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Nesting of the *Acrocephalus* warblers

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Abstract. The paper contains data concerning nest sites, material, construction, shape, and sizes in the majority of *Acrocephalus* species. The descriptions are based on field studies, museum specimens, and literature. The system proposed by CLEMENTS (2000) including 36 species in the genus *Acrocephalus* has been adopted. Similarities and differences in nesting of 32 species and four subspecies are studied in the last chapter on the basis of 38 characters assembled in Table XLI. They do not always reflect systematic relations of warblers within the genus *Acrocephalus* on the basis of molecular data.

Key words: genus *Acrocephalus*, nest site, nest material, nest construction, nest shape, nest sizes.

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I. INTRODUCTION

The genus *Acrocephalus* seems not to be defined unequivocally. From time to time it resembles a "witch's sack", to which various ornithologists place, according to their predilections, various species of Sylviinae, apart of a few, which are always in this genus. Those additional species are included in other genera, set up especially for them by other researchers . This causes serious divergences in the numbers of species, which are also enlarged by the differences in treatment of particular forms at the species/subspecies level. For instance, WILLIAMSON (1960) includes 13 species in the genus *Acrocephalus*, CLEMENTS (1974) – 16, WOLTERS (1980) also 16 (but a part of them only is listed by CLEMENTS 1974). According to MORONY et al. (1975) and COURTNEY-HAINES (1991) there are 27 species, and according to HOWARD and MOORE (1991) – 28; they also list in the genus *Acrocephalus* species which other authors include in the genera *Lusciniola*, *Calamodus*, *Conopoderax*, *Calamocichla* (part) and *Phragmaticola*. SIBLEY and MONROE (1990) mention 32 species, treating several subspecies as valid species. None of the above mentioned authors write about *Acrocephalus sechellensis* and *A. rodericanus*, listed by them in *Bebrornis*. KOMDEUR (1996) and SIBLEY (1996), however treat them as them as real acrocephalines which was accepted by CLEMENTS (2000), who in the genus *Acrocephalus* listed altogether 36 distinct species.

The present paper is not strictly systematic, hence, as a starting point, the authors have generally adopted the system and species English names proposed by CLEMENTS (2000). They know that treating particular forms, especially controversial ones, may not be approved by all researches.

They hope, however, that the materials presented here may, at least in part, explain the above-mentioned controversies and help a little to set in order the systematics of the genus.

According to MAYR (1958) and GREENWOOD (1997), the elements of animal behavior, especially these connected with reproduction, are diagnostic characters equal to morphological and molecular characters. One of them are innate methods of nest formation in birds. This was documented by experiments of PROMPTOV (1945) and stereotype activity of nest cup formation performed by young birds observed by GOODWIN (1954), DILGER (1956) and the HEINROTHS (1965).

First of all the authors describe here the nesting of European species, because for them we obtained the largest numbers of nests to study. As a background they gathered as much data as possible on the nests of extra-European species, studying specimens in several collections. However, in many cases they failed to collect data because the species grouped in the genus *Acrocephalus* inhabit huge territory (the Palaearctic, Ethiopian, Indo-Malayan, Oriental, Australian regions and selected islands of the Pacific, Indian and Atlantic Oceans – Fig. 1), and many endemic species are not represented in the collections. They were not able to study in person the nests of 18 species listed by CLEMENTS (2000) in the genus *Acrocephalus*. They are listed below in alphabetical order (together with distribution data): *aequinoctialis* (Christmas and Fanning Islands), *atyphus* (Tuamotu Archipelago), *baeticatus* (E & S Africa) *brevipennis* (Cape Verde Islands), *caffer* (Society Islands), *gracilirostris* (Subsaharan Africa), *griseldis* (S Iraq), *kerearako* (Cook Islands), *luscinius* (Mariana Islands), *orinus* (N India – known from one skin only), *rehsei* (Nauru Islans), *rimitarae* (Tubuai Islands: Rimitara), *rodericanus* (Rodrigues Island), *rufescens* (Subsaharan Africa), *sechellensis* (Seyshelles Islands), *sorgophilus* (NE China – according to PARKER & HARRISON 1963,

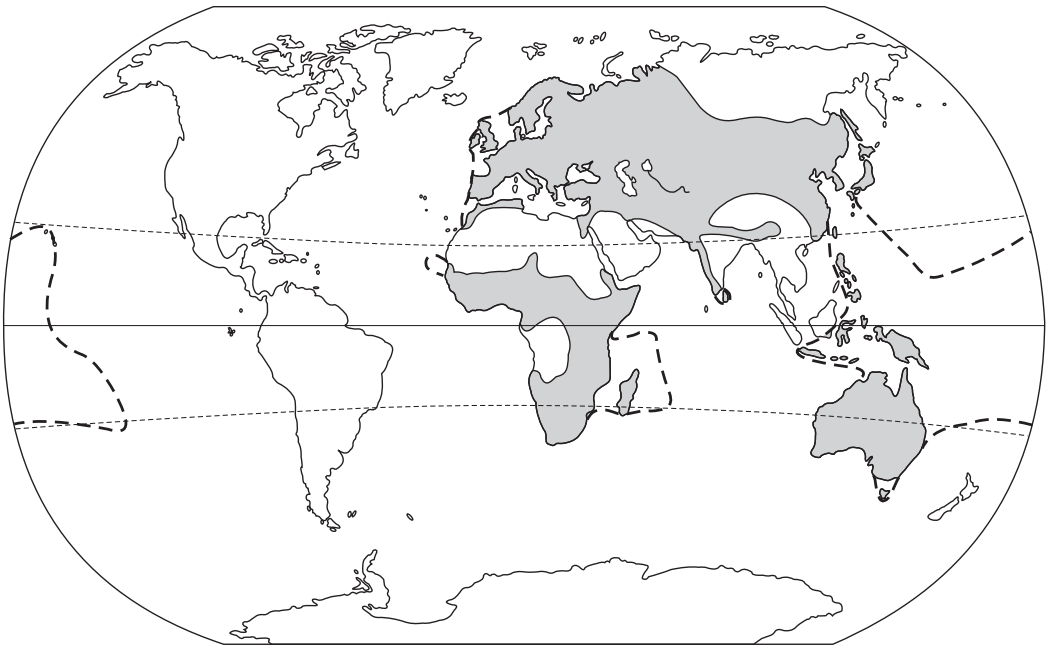


Fig. 1. General limits of the breeding distribution of all species included by CLEMENTS (2000) in the genus *Acrocephalus*, compiled after ALI & RIPLEY (1973), BAKER (1951), CHENG (1976), CRAMP (1992), FLINT et al. (1968), HARRISON (1982), KOVSHAR (1972), NECHAEV & FUJIMAKI (1994), PTUSHENKO (1954), SMITHIES (1968), SONOBE (1982), URBAN et al. (1997).

COURTNEY-HAINES 1991 and SIBLEY 1996 its breeding biology is unknown), *taiti* (Henderson Island) and *vaughani* (Pitcairn Island). An attempt was made to gather descriptions of their nests scattered in ornithological literature. In many cases this was successful, but those descriptions are not always satisfactory. Finally, the authors were unable to find any data concerning the nests of five species (i.e. *griseldis*, *orinus*, *rodericanus*, *sorgophilus* and *tangorum*).

Many persons helped in gathering the materials for the present paper. Dr E. N. KUROCHKIN, Dr O. LANGRAND, Prof. Dr R. MACKOWICZ, the late Capt. J. H. MACNEILE, Mr T. OLEŚ, Dr T. TOMEK, and Prof. Dr J. WITKOWSKI collected the nests or the data for nest record cards being in the authors' charge. Prof. Dr K. HUDEC permitted the studying of nest record cards stored at the Institute of Vertebrate Biology, Czech Rep. Ac. Sc. in Brno. The late Prof. Dr A. P. KUZYAKIN and Dr V. V. LEONOVICH permitted examination of the nests at their private collections. Dr P. DEVILLERS (Brussels), Prof. Dr V. E. FLINT (Moscow), Dr C. HARRISON (Tring), Dr G. F. MEES (Leiden) gave access to specimens in the collections being in their charge. Dr Ph. HORTON (Adelaide) lent two nests of the Australian Reed Warbler and took measurements of another two nests. Prof. Dr R. MACKOWICZ, Mrs Z. MALCHER and Mrs J. PAŁKA helped in gathering the literature. Ms K. OCHMAN M.Sc. helped with statistics, Mr M. FINIK made two drawings based on photographs, Mrs M. MATYJASZKIEWICZ M.Sc. prepared computer version of drawings, dr Z. M. BOCHEŃSKI prepared computer version of photographs (original and reproduced), Mr Ch. PAYNE of Oxford University Press, Mrs A. BIELSKAS of the American Museum of Natural History Library, Mrs J. C. LUCENTE of "The Wilson Bulletin", Prof, dr Ch. FEARE of the "Bulletin of the British Ornithologist's Club", and Dr J. P. DEJONGHE of "Alauda", sent the permissions for reproducing figures (photographs and drawing) published in journals represented by them. We owe our heartfelt gratitude to them all. We are also greately indebted to Prof. Dr A. DYRCZ and Dr B. LEISLER for their reviews of the manuscript.

II. MATERIAL AND METHODS

The results of field observations were noted on nest record cards. The data consist of the nest measurements, nest site, material used for building, some characters of nest construction; sketches of the nest sites are often presented. Photographic documentation is provided for many nests. In the case of the Marsh Warbler and Sedge Warbler also used were the data from nest record cards collected before 1967 from the territory of former Czechoslovakia and stored at the Institute of Vertebrate Biology in Brno. Most probably they constitute a part of data used then by HUDEC (1983). The nests stored in several museums as well as in private collections were also studied.

Original descriptions of nests, made in the field or in collections, are completed by data taken from literature. This especially concerns the species of very vide distribution, if studied specimens come from a part of their breeding areas. The places from which the described nests come are shown on maps, on the background of general limits of the breeding distribution of given species; non-inhabited areas within those limits are not indicated. The finding places of specimens described in fields or in collections are indicated by black dots. Descriptions from literature concerning nests from large areas are indicated with empty asterisks. The scales of maps and their projections are not unified.

In describing the nest site, the species of plant (or its kind only), number of stems (or branches), and height above water or ground, were taken into account. The nest sites of the *Acrocephalus* warblers are diversified, therefore a few general types of them were established. They are shown in Fig. 2. Unfortunately, the labels of nests housed in collections do not always contain sufficient data concerning their sites.

The material used for the building of nests is described with various accuracy: in the field, describing the nests containing eggs or chicks was, as a rule, limited to their external view (from the sides and above), while the nests stored in collections allowed more precise analysis, although they were not taken to pieces. Plant material elements were usually not identified to the species level, be-

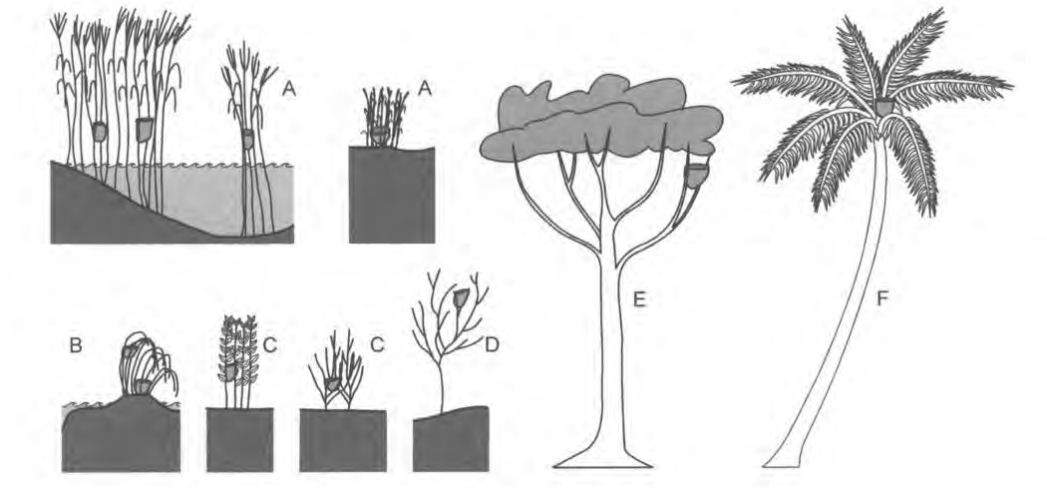


Fig 2. General types of the nest sites observed in acrocephaline warblers: A – nest hanging among vertical stems of emergent water plants (reed, red-mace, papyrus and others), or among such grasses as elephant grass in terrestrial habitats, B – nest "pressed" into sedge or grass tussock, C – nest attached to various land herbs such as *Arthemisia*, D – nest in forked branches of such bushes as willow, E – nest in forests (mainly on Pacific islands) in forked branches under or in the canopy, F – nest on palm trees.

ing counted only to different types, for example grass stalks, grass leaves (probably, sedges were often numbered in these categories), plant fibers, and so on.

In analysing the nest construction attention was paid to the following details: (1) the manner of attachment to plants supporting it (i.e. if the nest material is woven around supporting stems or not); (2) the traces of using by birds of wet or washed materials; (3) presence or absence of firmly woven ring at the rim; (4) the way of bending of long stems or stalks i.e. if they are curved or angular (depending on stiffness); (5) protruding outside stiff endings of long stems or stalks; (6) eventual transparency of some parts of walls or bottom.

All the nests were measured. In the case of nests which were of elliptic or irregular shape the external diameter as well as the diameter of the nest cup were measured crosswise and the means of those two measurements were taken into account in further calculations. Some nests studied at collections were stored in boxes too small for them and so somewhat pressed – this was taken into consideration, especially when the outer diameter and height of the nest were taken. Results of measuring are presented in tables. Their form depends on the number of studied specimens. In the case of very few nests studied – the measurements of each of them are given, whereas the data on larger series of specimens are summarized as follows: minimum and maximum mean of crossweise measuring (see above), arithmetic mean of all nests, its standard deviation, and coefficient of variation.

As in the case of *Sylvia* warblers (BOCHEŃSKI 1985), the following types of nest shapes have been distinguished on the basis of mutual relations between particular dimensions: flat nests – when the nest height is smaller than half the outer diameter; hemispheric nests – when the height is more or less equal to half the outer diameter; high nests – when the height is greater than half of the diame-

ter; and very high nests – when the height exceeds the total outer diameter. Similarly, in the descriptions of inner cups four categories have been introduced: shallow, hemispheric, deep, and very deep (in practice, flat and shallow nests are not encountered in the genus *Acrocephalus*).

