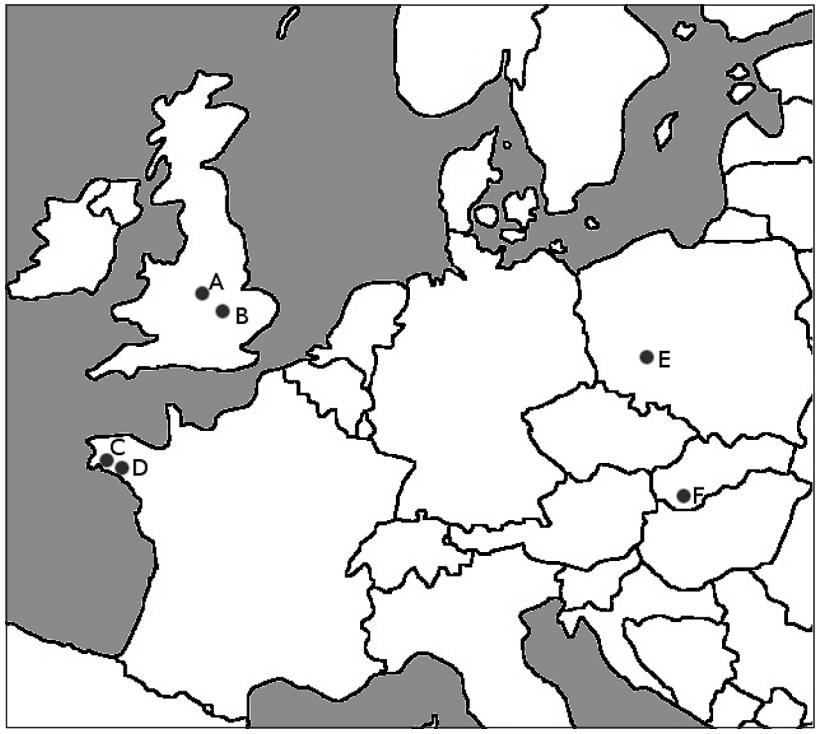

Fig. 1. Study areas of colour-ringed populations of Reed Warblers. A – Attenborough, Nottinghamshire, UK (Catchpole 1971), B – Wicken Fen, Cambridgeshire, UK (Duckworth 1992, Davies *et al.* 2003), C – Bay of Audierne, France (Bargain & Henry 2000), D – Guérande, France (Taillandier 1990), E – Milicz fishponds, Poland (this study), F – Velké Blahovo fishponds, Slovakia (Hoi *et al.* 2013)

from the time of arrival of the first individuals, mist-netted and individually marked birds (combinations of 3 colour and one metal ring), mapped singing males every 1–2 days, and started looking for a pair when a male ceased singing. The majority of nests (ca. 85% of all those found) were discovered at the building stage by observing nest-building and mate-guarding behaviour (total number of nests found: n = 1,061, on average 76 per season). From 1980 to 2005 we identified birds using standard methods applied in other studies (males while singing in territories, both mates during nest-building stage and at nests with chicks). Starting in 2006 we also studied mate-guarding behaviour, so most pairs were observed continuously for about 2 h at the building stage. Additionally, from 2006 to 2013 we identified parental birds at each nest by video-recording (JVC Everio GZ330) on three occasions: on the day of laying of the 2nd egg (this helped to identify secretive birds at nests that were lost during egg-laying or early incubation), during the incubation stage, and on the 8th day after hatching. The use of cameras greatly facilitated the identification process and enabled more efficient targeting of mist-nets. A total of 865 Reed Warblers were identified at 862 nests, including 490 males identified at 793 nests. Full details of the study area and research methods are presented elsewhere (Halupka *et al.* 1998).

