

Increased male singing in response to predator presence may represent reproductive investment in a promiscuous species, the Aquatic Warbler *Acrocephalus paludicola*

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Abstract. Males of the promiscuous Aquatic Warbler are regarded as emancipated from any parental duties, and in most of the broods nestlings are sired by two or more males. During a long-term study on the reproductive biology of the species on fen mires on the river Biebrza in north-eastern Poland, we frequently heard males singing more intensely or uttering warning calls close to nests. Here we test whether this behaviour is reproducible and therefore constitutes a mate investment or paternal investment. During the incubation periods, hides were erected ca. 30 m from nests. During 30-min periods male song bouts were counted while a test person was either concealed inside or placed outside the tent, hence well visible as a potential predator. The production of song showed a sevenfold increase during the presence of a clearly visible test person. This observation indicates that male song in Aquatic Warbler serves as a warning signal and hence can be regarded as a type of mate or paternal investment.

Key words: Aquatic Warbler, *Acrocephalus paludicola*, promiscuity, song function, predator, male reproductive investment

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The Aquatic Warbler is a small insectivorous passerine living in open wet grasslands and sedge fen mires (Wawrzyniak & Sohns 1977, Schulze-Hagen 1991, Cramp 1992). Its mating strategies can best be described as promiscuous, which is unique not only within the genus *Acrocephalus* (Leisler & Catchpole 1992, Birkhead 1993, Bairlein et al. 2006, Dyrzcz 2006), but also among passerines in general (Clutton-Brock 1991, Birkhead & Møller 1992). The enormous abundance of food in the flooded and permanently wet *Carex* vegetation permits uniparental care by females (Schulze-Hagen et al. 1989, Dyrzcz & Zdunek 1993), while males are emancipated from the care of the young (Heise 1970, Dyrzcz 1993). However, males sing throughout the whole breeding season with more or less constant intensity (Dyrzcz & Zdunek 1993). Paternity analyses have shown rates of multiple paternity as high as 80%, with single broods being fathered by up to five different males (Schulze-Hagen et al. 1993, Dyrzcz et al. 2002). Therefore sperm competition is intense, and males have

extraordinarily large testes and cloacal protuberances containing sperm storage structures. Moreover, copulations in this species are extremely prolonged and can last up to 50 minutes (Schulze-Hagen et al. 1995), thus constituting a considerable investment for males. In a number of cases males have been observed inspecting nests during the laying and early incubation period (own observations; B. Leisler in Hungary, B. Giessing in Ukraine), a behaviour not uncommonly recorded in the aviary (own observations; Schulze-Hagen 1995). When observing nests, we frequently heard males uttering song bouts or “teck”-calls, which function as alarm or warning signals (Halupka 1999). In this study we test whether this behaviour can be regularly provoked in close vicinity to nests, being then an indicator of a male reproductive contribution.

Tests were conducted from May until July in 1992 and 2010 on fen mires on the river Biebrza in north-eastern Poland (53°20'N, 22°40'E) as a part

of a long-term study on the species' reproductive biology. The study area constituted a bed of *Carex* tussocks with *Carex appropinquata* as the dominant species. Mosses were also abundant, and small (1–1.5 m) willow bushes *Salix* spp. were scattered throughout. The height of sedges generally did not exceed 80 cm. Water between the tussocks was a few centimeters deep (Dyrz 1993). In 1992 and 2010 hides were erected ca. 30 m away from nests during the incubation or early nestling stage. This distance was found to be the minimum distance from females that did not produce a disturbance reaction. On the next day the observer, escorted to the hide by another person, spent 30 min concealed inside the hide and another 30 min standing just beside it, thus well visible as a potential predator. The following day the test was repeated in reverse order. Tests were conducted outside the daily maxima of singing, which are before sunrise and particularly at dusk (Dyrz & Zdunek 1993). During the 30-min periods all song bouts uttered by males close to a given nest were counted. The difference was tested with the Wilcoxon test (Zar 1984). Most males were individually colour ringed.

In 28 out of 32 tests the singing activity was higher (in most cases much higher) in the presence of a "potential predator" (observer) than in his absence (Wilcoxon signed rank test with continuity correction, two-tailed: $V = 470.5$, $p < 0.001$) (Fig. 1). This 7–8-fold and highly significant increase in song output indicates that song in Aquatic Warbler male serves as a warning signal.

Other observations confirm that male song is a warning signal to females, which are probably on or near their hidden nests. When an observer approached the nest to check the nest contents, one or even several males, which had been previously silent, started singing as soon as the observer's distance to the nest fell below ca. 30 m. This behaviour was observed particularly during the first of several nest controls on a given day. Later in the day, after observers had crisscrossed the study area several times, a certain habituation may have taken place and male reactions decreased. In two cases later on, from hides close to nests we were able to observe Marsh Harriers *Circus aeruginosus* approaching on the wing. Immediately a male Aquatic Warbler started singing, while the incubating female quickly left her nest and climbed to the top of a *Carex* clump, took a look and then disappeared into the cover of dense vegetation.

