J Ornithol (2017) 158:925–933
DOI 10.1007/s10336-017-1466-3

ORIGINAL ARTICLE

# Great Reed Warbler singing behavior and conspicuous song structures are not nest-location cues for the Common Cuckoo

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Received: 1 December 2016 / Revised: 12 April 2017 / Accepted: 29 May 2017 / Published online: 6 June 2017

**Abstract** In some systems, brood parasites may be attracted by vocal or visual signals connected with host breeding. We studied a Great Reed Warbler (*Acrocephalus arundinaceus*) population where annually 30–50% of nests are parasitized by the Common Cuckoo (*Cuculus canorus*). We observed host males and quantified their song-related behaviors, including time spent singing, distance of movements and time spent singing in particular positions on a reed stem. We predicted that nests of more exposed males (i.e., those spending more time singing, moving a larger total distance, and spending more time on the top of stems) would be more likely to be parasitized than the nests of less exposed males. Additionally, we measured male song characteristics that we assumed to be most audible, and thus potentially the most conspicuous to the Common Cuckoo. We counted the number of "kara" syllables per song and measured their peak frequencies. Since these song structures are of low frequency and thus might be audible at longer distances, we predicted that males producing more kara syllables or uttering kara syllables of lower peak frequencies would also be more parasitized. However, we found that neither male singing behavior nor conspicuous song characteristics were significant predictors of parasitism. Only the visibility of host nests to the parasite, which we treated as a covariate, proved to be significant. Visible nests were more often parasitized than hidden nests. Our findings indicate that the Cuckoo females use nest visibility, or host behavior other than male singing, as the cue to locate host nests.

**Keywords** *Acrocephalus arundinaceus* · Brood parasitism · *Cuculus canorus* · Eavesdropping · Host activity hypothesis

## Zusammenfassung

### Drosselrohrsänger (*Acrocephalus arundinaceus*): Weder ihr Singverhalten, noch auffallende Strukturelemente in den Gesängen dienen dem Kuckuck (*Cuculus canorus*) als Hinweise auf den Standort der Nester

Es gibt Fälle, in denen Brutparasiten von akustischen oder visuellen Signalen, die mit der Brutaktivität des Wirts verbunden sind, angezogen werden. Wir untersuchten eine Population des Drosselrohrsängers (*Acrocephalus arundinaceus*), in der jedes Jahr 30–50% der Nester vom Kuckuck (*Cuculus canorus*) parasitiert werden. Hierfür beobachteten wir die Wirts-Männchen und quantifizierten ihre mit dem Singen verknüpften Verhaltenselemente, inklusive der mit Singen verbrachten Zeit, ihrer räumlichen Bewegungsmuster und der Zeit, die sie singend in ganz bestimmten Körperstellungen an einem Schilfhalm zubrachten. Wir sagten vorher, daß Nester von stärker exponierten Männchen (z. B. jenen, die mehr Zeit mit Singen verbrachten, beim Herumhüpfen größere

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Communicated by S. Kipper.

**Electronic supplementary material** The online version of this article (doi:10.1007/s10336-017-1466-3) contains supplementary material, which is available to authorized users.

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Entfernungen zurücklegten und mehr Zeit auf ein und demselben Schilfrohr hockten) eher parasitiert würden als weniger exponierte Männchen. Zusätzlich maßen wir die Längen derjenigen charakteristischen Gesangselementen, die am klarsten herauszuhören und damit für die Kuckucke potentiell am auffälligsten waren. Wir zählten die Anzahl der Kara-Silben pro Gesang und bestimmten deren Frequenzspitzen. Da diese Gesangselemente eher niedrigere Frequenzen aufweisen und somit über längere Entfernungen zu hören sind, mutmaßten wir, dass Männchen, die mehr Kara-Silben produzierten, oder mehr solche mit niedrigeren Frequenzen, häufiger parasitiert würden. Wir fanden jedoch heraus, dass weder das Sing-Verhalten der Männchen, noch auffällige Gesangsmuster signifikante Prädiktoren für Parasitismus waren. Einzig die Sichtbarkeit der Wirts-Nester für die Parasiten, von uns als Kovariante behandelt, stellte sich als signifikant heraus. Leicht sichtbare Nester wurden häufiger als versteckte Nester parasitiert. Unsere Ergebnisse legen nahe, dass Kuckucks-Weibchen die Nest-Sichtbarkeit oder aber Verhaltensweisen der Wirte, die nichts mit dem Gesang der Männchen zu tun haben, als Mittel benutzen, Nester von Wirten zu finden.

## Introduction

Signals are transmitted in communication networks in which multiple signalers and receivers are present, but individuals other than those interacting with the signaler can also be informed by these signals (McGregor 2005). In birds, auditory and visual signals are most often used, at the intraspecific level, to compete for a territory or mate, for mate choice and in parent–offspring communication (Kroodsma and Miller 1982; Catchpole and Slater 2008; Bradbury and Vehrencamp 2011). At the interspecific level, they are mostly used in predator–prey interactions (Whitear and Stehlik 2009).

