The breeding system of the Aquatic Warbler *Acrocephalus paludicola* – a review of new results

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Schulze-Hagen, K., B. Leisler, H. M. Schäfer & V. Schmidt 1999: The breeding system of the Aquatic Warbler *Acrocephalus paludicola* – a review of new results. Vogelwelt 120: 87 – 96.

Since 1991/1992 (SCHULZE-HAGEN 1991; CRAMP & BROOKS 1992) much has been contributed to the understanding of the breeding system of the Aquatic Warbler, a species with a mating system showing elements of scramble competition, polygyny and promiscuity. The species has been studied by our Polish-German working group in a 48 ha area in the southern basin of the Biebrza valley, NE Poland, since 1984. With the help of radio telemetry it was possible to show that ♂ cover home ranges of up to 7.8 ha. Home ranges may overlap widely and are frequently shifting. Core areas are occupied more intensively but not constantly (SCHÄFER 1998). The ♂' mobility correlates negatively with the number of fertile ♀ present, and non-aggressive searching for ♀ was more pronounced when fewer fertile ♀ were available. Song activity did not vary seasonally but showed marked diurnal peaks with a maximum between 18.00 h and 22.00 h. After sunset, short A-songs are performed, mainly for intrasexual communication and ♂ spacing. Our molecular analyses revealed that more than 60 % of the broods are fathered by 2 to 4 ♂. Hatching success in mixed paternity clutches was sometimes higher than in broods sired by a single ♂. In captivity, the duration of copulation averages 24 min, which is extraordinarily long and can be regarded as a kind of contact mate guarding. Very large cloacal protuberances, testes and seminal glomera with a high number of sperm are ♂ adaptations to intense sperm competition. Short breeding intervals, long brooding phases, short foraging flights and high feeding frequency as well as a lower growth rate of nestlings seem to be related to uniparental care by the ♀.

Key words: *Acrocephalus paludicola*, breeding biology, mating systems, promiscuity.

1. Introduction

To be able to protect the globally threatened Aquatic Warbler, information is needed concerning the species' habitat requirements and breeding biology. Research and conservation stimulate each other and are now inseparably interwoven. This is the special contribution of Prof. A. DYRCZ who, by his untiring research activities in Poland, has made the Aquatic Warbler a flagship species for the endangered flora and fauna of fen mires in European nature conservation.

For 15 years, our Polish-German working group has carried out studies on the Aquatic Warbler's breeding biology at the study site in the southern basin of the Biebrza valley, NE Poland. The principal share of the field work was done by Andrzej DYRCZ and his co-worker Wanda ZDUNEK. The species' accounts published in the "Handbuch der Vögel Mitteleuropas" (SCHULZE-HAGEN 1991) and in CRAMP & BROOKS (1992) summarise the knowledge at that time. Apart from the two seminal studies of HEISE (1970) and WAWRZYNIAK & SOHNS (1977), the knowledge about breeding biology is based on research of our team (DYRCZ 1989; LEISLER 1981, 1985, 1988; SCHULZE-HAGEN *et al.* 1989). Since 1991, a series of studies was published revealing new aspects of the biology of this promiscuous passerine. This review summarises the new results published since 1991/92 as well as some recent unpublished findings which contribute to a better understanding of the Aquatic Warbler's reproductive biology.

2. Study sites and methods

The 48 ha study plot (Grobla Honczarowska, 53°20' N, 22°40' E) is part of a fen mire in the non-flooded zone 5-6 km from the river Biebrza. The dominant plant species is *Carex appropinquata*, forming tussocks of varying height. Other *Carex* species *(C. elata, C. rostrata* and *C. limosa)* dominate in mossy areas *(Caliergonella cuspidata, Drepanocladus intermedius* and *Bryum ventricosum).* The height of sedges does not exceed 80 cm while water level is 5-25 cm. Small *Salix* bushes (1-1.5 m) are scattered throughout. Extensive hay making had ceased in this area during the early 1970s. The plot divided into 100 x 100 m squares with coloured poles and into 50 x 50 m squares for the radio tracking study. The whole area of Biebrza marshes was declared a National Park in 1993 (SCHÄFFER 1996).

Since 1986, the number of singing ♂ has been censused and nests were searched. All ♂, ♀ and nestlings were colour-ringed, and, in several years (1990, 1993, 1994, 1997), blood samples were taken from adults and young for molecular analyses (DNA-fingerprinting, microsatellite-PCR). Intensive observations (partly from a hide) shed new light on territorial behaviour and song activity of the ♂ as well as on breeding and feeding activity of the ♀. In 1990 and 1993 songs were recorded and analysed spectrographically. After a pilot study in 1996, in 1997 25 ♂, and in 1998 three ♂ and ten ♀ were equipped with small radiotransmitters (SCHÄFER 1998). Continuous direct observation of the birds is hampered by the dense vegetation of their prefered habitat, which allows a range of visibility of only up to 20 cm, and by the skulking behaviour of the birds, particularly the ♀ prior to the breeding period. Like rails, Common Quail *Coturnix coturnix* or *Locustella* warblers, Aquatic Warblers remain virtually completely hidden from the observer. Therefore, it was necessary to hand-raise several nestlings and keep them in aviaries under semi-natural conditions for close observations.

