Are there habitat dependent differences in male quality in Eurasian Reed Warblers? The role of male song and feeding investment

Existujú habitatové rozdiely v kvalite samcov trsteniarika bahenného? Úloha samčieho spevu a investície do kŕmenia

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Abstract. *Individuals of a species are usually adapted to a specific environment in terms of behavior, morphology or physiology. The question is whether fine tuned adaptations in a species may even exist within a habitat, but slightly different habitat features. Here we examine whether a marsh habitat consisting of patches of two different vegetation types (reed and reed mace) may result in male quality differences occupying them. We have already shown that in Eurasian Reed Warblers (*Acrocephalus scirpaceus*) egg investment of females, but not their quality or condition differs between individuals breeding in the two vegetation types. In this study we want to know, whether these habitat dependent investment strategies might be a consequence of differential allocation due to variation in male quality. To determine male quality we used i) song in terms of song speed, song complexity and redundancy of male Eurasian Reed Warblers singing in reed and reed mace and ii) paternal investment in terms of feeding contribution of males breeding in reed or reed mace. Our results revealed differences in feeding rates between broods raised in reed and reed mace territories but neither male song nor male feeding contribution varies between reed and reed mace territories. Thus different female egg investment is due to habitat rather than male quality. Habitat parameters influencing nest protection and offspring survival remain to explain differences in maternal egg investment.*

Key words: *Eurasian reed warbler, behavior, reed, reed mace, paternal investment, male attractiveness*

Introduction

Eurasian reed warblers (*Acrocephalus scirpaceus*) breed in different marsh habitats based on vegetation types, namely reed (*Phragmites australis*) and reed mace (*Typha* spp.) (Catchpole 1974, Glutz von Blotzheim & Bauer 1991, Honza et al. 1998, Borowiec 1992). Vegetation structure and in particular vegetation density differ between reed and reed mace (Catchpole 1974, Trnka et al. 2009, Darolová et al. 2014). In line with this we showed that nest predation was lower and reproductive success significantly higher in reed mace stands providing better nest cover. Surprisingly, this fitness advantage did not seem to convert into a clear preference for reed mace stands examining settlement order, but at least nest density was found to be higher in reed mace stands (Darolová et al. 2014). One prediction in line with a different offspring survival probability would be that females adjust egg investment accordingly (see

also Coslovsky et al. 2012). In this context we found differences in egg investment of female Eurasian reed warblers depending on the nesting habitat. Namely, females breeding in reed mace invest more into their eggs than females breeding in reed stands (Darolová et al. 2014). Beside habitat dependent variation in maternal investment it is also possible that the quality or attractiveness of the male partner can affect maternal investment (Petrie & Williams 1993, Garcia-Fernandez et al. 2010, Loyae & Lacroix 2010, McFarlane et al. 2010, Grenna et al. 2014, Sardell & DuVal 2014, Krištofík et al. 2014). Recently we have showed that in the Eurasian reed warbler (*Acrocephalus scirpaceus*), male song is an important feature of female mate choice. Furthermore maternal investment is influenced by the song characteristics of her partner (Krištofík et al. 2014), rather than the condition and quality of the female itself (Krištofík et al. 2013).

Consequently it would be important to investigate whether habitat dependent variation in maternal investment is mediated by habitat dependent variation in male quality.

In this study we therefore examined differences in male quality in terms of parameters found to be important in mate choice, including mating and paternal behavior, between the two vegetation types. In particular we examined male song quality and male feeding propensity of male Eurasian reed warblers. In terms of song we use different song parameters, which have been shown to be important for female egg investment (Krištofík et al. 2014). In terms of parental behavior we determined feeding contribution of male Eurasian reed warblers.

Materials and methods

Study area

We studied Eurasian reed warblers over three years (2011–2013) in the fishpond area of Veľké Blahovo, West Slovakia (48°03′09″ N, 17°35′38″ E, 112 m a.s.l.). The area consisted of three fishponds covering an area of approximately 70 ha. The pond area was partly covered with marsh stands consisting of *Phragmites australis*, *Typha angustifolia*, *T. latifolia* and partly *Carex* spp. In all three study years the entire area was inspected daily between 6h00 and 18h00, starting on April 1 until July 10.

Song recordings

Prior to mating, starting April 1, song was recorded from each male included in this study. We collected two to three song samples recorded two to five days apart. For standardization and to reduce the possibility of variability in song recordings throughout the pre-mating period, recordings were done only in the morning hours (between 6h00 and 10h00) and under acceptable accoustic conditions (e.g. avoiding events of strong wind, rain or heavy air traffic). The first recording was always done on male arrival day at the territory or one day later (Krištofík et al. 2014).