Brood parasites use similar cues to locate nests as avian nest predators (Grieef 1994). They may find nests by habitat searching (Robinson and Robinson 2001) or observation from a nearby perch (Alvarez 1993; Hauber and Russo 2000; Honza et al. 2002; Begum et al. 2011). The success of finding a nest by a parasite may be affected by nest-site characteristics including vegetation type, nest position and height above the ground, distance to habitat edge and to the nearest tree (Honza et al. 1998), as well as by vegetation cover (Moskát and Honza 2000; Fiorini et al. 2012), nest size (Briskie et al. 1990; Soler et al. 1995; McLaren and Sealy 2003; but see Grim et al. 2011; Jelínek et al. 2015) and nest visibility (Jelínek et al. 2014). Moreover, host vocal and visual conspicuousness due to territorial, nest-building or egg-laying behavior may also attract nest parasites (Uyehara and Narins 1995; Clotfelter 1998; Dabelsteen et al. 1998; Banks and Martin 2001). In this respect, some parasitic females even use host nest-defense responses directed toward them as a nest-location cue (Seppä 1969; Smith 1981; Gill et al. 1997).

Apart from using nest-location cues, brood parasites might also search for hosts that are best suited for their offspring (Parejo and Avilés 2007). Thus, they may choose hosts that will rear young parasite(s) successfully (Rothstein 1990). In some hosts, nest size reflects parental ability, and it is positively correlated with the probability of parasitism (Briskie et al. 1990; Soler et al. 1995; McLaren and Sealy 2003). Parasites also prefer high-quality hosts, as suggested from host females' body condition and egg color (Polačiková et al. 2009). Song output might be an reliable indicator of male condition (Greig-Smith 1982; Poesel et al. 2001; Searcy and Nowicki 2000) or food resources in a territory (Radesäter and Jakobsson 1989; Manica et al. 2014). If so, the parasites may also utilize these signals when searching for suitable nests.

Though there has been considerable effort to identify cues that brood parasites employ to find host nests (Vogl et al. 2002; Antonov et al. 2007; Parejo and Avilés 2007; Patten et al. 2011; and citations above), only a few studies have focused on host singing and movement (e.g., Clotfelter 1998; Banks and Martin 2001; Garamszegi and Avilés 2005). Studies focused on parasitic Cowbirds either supported the host activity hypothesis, i.e., that parasites are attracted by host nest-building or other behavior (e.g., Briskie et al. 1990; Grieef 1994; Banks and Martin 2001; Svagelj et al. 2009) or contradicted it (Fiorini et al. 2009; Steckler and Conway 2012). Studies on parasitic Cuckoo species also had equivocal findings. Soler and Pérez-Contreras (2012), who studied the Great Spotted Cuckoo (*Clamator glandarius*)—Eurasian Magpie (*Pica pica*) system, found that the parasite's observation of host activity near the nest determined its egg-laying decision. In the Common Cuckoo (*Cuculus canorus*), hereafter "Cuckoo," this topic has been investigated by Avilés et al. (2009) only. The authors reported that neither nest size nor song output of the Great Reed Warbler (*Acrocephalus arundinaceus*) hosts predicted their probability of being parasitized. Thus, Avilés et al. (2009) did not support the hypothesis that Cuckoos eavesdrop on signals likely reflecting host parental abilities.

Here we extended the study of Avilés et al. (2009) by marking host males and verifying their identity before we analyzed the effect of host vocal and visual stimuli on the probability of nest parasitism by Cuckoo females. Knowing the identity of male Great Reed Warblers is important because they sometimes change their territories over the course of the breeding season. In places with high breeding density, their territories may also be quite close to each other or partly overlap and males then may make relatively long flights into the territories of their neighbors.

The Great Reed Warbler is a polygynous species that has evolved a conspicuous singing behavior with variable song structures and repertoire size (Catchpole et al. 1985). Unpaired males sing a long advertising song that usually ceases after pair formation but often reappears when the males attempt to attract another female (Hasselquist and Bench 1991). Shorter territorial song is used by both paired and unpaired males in territorial defense (Cramp 1992). Singing males typically perch high on reed stems and often move between different song posts, while exhibiting their song-related behaviors (Kennerley and Pearson 2010). They are noisy, conspicuous, less secretive and much more easily detected than males of most other *Acrocephalus* warblers. Paired males also sing near nests, guard them and often follow females when they are collecting nest material (Cramp 1992). Thus all the above-mentioned cues might potentially be used by female Cuckoos to locate host nests. Studies on Cowbirds revealed that brood parasitic females use the activity of hosts to locate nests (Clotfelter 1998; Jaramillo and Burke 1999; Banks and Martin 2001). Based on this knowledge, we predicted that nests of more exposed males (i.e., those spending more time singing, moving larger total distances, and spending more time on the top of reed stems) would be parasitized more than the nests of less exposed males. Additionally, we predicted that males producing a higher number and/or lower peak frequencies of kara syllables would also be more parasitized, because these low-frequency song structures are audible at longer distances (Jilka and Leisler 1974).