The acronyms of museums and collections follow the descriptions of particular nests. They are as follows: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Krakow (ISEA), Provincial Museum at Radom, Poland (MOR), British Natural History Museum, Sub-Department of Ornithology at Tring (BMNH), Royal Museum of Natural History in Brussels (MRHN), Royal Museum of Natural History in Leiden (RMNH), Zoological Museum of Moscow State University (ZMMSU), South Australian Museum in Adelaide (SAM), and private collections of Dr V.V. LEONOVICH (VVL) and Prof. Dr A.P. KUZYAKIN (APK) in Moscow, which after his death was deposited in ZMMSU.

III. MOUSTACHED WARBLER *Acrocephalus melanopogon* (TEMMINCK, 1823)

One nest collected at Lake Valencei, W Hungary (ZMMSU) belongs to the nominative form *melanopogon* (TEMMINCK, 1823); the other six nests of the subspecies *mimicus* (MADARASZ, 1903) come from Lake Akgel in Azerbaijan (VVL). The locations of these places are shown in Fig. 3 against the breeding range of the species.

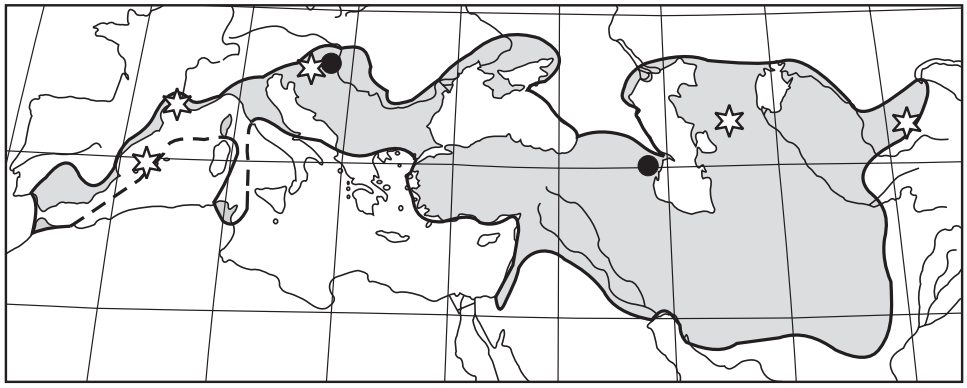


Fig. 3. Breeding area of the Moustached Warbler *Acrocephalus melanopogon* (grey), compiled from CRAMP (1992), PTUSHENKO (1954) and HARRISON (1982). Black dots – finding places of nests included in the present paper (described in the fields and in collections), asterisks – finding places of nests cited from literature. Dots and asterisks may also concern wider areas, such as provinces, if exact places are not indicated.

Nest site

Five of the nests from Lake Akgel were placed among reeds, hence they represent the type "A" of the nest site. They were situated above ground (1 nest) or above the water surface (3 nests). The height of the nest site, noted for 5 nests, was between 40 and 80 cm (54 cm on average; median = 40 cm).

Nest material and construction

Essential nest material of the Asiatic subspecies consists of the leaves of reed or reed-mace. The compactness of nest walls and vertical impressions of stems among which the nests were placed indicate that at least some leaves (and in one nest green algas) were taken wet from the water surface. In three cases particular supporting stems were surrounded by nest material. The plant wool of the previous year reed-maces in various amount was used for building the lower part (bottom) of four nests. At the rim of all nests there were conspicuous solid rings woven from dry material, i.e. strips

of reed leaves and inflorescences (thin stalks). The ring narrows the opening of the cup in relation to its interior. The nest of the nominative form from Hungary did not differ from the Asiatic ones.

Shape and size of the nest

The height of the majority of nests under study was similar to their largest outer diameter measured distinctly below the rim. As a result the nests look like spheres with cut upper parts (Fig. 4). The cup depth is similar or slightly larger than the diameter of the nest opening – in the latter case it may be similar to the largest diameter of the nest interior (in one case the size of the nest opening was 40x50 mm, that of the interior – 55x55 mm, whereas the depth – 53 mm). The measurements of all 7 nest are given in Table I.

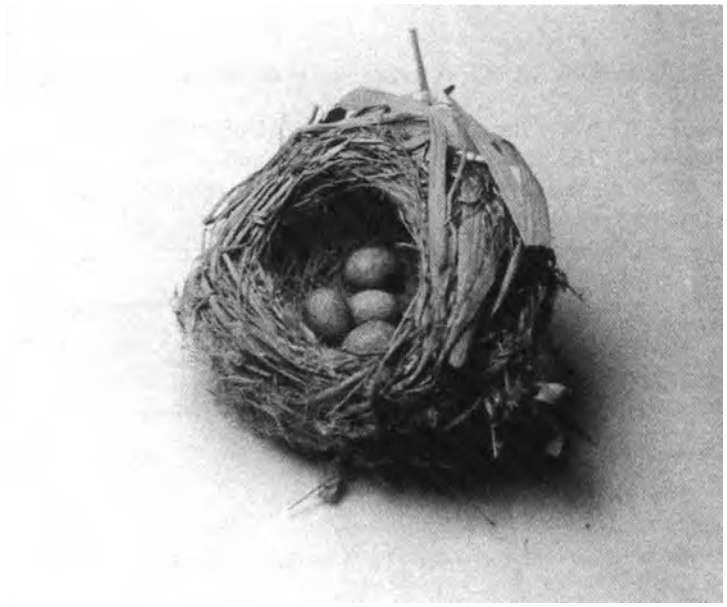


Fig. 4. The nest of the Moustached Warbler *Acrocephalus melanopogon* from the Lake Akgel, Azerbaijan (VVL collection).

Additional literature data and comments

The authors describing nesting habits of the Moustached Warbler (GLUTZ 1991, RADETZKY 1985, CRAMP 1992, MUNN 1948) write that it builds its nests in large areas of dense reed beds, always above the water surface. These descriptions deal with the typical form only. One of the *mimicus* nests now described was situated above ground, this not being exceptional since PTUSHENKO (1954) mentions a similar nest. The height of the nest site may be exceptionally greater than that mentioned here and attain 124 cm above the water surface (GLUTZ 1991 after LEISLER 1970) and 130 cm above ground (PTUSHENKO 1954). Besides reed and reed-mace as plants supporting the nest, there are mentioned rushes, *Cladium*, *Sparangium*, *Lythrum*, *Osmunda*, and also willow and tamarisk shrubs – hence, besides the type "A", they belonged to types "C" and even "D" of Fig. 2 (GLUTZ 1991, KOVSHAR 1972, PTUSHENKO 1954). GLUTZ (1991) emphasizes that the nests are placed below overhanging plant elements pulled by birds with plant fibres. MAKATSCH (1976) writes about nests placed among old reeds whose upper parts were bound together by man, and according to RADETZKY (1985) the nests may be hidden from above with artificial, man-made objects such as net floats.

Table I

The measurements (in mm) of the nests of two subspecies of the Moustached Warbler *Acrocephalus melanopogon*. Literature data cited below own materials. [Arithmetic means are given in square brackets]

Specimen and collection	Outer diameter	Opening diameter	Height	Depth
A. m. melanopogon:				
Lake Valencei (ZMMSU)	80x85	50x52	80	45
A. m. mimicus:				
Lake Akgel, Azerbaijan (VVL)	80	40x50	75	53
Lake Akgel, Azerbaijan (VVL)	80x100	50	70	40
Lake Akgel, Azerbaijan (VVL)	85	50	70	45
Lake Akgel, Azerbaijan (VVL)	75	49	75	52
Lake Akgel, Azerbaijan (VVL)	80	50	65	53
Lake Akgel, Azerbaijan (VVL)	80	50	85	55
Own data (both subspecies):	75-90 [81.8]	45-51 [49.3]	65-85 [74.3]	40-55 [49.0]
Literature data (*A.m.melanopogon* only):				
Balearic Islands (KOENIG 1929) (N=2)	85	40, 47	64	40, 60
Southern Europe (MAKATSCH 1976) (N=1?)	75	40	115	60
Camargue (LEISLER 1970) (N=9)	75-85 [78.2]	45-54 [49.2]	65-120 [96.1]	45-54 [49.1]
Lake Neusiedler (LEISLER 1970) (N=64)	65-95 [79.2]	40-60 [50.9]	45-145 [89.3]	35-60 [47.7]

Essential nest materials cited in the literature (MUNN 1948, PTUSHENKO 1954, MAKATSCH 1976, GLUTZ 1991, CRAMP 1992) are similar to those used for building the nests now described. GLUTZ (1991) additionally listed roots of reed and reed-mace, long filiform algae, insect pupae skins, follicles, and cocoons, and in the lining from time to time water bird feathers, fragments of tamarisk and willow leaves. Two nests described in Kazakhstan (KOVSHAR 1972) were built of stems mixed with reed-mace wool. The descriptions of nest construction are controversial: according to MUNN (1948), CRAMP (1992), and URBAN et al. (1997) it is a rather untidy, loosely-built structure, whereas according to GLUTZ (1991 after LEISLER 1970) it is a strong compact structure made of thick materials and therefore similar to the nests described by the present authors. Also only GLUTZ (1991) writes about wet materials (taken from the water surface), which strain when drying and cause an untidy appearance. IVANOV (1969) mentioned a nest observed in Pamiro-Altay which was built of reed-mace wool washed by female building in water.

The range of the cited nest measurements (Table I: literature data), which concern the nominative form only, are larger than those of the specimens described here. This is particularly well seen in the case of the maximum height, which in Camargue can reach 120 mm, and on Lake Neusiedler – 145 mm (GLUTZ 1991 after LEISLER 1970); arithmetic means indicate that high and very high nests are not exceptional there. According to GLUTZ (1991 after LEISLER 1970), the development of nestlings increases the inner diameter and diminishes the depth of nests.

IV. AQUATIC WARBLER *Acrocephalus paludicola* (VIEILLOT, 1817)

Of the 8 nests of the Aquatic Warbler 5 were described from the Biebrza Marshes (NE Poland), two were collected near Konin (W Poland) (MOR) while the last one was collected in Holland

(RMNH). Collection places are shown on the map on the background of the breeding range, which does not reach Holland recently (Fig. 5).

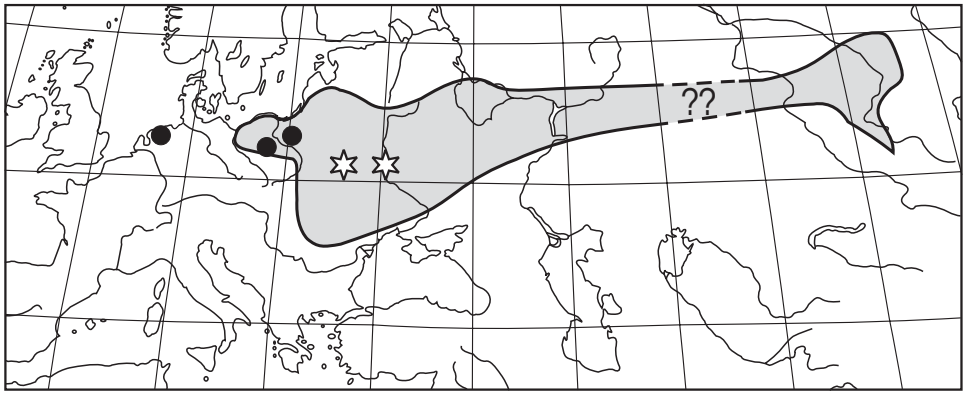


Fig. 5. Recent breeding distribution of the Aquatic Warbler *Acrocephalus paludicol*a, compiled from CRAMP (1992), FLINT et al. (1968), DYRCZ & SCHULZE-HAGEN (1997), Aquatic Warbler Conservation Team (1999) and finding places of the mentioned nests. (Dutch population does not exist now). Explanations as in Fig. 3.

Nest site

Nest sites were described only for those from the Biebrza marshes. One nest was situated among three vertical sticks of a young birch tree about 1 m high and from one side leaning against sedge tussock. The remaining four nests were built inside sedge tussocks amidst their stems (Fig. 6). In one of these tussocks a few horsetails were admixed. In two cases the nest bottom nearly touched the

A B

Fig. 6. The nests of the Aquatic Warbler *Acrocephalus paludi-cola* from the Biebrza National Park (east Poland): A – nest with nestlings seen from above, at Mocarze, 13 June 1968; B – nest inside a sedge tussock, collected at Budy in 1971 (ISEA collection).

ground, whereas in the other cases it was situated up to 22 cm above the ground. The nests situated inside sedge tussocks were well hidden by dry sedge leaves overhanging them. All nests represent the type "B" of the nest site (Fig. 2).

Nest material and construction

Long, narrow and soft sedge leaves circuitously and often loosely arranged constituted the main bulk of all 8 nests described. In the outer layer and the rim they were in most cases mixed with stems and, rarely, with thin herb stalks. Longer pieces of stalks and stems are often bent at an obtuse angle and their endings can slightly protrude. Usually there is no compact ring at the rim of a nest. If the ring is constructed, it may narrow the nest cup slightly. Soft nest material is not woven round sedge stems or sticks – only in one case was it found that one sedge was surrounded by nest material. Nothing indicated that the birds used wet material gathered from the water surface to firmly attach a nest to the stems. Some bits of moss were found in the basis (lower part of the bottom) in two nests. The nests are lined with very delicate plant material, consisting mainly of very thin stems, but also grass (sedge) leaves, fragments of grass inflorescences, and in one case of moss sporophite petioles. All these materials are circuitously and crosswise arranged and are bent only rarely.

Shape and size of the nest

In one nest only was its height nearly as large as the outer diameter; all other nests were more or less hemispheric in shape. Similarly, the depth of a nest cup is usually no larger than the inner diameter of the nest. Thus, the nests of the Aquatic Warbler should be placed in the category of high and deep nests. The measurements are shown in Table II. The most stable is the inner diameter of the nest, whereas its height is the most diversified variable.