2.3. Other populations

In addition to our Polish study, we also analysed data from studies of all colour-ringed populations of Reed Warblers (Fig. 1), where authors described the number of mated males and the rate of polygyny (Table 1). Individual ringing of Reed Warblers was also conducted by Catchpole (1971, 1974) in Great Britain, who first to note polygyny in the species (Catchpole 1971), although the frequency was not reported and so this study could not be used in the analyses. All cases analysed in this paper concern simultaneous polygyny (a male being mated simultaneously to two females) and not sequential polygyny (described also as mate-switching or within-season divorce). Frequency of polygyny was calculated as the percentage of polygynous males to all mated males in a population (Table 1). The authors of the studies used in

Table 1. Percentage of polygynous males in different European populations of Reed Warbler, and its 95% exact confidence limits (CL low, CL high). Number of study years, total number of mated males, percentage of nests with extra-pair offspring (and proportion of EPP young) and population densities are also shown. Densities reflect the number of breeding pairs per ha of a study area including a patch of reedbed. References: (1) Duckworth (1992); (2) Davies *et al.* (2003); (3) Taillandier (1990); (4) Bargain & Henry (2000); (5) this study; (6) Hoi *et al.* (2013).

Study area (reference)	*n* years	*n* mated ♂♂	% polygyn. ♂♂	CL low	CI high	% EPP nests (nestlings)	Density
UK, Wicken Fen (1)	2	30	6.7	0.8	22.1	–	1.3
UK, Wicken Fen (2)	2	52	1.92	0.05	10.3	15 (6)	1.6–2.8
France, Guérande (3)	2	40	2.5	0.06	13.2	–	1.3
France, Bay of Audierne (4)	4	44	0	0	8.0	–	6–8
All western Europe	–	166	2.4	0.7	6.1	–	–
Poland, Milicz fishponds (5)	14	490	0	0	0.8	21 (13)	10–21
Slovakia, Velké Blahovo fishponds (6)	1	31	0	0	11.2	57 (37)	–
All central Europe	–	521	0	0	0.7	–	–

analyses typically mapped singing males and looked for nests by observing nest-building behaviour, as we did. Birds were generally identified in the territories (males) and during feeding of the young (both mates). Davies *et al.* (2003) and Hoi *et al.* (2013) also performed observations during building/egg-laying that helped in bird identification. Mist-netting procedures were not described in detail, but according to the papers most (Duckworth 1992, Taillandier 1990) or all males (Bargain & Henry 2000, Davies *et al.* 2003, Hoi *et al.* 2013) were finally colour-ringed.

2.4. Statistics

To calculate exact 95% confidence intervals for the proportion of polygynous males we applied the Pearson–Klopper method, using R software (version 2.14; R Development Core Team, 2011) with package "binom" (ver. 1.0-5). To test whether differences in polygyny rate between our and other European populations exist we performed a likelihood ratio test. Data from two British and two French studies were pooled, as they concerned the same population studied in different years (Great Britain), or study areas were located close to one another in the same region of France – Brittany (Table 1). We also calculated the probability of not detecting polygynous males in the populations from central Europe. Reported p-values refer to two-tailed tests.

3. Results

Polygynous males have been found in most of the studied western populations (Table 1), although they represented a small proportion of the population (1.9–6.7%). The only exception to this is the study by Bargain & Henry (2000) in France, who did not record any cases of polygyny. However, the number of males observed in their population each year was very low (10–12).

Despite our many years of research, the large number of males identified at nests, and the addition of more sophisticated identification procedures we haven't found any case of polygyny in our study population. In 2006, attempted polygyny (Halupka *et al.* 2012) was recorded once during daily monitoring of the study plot: a male whose mate had laid her third egg on that day was observed mate-guarding another, newly arrived female, which began nest-building. The male accompanied this new female for several hours, though for less time than is typical at this stage. However, the new female disappeared the following day. We also never observed solitary feeding

Table 2. Average clutch size and annual production of fledglings per Reed Warbler female found in different study populations.