## Methods

### Fieldwork

We conducted the study from the end of April up to and including the beginning of July 2010 around fish ponds between Hodonín (48.85°N, 17.12°E) and Mutěnice (48.90°N, 17.03°E), in the Czech Republic. The host population consisted of ~100 breeding pairs of the Great Reed Warbler and experienced a relatively high parasitism rate [47% (Jelínek et al. 2014)]. Birds were mist-netted soon after territory establishment (males) or during nest building, egg laying or incubation (females). After capture, they were ringed with unique combinations of up to three plastic color rings and one aluminum ring. However, since many individuals had been marked in previous years, we did not disturb these unnecessarily and confirmed their identity by re-sighting. Based on our observations, 30 (29%) of 103 Great Reed Warbler males changed their territories over the course of the breeding season studied. The shortest and longest distances of such changes were 40 m and 5.4 km, respectively. Moreover, in some places with high breeding density, territories of some neighboring males were quite close to each other and partly overlapped, while other males made relatively long flights (even hundreds of meters) to change their song posts. Therefore, marking individual males as well as verifying their identity before observation of their behavior and before song recording were important prerequisites for collecting unbiased data.

We systematically searched for nests in male territories. The nests were found at the stage of building or at the beginning of egg laying, and were checked daily until clutch completion. At each visit, we numbered a newly laid egg with a waterproof pen according to its laying order and checked the nest content for the presence of a parasitic egg. Only clutches with a Cuckoo egg were recorded as parasitized.

Observations of color-ringed males started after male settlement and continued through the nesting stages potentially attractive to Cuckoos (i.e., nest building, egg laying) until the ultimate egg was laid (modal clutch size = 5 eggs). Observations were made by M. C., both in the morning (0500–1000 hours) and evening (1700–2100 hours), so that they covered the peaks of the highest Great Reed Warbler singing activity (Capek and Kloubec 2002; Kloubec and Capek 2011). Males were observed for 15 min after they had been detected, and after that their identity was verified using Vortex Viper 10 × 42 binoculars from a distance of 10–20 m. This distance was chosen to minimize observer effect, and to ensure correct identification of the focal male and reliable estimation of his positions. During the observation periods, we recorded the time the focal male spent singing (using a stopwatch), distances of his song-related movements exceeding 0.5 m as well as the time he spent singing at different positions on a reed stem. The position was estimated from the observer's viewpoint as a value on a scale (1–4) from the bottom to the top quarter of the stem. Sometimes, however, the male could not be properly located, either visually or acoustically. In such cases, we used the mean position value on the scale (i.e., 2.5) to express the unknown position. A song was defined as a continuous sequence of at least four syllables separated by a clear pause. Both types of song (short and long) were taken into account, similarly as in the studies of Catchpole et al. (1986) and Hasselquist and Bench (1991). Since the Great Reed Warblers might be expected to adjust their typical behavioral routines in response to strong wind or heavy rain, we avoided making observations during inhospitable weather, which could also influence males' detectability.

A total of 159 observations of 42 males belonging to 59 nests (25 of the nests were parasitized) were made. We made 96 observations in the morning and 63 in the evening, with a mean number of four observations per male (range 1–13) and three observations per nest of a particular male (range 1–6). Due to polygyny, some of the males had more than one nest, therefore the numbers of males and nests do not match.

We recorded the songs of 32 color-ringed males (of which 27 were also observed by M. C.) throughout the same nesting stages and periods of the day as above (though not necessarily on the same days). All recordings were made by Z. Š. from a distance 10–20 m, using a Marantz PMD 670 recorder and a Sennheiser ME-66 directional microphone. Again, we covered both types of song (sensu Catchpole 1983). All males included in this study had their nests in the same territories where the observations and/or recordings were made.

For each focal male we recorded the following breeding or nest characteristics (apart from parasitism): clutch initiation day (Julian date), nest status (monogamous—the nest of a monogamous male, primary—the nest belonging to the first female of a polygynous male, secondary—the nest belonging to the second female of the polygynous male), nest distance (in meters) to the nearest potential Cuckoo perch [shrub, tree or electric wire more than 5 m high (Jelínek et al. 2014)] and Cuckoo nest view (0 = no view, i.e., a Cuckoo could not see the nest from a perch nor locate it by host behavior; 1 = indirect view, i.e., a Cuckoo could not see the nest but could locate it by host behavior; 2 = direct view, i.e., the Cuckoo could directly see the nest from a perch; Øien et al. 1996; Jelínek et al. 2014). The last two variables were estimated by eye from the position of a nest.

### Variables and statistical analyses

From the observation protocols, we calculated total time a male spent singing, total distance of his movements and conspicuousness score as $\frac{\sum t_i p_i + t_u p_u}{t}$, where $t_i$ is the time spent at a particular position and $p_i$ is the position value on the scale 1–4 (see above), $t_u$ is the time spent at an unknown position, $p_u$ is the mean value on the scale (2.5) and $t$ is the total observation time (15 min). We averaged time spent singing, total distance of movements and conspicuousness score per nest of particular males.

Although we acquired more song recordings per male, we used only the most representative one (i.e., of the highest quality and containing at least 20 songs) for further detailed analyses. The recordings were analyzed in Avisoft SASLab Pro version 4.40 (Specht 2007) by J. C. S. As some temporal and structural parameters of the Great Reed Warbler song, like song length, repertoire size and syllable switching, have no effect on Cuckoo parasitism (Avilés et al. 2009), we focused on those structures and their spectral characteristics that make the song generally most conspicuous (Jilka and Leisler 1974). In each song, we thus counted the number of kara syllables and measured their peak frequencies (hertz), using the linear amplitude spectrum function (Fig. 1). Then we averaged these song-specific values per male.

As we observed and recorded the focal males at different breeding stages and these stages differ in the length of male song (see above), in further analyses we corrected time spent singing and number of kara syllables for the particular stage and used residual values of these song variables.