Additional literature data and comments

Descriptions of the nest site given by particular authors are differentiated. PTUSHENKO (1954) writes that the Aquatic Warbler builds its nest not above water but on the ground, most frequently near the foot of dense willow shrub. Similarly, FERIANC (1979) mentions generally dense perennial plants near water or shrubs which, according to HEISE (1970 after HARTERT 1910) are mixed with grasses. In contrast, CRAMP (1992) writes that nests are "in dense vegetation (usually old sedge *Carex* clump) over swampy ground or water", which seems to be repeated after NIETHAMMER (1937). The sites described by DYRCZ and ZDUNEK (1993) "differed from their surroundings in having deeper water between tussocks and having a higher abundance of dry sedges forming a roof above the nest". Hence, the above mentioned controversy may be caused by the descriptions based on local populations studied in different habitats. This is confirmed by the description of a single nest from Holland which was "12 inches above the ground and not over water" (ANONYMUS 1951). Similarly to our own material, many authors above of all mention sedges as plants supporting the nest. GLUTZ (1991) listed *Carex elata*, *gracilis* and *paradoxa*, and besides them grasses of the kinds *Agrostis* and *Agropyron*, NAUMANN (1905), and PTUSHENKO (1954) – willow shrubs (probably of various species). On the contrary, according to BANNERMAN (1953), in Holland the nests were never placed in reeds or low bushes. The heights of a nest site above the surface of the ground, or water, mud, or hard head of the sedge tussock (which is usually dry, protruding from water surrounding it) are unanimously given by above cited authors as very low: between just above the surface and about 30 cm, and only NAUMANN (1905) givess the upper limit as 40 cm.

The full, compiled list of materials used for building of nests distinctly exceeds this when based on our own analyses. Besides stems and leaves of sedges or grasses, herb stalks, various parts of moss and grass inflorescences, NAUMANN (1905) mentions among others fragments of the rush, *Galium*, rootlets (sometimes with mud), cocoons of insects, plant (willow) down, single feathers and in lining horse hair. WITHERBY et al. (1938) write about feathers in the lining, whereas according to BANNERMAN (1953) the nests in Holland contained no hair or feathers. CRAMP (1992) adds the spider's web, and GLUTZ (1991) cotton-grass wool. NIETHAMMER (1937) suggests that the nests are built of wet material collected from the water surface; according to GLUTZ (1991), it deals with a

Table II

The measurements (in mm) of 8 nests of the Aquatic Warbler *Acrocephalus paludicola*. Literature data cited below own materials. [Arithmetic means are given in square brackets]

Measurement	N	Min.	Max.	Mean	SD	CV
Outer diameter	8	75	110	87.3	11.29	12.93
Opening (inner) diameter	8	50	65	55.5	4.64	8.36
Height	7	45	85	61.7	16.90	27.38
Depth	7	20	55	39.2	10.92	27.90
General:	Outer diameter		Opening diameter		Height	Depth
Own data:	75-110		50-65		45-85	20-55
Literature data:						
Poland (GOTZMAN & JABŁOŃSKI 1972)	75-110		45-65		75-90	40-45
Germany (WAWRZYNIAK & SOHNS 1977)	65-90x70-100 N=22 [77x87]		40-60x45-65 N=2 1[50x56]		55-65 N=5 [60]	35-65 N=32[44]
(HEISE 1970)	82-106 N=10 [86]		52-50x65 N=11 [54]		–	36-46 N=12 [42]
East Galizia (W Ukraine) (NAUMANN 1905)	70-85		50-60		55-70	45-50
Kiev Province (NAUMANN 1905)	100-120		60-62		41	31
Orenburg Prov. (NAUMANN 1905):						
cup-shaped nests	100-120		50-80		65	40-50
cylindrical nest	150		50		120	55

part of the nests. SCHULZE-HAGEN (1995) observed female tearing off soft, macerated, often wet, sedge leaves, whereas others were collected from ground not more than 5 m from the nest; he never saw a bird using fresh plant material. The nest is generally a loose structure (NAUMANN 1905, HEISE 1970, GLUTZ 1991, CRAMP 1992) and vertical plant elements (most often stems) supporting it are not surrounded by nest material (PTUSHENKO 1954, HEISE 1970) as in the case of nests described by us.

Some authors write that the nest of the Aquatic Warbler is similar to that of the Sedge Warbler but smaller (NIETHAMMER 1937, WITHERBY et al. 1938, MAKATSCH 1976, ANONYMUS 1951). According to NAUMANN (1905), it may be similar to that of the Blyth's Reed Warbler, the Sedge Warbler, but there are also quite different ones. HEISE (1970) and GLUTZ (1991) after him write that the nest is more similar to that of the Reed Bunting than to the representatives of the genus *Acrocephalus*; it is also repeated by CRAMP (1992). This last statement does not agree with the present authors' data from the Biebrza Marshes: the bunting's nests observed there were always more solid and hard structures. As to the sizes and proportions, NAUMANN (1905) writes that the nests are high and very deep; this is surprising, because the measurements taken by PLESKE and PRAZAK and cited by him do not confirm this fact (with the exception of one cylindrical nest). On the contrary, ANONYMUS (1951), BANNERMAN (1953), and PTUSHENKO (1954), write about the hemispheric shape of nests. The depth larger than in the Sedge Warbler is emphasized by NIETHAMMER (1937), and in spite of the fact, that according to HEISE (1970), and according to measurements cited by GOTZMAN and JABŁOŃSKI (1972), it is not true, COURTNEY-HAINES (1991) repeats this version.

V. SEDGE WARBLER *Acrocephalus schoenobaenus* (LINNAEUS, 1758)

Altogether 44 nests are described: 23 from Poland (4 own nest record cards and 19 from MOR collection), 11 nest record cards from former Czechoslovakia (Istitute of Vertebrate Biology in Brno), 5 from Belgium (MRHN), 5 from the European part of the former USSR (ZMMSU, VVL). The finding places of the nests are plotted on the map against the background of the species range (Fig. 7).

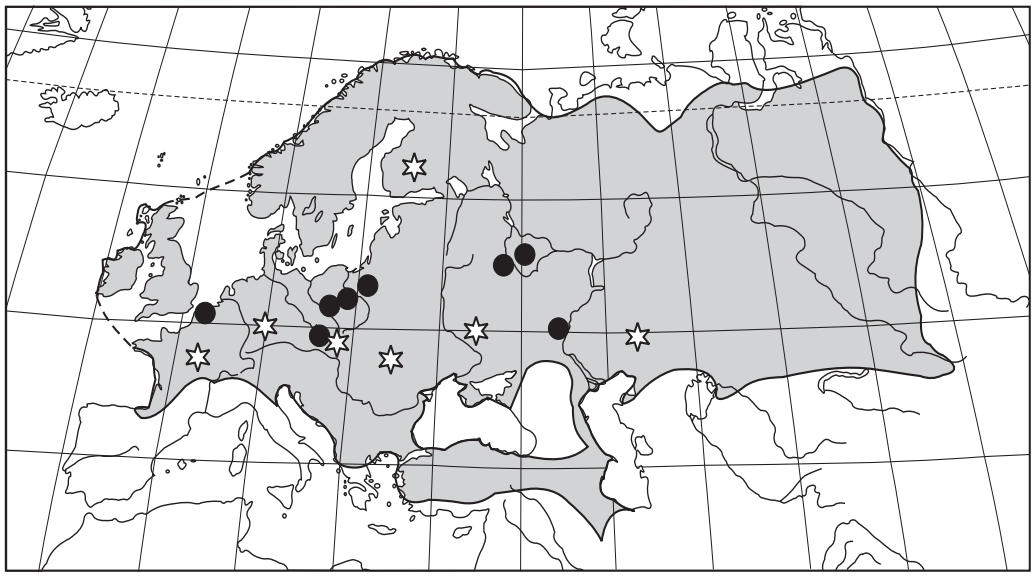


Fig. 7. Breeding distribution of the Sedge Warbler *Acrocephalus shoenobaenus*, compiled from CRAMP (1992), FLINT et al. (1968), and HARRISON (1982) and finding places of the mentioned nests. Explanations as in Fig. 3.

Nest site

All nests were found in various types of water-and-marsh habitats such as wet meadows, sedgy grounds and peatbogs overgrown to various degree by small shrubs or young trees, but also wet coasts of water bodies or rivers. It is a great pity that only in a few cards was it noted that the nest were situated above ground; of course, this does not mean that the remaining nests were built above water. Exact data concerning the nest height above water/ground and plants supporting the nest were noted in 18 and 19 cases respectively. The majority of nests were situated at a height not exceeding 50 cm (Table III: arithm. Mean = 28.4 cm, median = 24.5 cm). Even in the case of those situated inside the sedge tussocks their bottoms usually do not touch the ground – such a case being noted only once. The highest nest was built at 120 cm among the reedmace stems. The greater part represents type "B" of the nest site, but some may be encountered also to the type "A".

Table IV presents plant genera supporting the nests of the Sedge Warbler. There is no distinct dominant plant, though *Typha* and *Phragmites* slightly prevail.

Nest material and construction

The nests of the Sedge Warblers under study were rather firmly woven structures, with a more or less distinct ring at the rim. Various materials found in them are listed in Table V. The most characteristic for the base and outer layer are stems and leaves of sedges and/or grasses and green moss.

Table III

Nesting heights (in m) above ground or water of 17 nests of the Sedge Warbler *Acrocephalus schoenobaenus* in Poland

Nesting height	Number of nests	%
0 (just on a ground)	1	5.5
0.01-0.25	9	50.0
0.26-0.50	7	38.9
0.51-0.75	–	
0.76-1.00	–	
1.01-1.25	1	5.5

Table IV

Genera of plants supporting 17 nests of the Sedge Warbler *Acrocephalus schoenobaenus* in Poland

Plant genus	Number on nests	%
Typha	4	21.0
Phragmites	4	21.0
Carex	3	15.8
Calamagrostis	2	10.5
Urtica	2	10.5
Phragmites / *Carex*	1	5.3
Phragmites / *Urtica*	1	5.3
Typha / *Carex*	1	5.3
Graminaceae indet.	1	5.3

The latter is most frequently encountered in the base – in some nests it may constitute the main material. Stems in the outer layer of walls are usually circuitously arranged, long, reaching even more than 30 cm; they may be several times bent (broken) in various intervals, more often at obtuse angles than at acute ones. Examples of the intervals (in mm) are: 45-85-25-47, 40-64-50-14-46. Stem endings may protrude outside the nest up to several centimetres. Some herb stalks may be branched out. In the majority of nests the ring is compactly woven of material similar to the outer layer. Usually it narrows the opening of the nest cup in relation to the greatest width of the cup 1-2 cm below the rim up to ca 1 cm. Delicate materials of the lining (inner layer) are arranged circuitously and crosswise. In a very few cases the nest walls were in one side open-work (transparent) – but it is not clear if this is done by building birds or by mouse predators (such cases were observed in other passerines).

Shape and size of the nest

The Sedge Warbler's nests belong to categories of hemispheric (cup-shape), high and very high nests; in some cases the height may be nearly twice as great as the outer diameter (see Fig. 8). The measurements of 43 nests are given in Table VI. Their outer outlines as well as those of the nest cup openings are in most cases more or less elliptic. Differences between two crosswise measured outer diameters are usually higher than those of the inner ones. Some drastic examples are as follows: the nest containing 6 fresh eggs – outer d. 100x170 mm and opening d. of the same nest 50x55 mm, but

Table V

Materials used to build 39 nests by the Sedge Warbler *Acrocephalus schoenobaenus* (in descending order)

Kind of material	Number of nests	%
A. Bottom and outer layer (N=39)		
grass/sedge stems	29	74.3
grass/sedge leaves	24	61.5
moss	23	59.0
stalks of herbs	17	43.6
various bent stalks	15	38.5
rootlets	14	35.9
grass inflorescences	10	28.2
fibres of macerated leaves	8	20.5
reedmace leaves	2	5.1
plant wool (down)	2	5.1
feathers	2	5.1
reed leaves	1	2.6
spider's web	1	2.6
sweet grass (a piece)	1	2.6
B. Inner lining (N=36)		
inflorescence stalks	20	55.5
very delicate stems	13	38.1
very delicate herb stalks	6	16.6
feathers	3	8.3
rootlets	1	2.8
long hairs	1	2.8
"fibres"	1	2.8

other, empty nest – outer d. 100x120 mm and opening d. 65x80 mm. The opening diameter and depth may in some nests depend on the brood stage, as in one nest on 4 June (containing the first egg) they were 51x61 mm and 56 mm, whereas on 19 June (3 eggs just before hatching) – 52x65 mm and 49 mm respectively. The most stable is the opening diameter, whereas the height of the nest mostly varies (Table VI). Very high nests have a bottom and base much thicker than the others, so their depth does not vary more than in cup-shaped ones.

Additional literature data and comments

Nesting habits of the Sedge Warbler are diversified, so their descriptions differ from one another. It begins with the character of the surroundings of the nest site. According to CRAMP (1992), the nests are built above ground or water, NAUMANN (1905) writes that it is never above water but always above marsh or mud, GLUTZ (1991 after others) – 70% of nests are situated above water, 21% above wet ground and 9% above dry ground. Nests can also be built further away from water (WITHERBY et al. 1938). According to HAŁUPKA (1996) in Western Europe nests are generally built in drier places, whereas in Central and Northern Europe more often over water or wet ground. It is interesting that the nests studied by KOVSHAR (1972) in Kazakhstan were again built above ground. According to NIETHAMMER (1937), the nest is usually situated close to water, but there are exceptions: even 1 km apart.

Table VI

Measurements (in mm) of 43 nests of the Sedge Warbler *Acrocephalus schoenobaenus*. Literature data are cited below own materials. [Arithmetic means are given in square brackets]

Measurement	N	Min.	Max.	Mean	SD	CV
Outer diameter	43	70	135	101.5	12.96	12.77
Opening diameter	43	47	72	58.0	5.30	9.14
Height	39	60	180	84.8	21.46	25.30
Depth	42	20	62	44.6	8.31	18.62

General:	Outer diameter	Opening diameter	Height	Depth
Own data:	70-135	47-72	60-180	20-62
Literature data:				
Poland (GOTZMAN, JABŁOŃSKI 1972)	80-120	50-60	75-90	45-50
France (GLUTZ 1991)	–	49-52	70-110	–
Germany (SCHIERMANN 1927, cited by NIETHAMMER 1937 and CRAMP 1992)	95-120	50	70-95	45
Germany (GLUTZ 1991)	83-96	49-60	104	45
Former Czechoslovakia (HUDEC 1983)	60-130 [92]	40-66 [55]	60-120 [89]	35-60 [48]
Finland (GLUTZ 1991)	86-104	50-66	150-300	47-52
Eastern Galicia (W Ukraine) (NAUMANN 1905)	85-92	55-60	55-75	50-55
Ukraine, Kharkov Province (NABTOCHIY 1991)	82-109	44-67	60-116	38-63
Former USSR (PTUSHENKO 1954 after ZARUDNY 1888):				
cup-shaped nests	85-120	47-80	41-80	31-50
cylindrical nests	100-155	50	120	55
Kazakhstan (KOVSHAR 1972)*				
cup-shaped nests	100-120	50-80	65-80	40-50

*) KOVSHAR (1972) cites the same sizes of cylindrical nests after ZARUDNY (1888)

CRAMP (1992) writes that nests are generally situated in a variety of tall vegetation or low bushes. FERIANC (1979) similarly describes the bird's requirements. Besides various grasses (and reeds among them) noted by the present authors, sedges, reedmace, and nettles, are mentioned as more rarely noted rushes (KOVSHAR 1972, NABTOCHIY 1991) and *Claudium* (NIETHAMMER 1937, GLUTZ 1991), *Epilobium* (GLUTZ 1991) and *Filipendula* (NABTOCHIY 1991), *Tanacetum* (BOROWIEC 1999), willows (NAUMANN 1905: among fresh shoots but never in the bush itself, PTUSHENKO 1954, KOVSHAR 1972) and among them sallow (NABTOCHIY 1991), thorn bushes mixed with other plants (GLUTZ 1991), *Crategus* bushes (BOROWIEC 1999), young birches (CRAMP 1992, GLUTZ 1991), small spruce in herb stratum and junipers (GLUTZ 1991). Thus the nests represent also types "A", "C", and rarely even type "D" of the nest site. Besides, GLUTZ (1991) writes that the nest is often situated on broken stems and, in one case, on an old nest of the Song Thrush.