Study area	Clutch size	Fledglings / pair	Reference
UK, Lincolnshire	4.01	3.47	Brown & Davies (1949)
UK, Cambridgeshire	3.79	3.43	Duckworth (1990)
UK, Cheshire	3.90	3.33	Calvert (2005)
UK, different populations	3.89	4.09	Bibby (1978)
Germany	3.74	3.65	Ölschlegel (1981)
Sweden	4.00	3.64	Nilsson & Persson (1986)
France, Guérande	3.64	3.50	Taillandier (1990)
France, Bay of Audierne	3.96	3.98	Bargain & Henry (2000)
Poland	3.97	2.46	this study

of the young by a female, which could suggest polygyny (Duckworth 1992, see below). Polygynous males were also not recorded in the other central-European population, in Slovakia (Hoi *et al.* 2013). We performed a likelihood ratio test to test whether differences in polygyny rate between our and other European populations of Reed Warbler exist, assuming that polygyny is binomially distributed (the null hypothesis being an equal polygyny rate in all populations). We found significant differences in the frequency of polygynous males across Europe (likelihood ratio test: $\chi^2 = 12.56$, df = 3, $p = 0.0057$).We also calculated the probability of not detecting polygynous males in the two populations from central Europe, by comparing data from these sites with the most conservative estimate of polygyny rate in western Europe, i.e. 0.7% (lower 95% confidence limit for figures presented in Table 1). The probability of not finding polygynous males in the central European sample of 521 birds was 0.03. For the more likely estimate of 2.4% (mean value in the pooled data from western Europe), the respective probability was negligible (prob. = 0.000003). A similar probability was obtained when we compared only our Polish population with those from western Europe (prob. = 0.00001).

4. Discussion

We were not able to find any polygynous males in our long-term study of the Reed Warbler population at the Milicz fish ponds. Likewise, Hoi *et al.* (2013) did not report any cases of polygamy in Slovakia, so central European populations seem to be purely monogamous. In contrast, polygyny was regularly reported in western populations of Reed Warblers by several authors, despite shorter studies and smaller annual sample sizes compared to our study.

The comparative survey of different Reed Warbler populations indicates that polygyny is a widespread though infrequent event in the western populations. This pattern is especially apparent in Great Britain, where polygynous males were detected in every colour-ringing study. According to Owens & Hartley (1998) Reed Warblers should be classified as facultatively polygynous, and some authors describe the species in this way (Elphick 2007).

The most important study regarding costs and potential for polygyny in the species is that of Duckworth (1992), who found that secondary females incubated and fed their young unaided, but all nestlings successfully fledged. Experiments involving male removal also showed that widowed females can successfully raise fertile eggs to healthy fledglings, underlining the potential for successful polygyny in the species. However, removal experiments revealed some costs of solitary parental care; widowed females had lower overall breeding success, due to a higher rate of chick starvation (Duckworth 1992), but this pattern was detected only in late-season nests, when food conditions are generally deteriorating. This could indirectly suggest that food conditions may be responsible for the differences in the occurrence of polygyny in different populations of Reed Warblers, as suggested by Emlen & Oring (1977). If such mechanisms are involved, we should expect polygynous nests to occur relatively earlier in a season,

when food is abundant. In fact, all nests of polygynous birds whose timing was described were early or mid-season nests (Catchpole 1971, Duckworth 1992).

The comparison of annual production of fledglings per female in different European populations might suggest that rearing conditions are better in western Europe compared to the central populations (Table 2) as the between-population variation in clutch size is smaller than in fledgling production (respective variances are 0.017 *vs* 0.217, Table 2). However, other factors, e.g. differences in predation rate, partial losses associated with starvation or ectoparasites, number of pairs with second broods may also be involved (Schulze-Hagen 1991, Martin 2004). To determine whether food abundance affects differences in breeding success among sites and the incidence of polygyny, as Emlen & Oring (1977) suggested, food resources should be studied in different populations. However, as the species is an insect generalist and its prey varies significantly throughout the breeding season, between seasons, and with the age of nestlings (Bibby 1978, Cramp 1992, Dyrcz & Zdunek 1996) such studies would need to be performed at all sites in the same years and using the same methods.