To investigate whether the parasitism rate could be explained by male singing behavior, we fitted a generalized linear mixed model (GLMM) with a binomial error distribution and logit link function, where Cuckoo parasitism of individual nests was entered as a binary response variable (parasitized = 1, non-parasitized = 0). As fixed effects, we used male characteristics, i.e., mean residual time spent singing, mean total distance of movements and mean conspicuousness score. As covariates, we included nest distance to the nearest potential Cuckoo perch, Cuckoo nest view, nest status, clutch initiation day (centered in each nest status category) and second power of the clutch initiation day (to account for non-linear relationship). Male identifiers were included as a random effect, because more than one nest often belonged to particular males (especially when they were polygynous).

To explore whether the parasitism rate could be explained by conspicuous characteristics of male song, we fitted a generalized linear model (GLM) with a binomial error distribution and logit link function, where Cuckoo parasitism was entered as a binary response variable, mean residual number of kara syllables, their mean peak frequency as fixed effects, and all but one above-mentioned nest characteristics as covariates. We did not include nest status because nest numbers in particular categories were highly imbalanced, which could cause problems when fitting models.

All statistical analyses were conducted in R version 2.15.2 (R Core Team 2012). The GLMM was fitted in the package lme4 version 0.999999.0 (Bates et al. 2008), using Laplace approximation for parameter estimations (Bolker et al. 2009). In both the GLMM and the GLM, all input variables showed pairwise Spearman rank correlations lower than $|r_S| = 0.34$ and variance inflation factors less than 1.65. Thus, the models should not have been biased by multicollinearity. Residuals from the models did not exhibit any unnatural patterns and all Cook's distances were less than 0.60.

## Results

Host males with parasitized nests ($n = 25$) spent in total 10.6 ± 3.6 min (mean ± SD) singing while males with non-parasitized nests ($n = 34$) spent 10.9 ± 3.7 min of the 15 min of observation singing. Males with parasitized nests

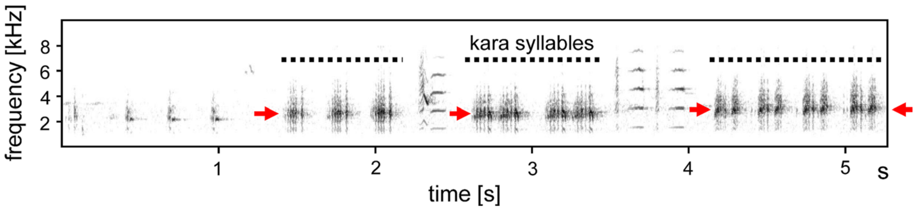

**Fig. 1** Example spectrogram of one Great Reed Warbler song with a typical composition; "kara" syllables are indicated by *dotted lines*, and their peak frequencies by *arrows* (for the sound recording, see the Electronic supplementary material (ESM)]

moved a total distance of 52 ± 38 m and reached a conspicuousness score of 2.6 ± 0.5, compared to males with non-parasitized nests, which moved 39 ± 39 m and were almost equally conspicuous (2.6 ± 0.4).

Neither the above-mentioned components of male singing behavior nor the nest characteristics (Cuckoo nest view, nest distance to the nearest Cuckoo perch and nest status, timing of the clutch) significantly explained the variation in the probability of Cuckoo parasitism (Table 1).

Males with parasitized nests ($n = 14$) produced 6.5 ± 2.2 kara syllables per song with a mean peak frequency of 2481 ± 147 Hz while males with non-parasitized nests ($n = 18$) produced 6.6 ± 2.1 kara syllables per song with a mean peak frequency of 2512 ± 97 Hz. The mean peak frequency of kara syllables was a marginally non-significant predictor of Cuckoo parasitism, with nests where males produced lower-pitched kara syllables showing a slight tendency to be more parasitized than those belonging to males producing higher-pitched kara syllables. The only important predictor, however, was the Cuckoo nest view: visible nests were statistically significantly more parasitized than hidden nests (Table 2).

## Discussion

We predicted that the Great Reed Warbler singing behavior and conspicuous song structures (i.e., kara syllables) may be used by Cuckoo females as nest-location cues. In general, the song of male passerines is critical for their reproductive success because it is used in territorial defense and mate attraction (McDonald 1989; Catchpole and Slater 2008). Thus, for males, the benefits of singing should outweigh the potential cost of reduced reproductive success if their nests are parasitized (Banks and Martin 2001).

Contrary to our expectations, neither the singing behavior of more exposed host males nor their potentially conspicuous song characteristics were significant predictors of parasitism. Only nest visibility from the Cuckoo's viewpoint, which we treated as a covariate, proved to be significant, at least in one of our analyses. More visible nests were more often parasitized than less visible nests. Our findings thus indicate that the parasitic females use nest visibility rather than male singing behavior as the best cue to locate Great Reed Warbler nests. This may be explained by the fact that the males of this host species do