The reports of various authors indicate that, similarly to the present authors' materials, the majority of nests are built up to 50 cm above ground or water. Nevertheless, nests built directly on the ground are rare. They are mentioned generally by CRAMP (1992) and NAUMANN (1905 after PRAZAK). According to the latter, it seems that sometimes nests only touch the ground, this also be-

Fig. 8. Two nests of the Sedge Warbler *Acrocephalus shoenobaenus* collected in the Kampinos National Park (central Poland), stored at ROM collection. Picture shows the character of nest material and various proportions: height of left nest is ca 60 mm, whereas that of the right one – 180 mm.

ing noted by PTUSHENKO (1954). The only nest touching the water surface is mentioned by KOVSHAR (1972). Nests situated more than one meter high are also rare. CRAMP (1992 after HAARTMAN 1969) reports the highest nest built at 1.95 m on a birch, whereas WITHERBY et al. (1938) mention a nest built at 12 ft. (= 3.7 m!). NIETHAMMER (1937) states generally that nests in bushes and trees up to two meters are rare, whereas according to GLUTZ (1991) the nests are situated between 5 and 95 cm and those built later in the breeding season are sited higher.

Various authors report much the same building materials as the present authors in Table V. BANNERMAN (1953) writes that nest foundation contains dead grass mixed with small pieces of dead thistle. GOTZMAN and JABŁOŃSKI (1972) write that grass or sedge leaves used for building of external layer are up to 4 mm wide. NABTOCHIY (1991) mentiones a duckweed and green algae. PTUSHENKO (1954) and KOVSHAR (1972) found in outer layer also spiders' cocoons and wings of butterflies, playing, according to the latter author, a decorative role only. In the lining of nest cup, CRAMP (1992) mentiones also plant down, NAUMANN (1905) – horse-hair and animal wool (among others sheep) and KOVSHAR (1972) – pinnated tops of grass. On the other hand, larger differences occur in the frequencies of using particular materials, which seems to be due to the kind of habitat, the place within the breeding range of the species, and the period of the breeding season. Thus, reed leaves noted only in one nest under study (Table V) are considered by GLUTZ (1991) as characteristic of the outer layer. Feathers were found only in five nests under study (Table V), whereas NAUMANN (1905) writes that they never lack, even if not numerous (he mentions feathers of ducks, Lapwing, Ruff, and others); according to HUDEC (1983), the nests are very often lined with feathers (of ducks, coots, pheasants, gulls, and others); NIETHAMMER (1937) and GLUTZ (1991) encounted feathers among frequent materials and, to the contrary, PTUSHENKO (1954) and KOVSHAR (1972) do not list them at all. NABTOCHIY (1991) found in the nests built in May a large amount of reedmace down (up to 50% of substance) while in June and July it was replaced by duckweed and green algae. None of the authors writes about the usage of wet material. Only PTUSHENKO (1954) mentions the soaked leaves in the inner layer of cylindrical nests (not stating whether they are wet or macerated

only). The above mentioned duckweed and algae were most probably gathered from the water surface and so were therefore used wet, but not for attaching the nest to the supporting plant stems.

KOVSHAR (1972) distinguished two layers in the nest structure, but PTUSHENKO (1954) and GLUTZ (1991) – three layers. According to CRAMP (1992), outer nest structure is loosely woven, a similar remark being made by NAUMANN (1905 after PRAZAK). It does not agree with the generally firmly woven nests under study, unless one takes into account a few most external pieces of material or stem endings protruding outside. CRAMP (1992) writes that the outer parts of nest are woven round vertical, supporting stems of plants. NAUMANN (1905) describes it more precisely – that nest sides are relatively loosely attached to vertical plants, but its lower part is always hanging loose; however PRAZAK (cited by NAUMANN 1905) emphasized that the nest is never suspended among reed stems. Similarly it is described by FERIANC (1979). According to PTUSHENKO (1954), stalks or branches among which the nest is situated are either surrounded by the wall material or only adhere to it – but even in that case they are tied with the material of the nest rim, i.e., according to GLUTZ (1991), with long fibres of reed or reedmace. KOVSHAR (1972) mentions only about firm adhering of the nest to stalks supporting it. It deals also with a part of the nests under study. The statement by NIETHAMMER (1937) that the nests situated high in bushes and trees are hanging, perhaps explains the diversity of descriptions presented above. In the nests under study there were more or less firmly woven rings at the rim, slightly narrowing the nest cup. Only NAUMANN (1905 after PRAZAK) reports such narrowing, which is, however, smaller than in the Reed Warbler's nest. KOVSHAR (1972) also describes a nest resembling a scroll of dry grasses, probably built by young birds.

CRAMP (1992) describes the Sedge Warbler's nest as a deep cup, rounded, to cylindrical. According to PTUSHENKO (1954) and KOVSHAR (1972), nest shape depends on its site, hence cup-shaped nests are most often situated above ground, whereas rarer, cylindrical, ones nearly always above water. According to NABTOCHIY (1991) and GLUTZ (1991 after KOSKIMIES), nest sites also affect their measurements (outer ones). Literature data cited in Table VI indicate that the differentiation of measurements is larger than in the case of the nests under study. Above all it deals with the nest height and then with the outer diameter. It seems to be connected with the number of cylindrical nests encountered.

GLUTZ (1991) considers that the diversity of nest sites chosen by the Sedge Warblers causes their breeding dominance in reedbeds. It seems that possibilities of adaptation in nest construction and material are also very important.

VI. BLACK-BROWED REED WARBLER *Acrocephalus bistrigiceps* SWINHOE, 1860

Description is based on five nests from the Far East: one from the Sakhalin I. (ZMMSU), three from Primorski Kray (ZMMSU, VVL, ISEA), and one from NE China (Manchuria) (ZMMSU). The places where these nests were collected are plotted against a background of the breeding range of the species in Fig. 9.

Nest site

Nesting heights were noted on three labels. They are: 40, 45 and 50 cm above the ground, in various types of vegetation close to the water; all those nests were situated not above the water level but above the ground. Three nests were attached to a few (3-4) vertical grass stems (in one case a thin branch of a willow was also used); one nest was supported by a few vertical stems of wormwood, and another one on 3 stems of unidentified herb, so they represent types "B" and "C" of the nest site.

Nest material and construction

Grass stems constitute the main nest material (observed in all nests under study); in outer layer grass leaves are also abundant. Vertical plant elements supporting the nest were surrounded by the

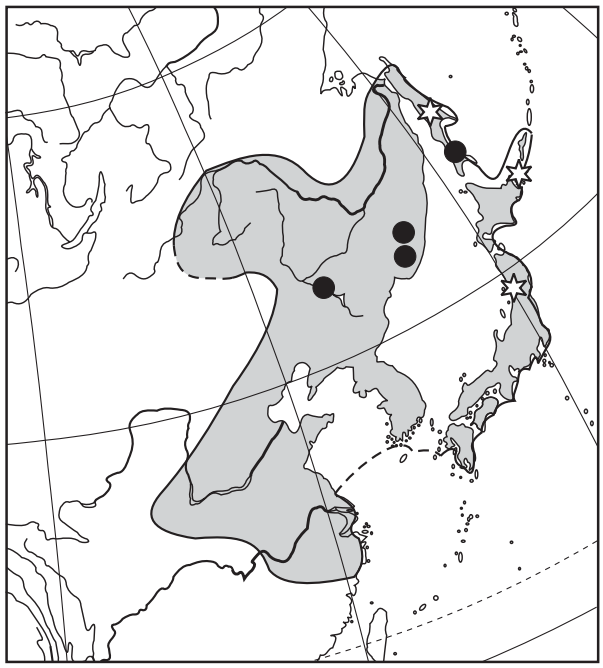
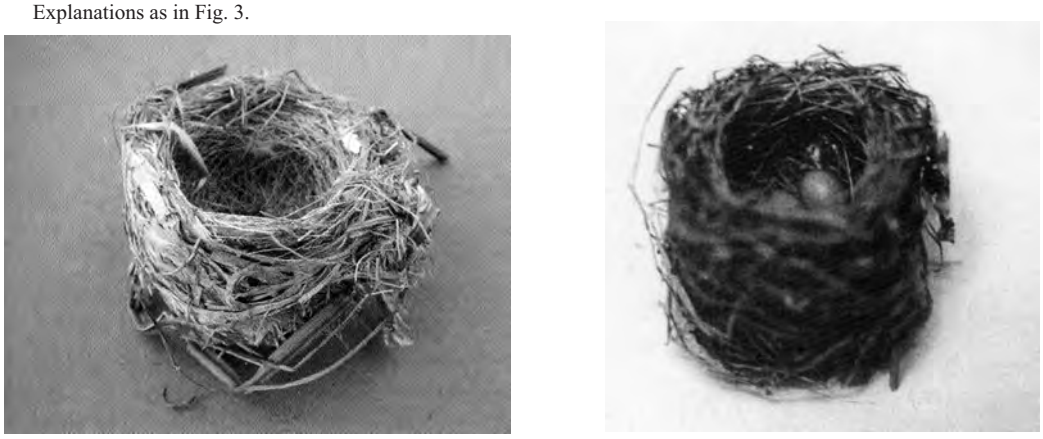


Fig. 9. Breeding distribution of the Black-browed Reed Warbler *Acrocephalus bistrigiceps* compiled from FLINT et al. (1968), CHENG (1976), SONOBE (1982), and NECHAEV & FUJIMAKI (1994), and finding places of the mentioned nests. Explanations as in Fig. 3.



A B

Fig. 10. Two nests of the Black-browed Reed Warbler *Acrocephalus bistrigiceps* from Primorye, Russian Far East: A – collected by Dr E. N. KUROCHKIN (and presented to ISEA collection), B – from River Iman (APK collection).

material to various degree, but weaving material round particular elements was not seen. At the rim of four nests there were conspicuous rings woven of plant fibres or grass stems (Fig. 10), in one case ending with small "ears". The ring slightly narrows the nest opening in relation to the diameter below it. Nest cups were lined with delicate, elastic, material (rootlets? inflorescence stalks?). The distinct ring was absent in the nest from Manchuria. Some of the stiff stems of the outer layer and the ring were bent into wide angles and some of their endings protruded from the nest. Four nests were relatively stiff and rather compact; two nests (from the Sakhalin I and from Manchuria) were slightly transparent (open-worked).

Shape and size of the nests

The nests of the Black-browed Reed Warbler belong to the category of deep or even very deep. Their outer contour is somewhat elliptic, whereas openings of the nest cup were circular in three cases and slightly elliptic in the other two nests (all of them were collected with full clutches in the first stage of incubation). The measurements of 5 nests under study compared with those cited by several authors are given in Table VII.

Additional literature data and comments

V. V. LEONOVICH (oral comm.) saw one nest built directly on the ground among grass stems which were not surrounded by nest material. Similarly KOBAYASHI (1932-1940) writes about nests that "seldom are found built at the roots of weeds on the ground". Usually, however, the nests are situated between 30 and 100 cm above the ground, these limits being cited by KOBAYASHI (1932-1940) from Japan and NECHAEV (1991) from the Sakhalin I. GIZENKO (1955) however, in the south of the Sakhalin found nests between 15 and 60 cm, and VOROBEV (1954) in the Ussuriiski Kray between just above the ground and slightly above 25 cm. According to JAHN (1942), the Black-browed Reed Warbler never builds its nests above 1 m, but TACZANOWSKI (1891) wrote that in East Siberia it may rarely nest up to 5 feet (1.6 m). PTUSHENKO (1954) writes that the nests are built in high, dense, grass and other herbaceous plants (such as *Artemisia* and *Galium*) which agrees with the data of KOBAYASHI (1932-1940) and NECHAEV (1991); the latter also mentions one nest situated on *Filipendula* in bifurcation of the stalk and a leaf. ILYASHENKO et al. (1988) found a nest in a rose bush.

The data concerning nest material agrees in general with the present descriptions, but NECHAEV (1991) writes precisely that the outer layer consists of fragments of the leaves and stems of grass, mainly *Calamagrostis*, *Poa*, *Phragmites*, rarely of the Kurilian bamboo and of cambium (of nettle,

Table VII

The measurements (in mm) of 5 nests of the Black-browed Reed Warbler *Acrocephalus bistrigiceps*. Literature data are cited below own materials. [Arithmetic means are given in square brackets]

Specimen and collection	Outer diameter	Opening diameter	Height	Depth
Primorski Kray (ZMMSU)	65x80	40x45	90	60
Primorski Kray (VVL)	78	50	60	48
Primorski Kray (ISEA)	72x78	45x55	60	ca 40
Sakhalin (ZMMSU)	90x100	50x50	80	50
Manchuria (ZMMSU)	90x95	47x47	80	42
Own data:	72.5-95 [82.6]	42.5-50 [47.9]	60-90 [74]	40-60 [48]
Literature data:				
Sakhalin (NECHAEV 1991) (N=12)	[79x83]	[50]	[80]	[48]
Sakhalin (GIZENKO (1955)	70	–	60	50
Former USSR – no locality (PTUSHENKO 1954)	70-85	42-53	54-60	34-46
Kunashir Island, Kuril Is (ILYASHENKO et al.1988) (N=4)	79-95 [85]	46-74 [56]	75-105 [86]	40-60 [50]
Japan (KOBAYASHI 1932-1940)	70-110	50-60	60-70	40-50

Filipendula and others), whereas inside there are thin strips of grass, horse-hair and, rarely, small feathers. GIZENKO (1955) mentions from the Sakhalin I nests built of thin tree bark.

