

Song post selection in the aquatic warbler *Acrocephalus paludicola*

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We investigated the microhabitat characteristics of song posts used by males of the aquatic warbler in Biebrza National Park (Poland). On average, song posts were located at a height of 94 cm and 32 cm from the top of the plant. Males preferred singing from living plants in habitat patches with tall vegetation and a low water level. The only factor significantly affecting the place chosen for singing was vegetation height, and males sang from a higher location as vegetation height increased. Where only lower vegetation was available, males used relatively higher places for singing in comparison with the total plant height. These observations support the hypothesis predicting the optimization of song post height.

Introduction

The acoustic defence of territory is a common behaviour of songbirds. This type of defence keeps intruders at a distance and physical fighting is minimized. Song is also a double-target signal, functioning simultaneously as a mate attractor (Catchpole & Slater 2008). For both of the above-mentioned reasons, the choice of place for singing, or to be more general, the whole spatiotemporal strategy of singing, is critical for fulfilling song functions. Although some species use quiet songs or calls in certain contexts (Dabelsteen *et al.* 1998, Ręk & Osiejuk 2011), the typical advertising song is loud and meant to reach potential receivers, i.e. mates and rivals

(Bradbury & Vehrencamp 2011). The amplitude of a bird's song depends on body size, structure of the syrinx and other organs involved in sound production (e.g. trachea length), and energy reserves (Fitch 1999, Mindlin & Laje 2005). Some of these constraints are strictly phylogenetic and can be overridden only within a relatively narrow range (e.g. body size is much less variable within than between species; Podos *et al.* 2004). It is likely that singers apply alternative strategies to increase or optimize the propagation of their songs. One of the most common strategies is choosing a song post in a high place. The signal and detection range of other bird signals is increased when a song post is in a high position (Mathevon *et al.* 1996). As some types

of environments (e.g. meadows) often do not provide high objects for singing, some species have evolved the extremely energy-consuming behaviour of singing during flight (Hedenström & Møller 1992, Hedenström & Ålerstam 1996). This is a good example of the importance of singing from the right place. However, singing from exposed objects or in flight also has a negative side. Being exposed and giving loud signals may attract predators (Møller *et al.* 2006, Møller 2011). It can be expected that signallers optimise the benefits and costs of signalling rather than simply maximizing the signal range.

The aquatic warbler *Acrocephalus paludicola*, is a small insectivorous passerine inhabiting open, wet grasslands and sedge fen mires. These habitats are characterised by an enormous abundance of food, resulting in uniparental care by females, and promiscuity (Dyrce 2006). Aquatic warbler males use songs for attracting mates and for rival deterrence (Dyrce 1993, Schulze-Hagen *et al.* 1999). The home range of aquatic warbler males may reach 8 ha and birds are not territorial during the breeding season (Schaefer *et al.* 2000). Recently, Dyrce *et al.* (2011) showed that males increase their song output in the presence of potential predators suggesting that song output may also serve as a warning signal to incubating females. Aquatic warblers reach high densities in vast fens with open fragments of sedges, and prefer habitats with tussocks of *Carex* sp. up to 80 cm high growing in water depths up to a few centimetres (Dyrce 1993). Much is known about the species' ecology and habitat preferences but there are no data available about choice of specific points from which males sing (Aquatic Warbler Conservation Team 1999, Tanneberger *et al.* 2009, Dyrce *et al.* 2011, Kubacka *et al.* 2013). As the structure of marshland vegetation may be uniform, the presence of a specific song post within it could be especially important for males. Information about male preferences for a specific plant species, plant height, vegetation density, water level and other factors could be practical for the conservation of this threatened species.