3. Short summary of knowledge up to 1991

The Aquatic Warbler's mating system differs from that of other *Acrocephalus* species in that the ♂ are completely emancipated from brood care and no pair bond is established. Breeding and feeding of the young is done exclusively by the ♀ (i.e. uniparental care; HEISE 1970; DYRCZ 1989). ♂ seem to be continuously ready to mate and are testing every ♀ for her willingness to copulate (SCHULZE-HAGEN 1991). Up to three nests were found in close proximity to song posts used for a longer period by individual ♂, which suggested a kind of resource defence polygyny (food, nest sites; LEISLER 1985; DYRCZ 1989).

The ♂ use home ranges in the homogeneous, dense, tangled vegetation intensively, and obviously do not defend them (WAWRZYNIAK & SOHNS 1977; DYRCZ 1989). The core areas of individual ♂ are about 0,11 ha (1100 m^2) and may partially overlap in optimal habitats (LEISLER 1985). In such habitat, densities of 9.5 to 12 singing ♂ are found per 10 ha (DYRCZ *et al.* 1984). Aggressive interactions between ♂ have rarely been observed.

Unlike ♂ in species with biparental care, Aquatic Warbler ♂ do not restrict their song activity to the early reproductive period, but sing with the same intensity throughout the whole breeding season. However, diurnal variation of song activity is pronounced showing a maximum at dusk when virtually all ♂ of a population are singing simultaneously. The song is short and simple and consists of three song types: A-song (rattles) mainly signals aggression and warning, B-song (introductory rattles followed by a sequence of tonal units) is an intermediate form, and C-song, which is longest and most complex, has a sexual function (CATCHPOLE & LEISLER 1989). Short song flights are performed mainly in the daytime (WAWRZYNIAK & SOHNS 1977).

The ♀ forage in immediate proximity to the nest (flights in a range of 10 to 50 m) and take mainly large prey, particularly spiders, caterpillars, Coleoptera, Diptera and Trichoptera (SCHULZE-HAGEN *et al.* 1989). The prey taken may vary greatly and is contingent on annually and seasonally changing food supply. Feeding frequency is high due to the habitat's richness in food. Low nest predation and a 50 % rate of second broods in some years guarantee a high reproductive output (WAWRZYNIAK & SOHNS 1977).

4. New results obtained after 1991

4.1. Arrival at breeding site, home ranges of ♂ and song

From the first observations of singing ♂ and the earliest egg-laying dates it can be inferred that the sexes arrive about simultaneously at the breeding site

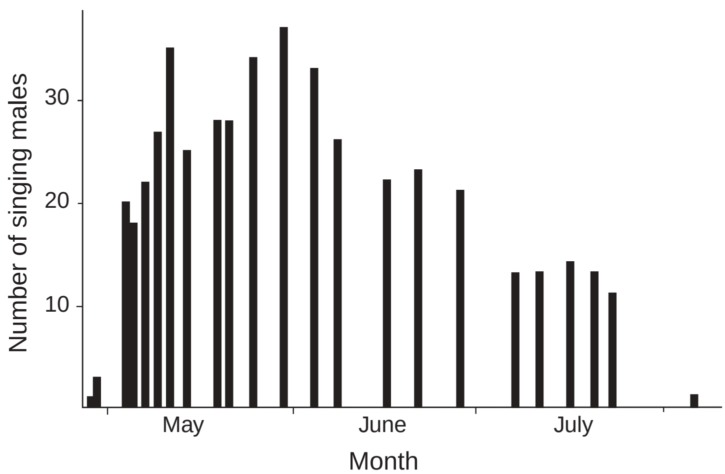

Fig. 1: Changes in abundance of singing ♂ Aquatic Warblers in a 48 ha study plot in Biebrza Marshes, Poland (from DYRCZ & ZDUNEK 1993b). – *Saisonale Änderungen der Zahl singender Seggenrohrsängermännchen auf einer 48 ha-Probefläche in den Biebrza-Sümpfen, Polen (aus DYRCZ & ZDUNEK 1993a).*

(DYRCZ & ZDUNEK 1993a). The number of singing ♂ in the study area increases continuously from the end of April to the end of May and afterwards decreases gradually up to the end of July (Fig. 1). Based on long-term observations of colour-ringed ♂, "territory size" in optimal habitats is 1.3 ± 0.82 ha (Fig. 2).

A radio telemetry study on 25 ♂ carried out in 1997 (SCHÄFER 1998; SCHÄFER *et al.* in prep.) revealed much more detailed information on the males' activity ranges. ♂ do not defend territories but hold overlapping home ranges (up to 74 % overlap; Fig. 2). Home ranges of up to 7.8 ha occur, which is distinctly larger than the "territory size" assessed previously by mere observation. Up to eleven radio-tracked ♂ were found within the home range of a single ♂. Some song posts are reported to be used by up to four ♂ successively. Yet, half of the time, the ♂ stay in isolated sections of 0.5 to 1.2 ha, which is only 16 % of the entire home range. These core areas overlap with the home ranges of other ♂ to a much smaller extent. They are used for 3 to 8 days on average and shift continuously throughout the breeding season (Fig. 3). Strikingly, ♂ frequently change their activity ranges. Mean duration of the male's presence at the study site was only 25 days (extremes 1-59 days).