For song recording we used an M-Audiotrack digital recorder connected to a condenser microphone mounted on a parabolic reflector (for details on recording set up, see Krištofík et al. 2014). For song analysis we used Avisoft Bioacoustics software. For the analyses we randomly selected 30 seconds of song usually originating from two of the recorded song material of each male. The 30 seconds of song of each male were printed and subsequently analyzed. For the analysis, samples were further divided into six-second intervals to determine structural parameters and the reliability of using 30 seconds of male song. That the choosen sample size is representative to characterize individual male song quality features was already demonstrated in an earlier study (Krištofik et al. 2014). For each song we determined syllables (for definition of syllables Catchpole & Slater 1995) as the smallest structural unit. Different syllables have a different structure and are separated by a short pause (Krištofík et al. 2014). To reduce analyzing errors due to variation in syllable discrimination, only one person (AD) did the visual analyses of the printed spectra. The following eight variables have been investigated. For details on the reliability of the selected song parameters, see Krištofík et al. (2014):

- Song speed: This parameter describes song speed in terms of the number of syllables a male produces per time unit. In this analysis therefore the number of syllables/30 seconds was used.
- Number of syllable types: This variable refers to the structural complexity of a male's song. It takes versatility but not necessarily innovative skills (for instance, the appearance of novel syllables) into account. It describes how many different syllable types a male produces in six-second intervals, independent of whether the same syllables have been observed in the former intervals. For the analysis the total number of syllable types of five six-second intervals (30 seconds) was used.
- Number of new syllables: This variable, describing structural song complexity, includes an innovative and a repetitive aspect of the song, and counts the number of novel syllables and how frequently they are used at every six-second interval.
- Number of new syllable types: This variable describes a purely innovative aspect of structural complexity, namely, the number of new syllable types appearing every six seconds over a period of 30 seconds. This count can only start after the first six-second interval, and consequently, the total number of new syllable types appearing over four intervals (following the first six second interval) is used for the analysis. Assuming high consistency over time, this variable would be the best predictor for repertoire size.
- Number of repeated syllables: This variable describes redundancy in terms of how frequently a syllable type appears in a six-second interval. The total number of syllable repetitions over five intervals (30 seconds) was used for the analysis.
- Number of repeated syllable types: Similarly, this variable describes how many different syllable types are repeatedly advertised per six-second interval. The total number of repeated syllables over five intervals (30 seconds) was used for the analysis.
- Number of immediately repeated syllables: This variable describes the number of syllables that are immediately repeated syllables over 30 seconds based on six-second intervals. The total number of repeated syllable types appearing over five intervals (30 seconds) was used for the analysis.
- Number of syllable switches: This complexity variable counts how frequently a male switches to a different syllable between successively produced syllables. Counts are again based on six-second intervals. The total number of syllable switches appearing over five intervals (30 seconds) was used for the analysis.

Determining of parental investment

To examine male parental behaviour we observed the total number of feedings per hour pooling the number of feeding trips of male and female Eurasian reed warblers. Males and females were identified by individual colour ring combinations. Therefore both parents were trapped before observations, females during the early feeding period (nestlings 2 to 5 days old) and males during territory settlement. For the analysis the proportion of male to female feedings as well as the total feeding rate (male and female feeding rates combined) were used. Feeding behaviour was observed from a hide, established one day prior to observation at a distance of five m from the nest. Behavioural observation were done in the morning hours between 06h00 and 10h00, and when nestlings were 6 to 8 days old.

Statistical analysis

All data fulfilled the requirements of normality, and therefore we used parametric tests throughout. Student t-tests were used to compare differences in the song parameters related to song speed, song complexity and song repetitions for males breeding in reed and reed mace vegetation. Since no variable significantly differed between the two vegetation types, p-values adjusted for Bonferroni are not presented. To examine the differences in the total feeding rate

Table 1. Different song parameters of males singing in reed (N = 11) or reed mace territories (N = 15). Given are means ± SE per 30 sec. of song; differences between habitats are not statsistically significant (P > 0.05).
Tabuľka 1. Charakteristiky spevu samcov s teritóriami v trstine (N = 11) alebo pálke (N = 15). Zobrazené sú priemerné hodnoty parametrov a ich štandardné odchýlky chyby zaznamenané počas 30 sekúnd spevu; rozdiely medzi habitatmi nie sú statisticky významné (P > 0.05).