In our study, we presented data on micro-habitat selection in aquatic warbler males with special reference to their choice of song posts. In particular, we checked how the distribution

of song-post heights chosen by males in relation to maximum height available and other characteristics of adjacent habitats fits the predictions of the two main hypotheses related to song propagation range and risk of predation. If males maximize signal propagation range in order to attract more females and keep rivals at a safe distance, then preference for singing from the tops of available plants within a patch is to be expected. If males optimize propagation range and predation risk, we would expect to observe birds singing from song posts located above some minimal height. Such song posts prevent reflections from the ground and other negative effects, which would weaken the signal (Consens & Falls 1984). Simultaneously, we would expect that birds avoid singing from the most exposed places. It is also likely that the height of a song post would be affected by habitat characteristics related to predation risk. For example, the proximity to shrubs or other hiding places of potential predators may induce more cautious behaviour. Another factor could be the plant species chosen as a song post. Stem rigidity may affect the choice of a song post in a simple mechanical way (the top of the plant should be strong enough to hold the bird). All these aspects of song post choice in the aquatic warbler are addressed in this paper.

Material and methods

The study was carried out in May and June 2012 at the Bagno Ławki marshland (53°17'24"N, 22°34'39"E) in Biebrza National Park, Poland. This area is the second most important breeding area for the aquatic warbler in the world. Singing males occur at densities from 4–12 per 10 ha, at an average of 7.3 per 10 ha. Observations were made on regularly mown meadows where aquatic warbler song posts were analysed by comparing habitat features around real song posts observed in the field with habitat of randomly selected points around them. The observers localized singing males along eight transects from 2.4 to 4.7 km (total length of 28.2 km) through an open peat bog. The observations were made during good weather conditions only, between 19:00 and 21:00, when males sing the

most intensively (Dyrce & Zdunek 1993, Kłoskowski & Krogulec 1999).

Vegetation was typical and consisted of clumps of sedges, small willows *Salix* sp., birches *Betula* sp., milk parsley *Peucedanum palustre*, and reeds *Phragmites australis*. Binoculars were used to initially localize singing males from a distance of 50–70 m. Therefore, males were not disturbed by the observer. When an exact song post was properly recognized, the observer came closer, measured the song post height, and noted all other habitat characteristics. The coordinates of the existing singing places were determined by GPS and then random points were selected for comparison. Each random point was localized 50 m south from the corresponding existing point within the area where birds could theoretically sing, but seven random points were not considered as they were located in completely unsuitable habitat (road, forest). The following variables, describing the song post and surrounding habitats were used: (1) plant species used as a song post, (2) condition of the song post (alive or dry), (3) song post height (m), (4) distance to the top of the plant chosen as the singing place (m), (5) vegetation structure (patched spatial pattern or mixed pattern with tussocks), (6) vegetation height (cm), (7) water level (cm) (8) reed density (stems m⁻²), (9) distance to compact reed belt (m), (10) distance to shrubs (m), (11) distance to forest (m), (12) distance to ditch (m). Measurements including per area calculations were done from 2 × 2 m quadrats. In some analyses we also refer to the height of the song post as the fraction of the entire plant's height in percentages. All mean values are given with their standard deviations (SD). We applied logistic and stepwise

logistic regressions to analyse aquatic warbler preference for particular habitat features selected on the basis of the species' biology. All statistical analyses were conducted using IBM SPSS Statistics ver. 21.

Results

Altogether 146 singing aquatic warbler males were observed. They were singing from an average height of 94 ± 26.0 cm. This accounted for, on average, 75% ± 13.1% of the total height of the plant, and, on average, 32 ± 19.8 cm from the top of the plant. More details on song post characteristics are given in Table 1. The majority of males sang from green, living plants (75%, *n* = 110) while others chose dead plants (25%, *n* = 36). Males sang from: reeds (*n* = 60), milk parsley *Peucedanum palustre* (*n* = 22), willows *Salix* spp. (*n* = 18), sedges *Carex* sp. (*n* = 9), horsetails *Equisetum* sp. (*n* = 8), birches *Betula* sp. (*n* = 8), bulrushes *Typha* sp. (*n* = 4) or other plants (*n* = 17). The plant structure at the song post had a spatial pattern of patches (*n* = 103, 70.5%) or a mixed pattern with both patches and tussocks (*n* = 43, 29.5%).