According to the assumptions of the model explaining the evolution of polygamy by Shuster & Wade (2003), the Reed Warbler seems to be especially predisposed to polygyny because of asynchronous breeding (receptive females dispersed in time), and extremely high densities in breeding populations (and hence of females). However, the proportion of polygynous individuals is lower in the Reed Warbler than in related species, such as Great Reed Warbler *Acrocephalus arundinaceus* or Sedge Warbler *A. schoenobaenus,* which are characterised by more synchronous breeding and lower densities (Leisler & Catchpole 1992). For example, in our study area, densities of Great Reed Warbler are several times lower than those of the Reed Warbler (11.5–38 pairs / 10 ha *vs* 90–216 pairs / 10 ha; Dyrcz 1981, Halupka *et al.* 2008, Dyrcz & Halupka 2009) and the number of days in a season when receptive females occur is lower in the Great Reed Warbler (Med = 63, n = 14 years) than in the Reed Warbler (Med = 78, n = 14 years; Mann–Whitney U-test: U = 23, p = 0.0002). The annual index of breeding synchrony of Great Reed Warblers studied in Sweden (Arlt *et al.* 2004) was lower than in our population of Reed Warblers (median values of *SI*: 20.7 and 15.97 respectively; Mann–Whitney U-test: U = 19, p = 0.0195, n_1 = 11, n_2 = 9).

As such, at the intraspecific level, we should expect more frequent polygyny in Reed Warbler populations with higher breeding densities and less synchronous breeding. Indexes of breeding synchrony (Kempenaers 1993, Arlt *et al.* 2004) have not been published for any population of Reed Warblers (all populations seem to breed highly asynchronously, although substantial interseasonal differences exist), but data on densities are often more readily available and more stable across years. For example, in the British Wicken Fen population (where polygyny was found regularly), and the French population studied by Taillandier (1990), breeding densities were much lower than in our study population (Table 1). However, in contrast to Shuster and Wade's (2003) suggestion, polygyny was found more often in the western populations.

Differences in the spatial distribution of territories can also explain some variation in the frequency of extra-pair paternity between the studied populations. In Britain, Davies *et al* (2003) found extra-pair young in 15% of broods (1–2 extra-pair nestlings per nest) (Table 1) whereas in our population extra-pair young occurred in 16%–33% of nests each year, and in some nests accounted for all of the young. In the other central European population studied recently (Hoi *et al.* 2013), extra-pair young constituted almost 40% of all nestlings and occurred in more than 57% of unmanipulated nests (Table 1).

We conclude that Reed Warblers may adopt different mating strategies, depending on local food resources but also the density and spatial distribution of territories. In those populations with more abundant food resources, and probably better prey quality, some birds may form polygynous trios. In other areas, however, where the breeding densities are higher and food conditions relatively poorer, and so where the costs of solitary rearing young are high, birds may engage more often in extra-pair copulations. This explanation is consistent with the idea that mating systems should be perceived as flexible and fluid in both ecological and evolutionary time (Johnson & Bur-

ley 1997). At present this hypothesis can be supported only by scarce observational data, and to test the prediction further requires more data from different colour-ringed populations (preferably collected simultaneously to control for the effect of season), including information on the polygyny rate, the share of extra-pair nestlings, food resources, and population productivity.

Acknowledgments. We would like to thank Bruno Bargain, Alžbeta Darolová, Will Duckworth and Leif Nilsson, who kindly answered our questions regarding their study populations of Reed Warblers. We are grateful to Giulia Casasole, Justyna Chachulska, Monika Czuchra, Alicja Dziachan, Maria Podżorska, Stachu Rusiecki, Magdalena Soboń, Łukasz Tomasik, Katarzyna Turzańska, Paulina Turowicz, Jolanta Wójcik and Jarosław Wróblewski for field assistance. Remarks of two anonymous reviewers helped us to improve substantially the manuscript. We are also very grateful to Richard Broughton who corrected the language of the paper. Calculations of the number of fertile days of Great Reed Warblers were possible courtesy of Andrzej Dyrcz. In 2006–07 the research was financially supported by the Polish State Committee for Scientific Research (grant 2P04F05330) and Max Planck Institute for Ornithology, and in 2006–2013 by the University of Wroclaw (projects 1018/S/IZ/2006-12 and 1073/S/SORM/13).