According to PTUSHENKO (1954) and VOROBEV (1954) the nests are compact and spherical with deep nest cup, which corresponds in general to the present data. The sizes of nests described from the Sakhalin (GIZENKO 1955, NECHAEV 1991) correspond to those under study, whereas four nests described by ILYASHENKO et al. (1988) from Kunashir I (S Kuril Is) and to some degree those from Japan (KOBAYASHI 1932-1940) are slightly larger (see Table VII).

VII. PADDYFIELD WARBLER *Acrocephalus agricola* (JERDON, 1845)

Two nests of the Paddyfield Warbler were collected in southern Ural (VVL) and on the Aral Sea (APK) hence they belong to the subspecies *A. a. agricola* (JERDON, 1845) (the nest collected by prof. KUZYAKIN is the same as that described by him – KUZYAKIN 1959). The places of their collection are plotted against the breeding range of the species in Fig. 11.

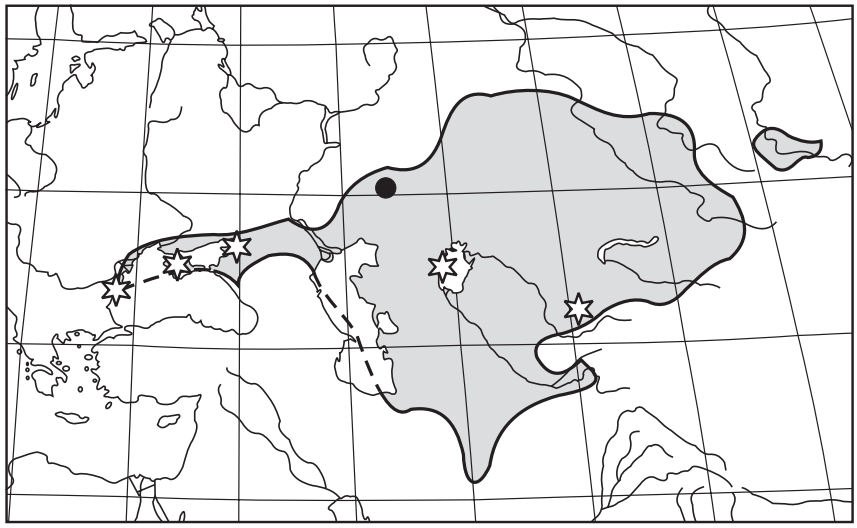


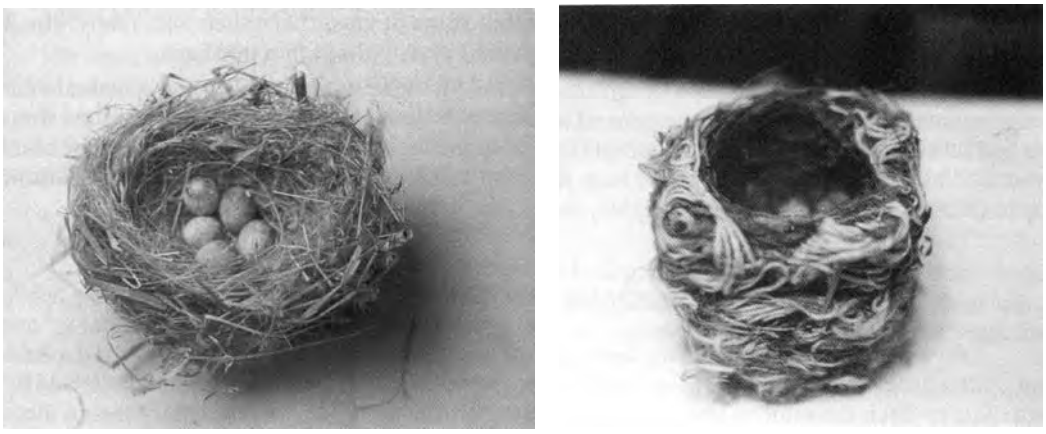
Fig. 11. Breeding distribution of the Paddyfield Reed Warbler *Acrocephalus agricola* compiled from FLINT et al. (1968), HARRISON (1982), GLUTZ (1991), and CRAMP (1992), and simplified. Finding places of the mentioned nests are plotted on the map. Explanations as in Fig. 3.

Nest site

Both nests were found in reedbeds and attached to thin reed stems (4 and 8). They represent the type "A" of the nest site. According to the label, the nest collected on the Aral Sea was situated ca 40 cm above the water level and 70 cm below the reed tops, this meaning that the reeds were not fully grown.

Nest material and construction

The nest collected in southern Ural was loosely built of stems, grasses and reed inflorescences. Reed stems supporting it were surrounded by nest material but pieces of material woven round particular stems were not visible, nor was there any compact ring of the material at the rim (Fig. 12). On the contrary, in the nest collected on the Aral Sea nest material was woven around the reed stems and, besides plant material, the birds also used white thread (Fig. 12).



A B

Fig. 12. The nests of the Paddyfield Reed Warbler *Acrocephalus agricola*: A – from the River Ilek, Ak-Bulak district (VVL collection), B – from Uzum-Kair Island, the Aral Sea (APK collection).

Shape and size of the nest

Both described nests of the Paddyfield Warbler belonged to the categories of high and deep nests. The outer contour of one of them and the opening of the nest cup were elliptic. The measurements of the nests under study and literature data are given in Table VIII.

Table VIII

Measurements (in mm) of two nests of the Paddyfield Warbler *Acrocephalus agricola* from Central Asia. Literature data are cited below own materials. [Arithmetic means are given in square brackets]

	Outer diameter	Opening diameter	Height	Depth
A.a.agricola:				
Ilek river, left tributary of the Ural r. (VVL)	95x80	65x50	75	ca 40
Uzun-Kair I. on the Aral Sea (APK)	95	50	80	45*
Literature data:				
A.agricola septimus **				
Bulgaria (NADLER & IHLE 1988)	–	50	–	45
	–	55	–	45
nest not fully completed	–	45	–	40
Black Sea Islands (KOSTIN 1983)	43-86	41-66	46-86	30-60
(N=28)	[72]	[47]	[72]	[50]
Black Sea Reserve (PIROGOV 1991)	60-95.5	40-65	35-105	30-85
(N=63)	[76.8]	[48.5]	[77.1]	[46.4]
A.agricola agricola				
Kazakhstan (KOVSHAR 1972 after ZARUDNY 1916, KUZYAKIN 1959, SHNITNIKOV 1949) (N=9)	75-95	37-55	80-130	48-55
Kirghizya ? (NAUMANN 1905)	64	42	130	64

* KUZYAKIN (1959) writes that the depth of this nest was 5.5 cm

** According to KNOX et al. (2002) the species is monotypic and *septimus* is the synonym of the nominate form.

Additional literature data and comments

Literature data concerning the Paddyfield Warbler cannot be cited credulously, because some authors (i.e. PTUSHENKO 1954 and COURTNEY-HAINES 1991) include in this taxon, as a subspecies, other Asiatic reed warblers numbered by the others in *bistrigiceps* and *concinens*, which differ in their nesting habits. It seems that some such controversies are repeated by CRAMP (1992). Thus, additional data come from the papers concerning *A. a. agricola* and *a. septimus* only (PTUSHENKO 1954: *a. agricola*; KOVSHAR 1972, NADLER & IHLE 1988, PIROGOV 1991).

The majority of the Paddyfield Warbler's nests were built in reeds above-water but also aboveground, usually near water but also as far as 30 m away (NADLER & IHLE1988); reedmace, pigweed, or small bushes seem to be used more rarely. On the other hand, there are possibly local preferences such as worm-wood in a belt where it was mixed with reeds, on the Lebyazhe Is by Krimea (KOSTIN 1983). Therefore, besides nest sites of the type "A", maybe also found those belonging to the type "C". According to PIROGOV (1991), the birds prefer dense, high, reedbeds and avoid low (up to 60 cm) and sparse ones. The height of nest site above ground or water ranges from 5 to 120 cm (extreme situations are rare) and seems to depend on plant kind: of the nests studied by PIROGOV (1991) those built in reeds were situated up to 68.5 cm, whereas those built in pigweed – up only to 11 cm above ground; the nests in worm-wood studied by KOSTIN (1983) were situated 10-40 cm above ground.

According to CRAMP (1992 after BAKER 1933), nest material is woven round 2-8 vertical stems of water plants. KOVSHAR (1972) writes that to build an outer layer the birds sometimes use wet plant strips floating on the water, which dry up the next, whereas PTUSHENKO (1954: *a. agricola*) treats it as a rule. This was not indicated by two nests under study, so perhaps KOVSHAR (1972) is right in stating that it refers to some nests only. Generally, all descriptions indicate that nests are firmly built and the endings of stems used do not protrude; KOVSHAR (1972) adds that the rim of the nest cup makes its round opening narrower than the inside. All authors agree that the commonest plant used for building nests is reed: its leaves (often wet) and inflorescences; stems and leaves of grass and plant down (poplar and other) are also commonly used, and sometimes various other water plants also. All these materials may be seen in the outer layer, though inflorescences, very delicate grasses and/or plant down are characteristic for lining of the nest cup. Additionally, PIROGOV (1991) mentions feathers and down of birds, which sometimes may be encountered both in outer and inner layers.

PTUSHENKO (1954) described nests of the Paddyfield Warbler as cylindrical or "spherical with cut upper part". The measurements listed in Table VIII (especially those based on large series of nests) indicate that sizes vary. The outer diameter of the two nests under study is close to its maximum range. The smallest differentiation is observed in opening diameter. The highest nests (13 cm) were encountered in Central Asia.

VIII. BLUNT-WINGED WARBLER *Acrocephalus concinens* SWINHOE, 1870

One badly preserved (flattened) nest (BMNH) was collected in China, therefore it belongs to the nominative form. This specimen was attached to two reed stems which were surrounded by nest material. Literature data concerning the nests of the Blunt-winged Warbler are rather general and scanty, and they deal with subspecies living in Asia but outside China. These data may be referred to as follows. The places from which the data come are shown on the background of the species breeding range (Fig. 13).

Nest site

BATES and LOWTHER (1952) write that the nests of *A. concinens haringtoni* WITHERBY, 1920, from Kashmir are usually situated near the ground but, rarely, even to 1 m high and adhered to thin reeds. According to ALI & RIPLEY (1973), the nests in northern Afghanistan are attached to or sus-

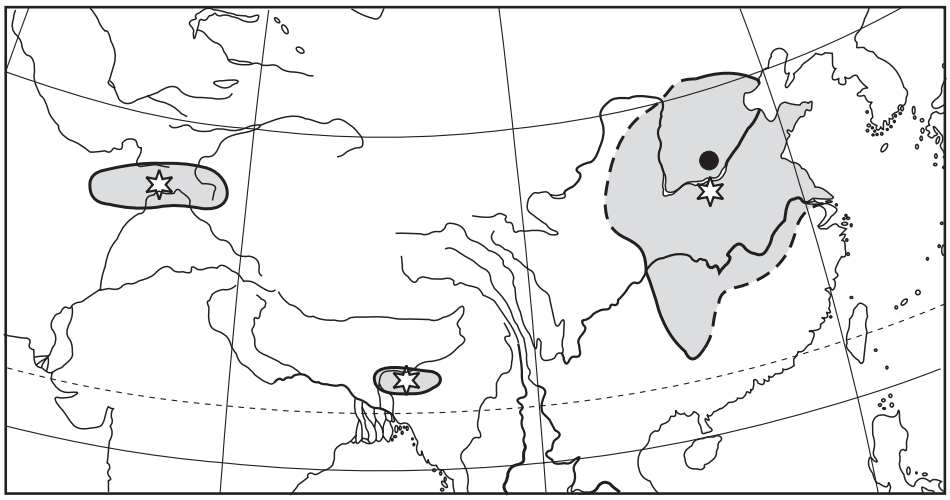


Fig. 13. Breeding distribution of the Blunt-winged Reed Warbler *Acrocephalus concinens* compiled from FLINT et al. (1968), ALI and RIPLEY (1973) and CHENG (1976), and places the nest descriptions come from. Explanations as in Fig. 3.

pended between several upright plant stems within 90 cm from the ground whereas, according to COURTNEY-HAINES (1991 after BAKER 1924), they are either attached to the stems of various weeds, such as nettles, or placed in low bushes. About the nests of *A. c. stevensi* the latter author writes that they are usually attached to several grass stems 60-90 cm (2 or 3 feet) above the ground. Thus, the nests represent the types "A" and "C" of the nest site (Fig. 2).

Nest material and construction

BATES and LOWTHER (1952) write about two different types of nests built by *A. c. haringtoni*. One of them is of coarse grass, with finer material of the same kind used inside. The other type is built, to a various degree, of moss (one of them "almost entirely of moss"), lined with grass and a few feathers. There are also nests of an intermediate type. ALI and RIPLEY (1973) describe nests from northern Afghanistan as a neat cup of grass, reed fibres, rush leaves, occasionally some moss, lined with wool, vegetable down, and sometimes feathers. In *A. c. stevensi* they are composed of grass and strips of reed-leaves, with the interior neatly lined with finer grasses (COURTNEY-HAINES 1991). No details about construction, such as the presence of rim, possible usage of wet material, or weaving of the material round vertical plant elements supporting the nest are given.

Shape of the nest

The shape is described only very generally, as "a small replica of the nest of the Great Reed Warbler" (BATES and LOWTHER 1952), or as a "smaller facsimile of that of the *A. stentoreus*" (COURTNEY-HAINES 1991 after BAKER 1924). The nests of *arundinaceus* and *stentoreus* are of the similar type, however in the photograph enclosed in the book by BATES and LOWTHER (1952) the nest resembles rather that of *A. palustris*. There are no detailed data on sizes of nests.