The general characteristics of song posts in comparison with random points are presented in Table 1. Logistic regression showed that aquatic warbler males preferred singing habitat patches with higher vegetation (*p* < 0.001) and a lower water level (*p* = 0.005) (Table 2). Water level variation was small with differences between average water levels at the song posts and at the random points being negligible (Table 1).

We used stepwise linear regression to verify which factors affected song-post height, with

Table 1. Descriptive statistics (mean ± SD) of habitat characteristics of aquatic warbler song posts and nearby random points.

| Variable | Song posts (<i>n</i> = 146) | Random points (<i>n</i> = 139) |
|--|------------------------------|---------------------------------|
| Vegetation height (cm) | 126 ± 30.0 | 83 ± 17.8 |
| Water level (cm) | 6.5 ± 2.84 | 7.4 ± 3.46 |
| Reeds density (stems m ⁻²) | 6.9 ± 16.68 | 2.7 ± 7.35 |
| Distance to compact reed belt (m) | 30.1 ± 44.12 | 34.1 ± 45.41 |
| Distance to shrubs (m) | 130 ± 141.6 | 147 ± 137.9 |
| Distance to forest (m) | 491 ± 466.0 | 534 ± 451.6 |
| Distance to ditch (m) | 130 ± 156.1 | 151 ± 185.1 |

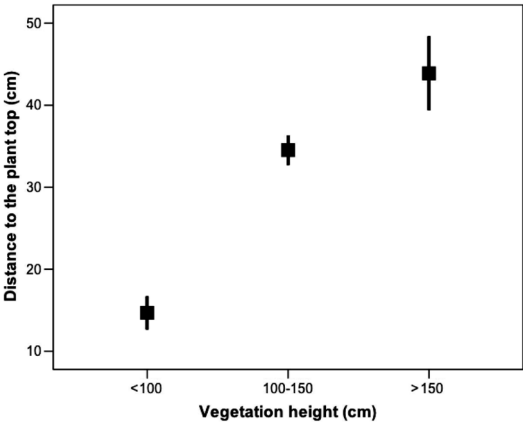


Fig. 1. Relationship between height of the plant chosen for singing and distance between a singing male and the top of the plant.

all song post characteristics as predictors. Our results showed that only vegetation height ($p < 0.001$, see Table 3 for details) was significant, explaining ca. 58% of the height variation of the song posts. In principle, the higher the vegetation, the higher the location of the song post. No significant relationships between the height of the song posts and any other habitat characteristic were found, except for some inter-correlations. For example, song post height correlated

with reed density ($r = 0.45$, $p < 0.001$), but this was an effect of a correlation between reed density and vegetation height ($r = 0.56$, $p < 0.001$).

The correlation of song post height and distance from the top of the plant was negative and very weak ($r = -0.16$, $n = 146$, $p = 0.05$). The height of song posts was characterized by much smaller variation (CV = 27.6%) than the distance from the top of a plant chosen for singing (CV = 61.7%). To explore this behaviour in detail, we divided all plants used as singing places into three vegetation-height-classes (up to 100 cm, 100–150 cm and > 150 cm). Then, we analysed which place on a plant was chosen for singing in relation to height of the plant. Males singing from shorter plants (up to 100 cm) chose significantly higher places on them (83% of plant height) in comparison with males singing from taller plants. Males singing from plants with a height 100–150 cm and > 150 cm on average chose places located relatively lower at 73% and 74% of the entire plant height, respectively (Kruskal-Wallis test: $\chi^2 = 13.83$, $df = 2$, $p = 0.001$; Fig. 1). This relationship is also reflected by a negative correlation between vegetation height and relative song-post height, measured as the ratio between song-post height and plant height (Spearman's correlation: $r_s = -0.22$, $n = 146$, $p = 0.008$).