Ei polygyniaa keskieurooppalaisissa rytikerttuspopulaatioissa

Keskustelu polygynian esiintymisestä on pitkälti keskittynyt laji- ja yksilötasoon. Tässä tarkastelemme polygynian astetta rytikerttusen eri populaatioissa. Länsi-Euroopan tilanteesta poiketen, rytikerttuset ovat puhtaasi monogaamisia tutkimuspopulaatiossamme lounaisessa Puolassa, sekä läheisessä slovakialaisessa populaatiossa. Keskustelemme tästä tuloksesta polygynian esiintymisen hypoteesien valossa. Ehdotamme, että eri puolilla Eurooppa voi olla eri strategioita lisääntymismenestyksen optimoimiseksi. Länsi-Euroopan rikkaammissa elinympäristöissä, joissa yksinäisetkin naaraat kykenevät kasvattamaan poikasiaan onnistuneesti, polygynia on tavallisempaa ja parisuhteen ulkopuoliset parittelut melko harvinaisia. Sen sijaan Keski-Euroopassa, jossa poikasten kasvattamisen kustannus on suurempi, koiraat eivät yritä houkutella toista naarasta, mutta harrastavat sen sijaan enemmän parisuhteen ulkopuolisia paritteluja.

References

Arlt, D., Hansson B., Bensch S., von Schantz T. & Hasselquist D. 2004: Breeding synchrony does not affect extra-pair paternity in Great Reed Warblers. — Behaviour 141: 863–880.

Bargain, B. & Henry, J. 2000: Breeding biology of Reed Warbler *Acrocephalus scirpaceus* in the Bay of Audierne (Brittany, France). — Alauda 68: 95–108. (In French with English summary)

Bateman, A.J. 1948: Intra-sexual selection in *Drosophila.* — Heredity 2: 349–368.

Bibby, C.J. 1978: Some breeding statistics of Reed and Sedge Warblers. — Bird Study 25: 207–222.

Bibby, C.J. & Thomas, D.K. 1985: Breeding and diets of the Reed Warbler at a rich and a poor site. — Bird Study 32: 19–31.

Brown, P.E. & Davies, M.G. 1949: Reed Warblers. — Foy Publications Ltd., East Moseley, Surrey.

Calvert, M. 2005: Reed warblers at Rostherne Mere. — English Nature, Shrewsbury.

Catchpole, C.K. 1971: Polygamy in Reed Warblers. — British Birds 64: 232–233.

Catchpole, C.K. 1974: Habitat selection and breeding success in the Reed Warbler (*Acrocephalus scirpaceus*). — Journal of Animal Ecology 43: 363–380.

Cramp, S. (ed.) 1992: The Birds of the Western Palearctic, vol. VI. — Oxford University Press, Oxford.

Davies, N.B., Butchart S.H.M., Burke, T.A., Chaline, N. & Stewart I.R.K. 2003: Reed warblers guard against cuckoos and cuckoldry. — Animal Behaviour 65: 285–295.

Duckworth, J.W. 1990: Parental care in the reed warbler. — D. Phil. Thesis, University of Cambridge.

Duckworth, J.W. 1992: Effects of mate removal on the behaviour and reproductive success of Reed Warblers *Acrocephalus scirpaceus*. — Ibis 134: 164–170.

Dyrcz, A. 1981: Breeding ecology of great reed warbler *Acrocephalus arundinaceus* and reed warbler *Acrocephalus scirpaceus* at fish-ponds in SW Poland and lakes in NW Switzerland. — Acta Ornithologica 18: 307–333.

Dyrcz, A. & Halupka, L. 2009: The response of the great reed warbler *Acrocephalus arundinaceus* to climate change. — Journal of Ornithology 150: 39–44.

Dyrcz, A. & Zdunek, W. 1996: Potential food resources and nestling food in the Great reed warbler *Acrocephalus arundinaceus* and Reed warbler *Acrocephalus scirpaceus* at Milicz fish-ponds. — Birds of Silesia 11: 12 –132. (In Polish with English summary)

Elphick, J. (ed.) 2007: The atlas of bird migration: Tracing the great journeys of the world's birds. — The Natural History Museum, London.

Emlen, S.T. & Oring, L.W. 1977: Ecology, sexual selection, and the evolution of mating systems. — Science 197: 215–223.