IX. REED WARBLER *Acrocephalus scirpaceus* (HERMANN, 1804)

The analysis of the nests of the Reed Warbler is based on 84 own nest record cards coming from a few places in Poland (mostly from the vicinity of Milicz). These data are supplemented by the nests collected in Central Poland and housed at the Radom District Museum (MOR), collected in Great Britain (BMNH), Denmark (ZMMSU), and Azerbaijan (VVL). All of them belong to the

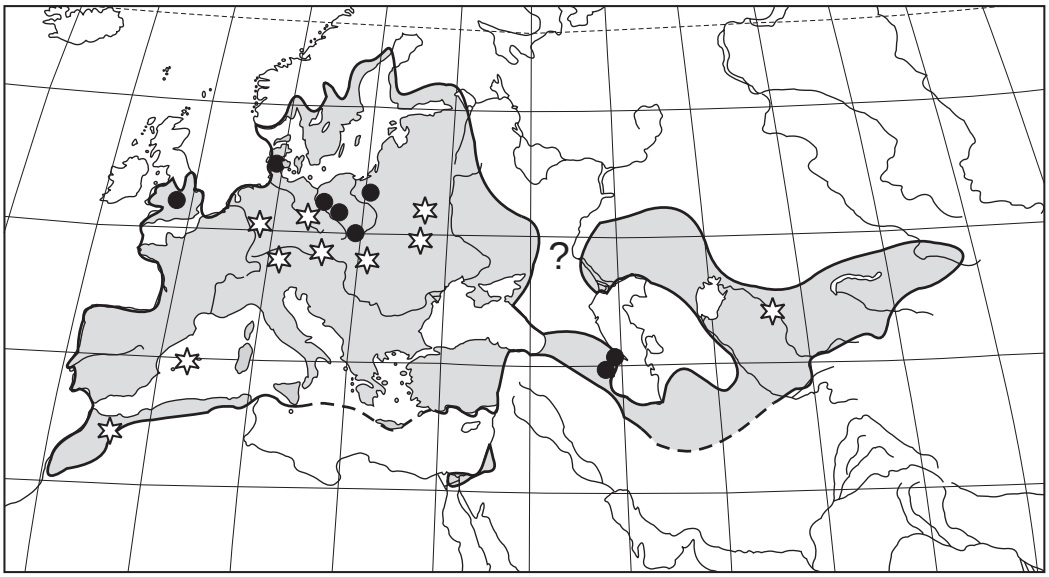


Fig. 14. Breeding distribution of the Reed Warbler *Acrocephalus scirpaceus* compiled from FLINT et al. (1968), HARRISON (1982), GLUTZ (1991), and CRAMP (1992), and simplified. Finding places of the mentioned nests are plotted on the map. Explanations as in Fig. 3.

nominative form *Acrocephalus s. scirpaceus* (HERMANN, 1804). The places of collection are plotted against the background of the breeding area in Fig. 14.

Nest site

Plant species in which nests of the Reed Warbler were built were noted in 79 cases (Table IX). More than 90 % of nests were hanging on reed stems; the age of reeds was noted in 53 cases: 27 nests were built in fresh (green) reeds, only 4 in dry (last year) reeds exclusively, and 22 in mixed, fresh, and dry reeds. The other kinds of plants in own material were scanty. Altogether, they belonged mainly to the type "A" and, rarely, the types "C" and "D" of the nest site. The majority of nests were situated above the water surface and only a few above ground, usually near water. All the

Table IX

Species of plants in which 79 nests of the Reed Warbler *Acrocephalus scirpaceus* were built

Plant species	No of nests	%
Phragmites communis	73	92.4
Phragmites / *Solanum dulcamara*	2	2.5
Salix sp.	2	2.5
Glyceria maxima	1	1.3
Undet. shrub	1	1.3
Total	79	100.0

nests were situated between 32 and 160 cm above water or ground level (arithm. mean = 66.6 cm, median = 60 cm); the highest was built in a willow bush above the ground. The heights of nests depending on their situation, are given in Table X. In spite of the fact that in both groups the majority of nests were situated between 51 and 75 cm above the surface, the nests above ground were built higher. Numbers of vertical plant elements (reed stems or other) to which 79 nests of the Reed Warbler were attached ranged from 2 to 8, arithm. mean = 3.63 (Table XI).

Table X

Nesting heights (in m) of 78 nests of the Reed Warbler *Acrocephalus scirpaceus*

Nesting height	Nests situated above water		Nests situated above ground		Total	
	No	%	No	%	No	%
0.26-0.50	23	32.4	–		23	29.5
0.51-0.75	30	42.2	4	57.1	34	43.6
0.76-1.00	11	15.5	1	14.3	12	15.4
1.01-1.25	7	9.9	1	14.3	8	10.2
1.26-1.50	–		–		–	
1.51-1.75	–		1	14.3	1	1.3
Total	71	100.0	7	100.0	78	100.0

Table XI

Number of reeds (or other vertical plant elements) to which 79 nests of *Acrocephalus scirpaceus* were attached

No of elements	No of nests	%
2	14	17.7
3	28	35.4
4	22	27.8
5	7	8.9
6	5	6.3
7	2	2.6
8	1	1.3
Total	79	100.0

Nest material and construction

The list of materials identified in 45 nests is given in Table XII. Most common are reed inflorescences and leaves or strips of them, which in some cases may be replaced by grass. Plant down (or cotton) is also very common. It may occur in various amounts, but always in the outer layer of the walls and bottom only – never in the lining. The plant down comes from reed-mace, willow, aspen, and poplar.

The nest is usually a basket-like structure, attached to several more or less vertical and parallel stems, with its bottom hanging among them (not supported from below). It concerns not only the nests built in reeds but also those built in bushes (Fig. 15C). The first stage of building is an open worked platform based on a solid circumference built of various material (grasses, strippes of reed leaves, reed inflorescences, fibres, plant down, etc.) wound round the stems, and joining stems with

Table XII

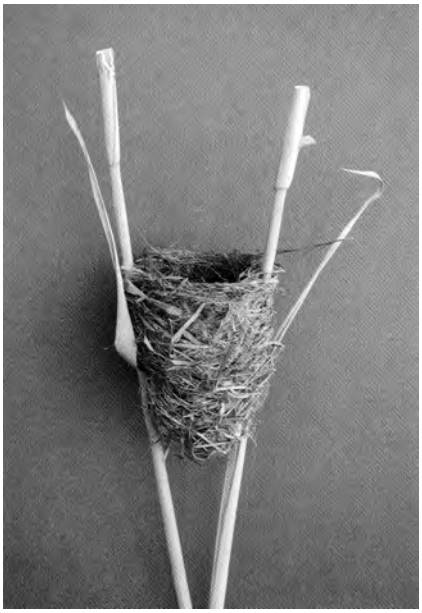
Material used for building of 45 nests of the Reed Warbler *Acrocephalus scirpaceus*

Kind of material	No of nests	%
A. outer layer of bottom and walls (N= 45)		
reed inflorescences	43	95.6
stripes of reed leaves	40	88.9
plant down	27	60.0
grass stems	18	40.0
grass inflorescences	6	13.3
spider's cocoons	4	8.9
grass leaves	3	6.7
moss	3	6.7
cobweb	3	6.7
sweet grass inflorescences	2	4.4
rootlets	2	4.4
dry algae	1	2.2
feather (duck)	1	2.2
duck down	1	2.2
green leaves of herbs	1	2.2
stalks of Compositae	1	2.2
sweet grass stalks	1	2.2
rush sporophite	1	2.2
B. Inner lining (N= 19)		
reed inflorescences	17	89.5
grass stems	3	15.8
sweet grass leaves	1	5.3
grass inflorescences	1	5.3
rootlets	1	5.3

each other. This is the base of solid, compact, and in most cases relatively thick and hard bottom. Usage of wet grasses was observed only once. However, the mixture of bottom material, its compactness and hardness, may indicate that wet material was used at least in some cases, and quickly dried. The walls are softer though they may also be thick. At the rim there is the ring, which is built mainly of reed inflorescences often mixed with cobweb, or plant down. Although the ring is soft, it narrows the opening to some degree in relation to the cup inside. Material of walls and ring surrounds and winds round the stems supporting the nest. Rarely, more distant reed stems may be tied with a kind of "ears" (or "basket handles") (Fig. 16). There is no evidence that upper parts of the nest are built of wet material. The nest cup is lined with long, very thin and elastic pinnacles of inflorescences or others. Some nests may be slightly transparent, but this was noted in a few cases only.

Shape and size of nests

Nests of the Reed Warbler under study belong to the categories of high and very high. The nest height ranges between 50 and 140 mm, but even the former measurement distinctly exceeds half of the outer diameter. The absolute majority of nests are 60-89 mm high, but the height of more than 40% of nests is between 70 and 79 mm. The nests are also deep and very deep, but usually the diameter of the nest opening does not differ greatly from the depth. In most cases the outer contour of the nest is elliptic or a little irregular. In about 30% only it is round or the difference between the



A

B

C

Fig. 15. The nests of the Reed Warbler *Acrocephalus scirpaceus*: A – attached to two reeds – nest walls are supported by reed leaves (ISEA collection), B – attached to four reed stems (ISEA collection), C – situated in a forked willow branch in south England – nest bottom hangs among twigs (BMNH collection).

largest and smallest diameters is no larger than 5 mm; in the remaining nests that difference is greater (extreme examples: 65x85 mm, 70x90 mm). The same is true to the opening – only about 17.5% were round or, if elliptic, the diameters differ up to 20 mm (extreme examples: 45x65 mm, 41x55 mm, 47x63 mm). It is interesting that the elliptic shapes of outer and opening diameters seem not to be correlated. On the other hand, they may be correlated to some degree with the number of reed stems supporting the nest (Fig. 16). The measurements of 93 nest are summarized in Table XIII.

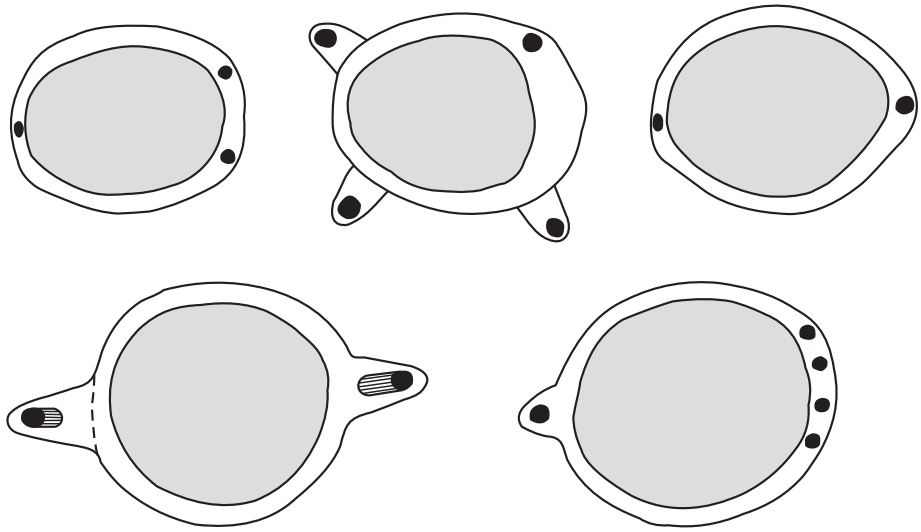


Fig. 16. A few examples of distribution of reed stems (black dots) supporting the nests of the Reed Warbler *Acrocephalus scirpaceus*. In two of them the "ears" (or "basket handles") are seen.

Table XIII

Measurements (in mm) of nn nests of *Acrocephalus scirpaceus*. Literature data are given below own material. [Arithmetic means in lower part are given in brackets]

Measurement	No	min.	max.	mean	SD	CV
Outer diameter	93	63.5	90.0	74.68	5.65	7.56
Opening diameter	93	43.0	57.5	50.73	2.99	5.89
Height	93	50.0	140.0	75.66	12.58	6.63
Depth	91	38.0	62.0	48.32	5.40	11.17
General:			Outer diameter	Opening diameter	Height	Depth
Own data:			63.5-90.0 [74.7]	43.0-57.5 [50.7]	50-140 [75.7]	38-62 [48.3]
Literature data:						
A.s.scirpaceus						
Poland (GOTZMAN, JABŁOŃSKI 1972)			60-90	45-60	50-80	40-50
Milicz ponds, Poland (BOROWIEC and DĄBROWSKA 1991) (N=201)			50-104 [72.7]	40-71 [56.0]	50-130 [74.3]	30-73 [49.7]
former Czechoslovakia (HUDEC 1983) (N=52)			60-110 [79]	35-70 [47]	50-115 [77]	25-60 [50]
East Galicia, W.Ukraine (NAUMANN 1905)			70-95	40-45	50-70	40-50
Kiev Province (NAUMANN 1905)			65-90	45-55	50-70	40-45
former USSR (PTUSHENKO 1954)			65-90	45-55	50-70	40-45
North Africa (URBAN et al.1997)			ca 80	ca 50	–	ca 55
A.s.fuscus						
Kazakhstan (KOVSHAR 1972)			65-90	45-55	50-110	40-57

Additional literature data and comments

Reeds, as the most common type of plant supporting nests of nominative subspecies of the Reed Warbler, are mentioned by all authors. GLUTZ (1991) writes that 76.1% of nests from Poland, Great Britain, and Germany were built in reeds. The list of other plants includes more than 20 kinds (GLUTZ 1991; MOLL 1958; NIETHAMMER 1937; ÖLSCHLEGEL 1981) and it seems that their share depends on the local conditions. Generally, according to GLUTZ (1991), the second most common plant supporting nests is the reed-mace *Typha* sp. (8.6 %), the third place belongs to various willows *Salix* sp. (4.5 %), which are followed by 14 other kinds of plants (10.7 %). The share of reed is even higher in rich material from the south Czech Republic cited by PROCHAZKA (2000), but he stated that proportions between sizes of nest numbers and stand area indicated a slight preference of the Reed Warbler to the reed-mace. In the case of the Asiatic subspecies *fuscus* from Kazakhstan, the situation seems to be similar (KOVSHAR 1972). The number of stems supporting the nest ranges between two and eleven. The latter number is exceptional and mentioned only by BOROWIEC and DĄBROWSKA (1991). In the present authors' material the nests attached to two stems, constitute less than 18%. A similar percentage was observed by DYRCZ (1981), but according to ÖLSCHLEGEL (1981) nests supported by two stems make up 30%. On the other hand, in the material described by BOROWIEC and DĄBROWSKA (1991), such nests constitute 4.3%, and only BANNERMAN (1953) does not mention them at all, writing about 3-7 stems.