Table 2. Results from a logistic regression predicting the occurrence of the aquatic warbler song posts by comparison of the characteristics of real song posts ($n = 146$) and random points ($n = 139$).

| Predictor | <i>B</i> | SE | Wald | df | <i>p</i> | Exp(<i>B</i>) |
|-------------------------------|----------|-------|--------|----|----------|-----------------|
| Vegetation structure | −0.014 | 0.4 | 0.001 | 1 | 0.972 | 0.986 |
| Vegetation height | 0.084 | 0.01 | 70.977 | 1 | < 0.001 | 1.088 |
| Water level | −0.162 | 0.057 | 8.057 | 1 | 0.005 | 0.851 |
| Reeds density | −0.011 | 0.014 | 0.599 | 1 | 0.439 | 0.989 |
| Distance to compact reed belt | 0.007 | 0.004 | 3.318 | 1 | 0.069 | 1.007 |
| Distance to shrubs | 0.000 | 0.002 | 0.008 | 1 | 0.93 | 1.000 |
| Distance to forest | 0.000 | 0.001 | 0.001 | 1 | 0.982 | 1.000 |
| Distance to ditch | 0.000 | 0.001 | 0.052 | 1 | 0.820 | 1.000 |
| Intercept | −7.408 | 1.091 | 46.088 | 1 | < 0.001 | 0.001 |

Table 3. Results of a stepwise linear regression with plant species, vegetation structure, vegetation height, water level, reed density, distance to reeds, distance to shrubs, distance to the forest and distance to a ditch, entered into the model.

| Model | <i>B</i> | SE | β | <i>t</i> | <i>p</i> |
|-------------------|----------|-------|---------|----------|----------|
| Intercept | 11.176 | 6.091 | – | 1.835 | 0.069 |
| Vegetation height | 0.656 | 0.047 | 0.76 | 13.952 | < 0.001 |

Discussion

The aquatic warbler is the rarest migratory bird in Europe and is an endangered species globally, with the category VU (Vulnerable) (IUCN 2013). The actual breeding range of the aquatic warbler is restricted to eight countries of eastern and central Europe, and eastern Asia. Therefore, there is an urgent need for further research on the biology and ecology of this species (Flade & Lachmann 2008). Results of the present study confirm the hypothesis stressing the importance of a compromise between signal propagation range and predation risk. Aquatic warbler males preferred patches with higher vegetation. Their song post heights were positively correlated with the plant height available for singing. However, males also clearly avoided singing from the tops of available plants. They selected places located lower than the top, and the distance between the song post and the top of the plant was greater on taller plants (Fig. 1). Consequently, on shorter plants, males chose proportionally higher song posts. Such a choice suggests there is some minimal singing height that the birds avoided at the expense of safety.

High song posts do not always benefit song transmission. High posts may be more important as a strategy for enhancing sound perception (Dabelsteen *et al.* 1993, Holland *et al.* 1998). In the case of the aquatic warbler, such reasoning is rather unlikely as males are forced to choose song posts in a very narrow height range and only up to 210 cm above ground. Acoustic communication that is 1–2 m above ground is exposed to the influence of boundary interference (Wiley & Richards 1982, Consens & Falls 1984). The presence of dense and patchily distributed vegetation may have a complicated and unpredictable effect on sound transmission (Wiley & Richards 1982). As other *Acrocephalus* warblers living in similar habitats, the aquatic warbler should benefit from a high singing position when it comes to propagation distance (Jilka & Leisler 1974). Therefore, the observed behaviour accurately reflects the trade off between song propagation and predation risk. It seems that the singing strategy is applied at a micro-habitat scale, as we did not find any significant relationships between song post height and dis-

tance to any landscape structures such as reed belts or forests.

On breeding grounds, aquatic warbler males sing from perches (Cramp 1992). Despite the fact that this species' habitat selection has been explored in detail (Tanneberger *et al.* 2010), here we present data on song post selection for the first time. Even though males do not defend territories, they sing from permanent posts which seems to be important for them in attracting females, deter rival males, and later, to protect incubating females against predators (Schulze-Hagen *et al.* 1999, Dyrce *et al.* 2011).

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