**Table 1** Estimates, SE and results from the ANOVA table (type III) of fixed effects from the full generalized linear mixed model explaining the variation in the probability of Cuckoo parasitism in relation to Great Reed Warbler singing behavior (time spent singing, total distance of movements and conspicuousness score), nest characteristics (Cuckoo nest view, distance to the nearest Cuckoo perch, nest status) and timing of breeding (clutch initiation day, clutch initiation day$^2$)

| | Estimate | SE | Wald $\chi^2$ | *P* |
|---|---|---|---|---|
| Probability of Cuckoo parasitism | | | | |
| Time spent singing | −0.13 | 0.12 | 1.2 | 0.28 |
| Total distance of movements | 0.02 | 0.01 | 2.3 | 0.13 |
| Conspicuousness score | 0.44 | 0.76 | 0.3 | 0.56 |
| Distance to the nearest Cuckoo perch | 0.05 | 0.04 | 1.6 | 0.20 |
| Cuckoo nest view | 1.12 | 0.76 | 2.2 | 0.14 |
| Nest status | – | – | 3.1 | 0.21 |
| Clutch initiation day | 0.01 | 0.03 | 0.1 | 0.73 |
| Clutch initiation day$^2$ | 0.00 | 0.00 | 1.0 | 0.31 |

For more details about predictors see the "Methods"

**Table 2** Estimates, SE and results from the ANOVA table (type III) of fixed effects from the full generalized linear model explaining the variation in the probability of Cuckoo parasitism in relation to conspicuous characteristics of Great Reed Warbler song (number of kara syllables and their mean peak frequency), nest characteristics (Cuckoo nest view, distance to the nearest Cuckoo perch) and timing of breeding (clutch initiation day, clutch initiation day$^2$)

| | Estimate | SE | Wald $\chi^2$ | *P* |
|---|---|---|---|---|
| *Probability of Cuckoo parasitism* | | | | |
| Number of kara syllables | −0.20 | 0.23 | 0.7 | 0.39 |
| Mean peak frequency of kara syllables | −0.01 | 0.00 | 3.2 | 0.07 |
| Distance to the nearest Cuckoo perch | 0.03 | 0.04 | 0.3 | 0.56 |
| Cuckoo nest view | 3.04 | 1.22 | 6.3 | 0.01* |
| Clutch initiation day | 0.15 | 0.09 | 2.7 | 0.10 |
| Clutch initiation day$^2$ | 0.01 | 0.01 | 1.1 | 0.29 |

For more details see "Methods" section

* $P < 0.05$

not always sing near their nests (Catchpole et al. 1985). Alternatively, the observation periods in our study might not have been long enough to provide a representative sample of male singing behavior across all the nesting stages potentially attractive to Cuckoos.

Although we failed to support the host activity hypothesis (Smith 1981; Clotfelter 1998; Banks and Martin 2001), Cuckoos may still exploit some aspects of the Great Reed Warbler song not measured by us. For example, Great Reed Warblers might be more conspicuous to Cuckoos if they sing louder or if they produce certain types of calls (e.g., alarm or contact calls). On the other hand, Cuckoos are known to exploit successfully various quiet or secretive species, whereas the Great Reed Warbler song and other vocal communications are generally relatively loud. It is also possible that other host behaviors (e.g., nest building or nest defense) may be relevant to Cuckoos when searching for nests. Once a nest is found, the parasitic females can rely on other signals of host quality, like egg coloration (Polačiková et al. 2009) or nest size (Soler et al. 1995), or simply choose nests on the basis of how well their own eggs match the appearance of host clutches (Antonov et al. 2012; Honza et al. 2014).

Old World parasitic Cuckoo species belong to an ancient avian group that has had enough time to specialize. Many of them lay mimetic eggs to deceive their particular host species (Davies 2000) and use various cues to locate suitable nests (Soler et al. 1995; Øien et al. 1996; Antonov et al. 2007; Begum et al. 2011). In the Cuckoo–Great Reed Warbler system, nest visibility from Cuckoo vantage points and the distance to the nearest parasitic female's perch substantially affect the likelihood of being parasitized (Moskát and Honza 2000; Jelínek et al. 2014; but see the non-significant effect of the latter in this study). These factors were shown as important also in other Cuckoo hosts (Alvarez 1993; Antonov et al. 2007; Welbergen and Davies 2009); however, host activity as a cue for nest searching has been reported only anecdotally (Löhrl 1950; Enkelaar 1959; Seppä 1969) or was not found at all (Avilés et al. 2009). So far, the host activity hypothesis has been well supported only for the Great Spotted Cuckoo (Soler and Pérez-Contreras 2012).

New World parasitic Cowbirds, on the contrary, are a relatively young lineage, consisting mainly of generalists with no special egg mimicry (Davies 2000). Some investigations on these brood parasites indicated that host activity, including song rates and aggression, may influence host nest detectability (Smith 1981; Arcese and Smith 1988; Banks and Martin 2001; Svagelj et al. 2009; but see Grieef 1994; Clotfelter 1998). Although in Clotfelter's study there was no evidence that male activity influenced the probability of parasitism, females whose nests were parasitized gave significantly more vocalizations during the egg-laying period than non-parasitized females. This suggests that, in some hosts, female (rather than male) vocalization might serve as a proximate cue for Cowbirds (Clotfelter 1998). Some recent studies, however, show that the more the hosts vocalize or are aggressive near their nests, the lower the probability of parasitism (Fiorini et al. 2009; Steckler and Conway 2012), which contradicts the host activity hypothesis. Host aggressiveness may also be an effective anti-parasite strategy in our study system as Great Reed Warblers are highly aggressive toward nest intruders including the Cuckoo (Bártol et al. 2002; Røskaft et al. 2002; Požgayová et al. 2013; Trnka and Grim 2013), which may even be killed by them (Molnár 1944; Janisch 1948; Mérő and Žuljević 2014).