The height of nest site above water or ground level varies in relations of various authors and seems to depend on local conditions, kind of plant to which it is attached, and also on the part of breeding season. The lowest nest site in reeds – 13 cm – above water level is noted by BOROWIEC and DĄBROWSKA (1991), another one – 15 cm – by ÖLSCHLEGEL (1981), but these are exceptions. According to DYRCZ (1981) the mean height in Poland is 66.9 cm, whereas on Swiss lakes – 79,7 cm; in former Czechoslovakia – 60.6 cm (HUDEC 1983) and 61.3 cm (PROCHAZKA 2000), and in England – 75.6 cm (CRAMP 1992: after CATCHPOLE 1974). However, the mean heights in the same population may vary in successive seasons and the differences may be statistically significant (BOROWIEC and DĄBROWSKA 1991). The highest values are cited as follows: FERIANC (1979) – "2.3 m and more", PTUSHENKO (1954) – 3.5 m., and KOVSHAR (1972) for *A. s. fuscus* in Kazakhstan – 3 m. Generally, according to CRAMP (1992: after CATCHPOLE 1974) the nests sited in reeds are lower than in other vegetation. The highest nests are usually situated in bushes (NIETHAMMER 1937). Also repeated nests are built higher than the first ones (FERIANC 1979). DYRCZ (1981) and CRAMP (1992) write that height increases during the breeding season. OLBERG (1952) connected this finding with the raising of the nests by growing reeds. However, it seems to be more complicated, because it should affect only the nests built in fresh reeds. To solve the problem it would be necessary to measure the height of a particular nest several times in the breeding season, but nobody writes about it. Our Table XIV may, indirectly and at least in part, explain it. The nests containing eggs, i.e. newly built, are sited at approximately similar mean height in the first ten days of June, i.e. in the beginning of the breeding season as a month later, when the reeds should be much higher. It refers to the nests built in fresh reeds as well. The highest situated nest (125 cm above water) still not complete and empty, was found on 9 of June. On the other hand, mean height of empty nests in the first ten days of July (at least in part left by youngs hatched in mid-June or so) is eight cm higher; to the contrary, mean height of the nests with young is distinctly lower. It may suggest that mainly empty nests, left by the youngs of the first brood, are raised.

All authors describing the Reed Warbler's nests from various parts of its breeding area mention grasses, reed leaves and inflorescences, as well as plant down. They also write that the material is woven round plant stems supporting the nest (BANNERMAN 1953, BOROWIEC and DĄBROWSKA 1991, CRAMP 1992, FERIANC 1979, KOVSHAR 1972, MOLL 1958, MUNN 1931, NAUMANN 1905, PTUSHENKO 1954, URBAN et al. 1997). PTUSHENKO (1954), GOTZMAN & JABŁOŃSKI (1972), and KOVSHAR (1972) point to another characteristic feature i.e. that the nest opening is narrower than the inside cup below it. According to GOTZMAN and JABŁOŃSKI (1972), complete lacking of stiff (and bent) materials in the rim is also very characteristic. The descriptions of nest materials by the

Table XIV

Numbers: mean nesting heights [and ranges] of the Reed Warbler *Acrocephalus scirpaceus* nests measured (in cm) in successive ten days intervals of the breeding season in dry, mixed and fresh reeds

Age of reeds	Dates of measuring			
	1-10 Jun	20-30 Jun	1-10 Jul	after 11 Jul
last year (dry)	1: 43		3: 48.3 [40-60]	
mixed	4: 87.5 [50-125]	2: 95.5 [86-105]	14: 69.3 [45-110]	2: 84 [66-102]
fresh	5: 65.6 [52-82]		22: 65.8 [43-110]	
total: mean	10: 72.1		39: 65.7	
among them with eggs	5: 67.4		17: 68.7	
nests in fresh reeds containig eggs			10: 68.2	
containing youngs			7: 54.7	
empty (leaved?)			5: 76.2	

above mentioned authors indicate that many kinds of material listed in our Table XII, such as plant down, cobweb, or feathers, may be used more often. According to MOLL (1958) the spider's web may also be wound round the supporting stems and, according to FERIANC (1979), it works as an adhesive substance in the material. The authors also mention the materials which were not found by us. Hence, BANNERMAN (1953) writes about wool, of which the exterior of exceptional nests was composed almost entirely. NAEUMANN (1905) refers to the insect's yarn, whereas CRAMP (1992), KOVSHAR (1972), PTUSHENKO (1954) and WITHERBY et al. (1938) mention horse-hair in the lining. BOROWIEC and DĄBROWSKA (1991) mention also pieces of string, cotton yarn, and coloured thread, also those of steelon. The birds often use materials taken off their old (last year) or abandoned nests (BOROWIEC and DĄBROWSKA 1991, GARLING 1942). In some nests of the Asiatic subspecies *fuscus* both PTUSHENKO (1954) and KOVSHAR (1972) mention clay; their descriptions suggest that the birds bring it to the nests together with stalks which are covered with it. In such cases "nest walls are very smooth inside, and like as polished".

The using of wet material is a separate and controversial problem. Many authors do not mention it at all (BANNERMAN 1953, BOROWIEC and DĄBROWSKA 1991, CRAMP 1992, FERIANC 1979, KOVSHAR 1972, MUNN 1931, NAUMANN 1905, PTUSHENKO 1954, URBAN et al. 1997, WITHERBY et al. 1938). MOLL (1958) writes that he had never found nests built of wet material, but cites ZIMMERMANN who mentioned it. ZIMMERMANN's data are also cited by NIETHAMMER (1937). KOVSHAR (1972) writes about a nest from Kazakhstan, with an outer layer built of wet reed leaves. Wet reed leaves and inflorescences are mentioned also by SPRINGER (1960). Nobody, however, has observed birds gathering material from water surface. The above data and our own do not allow us to state whether the using of wet material is exceptional (the statement of MOLL 1958) or if it is common but usually overlooked.

The shape of the Reed Warbler's nest is commonly characterized as a deep cylindrical, basket-like cup (i.a. CRAMP 1992, HARRISON 1975, KOVSHAR 1972, WITHERBY et al. 1938). The nest measurements cited by several authors are given in the lower part of Table XIII. The results are generally similar, especially those regarding the means. The most variable, as in our data, seems to be the nest height, but it concerns the upper limit of this measurement only – the lower limit is always the same.

X. AFRICAN REED WARBLER *Acrocephalus baeticatus* (VIEILLOT, 1817)

The systematic position and composition of the African Reed Warbler is not quite clear, and statements of various authors are controversial to some degree. In the present paper the authors follow the systematics by CLEMENTS (2000), including among others *A. cinnamomeus* REICHENOW, 1908, as the subspecies, in spite of its being treate as a valid species by some authors (among others: WOLTERS 1980, HOWARD & MOORE 1991, STEYN 1996). The present authors have not seen any nest of *A. baeticatus*, thus all the data have been compiled from the literature. The places from which the nests were desribed are plotted against the breeding range (Fig. 17).

Fig. 17. Breeding distribution of the African Reed Warbler *Acrocephalus baeticatus* after URBAN et al. (1997) and places from which the nest descriptions come from. Explanations as in Fig. 3.

Nest site

The literature data indicate that the nest site varies, being different in different parts of the large breeding area of the bird. First of all, according to STEYN (1996), the bird is not necessarily associated with water and may nest at some distance from it. Hence, BOURNE (1955, after MOREAU 1940) writes that on the continent it has been found in reed-beds, whereas on Zanzibar and other islands it occurs in gardens, mangrove swamps, and *Casuarina* scrub. In Rhodesia the nest described by BENSON and PITMAN (1956) was built in long rank grass in shallow stagnant flood-water. WINTERBOTTOM (1971) writes about the nests placed in reeds, weed plants or other vegetation usually near water, whereas according to ROBERTS Birds of South Africa (1958) the nest is more often recorded in low weeds and bushes than in reeds; it may also be attached to drooping branches of willow or woven to fork in slender mangrove shoot (URBAN et al. 1997). Hence, the nest sites represent type “A” and “C” of the nest site.

The height of nest sites above ground or water also varies: usually 0.6-1.5 m, but on the Sudan coast c. 20 cm above mud (URBAN et al. 1997); in Rhodesia – 1.2 m (BENSON & PITMAN 1956).

Nest material and construction

The nest is built of dry grass, reeds, or leaves and lined with finer material (ROBERTS Birds of South Africa 1958, URBAN et al. 1997); COURTNEY-HAINES (1991) mentions a nest from Transvaal

lined with finer white seed fluff. It is a small deep cup, bound to some support such as a few (4-6) upright stems of reeds, sedges, or grasses (URBAN et al. 1997). According to STEYN (1996) it "is not as neatly finished as the nests of other 'reed' warblers". In the photograph he encloses (Fig. 18) the nest built in dense reed bed is attached to 2 (3?) reed stems, one of them green (visible in the picture)

Fig. 18. The nest of the African Reed Warbler *Acrocephalus baeticatus* (drawing by M. FINIK from the photograph published by STEYN 1996).

being wrapped with nest material – its endings (up to several cm long) loosely hang down from the walls; the ring round the opening is distinctly woven; inside it is smoothly lined with fine material. FRY et al. (1974) write that the nests of *baeticatus* generally resemble that of *A. scirpaceus*. They cite, however, G. MOREL who in Senegal found a nest "attached to three stems of *Typha australis*. It was suspended from one stem by a 'rope' about 80 mm long, a construction recalling the 'basket--handles' that characterize nests of *A. palustris*". In the literature cited there is no data concerning the use of wet materials by birds.

Shape and size of the nests

According to "ROBERTS Birds of South Africa" (1958), the nest is a small deep cup, bound to some support but not tapering in the same way as in *A. gracilirostris*, giving it a flatter appearance. However, COURTNEY-HAINES (1991) writes that the nests conical in shape, being wide at the top and tapering towards the bottom, may be "in reality, merely normal ball-shaped structures placed on top of well developed cock nests, the two combining to form, in outward appearance, a cone-like assemblage".

Table XV

The measurements (in mm) of nests of the African Reed Warbler *Acrocephalus baeticatus* based on the literature data

Locality and author	Outer diameter	Opening diameter	Height	Depth
Nortern Rhodesia (BENSON & PITMAN 1956)	70	40	80	35
Lake Chad (FRY et al. 1974)	–	45	–	50
Tropical West Africa (BANNERMAN 1939)	–	45	–	40

The measurements of nests of the African Reed Warbler are cited by BENSON and PITMAN (1956) and FRY et al. (1974), and in the case of *cinnamomeus* by BANNERMAN (1939). They are given in Table XV.

XI. BLYTH'S REED WARBLER *Acrocephalus dumetorum* BLYTH, 1849

The description of the Blyth's Reed Warbler's nests is based on 10 specimens of Moscow collections (APK next deposed at ZMMSU, ZMMSU and VVL) and coming mainly from the Krasnoyarski Kray and the surroundings of Moscow. These places are shown on the map also giving the limits of breeding area of the species (Fig. 19).

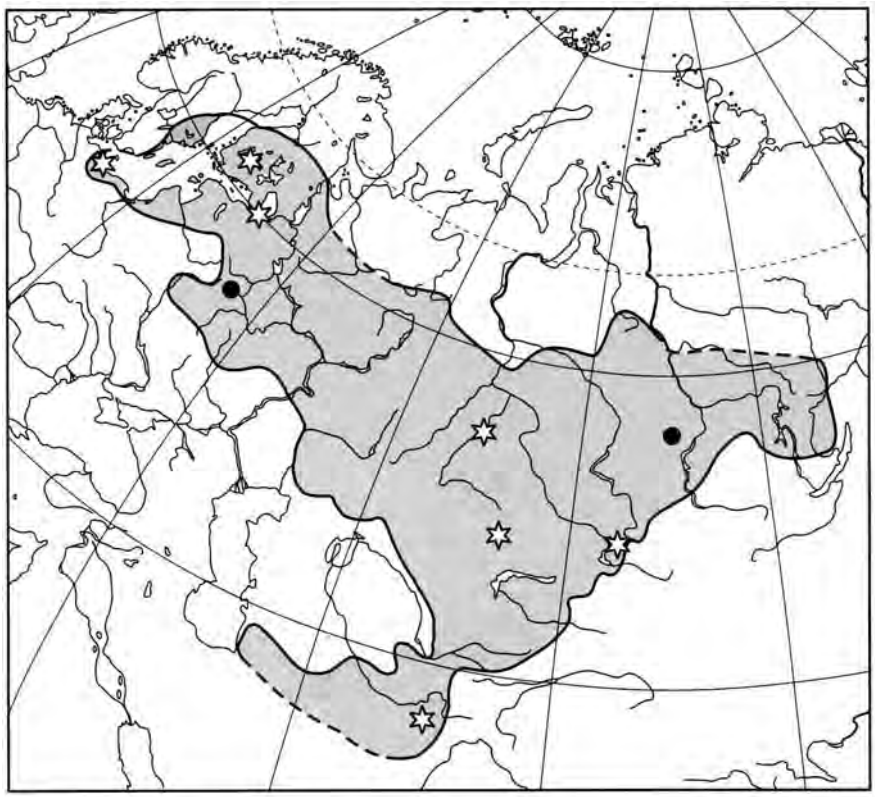


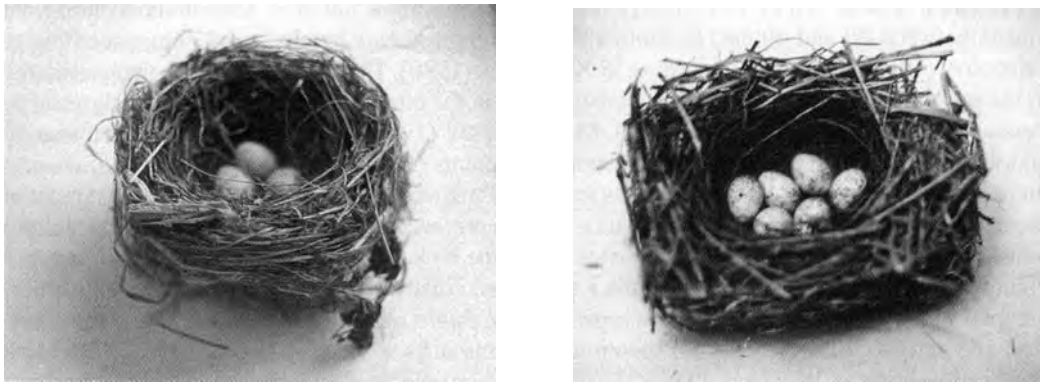
Fig. 19. Breeding distribution of the Blyth's Reed Warbler *Acrocephalus dumetorum* after PORTENKO and STUBS (1976) sligtly actualized after CRAMP (1992), and finding places of described nests. Explanations as in Fig. 3.