Song parameter / Charakteristika spevu	Reed / Trstina	Reed mace / Pálka
Number of syllables (song speed)[1]	179.4 ± 9.9	176.9 ± 9.1
Number of syllable types [2]	68.2 ± 4.0	73.9 ± 3.5
Number of new syllables[3]	100.11 ± 9.3	111.77 ± 6.0
Number of new syllable types[4]	42.22 ± 4.2	49.3 ± 4.2
Number of repeated syllables[5]	153.8 ± 10.7	144.9 ± 5.5
Number of repeated syllable types[6]	43.0 ± 2.5	43.07 ± 1.1
Number of immediately repeated syllables[7]	124.0 ± 14.1	113.6 ± 17.3
Syllable switches[8]	85.7 ± 5.8	88.4 ± 0.5

[1] Počet slabík (rýchlosť spevu), [2] Počet typov slabík, [3] Počet nových slabík, [4] Počet nových typov slabík, [5] Počet opakovaných slabík, [6] Počet opakovaných typov slabík, [7] Počet bezprostredne opakovaných typov slabík, [8] Zmena slabiky.

and the male to female feeding rate between reed and reed mace, we used a GLM with vegetation type as fixed factor, and brood size as covariate.

Results

We did not find any difference in male song performance when examining different song characteristics of males breeding in reed or reed mace. Song speed did not vary between reed and reed mace males (Table 1). Also, structural song complexity in terms of syllable changes and song redundancy in terms of syllable repetitions did not vary between reed and reed mace males (Table 1).

Examining the total feeding rate we found a significant difference in overall feeding investment (number of feeding trips of males and females) between the two vegetation types ($F = 3.4$, $P = 0.008$, Fig. 1). The results suggest that feeding investment is higher in reed than in reed mace.

However, examining male to female feeding effort, we did not find a difference between the two vegetation types ($F = 0.2$, $P > 0.9$, Fig. 1).

Discussion

In this study we found differences in parental feeding behaviour, but no evidence for vegetation type dependent variation in male quality related to song or paternal characteristics. Thus male quality differences can be neglected to explain vegetation type dependent variation in maternal investment.

Early maternal investment is an important factor influencing offspring development (Mousseau & Fox 1998, Müller et al. 2007). There are several factors or pathways through which maternal investment can be influenced. One major route would be that, maternal investment depends on the environment. In line with this resource availability may influence maternal investment (Mousseau & Fox 1998). Alternatively, female habitat selection may also depend on her intrinsic quality and/or her condi-
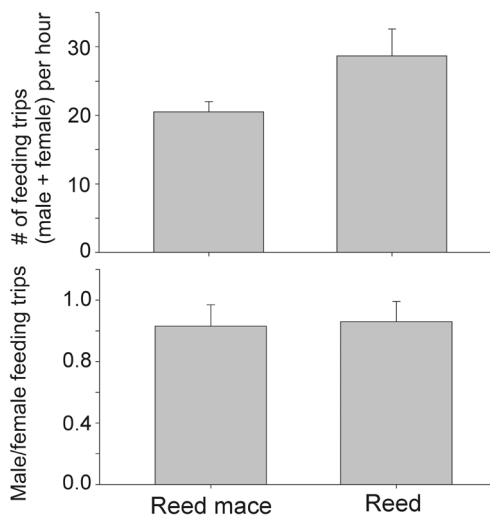

Fig. 1. Number of feeding trips per hour combined for males and females (upper graph) and male to female feeding trips per hour (lower graph) for broods in reed mace (N = 16) and reed (N = 15) respectively (given as (means ± SE).
Obr. 1. Počet kŕmení mláďat za hodinu spolu samcami a sae micami (horný graf) a pomer počtu kŕmení mláľat samcami /samicami (dolný graf) v hniezdach v pálke (N = 16; reed mace) a trsti (N = 15; reed). Zobrazené sú aritmetické priemery ± stredná chyba.

tion (Moreno et al. 2006, Zanollo et al. 2013) and reflected in maternal investment.

At the first glance egg investment in female Eurasian reed warblers seems to be directly related to environmental differences. Egg yolk weight was significantly bigger in reed mace than in reed (Darolová et al. 2014).

Do differences in food availability, provided by the two vegetation types, directly influence female condition and consequently maternal investment? A strong, direct effect of vegetation type on maternal investment is not expected, because Eurasian reed warblers frequently hunt outside the breeding territory and vegetation, and even forage in adjacent habitats (Catchpole 1973, Borowiec 1992). For example, 64% of all foraging events of Eurasian reed warblers occur outside the marsh (Catchpole 1973). Alternatively, environmental affects via female condition have not been observed since female condition did not differ between the two habitats (Krištofík et al. 2014) and there is also no habitat-dependent body size difference, which would suggest that superior and more competitive females nest in reed mace stands (see (Krištofík et al. 2013).