In Aquatic Warbler, male song has a function in attracting females and in intrasexual competition (Schulze-Hagen 1991, Dyrz 1993). Here we offer indications for another function of song in this species, namely as a warning signal in front of a predator close to a nest. Warning song near the nest is also known in other Acrocephalidae. These species are characterised by a genetically monogamous mating system and biparental care (Reed Warbler *A. scirpaceus*: Brown & Davies 1949; Marsh Warbler *A. palustris*: Dowsett-Lemaire 1979). However, in a promiscuous species featuring a bond-free sociality warning song appears unexpected. Like the observed nest visits or controls by males during laying and early incubation phases, warning song in front of a predator near a nest may also reflect an investment strategy in the form of mate and paternal investment, which correlates with mating success. In another promiscuous bird, the fowl *Gallus gallus*, it could be experimentally demonstrated for the first time that males increase their alarm-calling rate as a function of their recent mating success (Wilson & Evans 2008). This provides support for a costly mate investment. As female Aquatic Warblers raise their offspring unaided, nestling growth is the slowest and the nestling period the longest among all *Acrocephalus* species (Wawrzyniak & Sohns 1977, Dyrz 1993). As a longer nestling period implies a greater predation risk, a male

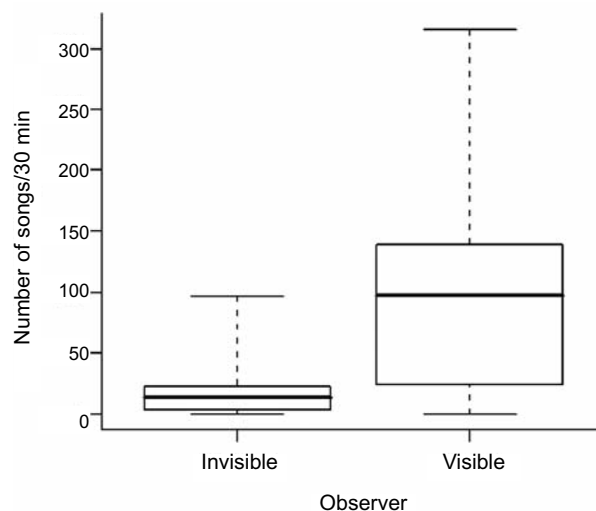


Fig. 1. Singing activity of Aquatic Warblers during two 30-minute sessions when the observer was visible in the vicinity (~30 m) of the nest (out of the hide), and when he was invisible (in the hide). All nests were at the incubation stage. Median values, quartiles and ranges are shown (solid line, box and whiskers respectively).

investment directed towards a mate and/or offspring would represent a potential fitness benefit.

We have not carried out these experiments throughout the whole nesting period from egg laying to fledging of nestlings, nor controlled the paternity status in the tested nests. Therefore our results are only suggestive. In a further study it would be useful to (1) to expand standardised tests over full nest cycles, (2) conduct playback experiments at the nest and record female reactions, and (3) analyse paternity relationships of broods tested. If several males join in warning song near a nest, as sometimes observed, then it has to be shown whether these individual males share multiple paternity in such a brood.

Our observational tests are also an indication that promiscuous strategies constitute a wide range of transitions, from completely bond-free relationships to different forms of male reproductive investment, which depend on ecological conditions and which can vary within populations (Shriver et al. 2007).

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STRESZCZENIE

[Zwiększona intensywność śpiewu samca w reakcji na obecność drapieżnika — forma inwestycji rodzicielskiej u promiskuitycznej wodniczki?]

Wodniczka, niewielki owadożerny ptak wróblowy zasiedlający podmokłe łąki i torfowiska, jest gatunkiem promiskuitycznym, u którego w większości lęgów pisklęta pochodzą od dwóch lub więcej samców. Budową gniazda, wysiadywaniem jaj oraz karmieniem piskląt zajmuje się wyłącznie samica. W związku z tym dotychczas uważano, że samiec tego gatunku nie przejawia żadnej formy opieki rodzicielskiej. W czasie wieloletnich badań nad biologią rozrodu tego

gatunku prowadzonych na torfowiskach Kotliny Biebrzańskiej, zauważono wzrost intensywności śpiewu samców i wydawanie przez nie głosów alarmowych w momencie, gdy obserwator przechodził w pobliżu gniazda. W niniejszej pracy testowano czy takie zachowania są adresowane do wysiadujących samic, co mogłoby wpływać na obniżenie strat powodowanych przez drapieżniki, a tym samym zwiększać sukces rozrodczy. W tym celu w odległości ok. 30 m od gniazda z wysiadującą samicą stawiano przenośną

kryjówkę do obserwacji. W czasie 30 minutowych sesji notowano liczbę piosenek wydawanych przez samce w czasie, gdy obserwator był niewidoczny w kryjówce i w czasie, gdy stał obok kryjówki, dobrze widoczny jako potencjalny drapieżnik. W tym ostatnim przypadku intensywność śpiewu wzrastała siedmiokrotnie (Fig. 1). Obserwacje te sugerują, że śpiew samca wodniczki, poza innymi funkcjami, służy jako sygnał ostrzegawczy w okresie lęgowym, co można uznać za formę inwestycji rodzicielskiej.