Despite the considerable effort to identify cues and search modes that brood parasites use to find host nests (e.g., Antonov et al. 2007; Parejo and Avilés 2007; Patten et al. 2011), within the Old World host–parasite systems, there is only one study that explored female Cuckoo preference for certain nests in relation to host singing behavior (Avilés et al. 2009). Avilés et al. (2009) hypothesized that song output differs with host age or quality and thus may be used by Cuckoos as an indicator of host rearing abilities, because young or low-quality hosts are expected to give offspring less care than older or high-quality hosts. Avilés et al. (2009), however, could not support their hypothesis as none of the measured Great Reed Warbler song characteristics (i.e., proportion of time spent singing, song length, repertoire size and syllable switching) possibly reflecting host parental abilities predicted the probability of Cuckoo parasitism. Unfortunately, we could not test for age-related effects of male singing behavior and conspicuous song traits on the probability of parasitism because only a small proportion of males in our dataset were young [i.e., determined as first-year breeders based on Procházka et al. (2012)]. However, as age-specific differences in certain Great Reed Warbler song characteristics have recently been found (Forstmeier et al. 2006; Węgrzyn et al. 2010; Leniowski and Węgrzyn 2013), further studies of this in males of different age cohorts might be desirable.

## Conclusion

In the Great Reed Warbler, nest visibility is probably a more important determinant of parasitism than male singing behavior or conspicuous song structures. Well-concealed nests have a better chance of escaping parasitism than nests which are easy to detect (Moskát and Honza 2000). However, the host activity hypothesis might still be valid if other host behaviors (e.g., nest building or aggressiveness) can reveal the nest and thus attract Cuckoos.

**Acknowledgements** We thank V. Jelínek, M. Šulc, K. Morongová and T. Bolcková for their invaluable help in the field. We are also grateful to the management of Fish Farm Hodonín for enabling us to work on its properties, and local conservation authorities for giving us permission and the licenses to conduct the research. This paper has greatly benefited from the suggestions of two anonymous referees.

### Compliance with ethical standards

**Funding** Financial support for this research was provided by the Czech Science Foundation (grant 17-12262S) and institutional support (RVO 68081766).

**Ethics statement** All the work adhered to the Animal Care Protocol of the Academy of Sciences of the Czech Republic (license number 0008/98-M103) and complies with current Czech law on the protection of animals against mistreatment, as well as with instructions on the activity of collaborators of the Czech Bird Ringing Center.

## References

Alvarez F (1993) Proximity of trees facilitates parasitism by Cuckoos *Cuculus canorus* on Rufous Warblers *Cercotrichas galactotes*. Ibis 135:331

Antonov A, Stokke BG, Moksnes A, Røskaft E (2007) Factors influencing the risk of Common Cuckoo *Cuculus canorus* parasitism on Marsh Warblers *Acrocephalus palustris*. J Avian Biol 38:390–393

Antonov A, Stokke BG, Fossøy F, Ranke PS, Liang W, Yang C, Moksnes A, Shykoff J, Røskaft E (2012) Are Cuckoos maximizing egg mimicry by selecting host individuals with better matching egg phenotypes? PLoS One 7:e31704. doi:10.1371/journal.pone.0031704

Arcese P, Smith JNM (1988) Effects of population density and supplemental food on reproduction in Song Sparrows. J Anim Ecol 57:119–136

Avilés JM, Moskát C, Bán M, Hargitai R, Parejo D (2009) Common Cuckoos (*Cuculus canorus*) do not rely on indicators of parental abilities when searching for host nests: the importance of host defenses. Auk 126:431–438

Banks AJ, Martin TE (2001) Host activity and the risk of nest parasitism by Brown-headed Cowbirds. Behav Ecol 12:31–40

Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T (2002) Responses of Great Reed Warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a Cuckoo *Cuculus canorus* dummy and egg mimicry. J Avian Biol 33:420–425

Bates D, Maechler M, Dai B (2008) lme4: linear mixed-effects models using S4 classes. R package version 0.999375-28. http://lme4.r-forge.r-project.org/. Accessed 20 October 2016

Begum S, Moksnes A, Røskaft E, Stokke BG (2011) Factors influencing host nest use by the brood parasitic Asian Koel (*Eudynamys scolopacea*). J Ornithol 152:793–800

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bradbury JW, Vehrencamp SL (2011) Principles of animal communication, 2nd edn. Sinauer, Sunderland

Briskie JV, Sealy SG, Hobson KA (1990) Differential parasitism of Least Flycatchers and Yellow Warblers by the Brown-headed Cowbird. Behav Ecol Sociobiol 27:403–410

Capek M Jr, Kloubec B (2002) Seasonal and diel patterns of song output by Great Reed Warblers *Acrocephalus arundinaceus*. Biologia 57:267–276

Catchpole CK (1983) Variation in the song of the Great Reed Warbler *Acrocephalus arundinaceus* in relation to mate attraction and territorial defence. Anim Behav 31:1217–1225

Catchpole CK, Slater PJB (2008) Bird song: biological themes and variations. Cambridge University Press, Cambridge