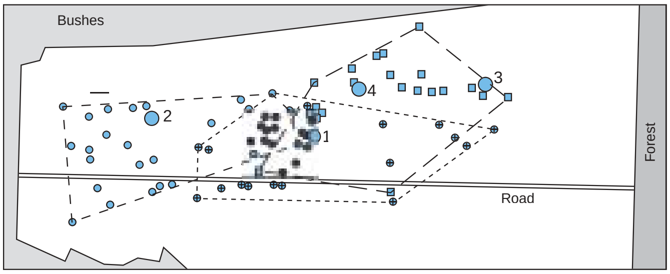

Fig. 2: Location of "territories" and song posts of three Aquatic Warbler ♂ and nests (numbered dots) at a site ca. 8 km distant from the Biebrza Marshes study site (from DYRCZ 1989). – *Verteilung von "Territorien" und Singwarten von drei Seggenrohrsängermännchen sowie Neststandorte (numerierte Punkte) auf einer Fläche, die ca. 8 km von der Probefläche entfernt liegt (aus DYRCZ 1989).*

♂ mobility correlates with the number of fertile ♀ in the area. ♂ cover larger distances and are more mobile when there are only few receptive ♀ available and are less mobile with many fertile ♀ present. ♂ manifest their presence by intensive song. So far, no evidence is available for a relationship between the males' activity ranges and the females' nest sites (SCHÄFER 1998) since fertilisation success of individual ♂ has not yet been analysed.

Daily song activity (time with/without song) of ♂ tracked by telemetry does not change in the course of the breeding season. However, variation within the day is pronounced and reaches a maximum between 18:00 and 22:00 h (SCHMIDT 1998; SCHMIDT *et al.* in prep). The same is true of song rate (i.e. number of songs per unit time), which is at its peak between 2:00 h and 4:00 h and between 20:00 h and 22:00 h. The proportion of C-songs (presumably with sexual function) declines in the course of the season and has a diurnal peak between 18:00 h and 20:00 h. A-song with intrasexual function (♂ spacing) is most frequent after sunset.

♂ reacted in different ways to the playback of A- and C-songs. At the playback of A-song they approached and responded with an increasing proportion of A-songs. However, this reaction was performed only during the first half of the breeding season. ♂ did not show any reaction to the playback of C-song (SCHMIDT 1998). Song flights presumably serve to increase au-

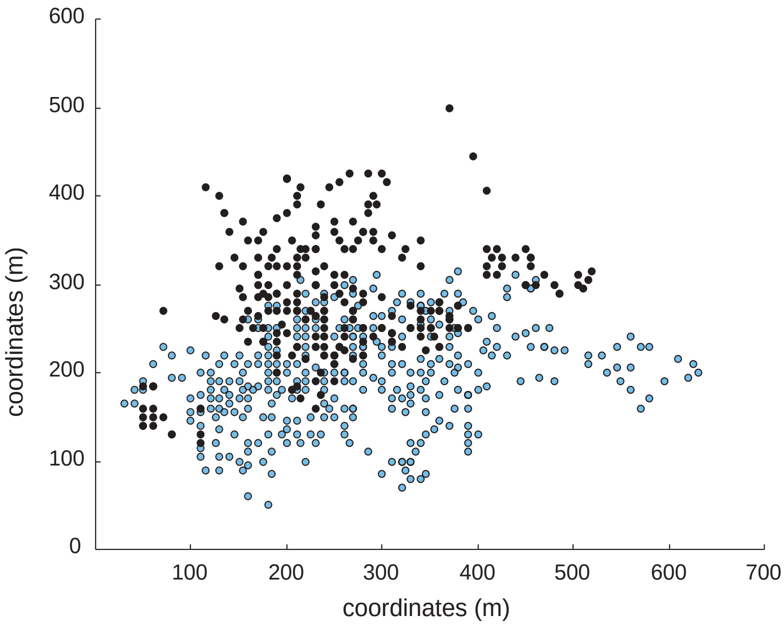

Fig. 3: Seasonal shift of a ♂ Aquatic Warbler home range as revealed by use of microtransmitters (○ records 18.-22. May 1998; ● records 25.-29. May 1998) (from SCHÄFER 1998). – *Beispiel für die saisonale Verschiebung eines Streifgebietes eines Seggenrohrsängermännchens, das einen Transmitter trug* (○ Ortungen 18.-22. Mai 1998; ● Ortungen 25.-29. Mai 1998) *(aus SCHÄFER 1998).*

Fig. 4: Typical song flight of Aquatic Warbler. – *Singflug des Seggenrohrsängers.* Drawing by D. QUINN.

dibility. Frequency of song flights was higher in the middle of the breeding season when the number of fertile ♀ was low. Song flights contained more C- and fewer B-songs than songs given from song posts and were performed more often during the second half of the day (SCHMIDT 1998; SCHMIDT *et al.* in prep.).