Halupka, L., Dyrcz, A. & Borowiec, M. 2008: Climate change affects breeding of reed warblers *Acrocepha-*

lus scirpaceus. — Journal of Avian Biology 39: 95–100.

Halupka, L, Sztwiertnia, H. & Tomasik, Ł. 2012: Single polygyny attempt in Reed Warbler *Acrocephalus scirpaceus* on Milicz fish-ponds. — Ornis Polonica 53: 300–302. (In Polish with English summary)

Henry, C. 1978: Feeding nestlings in Reed Warbler (*Acrocephalus scirpaceus*). Food selection. — Le Gerfaut 68: 25–52. (In French with English summary)

Hoi, H., Krištofik, J. & Darolová, A. 2013: Experimentally simulating paternity uncertainty: immediate and long-term responses of male and female reed warblers *Acrocephalus scirpaceus*? — PLoS ONE 8: e62541.

Jakubas, D. & Wojczulanis-Jakubas, K. 2010: Sex- and age-related differences in the timing and body condition of migrating Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus choenobaenus*. — Naturwissenschaften 97: 505–511.

Jonnson, K.J. & Burley, N.T. 1997: Mating tactics and mating systems of birds. — Ornithological Monographs 49: 21–60.

Kempenaers, B. 1993: The use of breeding synchrony index. — Ornis Scandinavica 24: 1.

Lack, D. 1968: Ecological adaptations for breeding in birds. — Methuen, London.

Leisler, B. & Catchpole, C.K. 1992: The evolution of polygamy in European reed warblers of the genus *Acrocephalus*: a comparative approach. — Ethology, Ecology & Evolution 4: 225–243.

Martin, T.E. 2004: Avian life-history evolution has an eminent past: does it have a bright future? — Auk 121: 289–301.

Møller, A.P. & Birkhead, T.R. 1993: Certainty of paternity covaries with paternal care in birds. — Behavioral Ecology and Sociobiology 33: 261–268.

Nilsson L. & Persson H. 1986: Choice of nest site, clutch size and nesting success in a population of Reed Warblers, *Acrocephalus scirpaceus*, in south Sweden — Var Fagelvarld. 45: 340–346. (In Swedish with English summary)

Owens, I.P.F. & Hartley, I.R. 1998: Sexual dimorphism in birds: why are there so many different forms of dimorphism? — Proceeding of the Royal Society of London B 265: 397–407.

Ölschlegel, H. 1981: Ergebnisse zehnjähringer Beobachtungen an einer Population des Teichrohrsängers, *Acrocephalus scirpaceus*, während der Brutzeit. Beitr. Vogelkd. — Beiträge zur Vogelkunde 27: 329–362. (In German)

Schulze-Hagen, K. 1991: *Acrocephalus scirpaceus*. — In Handbuch der Vogel Mitteleuropas (ed. Glutz von Blotzheim, U.N. & Bauer, K.M.),vol. 12/I: 433–486. AULA Verlag, Wiesbaden. (In German)

Schulze-Hagen, K., Leisler, B. & Winkler, H. 1996: Breeding success and reproductive strategies of two *Acrocephalus* warblers. — Journal of Ornithology 137: 181–192.

Shuster, S.M.& Wade, M.J. 2003: Mating systems and strategies. — Princeton University Press, Princeton and Oxford.

Stutchbury B.J. & Morton E.S. 1995: The e ffect of breeding synchrony on extra-pair mating systems in songbirds. — Behavior 132:675–690.

R Development Core Team 2011: R: a language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna.

Taillandier, J. 1990: First information about population dynamics of Reed Warbler (*Acrocephalus scirpaceus*) at salty marshes of Guérande (Loire region). — Alauda 58: 21–28. (In French with English summary)

Trivers, R.L. 1972: Parental investment and sexual selection. — In Sexual selection and the descent of men (ed. Campbell B.): 136–179. Aldine, Chicago.

Westerdahl, H., Bensch, S., Hansson, B., Hasselquist, D. & von Schantz, T. 2000: Brood sex ratios, female harem status and resources for nestling provisioning in the great reed warbler (*Acrocephalus arundinaceus*). — Behavioural Ecology & Sociobiology 47: 312–318.