Catchpole CK, Leisler B, Winkler H (1985) Polygyny in the Great Reed Warbler *Acrocephalus arundinaceus*: a possible case of deception. Behav Ecol Sociobiol 16:285–291

Catchpole CK, Leisler B, Dittami J (1986) Sexual differences in the responses of captive Great Reed Warblers *Acrocephalus arundinaceus* to variation in song structure and repertoire size. Ethology 73:69–77

Clotfelter ED (1998) What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird nests? Anim Behav 55:1181–1189

Cramp S (ed) (1992) The birds of the Western Palearctic, vol 6. Oxford University Press, Oxford

Dabelsteen T, McGregor PK, Lampe H, Langmore N, Holland J (1998) Quiet song in songbirds: an overlooked phenomenon. Bioacoustics 9:89–105

Davies NB (2000) Cuckoos, Cowbirds and other cheats. Poyser, London

Enkelaar H (1959) Van allerlei over de koekoek. Vreemde gedragingen van een koekoek. Vogeljaar 7:204–205

Fiorini VD, Tuero DT, Reboreda JC (2009) Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by Shiny Cowbirds on Chalk-browed Mockingbirds. Behaviour 146:1387–1403

Fiorini VD, Tuero DT, Reboreda JC (2012) Dense canopy cover over House Wren (*Troglodytes aedon*) nests increases latency of brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*). Emu 112:55–59

Forstmeier W, Hasselquist D, Bensch B, Leisler B (2006) Does song reflect age and viability? A comparison between two populations of the Great Reed Warbler *Acrocephalus arundinaceus*. Behav Ecol Sociobiol 59:634–643

Garamszegi LZ, Avilés JM (2005) Brood parasitism by Brown-headed Cowbirds and the expression of sexual characters in their hosts. Oecologia 143:167–177

Gill SA, Grieff PM, Staib LM, Sealy SG (1997) Does nest defense deter or facilitate Cowbird parasitism? A test of the nesting-cue hypothesis. Ethology 103:56–71

Greig-Smith PW (1982) Song-rates and parental care by male Stonechats (*Saxicola torquata*). Anim Behav 30:245–252

Grieef P (1994) Cues used by brood parasites and predators to locate nests. UFS (Delta Marsh) annual report, vol 29. http://umanitoba.ca/science/delta_marsh/reports/1994/grieef/grieef.html. Accessed 23 November 2016

Grim T, Samaš P, Moskát C, Kleven O, Honza M, Moksnes A, Røskaft E, Stokke BG (2011) Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? J Anim Ecol 80:508–518

Hasselquist D, Bench S (1991) Trade-off between mate guarding and mate attraction in the polygynous Great Reed Warbler. Behav Ecol Sociobiol 28:187–193

Hauber ME, Russo SA (2000) Perch proximity correlates with higher rates of Cowbird parasitism of ground nesting Song Sparrows. Wilson Bull 112:150–153

Honza M, Øien IJ, Moksnes A, Røskaft E (1998) Survival of Reed Warbler *Acrocephalus scirpaceus* clutches in relation to nest position. Bird Study 45:104–108

Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, Moksnes A, Røskaft E (2002) Behaviour of female Common Cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. Anim Behav 64:861–868

Honza M, Šulc M, Jelínek V, Požgayová M, Procházka P (2014) Brood parasites lay eggs matching the appearance of host clutches. Proc R Soc B Biol Sci 281:20132665

Janisch M (1948) Fight between *Cuculus c. canorus* L.—Cuckoo—and *Acrocephalus a. arundinaceus* L.—Great Reed Warble. Aquila 55:291

Jaramillo A, Burke P (1999) New World blackbirds. Helm, London

Jelínek V, Procházka P, Požgayová M, Honza M (2014) Common Cuckoos *Cuculus canorus* change their nest-searching strategy according to the number of available host nests. Ibis 156:189–197

Jelínek V, Procházka P, Honza M (2015) Experimental enlargement of nest size does not increase risk of predation or brood parasitism in the Great Reed Warbler *Acrocephalus arundinaceus*. Ibis 157:396–400

Jilka A, Leisler B (1974) Die Einpassung dreier Rohrsängerarten (*Acrocephalus schoenobaenus*, *A. scirpaceus*, *A. arundinaceus*) in ihre Lebensräume in bezug auf das Frequenzspektrum ihrer Reviergesänge. J Ornithol 115:192–212

Kennerley P, Pearson D (2010) Reed and bush warblers. Helm, London

Kloubec B, Capek M (2011) Great Reed Warbler (*Acrocephalus arundinaceus*)—singing activity. In: Šťastný K, Hudec K (eds) Fauna of the Czech Republic. Birds 3/I. Academia, Praha, pp 520–521 **(in Czech with a summary in English)**

Kroodsma DE, Miller EH (eds) (1982) Acoustic communication in birds, vol 1 and 2. Academic Press, New York

Leniowski K, Węgrzyn E (2013) Organization, variation in time, and impacting factors in the song strophe repertoire in the Great Reed Warbler (*Acrocephalus arundinaceus*). Ornis Fenn 90:129–141

Löhrl H (1950) Zur Biologie des Kuckucks. Ornithol Ber 3:120–125

Manica LT, Maia R, Dias A, Podos J, Macedo RH (2014) Vocal output predicts territory quality in a Neotropical songbird. Behav Process 109:21–26