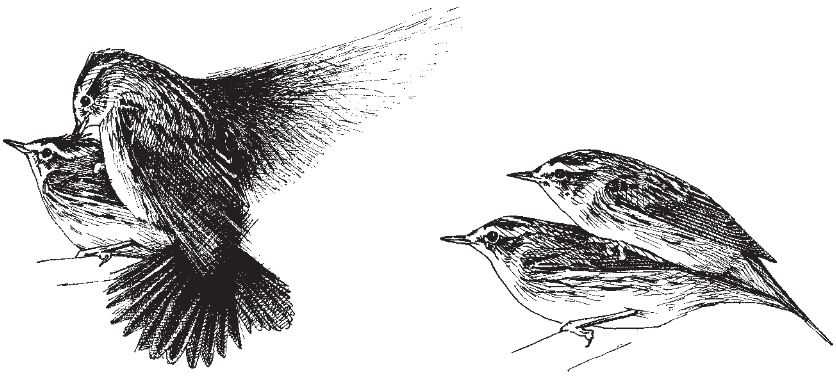

Fig. 5: Left: Copulation in Aquatic Warblers. Cloacal contact during a copulation bout: the fluttering ♂ twists his abdomen towards the female's cloaca for 1-5 sec. Right: ♀ and ♂ resting in close physical contact for several minutes between cloacal contacts (drawings by R. LOTTMANN; from SCHULZE-HAGEN *et al.* 1995). – *Links: Kopula beim Seggenrohrsänger. Der Kloakenkontakt dauert 1-5 sec. Rechts: Zwischen zwei Inseminationen ruhen Weibchen und Männchen für mehrere Minuten in engem Körperkontakt (Zeichnung R. LOTTMANN. Aus SCHULZE-HAGEN et al. 1995).*

4.2. Mating system and reproductive organs

Molecular studies (DNA-fingerprinting from blood samples from ♂, ♀ and nestlings, n = 120) revealed a very high rate of broods with multiple paternity (SCHULZE-HAGEN *et al.* 1993). These results were confirmed with the help of microsatellite PCR of about 315 nestlings from 72 broods and 170 adults from three years (DYRCZ *et al.*, in prep.). On average, 39 % of the broods were sired by one father, whereas 61 % were multipaternal with 2-4 fathers. The proportion of young sired by a second or third ♂ (young of additional fathers) averaged 23.8 %. The rate of multiple paternity was equal in first and second broods, but varied between years, presumably depending on weather conditions, i. e. food supply (DYRCZ *et al.* in prep.). There was no significant difference between single and multipaternal broods in terms of ♀ traits and breeding parameters (e.g. date of the first egg, clutch size etc.). However, there was