However our results demonstrate that the feeding effort in terms of total number of feeding trips per hour significantly vary between the two habitats. This result may indicate different insect availability in the two vegetation types. For instance, the higher feeding frequency in reed may be due to differences in prey size. Reed, in contrast to reed mace is frequently covered with aphids, and Eurasian reed warblers use them to feed offspring (Catchpole 1973, Grim & Honza 1996). Smaller prey loads may hence require more frequent feeding trips. Thus, a different food supply related to the two vegetation types cannot necessarily be derived from our results. Consequently, feeding rate may not be a proper determinant of food availability and no strong conclusions can be drawn in relation to vegetation type dependent variation in food availability.

Beside the environment there are other factors, related to the social environment which could influence maternal investment, e.g. the quality or attractiveness of the mate (Hofstad et al. 2002, Remeš 2011, Okanoya & Soma 2013, Grenna et al. 2014, Krištofík et al. 2014).

In several species it is known that female choice is based on male parental quality (Greig-Smith 1982, Hoelzer 1989, Hoi-Leitner et al. 1995, Keyser & Hill 2000). There is in fact variation in male feeding investment in Eurasian reed warblers and males rather than females adjust investment also according to the needs of young (Kleindorfer et al. 2003).

In fact male Eurasian reed warblers differ in size between the two vegetation types. Reed mace males are bigger in terms of tarsus length than reed males (Darolová et al. 2014). Thus, one could assume that superior males settle in reed mace.

Here we show that feeding behaviour in general differs between the two vegetation types but male feeding contributions did not, which suggests, that although reed and reed mace males differ in morphology, they do not differently invest in offspring feeding. Consequently, there is no obvious difference in paternal quality (feeding investment), which may help to explain habitat dependent variation in maternal egg investment.

Because in the monomorphic Eurasian reed warbler (Krištofík et al. 2014) as well as other *Acrocephalus* warblers (Catchpole et al. 1984, Bensch & Hasselquist 1992, Catchpole 1996, Buchanan & Catchpole 1997), song is the most important feature for female choice we would expect that male quality differences between vegetation types should be most pronounced in their song performance. Even more that maternal investment has been demonstrated, to be affected by male song performance (Krištofík et al. 2014). Thus maternal investment could be a response to male habitat dependend variation in song performance.

Our results, however, revealed that there is no evidence that, males differ in song quality (see Table 1). Neither song speed, nor song complexity or redundancy varied between males performing in reed or reed mace. Therefore the male song features investigated, which are known to be related to mate choice and maternal

investment, do not help to explain female allocation rules between the two vegetation types.

To conclude, differences in male attractiveness or quality can be neglected to be responsible for differences in female egg investment between the two vegetation types. Also, vegetation-type dependent variation in food availability, female condition or intrinsic quality, are unlikely to influence maternal egg investment (Krištofík et al. 2013). In the end it seems that only certain environmental features related to nest site and offspring protection remain to explain resource allocation into eggs. One could imagine that nest site features like vegetation density may influence the perceived visual protection from predators when building or sitting in the nest, for example. In fact, visual protection has been shown to influence incubating female risk assessment and consequently her defense behavior (Schneider & Griesser 2013), and there is also evidence that visual cues are responsible to influence female egg investment (Coslovsky et al. 2012). This is one interesting assumption, which should be further explored.

Súhrn

Jedince určitého druhu sú obvykle adaptované na špecifické prostredie správaním, morfológiou alebo fyziológiou. Je otázne, či jemne ladené adaptácie druhu môžu byť aj v rámci habitatu s nepatrnými odlišnosťami jeho vlastností. V tejto štúdii sme sa snažili preveriť, či mokradný biotop pozostávajúci z dvoch odlišných typov vegetácie (trsť a pálka) môže vyústiť do odlišností kvality samcov v nich. Už sme zistili, že investície samíc trsteniarika bahenného do vajec sa líšila medzi jedincami hniezdiacimi v týchto dvoch typoch vegetácie, pričom kondícia samíc sa však nelíšila. V tejto štúdii sme chceli zistiť, či tieto investičné stratégie samíc závislé do typu habitatu môžu byť dôsledkom variability kvality samcov. Na hodnotenie kvality samcov sme použili a) spev – jeho rýchlosť, komplexnosť a redundanciu trsteniarikov bahenných spievajúcich v trsti a pálke a b) otcovské investície samcov v spolupodieľaní sa na kŕmení mláďat v hniezdach v trsti a pálke. Naše výsledky ukázali rozdiely v intenzite kŕmenia medzi hniezdnymi teritóriami v trsti a pálke. Rozdiely v materských investíciách samíc do vajec môžu vysvetliť parametre habitatu ovplyvňujúce ochranu hniezd a prežívanie mláďat.

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