McDonald MV (1989) Function of song in Scott's Seaside Sparrow, *Ammodramus maritimus peninsulae*. Anim Behav 38:468–485

McGregor PK (2005) Animal communication networks. Cambridge University Press, Cambridge

McLaren MC, Sealy SG (2003) Factors influencing susceptibility of host nests to brood parasitism. Ethol Ecol Evol 15:343–353

Mérő TO, Žuljević A (2014) From the ornithological notebook—Great Reed Warbler *Acrocephalus arundinaceus*. Acrocephalus 34:130

Molnár B (1944) The Cuckoo in the Hungarian Plain. Aquila 51:100–112

Moskát C, Honza M (2000) Effect of nest and nest site characteristics on the risk of Cuckoo *Cuculus canorus* parasitism in the Great Reed Warbler *Acrocephalus arundinaceus*. Ecography 23:335–341

Øien IJ, Honza M, Moksnes A, Røskaft E (1996) The risk of parasitism in relation to the distance from Reed Warbler nests to Cuckoo perches. J Anim Ecol 65:147–153

Parejo D, Avilés JM (2007) Do avian brood parasites eavesdrop on heterospecific sexual signals revealing host quality? A review of the evidence. Anim Cognit 10:81–88

Patten MA, Reinking DL, Wolfe DH (2011) Hierarchical cues in brood parasite nest selection. J Ornithol 152:521–532

Poesel A, Foerster K, Kempenaers B (2001) The dawn song of the Blue Tit *Parus caeruleus* and its role in sexual selection. Ethology 107:521–531

Polačiková L, Procházka P, Cherry MI, Honza M (2009) Choosing suitable hosts: common Cuckoos *Cuculus canorus* parasitize Great Reed Warblers *Acrocephalus arundinaceus* of high quality. Evol Ecol 23:879–891

Požgayová M, Procházka P, Honza M (2013) Is shared male assistance with antiparasitic nest defence costly in the polygynous Great Reed Warbler? Anim Behav 85:615–621

Procházka P, Jelínek V, Požgayová M, Honza M (2012) How to age Great Reed Warblers (*Acrocephalus arundinaceus*) after complete moult. Sylvia 48:57–73 **(in Czech, with a summary in English)**

R Core Team (2012) R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna. http://www.Rproject.org/. Accessed 20 October 2016

Radesäter T, Jakobsson S (1989) Song rate correlations of replacement territorial Willow Warblers *Phylloscopus trochilus*. Ornis Scand 20:71–73

Robinson WD, Robinson TS (2001) Is host activity necessary to elicit brood parasitism by Cowbirds? Ethol Ecol Evol 13:161–171

Røskaft E, Moksnes A, Stokke MG, Bičík V, Moskát C (2002) Aggression to dummy Cuckoos by potential European Cuckoo hosts. Behaviour 139:613–628

Rothstein SI (1990) A model system for coevolution: avian brood parasitism. Annu Rev Ecol Evol 21:481–508

Searcy WA, Nowicki S (2000) Male-male competition and female choice in the evolution of vocal signaling. In: Espmark Y, Amundsen T, Rosenqvist G (eds) Animal signals. Tapir Academic, Trondheim, pp 301–315

Seppä J (1969) The Cuckoo's ability to find a nest where it can lay an egg. Ornis Fenn 46:78–79

Smith JNM (1981) Cowbird parasitism, host fitness, and age of the host female in an island Song Sparrow population. Condor 83:152–161

Soler M, Pérez-Contreras T (2012) Location of suitable nests by Great Spotted Cuckoos: an empirical and experimental study. Behav Ecol Sociobiol 66:1305–1310

Soler JJ, Soler M, Møller AP, Martínez JG (1995) Does the Great Spotted Cuckoo choose Magpie hosts according to their parenting ability? Behav Ecol Sociobiol 36:201–206

Specht R (2007) Avisoft-SASLab Pro version 4.40. Sound analysis and synthesis software. Avisoft Bioacoustics, Berlin

Steckler SE, Conway CJ (2012) Frequent vocalizing is negatively associated with brood parasitism in a host of the Brown-headed Cowbird. Condor 114:219–226

Svagelj WS, Fernández GJ, Mermoz ME (2009) Effects of nest-site characteristics and parental activity on Cowbird parasitism and predation in Brown-and-Yellow Marshbirds. J Field Ornithol 80:9–18

Trnka A, Grim T (2013) Color plumage polymorphism and predator mimicry in brood parasites. Front Zool 10:1–10

Uyehara JC, Narins PM (1995) Nest defense by Willow Flycatchers to brood-parasitic intruders. Condor 97:361–368

Vogl W, Taborsky M, Taborsky B, Teuschl Y, Honza M (2002) Cuckoo females preferentially use specific habitats when searching for host nests. Anim Behav 64:843–850

Węgrzyn E, Leniowski K, Osiejuk T (2010) Whistle duration and consistency reflect philopatry and harem size in Great Reed Warblers. Anim Behav 79:1363–1372

Welbergen JA, Davies NB (2009) Strategic variation in mobbing as a front line of defense against brood parasitism. Curr Biol 19:235–240

Whitear AK, Stehlik I (2009) Use of auditory predation cues in the Ruby-throated Hummingbird (*Archilochus colubris*). Univ Tor J Undergrad Life Sci 3:47–49