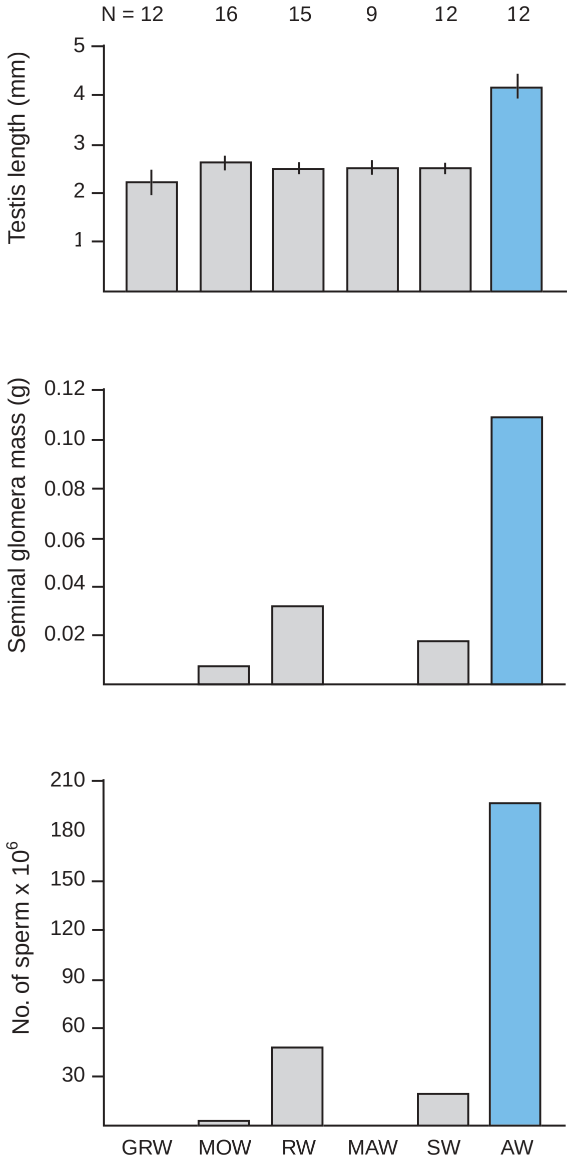

Fig. 6: Comparison of ♂ reproductive anatomy between *Acrocephalus* warblers: GRW Great Reed Warbler, MOW Moustached Warbler; RW Reed Warbler; MAW Marsh Warbler; SW Sedge Warbler; AW Aquatic Warbler. (Top) Testes length (corrected for body mass by dividing by cube root of mass), determined by laparotomy; values are means + s. d. (n). (Middle) Seminal glomera mass; data for single specimens except for the Aquatic Warbler, where n = 2; no data for Great Reed Warbler or Marsh Warbler. (Bottom) Numbers of spermatozoa in the seminal glomera; no data for Great Reed Warbler or Marsh Warbler (from SCHULZE-HAGEN *et al.* 1995). – *Vergleich der Anatomie der Sexualorgane bei Rohrsängermännchen: GRW Drosselrohrsänger; MOW Mariskensänger; RW Teichrohrsänger; MAW Sumpfrohrsänger; SW Schilfrohrsänger; AW Seggenrohrsänger. Oben: Hodengröße (körpergewichtskorrigiert; Messung durch Laparotomie; Durchschnitt und Standardabweichung). Mitte: Gewicht der glomera seminales; Messung jeweils bei 1 Männchen, beim Seggenrohrsänger n = 2; keine Angaben für Drossel- und Sumpfrohrsänger. Unten: Spermatozoenzahl in den glomera seminales; keine Angaben für Drossel- und Sumpfrohrsänger (aus* SCHULZE-HAGEN *et al. 1995).*

a marked difference in the rate of unhatched eggs and of starved or disappeared nestlings, which was lower in multipaternal broods (DYRCZ *et al.* in prep.).

The promiscuous mating system of *A. paludicola* with a high level of multipaternity indicates intense sperm competition. In choice experiments carried out in aviaries ♀ reacted more promptly and for longer periods to the playback of C-songs than to the playback of A-song (CATCHPOLE & LEISLER 1996), partly performing wing-quivering. Under aviary conditions, the ♂ are trying to copulate continuously during the females' fertile period (SCHULZE-HAGEN *et al.* 1995). ♀ unwilling to copulate will hide in the vegetation. The copulation, in other birds usually lasting only 1-2 sec, is extraordinarily long in Aquatic Warbler (Fig. 5). The ♂ stays mounted for 23.7 ± 11.8 min on an average and has up to 6 cloacal contacts (inseminations). Prolonged copulation may have evolved, on the one hand, to allow ♀ to assess ♂ quality and, on the other hand, to allow ♂ contact mate guarding. Copulations are most frequent some days before egg-laying and during the early laying period with peaks in the evenings and in the early mornings. The ♀ is able to interrupt copulation at any time by escaping the ♂ (SCHULZE-HAGEN *et al.* 1995).

The reproductive organs are also extremely well adapted to intensive sperm competition with cloacal protuberance, testes and seminal glomera being extraordinarily large compared to other *Acrocephalus* species and birds in general (Fig. 6). The numbers of sperm in the seminal glomera is very high, whereas the length of the spermatozoa is not conspicuous (SCHULZE-HAGEN *et al.* 1995).

4.3. Breeding biology

In the aviary, ♀ willing to construct a nest often returned to a selected tuft of vegetation, climbed around and performed movements at its bottom. Soon afterwards they carried nesting material. Nest construction is done mainly in the mornings and in the evenings. It takes about 2 to 3 days to construct the outer layer and two days to line the interior of the nest (SCHULZE-HAGEN 1995).

Clutch initiation is well synchronised within the population. Up to 80 % of the ♀ start egg-laying within one week (DYRCZ & ZDUNEK unpubl.). The nests are not distributed evenly over the study plot but are clustered (Fig 7). Nest sites differ from randomly chosen places in having a higher water level and a larger proportion of dry, last year's grass covering the nest

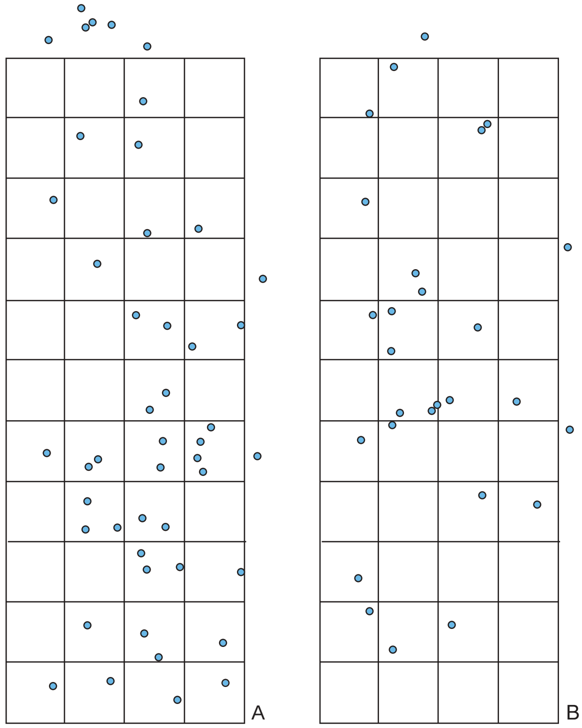

Fig. 7: Distribution of Aquatic Warbler nests on the Biebrza Marshes study plot in 1990 (squares 100 x 100 m); (A) first brood; (B) second brood (from DYRCZ & ZDUNEK 1993a). – *Verteilung von Seggenrohrsängernestern auf der Probefläche 1990. (A) Erste Brut; (B) zweite Brut (aus DYRCZ & ZDUNEK 1993a).*

(DYRCZ & ZDUNEK 1993). Also abundance of prey is of importance in the choice of the nest site: the density of arthropods is distinctly higher in the immediate proximity of the nest than in plots chosen at random. This correlates with the observation that the principal share of the food is collected at a distance of 18 to 30 m from the nest (SCHULZE-HAGEN *et al.* 1989; DYRCZ & ZDUNEK 1993a). Particularly where nests are clustered, density of potential prey is distinctly higher (Tab. 1). In several cases, two nests were situated within less than 10 m of each other. In such cases the foraging areas did not overlap (DYRCZ & ZDUNEK 1993a), while aggressive interactions among foraging ♀ are frequent (SCHULZE-HAGEN 1991).

During the period of incubation, which is performed by the ♀ alone, the time spans of nest attendance and absence are very short, averaging 11 and 5 min, respectively. These are the shortest phases ever recorded in Passerines. They may be interpreted in relation to uniparental care by a small insectivorous bird with a high metabolic rate in an environment with variable microclimate (DYRCZ 1993). Incubation lasts 12 to 14 days (SCHULZE-HAGEN 1995). Compared to other *Acrocephalus* species, feeding activity is lower and brooding more intensive during the first days after hatching. With the beginning of thermoregulatory independence of the nestlings and their rapidly increasing demand for food, brooding decreases from the 7th or 8th day onwards. Feeding frequency now increases markedly and is higher than in Marsh Warblers *A. palustris*, where both parents participate in rearing the young (DYRCZ 1993; SCHULZE-HAGEN *et al.* 1989). With 15 to 16 days, the fledgling period is by far the longest among all *Acrocephalus* warblers and reflects the low feeding frequency during the first days after hatching. Compared to other *Acrocephalus* species, the young show a clearly retarded growth rate (DYRCZ 1993; DYRCZ *et al.* 1994). In one case, two young were still being fed 14 and 16 days after fledging (SCHULZE-HAGEN 1995).

Only 17 % of the ♀ stayed at the study site, where they have bred successfully, to start a second brood. Thus, the majority of ♀ breeding at any time moved into the area a short time before (DYRCZ & ZDUNEK 1993a). Similar movements prior to the start of the second brood also seem to be of major importance elsewhere (WAWRZYNIAK & SOHNS 1977, M. FLADE & A. KOZULIN, pers. com.).

Aquatic Warbler ♀ are very cryptic and shy in the surroundings of their nests, particularly when breeding or during the early nestling period. Only later does the frequency of warning calls at the approach of predators increase. In contrast to Meadow Pipit *Anthus pratensis* and Reed Bunting *Emberiza schoeniclus*, Aquatic Warbler ♀ display less risky antipredatory behaviour such as warning calls from the distance, only minor approaches and

Tab. 1: Comparative abundance of potential prey (dry weight arthropods) in different nesting situations of Aquatic Warblers in 1991; sampling of arthropods by standardised sweep-netting. Aggregated nests < 30 m apart; isolated nests > 50 m from next nest apart (from DYRCZ & ZDUNEK 1993a). – *Beziehung zwischen Nahrungsangebot (Trockengewicht von Arthropoden) und Neststandorten 1991. Proben wurden mit standardisierten Kescherfängen gesammelt (aus DYRCZ & ZDUNEK 1993a).*

site	dry weight (mg)	significance
directly at nest (n=30)	81.1 ±61.8	t_{73} = 1.62; n. s.
within 30 m of nest (n=45)	107.9 ± 75.0	
at nest aggregations (n=15)	155.6 ± 61.2	t_{43} = 2.98; p < 0.01
at isolated nests (n=30)	87.1 ± 77.8	
first brood (n=55)	111.1 ± 74.0	t_{73} = 6.75; p < 0.001
second brood (n=20)	58.8 ± 43.0	

Fig. 8: Aquatic Warbler. – *Seggenrohrsänger.* Photo: M. WOIKE.

Fig. 11: Aquatic Warbler with typical leg posture, in which they also climb through dense tufts of sedges. Yaselda marshes, summer 1998. – *Seggenrohrsänger in typischer Beinhaltung (mit gespreizten Beinen unterschiedliche Stengel greifend), die auch beim Klettern durch dichte Seggenbüschel häufig zu beobachten ist; Jaselda-Talmoor, Sommer 1998.* Photo: A. KOZULIN.

Fig. 9 and 10: Compared to other *Acrocephalus* species, Aquatic Warblers feed relatively large prey to their young; Yaselda marshes, summer 1998. – *Im Vergleich mit anderen Rohrsängerarten verfüttern Seggenrohrsänger relativ große Beutetiere an ihre Jungen; Jaselda-Talmoor, Sommer 1998.* Photo: A. KOZULIN.

no attacks. In experiments, they approach nearer to small mammals than to birds of prey (HALUPKA 1993). The shy and cryptic behaviour near the nest seems to be related to unaided rearing of the young by the ♀. Whether ♂ begin to sing when potential predators approach the nest has to be clarified. Possibly, this is a weak manifestation of ♂ investment (DYRCZ & SCHULZE-HAGEN unpubl.).

4.4. Breeding statistics

Clutch size amounts to 3-6 eggs with a median of 5 eggs (Tab. 2). First clutches are somewhat larger than second clutches (see appendix). Losses are remarkably small and breeding success is among the highest ever recorded in open nesting passerine birds. Total losses occur in only 20 % of the broods (according to a simple calculation; the MAYFIELD method appears to yield too low an estimate given the high breeding success of this species (DYRCZ & ZDUNEK 1993b). The percentage of successfully fledged nestlings amounts to 62 % (n = 677 eggs; DYRZC & ZDUNEK 1993b). Losses in first broods are smaller than in second broods. Total breeding success may vary considerably from year to year. It has still to be tested whether breeding success is higher in aggregations or in isolated nests.

Losses during the time of egg-laying and incubation are distinctly smaller than during the nestling phase. The proportion of unhatched eggs (infertile, dead embryo) is 8,6 %. The main causes of losses are predation, flooding, starvation and abandoning of broods. Harriers *Circus* spec. seize nestlings which attract attention by their begging calls in rainy and cold weather (DYRCZ & ZDUNEK 1993b and pers. com.). In one case where the complete brood died from starvation, the ♀ extended its foraging flights to 86 m on average and frequently as far as 200 m, feeding conditions in the approximity of the nest obviously being unfavourable (DYRCZ 1993). Unlike other *Acrocephalus* fledglings, young Aquatic Warblers soon behave in a solitary way. As a response to disturbance they tend to fly upwards, performing high jumps. Both behaviours may be interpreted as antipredator strategies against small ground-dwelling mammals.

5. Discussion

High productivity of the Aquatic Warbler's habitat is the essential prerequisite for uniparental care by the ♀ and the high degree of ♂ emancipation (LEISLER & CATCHPOLE 1992). Yet, the fact that (1) breeding conditions are unpredictable due to watertable changes (LEISLER 1985), (2) the resources are not economically defendable (SCHÄFER *et al.* in prep.) and (3) ♂ aggregate, resulted in a "lek-like" mating system (WIKELSKI & TABORSKY 1997) or in a sort of scramble competition. Since 1991, particularly molecular genetic techniques and radio telemetry have added much to our understanding of the Aquatic Warbler breeding system. The high frequency of broods with multiple paternity, prolonged copulation and adaptations to high sperm production are all indications of intense sperm competition, which may act as a selection factor (BIRKHEAD 1993; SCHULZE-HAGEN *et al.* 1995; general see PARKER 1970; REYNOLDS 1996). Against this background, the males' far reaching movements and constant song activity throughout the breeding period indicate continuous advertisement and readiness to mate. Prolonged copulation and high sperm production can be seen as the only available strategy of effective paternity assurance. Apparently, receptive ♀ choose nest sites and feeding areas as a function of habitat parameters such as prey availability, which may result in a more scattered or a more concentrated distribution of nests in suboptimal or optimal habitat patches, respectively (DYRCZ & ZDUNEK 1993). On the other hand, ♂ tend to aggregate in places where fertile ♀ are likely to be available. However, whether some ♂ succeed in monopolising access to ♀ still remains unclear. The high degree of synchronisation of egg-laying at the beginning of the breeding period may restrict ♂ access to ♀ in time. In contrast to "classical" systems with scramble competition, the mobility of ♂ is lower when many fertile ♀ are available (SCHÄFER 1998; SCHÄFER *et al.* in prep.). This could mean that fertile ♀ visit advertising ♂ in a given area. Preliminary results from our radiotracking study suggest, that females do some mate sampling and that males may switch between different mating tactics (being mobile or stationary).

Why some ♀ mate with only one ♂, but others mate with several ♂, is still an unresolved question both in terms of the mechanism and the function. A comparison of data from three years with different weather conditions revealed that in 1997, a year with unfavourable weather, not only was the rate of broods with multiple paternity higher, but also the rate of unhatched eggs and of starved/disappeared nestlings was significantly lower in broods with multiple paternity than in broods with single paternity (DYRCZ *et al.* in prep.). Such year-to-year variation will

Tab. 2: Breeding statsitics of the Aquatic Warbler population in the lower Biebrza basin (from DYRCZ & ZDUNEK 1993 a, b; SCHULZE-HAGEN 1991, 1995). – *Brutbiologische Parameter (aus DYRCZ & ZDUNEK 1993a, b; SCHULZE-HAGEN 1991, 1995)*

duration of nest building	3-5 days
laying period	early May until late July
first egg (median)	1st clutch 18 May 2nd clutch: 29 June
clutch size (average) first clutch	5.11 ± 0.60 eggs
clutch size (average) second clutch	4.37 ± 0.60 eggs
total clutch size (average; n = 157)	4.81 ± 0.73 eggs
length of incubation	12 to 14 days
length of nestling phase	15 to 16 days
time feeding fledglings (one case)	12 to 14 days
interval between first and second clutch	41 days
time between loss of clutch and first replacement egg	7 days
rate of second clutches	ca. 50 %
breeding success (% eggs producing fledglings; n = 677)	62 %
unhatched (infertile, dead embryo)	8.6 %
losses during egg stage	11.9 %
losses during nestling stage	30.4 %

offer the opportunity to identify important ecological factors that might influence ♂ and ♀ mating tactics. Whether mate sampling is costly for ♀ and which criteria they use for mate choice is still unknown. Probably variation in the extent of knowledge about potential ♂ partners explains variation in the number of fathers per brood. For example, multiple matings could allow ♀ to correct an initial choice of a partner (in a similar way as in the Common Quail, RODRIGO-RUEDA *et al.* 1997). Alternatively, only some ♀ may succeed in pairing with more than one ♂. Data on the fertilisation success of individual ♂ and their distribution are necessary to test these ideas. Development of additional microsatellite primers to find out which ♂ are sires within one brood and to determine overall fertilisation success of individual ♂ is under way. Benefits which may accrue to ♀ from multiple matings could be fertilisation insurance, genetic diversity or avoidance of negative inbreeding effects. Further study of the molecular structure of different Aquatic Warbler populations in Eastern Europe and further radio tracking studies to assess the spatio-temporal association of the sexes should help to answer these open questions. Simple experiments in the wild are aimed at clarifying whether ♂ warn ♀ about potential predators, a way in which ♀ might benefit directly (DYRCZ & ZDUNEK 1993a). Examination of sperm morphology and physiology as well as the structure of the ♀ genitalia should help to better understand the mechanism of sperm competition.

The comparative analysis of several *Acrocephalus* species with mating systems varying from monogamy to polygyny and promiscuity proved to be especially fruitful for understanding many aspects of the Aquatic Warbler's reproductive biology (LEISLER & CATCHPOLE 1992).

Acknowledgments: The principal share of this long-term study was done by Prof. Andrzej DYRCZ and Wanda ZDUNEK, who, throughout many years, spent the whole breeding season in the Biebrza region. They merit our special thanks. Furthermore, we wish to thank all those who participated in this project, in particular: Prof. Michael WINK, Dr. Beat NAEF-DAENZER, Prof. Tim BIRKHEAD, and David QUINN. Grants were offered generously by the DFG and the research commission of the DO-G and the Schweizerische Nationalfonds.

6. Zusammenfassung

Schulze-Hagen, K., B. Leisler, M. Schäfer & V. Schmidt 1999: Brutbiologie des Segggenrohrsängers *Acrocephalus paludicola* – Überblick über die neuesten Ergebnisse. Vogelwelt 120: 87 – 96.

Neue Forschungsergebnisse zur Brutbiologie des Seggenrohrsängers, die nach 1991 (SCHULZE-HAGEN in GLUTZ & BAUER 1991) gewonnen wurden, werden beschrieben. Die Ergebnisse stammen von einem polnisch-deutschen Team, dass seit 1986 auf einer 48 ha großen Probefläche im Südbecken der Biebrza-Niederung (Nordost-Polen) am Seggenrohrsänger forscht. Telemetriestudien haben gezeigt, dass die Aktionsräume (home ranges) der ♂ bis zu 7,8 ha groß sind, sich oft überlappen und häufig wechseln. Die Kerngebiete der home ranges werden intensiver genutzt. Die Beweglichkeit der ♂ (Häufigkeit und Ausmaß der Ortswechsel) korreliert positiv mit der Anzahl anwesender fruchtbarer ♀. Die Gesangsaktivität hat ihren Höhepunkt während und nach dem Sonnenuntergang zwischen 18:00 und 22:00 Uhr, wenn vorwiegend kurze Strophen des A-Typs vorgetragen werden. Molekulargenetische Analysen haben ergeben, dass etwa die Hälfte aller Bruten von mehreren (2-4) Vätern stammt. Bei in Gefangenschaft gehaltenen Vögeln wurde festgestellt, dass die Kopulation ungewöhnlich lange (im Durchschnitt 24 min) dauert, was als eine Form von "mate-guarding" angesehen werden kann. Die ♂ sind sehr gut an extrem intensive Spermienkonkurrenz (sperm competition) angepasst (sehr große Kloake, Hoden und Samenreservoire sowie eine hohe Spermienmenge). Kurze Bebrütungsintervalle, eine lange Bebrütungszeit, kurze Nahrungsflüge und hohe Fütterungsfrequenz sind ebenso wie verzögerte Nestlingsentwicklung und spätes Ausfliegen der Jungvögel als Anpassungen an die uniparentale Brutpflege anzusehen (Bebrütung und Jungenaufzucht werden ausschließlich vom ♀ übernommen).

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