Nest site

All nests were situated above ground. Nest height was noted for 8 of them and ranged from 25 to 50 cm. The mean height is 38.7 cm (median = 40 cm). Three nests were built in *Spirea*, two in *Rosa* shrubs, two among *Urtica* stems, one in *Rubus idaeus* mixed with *Urtica* and one in *Rubus* mixed with *Urtica* and *Epilobium angustifolium*. Thus, they represent type "C" of the nest site (Fig. 2).

Nest material and construction

All nests were solid and compact (Fig. 20), though the most external layer, built of long plant elements, was looser than deeper layers. The materials used by birds are listed in Table XVI. Most characteristic are dry grass stalks and leaves. At least some of the stiff grass stalks and stems of herbs of external layer are bent and their endings may slightly protrude. No traces indicated the use of wet material for building outer parts of the nest walls. Vertical stems or branches supporting the nests were surrounded by nest material; the exact weaving of material round stems was noted only in two cases. At the nest rim there is a more or less firmly woven ring, which in most cases makes the nest opening narrower than the inside of the cup. In one case only the lack of distinct ring and of surrounding the supporting elements by nest material was noted, but the specimen appeared to be a lit-



A B

Fig. 20. Two nests of the Blyth's Reed Warbler *Acrocephalus dumetorum*: A – from Moscow surroundings (ZMMSU collection), B – from Krasnoyarski Kray (APK collection).

Table XVI

Material used to build ten nests by the Blyth's Reed Warbler *Acrocephalus dumetorum* (in descending order)

Kind of material	Number of nests	%
A. Bottom and outer layer:		
dry stems and leaves of grass	10	100
dry herb stalks	5	50
plant fibres	5	50
rootlets	2	20
green fragments of plants	1	10
leaves	1	10
B. Innner lining:		
very delicate stems	9	90
undulated thin rootlets	2	20

tle damaged. The nest cup is usually lined with very delicate material, mainly with thin stems – in two nests with undulated rootlets, which in one of them totally replaced the stems.

Shape and size of the nest

Nests of Blyth's Reed Warbler are high, only one nest being very high (i.e. its height exceeded the outer diameter). The outer contour was circular in six nests under study and in the remaining four nests slightly elliptic (the most elliptic nest was 93x110 mm). Nest cup was always deep but the depth was never greater than the diameter of the nest opening, which in seven nests was circular and in another three elliptic (the most: 45x56 mm). The measurements of studied specimens are given in Table XVII. The most stable is the diameter of the nest opening, whereas the outer diameter and the height are the most diversified measurements. The depth does not depend on the nest height.

Additional literature data and comments

Literature data not only complete those presented above; some of them come from other parts of the large breeding range of the species. The greatest range of the nest site height above ground, 8-150 cm, was observed by TOTUNOV (1981) in Western Siberia, but most nests found by him were placed between 20 and 40 cm. In southern Finland approximate height was 43 cm, according to ERIKSSON (1969), and 38 cm according to KOSKIMIES (1980). Thus it was similar to that calculated in the present work – also the ranges were similar. On the other hand, from the surroundings of St Petersburg (i.e. quite near to S Finland), MALCHEVSKIY (1959) described nests sited between 50 and 90 cm; this may be connected with supporting plants (*Sambucus*, *Ribes nigrum*, *Filipendula*) there preferred by the birds. 78% of nests found by TOTUNOV (1981) were sited in shrubs: most of them in *Rosa*, and 22% in herbaceous plants. Various preferences in various parts of Kazakhstan are pointed out by KOVSHAR (1972); he writes that in the Kokchetavski Upland nests were found in young birches, in nettles and reeds, in the Karkaralinski district mainly in the black currant shrubs, whereas in the Altai in *Lonicera*, *Ribes nigrum*, *Rosa*, *Rubus caesius*, *Filipendula*, young bird cherries, and nettles. JOHANSEN (1954) mentioned fern tussocks while PTUSHENKO (1954) listed also shrubs of jasmine, willow (type "D" of the nest site), hop, and dock and suggested that the most important factor for the bird in choosing a nest site is the connection of vegetation density and abundance of light at the edges. According to GLUTZ (1991), the height of nest site grows during the breeding season together with growing of vegetation but, on the other hand, nests site above 70 cm are very rare.

Nest material listed in Table XVI should be completed in the outer layer by plant down, often with spider webs (ABDUSALYAMOV 1973, CRAMP 1992), feathers (KOVSHAR 1972), and sometimes spider's cocoons (PTUSHENKO 1954). All the cited authors mention horse-hair used for lining the nest cup. The nest is a neat and compact cup, sometimes conical (CRAMP 1992), with rim edges slightly constricting the nest opening (ABDUSALYAMOV 1973, KOVSHAR 1972). According to PTUSHENKO (1954), the nest is smooth inside and outside, which does not agree with the protruding stem and stalk endings described above as well as seen in photographs published by ERIKSSON (1969) and DAUBER & HELBIG (1983). None of the cited authors write about the use of wet materials for building. GLUTZ (1991) writes that in general the nest is similar to that of the Marsh Warbler and differs from it in having "loops" and the presence of a plant down.

Nest sizes (Table XVII) show some differences between populations living in particular parts of the breeding area, but they deal more with the outer measurements than with those of the nest cup. It is interesting, on the other hand, that although *A. dumetorum* is approximately of the same size as *A. scirpaceus*, and accordingly, the inner measurements of its nests are similar to those of *scirpaceus*, both outer diameter and height are in *dumetorum* nests much larger (see Tables XIII and XVII).

Table XVII

The measurements (in mm) of ten nests of the Blyth's Reed Warbler *Acrocephalus dumetorum*. Literature data cited below own materials. [Arithmetic means are given in square brackets]

Measurement	N	Min.	Max.	Mean	SD	CV
Outer diameter	10	92.5	115.0	101.8	5.79	5.69
Opening diameter	10	50.5	60.0	56.8	3.73	6.56
Height	10	65.0	110.0	87.2	13.92	15.96
Depth	10	43.0	50.0	46.0	2.87	6.24

General:		Outer diameter	Opening diameter	Height	Depth
Own data		92.5-115	50.5-60	65-110	43-50
		[101.8]	[56.8]	[87.2]	[46.0]
in it: vicinity of Moscow,	(N=3)	[97.5]	[56.7]	[71.6]	[46.3]
Krasnoyarski Kray,	(N=7)	[103.6]	[56.9]	[93.9]	[45.9]
Literature data:					
Finland (ERIKSSON 1969), (N=10)		90-105	58-60	75-115	40-41
former USSR (PTUSHENKO 1954)		90-130	50-63	65-95	33-40
Western Siberia (TOTUNOV 1981)		86-117	49-65	73-78	41-48
	(N=23)	[102.6]	[56.5]	[76.0]	[44.3]
Kazakhstan (KOVSHAR 1972),	(N=8)	80-115x125	45x50-55x65	60-105	–
Tadjikistan (ABDUSALYANOV 1973)		–	56	85	36

XII. MARSH WARBLER *Acrocephalus palustris* (BECHSTEIN, 1798)

The description of the Marsh Warbler's nests is based on 25 of the author's own nest record cards, 24 nest record cards of the Institute of Vertebrate Biology in Brno, 7 nests stored at the Radom Museum (MOR), and 3 nests collected in the European part of the former USSR (ZMMSU). The places from which the nests have been derived are plotted against the breeding range of the species on the map in Fig. 21.

Nest-site

The height at which 45 nests were situated ranges from 25 cm to 84 cm (in raspberry bush) above ground, 44.9 cm on average (median = 45 cm). The distribution of nesting heights is presented in Table XVIII. It shows that more than the half of them lie in the height group between 25 and 50 cm.

The list of plant species supporting the nests (to the stems of which the nests were attached) is fairly numerous (Table XIX). The nettles are absolute dominants supporting 23 nests, i.e. nearly 48%; another five nests were attached both to nettles and other plants (Fig. 22). The nests belonged mainly to the type "C", but rarely also to the type "D" of the nest site (Fig. 2).

Nest material and construction

The list of materials used for building 51 nests is given in Table XX. The most common are grass stalks, foundd in 50 nests, while in the remaining nests they were replaced by various stems. Some stiff stalks and stems, used for building of the outer layer, may be bent and their endings may slightly protrude from the walls. The nests are usually attached to several more or less vertical plant

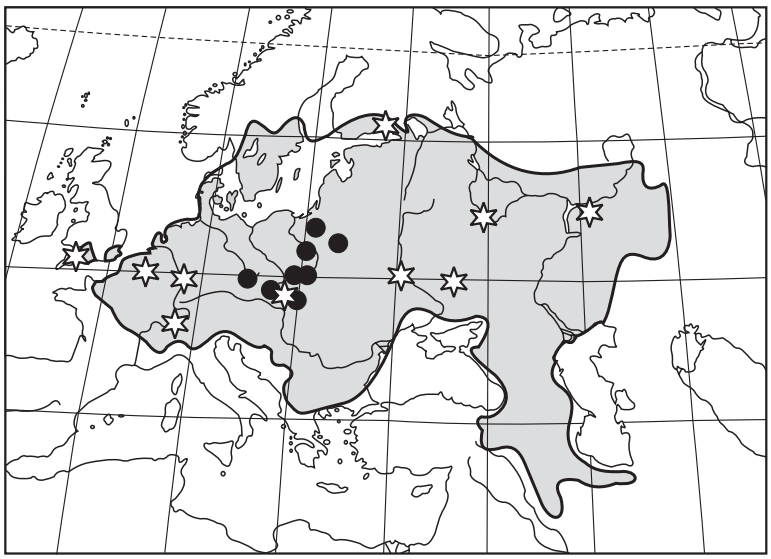


Fig. 21. Breeding distribution of the Marsh Warbler *Acrocephalus palustris* after PORTENKO and STUBS (1976) and finding places of the mentioned nests. Explanations as in Fig. 3.

Table XVIII

Nesting heights (in m) of 46 nests of the Marsh Warblers *Acrocephalus palustris* in Poland and in former Czechoslovakia

Nesting height	Number of nests	%
0-0.25	5	11.1
0.26-0.50	26	57.8
0.51-0.75	12	26.7
0.76-1.00	2	4.4
Total	45	100.0

elements, which are bound by soft material of the nest walls. It concerns, however, very often a part of the wall height, usually the upper one. At the rim there is usually a ring of long stalks and other soft materials, woven not very solidly. In the majority of cases it makes the nest opening slightly narrower than the diameter of a cup below it. In some cases walls may be to some degree transparent, but this is never the case with the bottom. The authors did not note any traces of using wet materials. The inside lining is made of very delicate and resilient, thin, and at least several cm long, pieces of plant or hair.

Shape and size of the nest

The nests under study belonged to the categories of high to very high and deep to very deep nests. Very high nests made up ca 33% of the total and very deep nests below 9% only. The nests are more or less conical in shape, or cylindrical with a hemispheric bottom. Their outer contour seen from above is round (ca 20% cases) to elliptic (or irregular, for example triangular, depending on the arrangement of supporting elements). However, the difference between longer and shorter diameters are greater than 10 mm only in a few cases (the greatest: 72x95 mm). Similarly, the shape of

Table XIX

Genera of plants in which 48 nests of the Marsh Warbler *Acrocephalus palustris* were built

Plant genus	Number of nests	%
Urtica sp. (pure)	23	47.9
Undet. *Graminaceae*	4	8.3
Phragmites	3	6.2
Salix sp.	3	6.2
Rubus idaeus	3	6.2
Urtica/*Rubus fruticosus*	2	4.2
Artemisia sp.	2	4.2
Undet. thistle	2	4.2
Urtica sp./*Tanacetum vulgare*	1	2.1
Urtica sp./*Grossularia*	1	2.1
Urtica sp./ stem of undet.plant	1	2.1
Solidago sp.	1	2.1
Rosa sp.	1	2.1
Artemisia / *Phragmites*	1	2.1
Total	48	100.0

A

B-C

Fig. 22. Typical nest sites of the Marsh Warbler *Acrocephalus palustris*: A – on blackberry and nettles, B, C – on one branch of gooseberry bush and three stems of nettles (two sights).

Table XX

Material used to build 51 nests of the Marsh Warbler *Acrocephalus palustris* (in descending order)

Kind of material	Number of nests	%
A. Bottom and outer layer (N=51):		
grass stalks	50	98.0
grass blades	29	56.9
various plant fibres *	23	45.1
stems of herbs **	13	25.5
rootlets	4	7.8
grass inflorescences	4	7.8
cocoons	3	5.9
stiff branched stems	2	3.9
sedge leaves	1	2.0
B. Inner lining (N=44):		
plant fibres	24	54.6
very thin stalks	15	34.1
grass pedicles	4	9.1
hairs (black)	2	4.5

* among them fibres of macerated nettle stems ** nettle stems and other

the cup opening is round in ca 20%; in the remaining nests it is elliptic, but in 20% only the difference between the two diameters exceeds 5 mm. The measurements of nests are given in Table XXI.

Additional literature data and comments

The nests of the Marsh Warbler have been described in many papers concerning the populations inhabiting various parts of the breeding area of the species (see map: Fig. 21). Generally, it nests above dry ground at various distance from water (GLUTZ 1991; GOTZMAN & JABŁOŃSKI 1972; NIETHAMMER 1937; PTUSHENKO 1954). KUSHNAREV (1987), however, found five nests (of 70) sited above water.

As to the height above ground, stated by the authors as 25-84 cm, the same or very similar limits are cited by ERIKSSON (1969: Finland), GLUTZ (1991: Germany, Belgium, Switzerland), SCHULZE-HAGEN (1984: Germany), WIPRACHTIGER (1976: Switzerland). NAUMANN (1905: Central-East Europe) also cites similar limits as general, and adds that the nests sited below 30 cm are rare but never immediately above the ground. The same hights are given by KNYSH (1999: Ukraine) and NIETHAMMER (1937: Germany), the latter, however, mentions also rare nests built higher, exceptionally even 6.5 m. High built nests (up to 2 m) are also described by DOWSETT-LEMAIRE (1981: Belgium). On the other hand, PTUSHENKO (1954) and ZATSEPINA (1968) mention nests built immediately above ground (up to 15 cm). Average height increases through the season (DOWSETT-LEMAIRE 1981; FRANZ 1981; KNYSH 1999; SCHULZE-HAGEN 1984; WIPRACHTIGER 1976), but it seems that the height also depends on the kind of vegetation in which the nest is sited. It may be also that in the eastern part of the breeding area the birds generally nest lower than in the western part.

The number of plant species in which the nests are built is high. BANNERMAN (1953), DOWSETT-LEMAIRE (1981), FRANZ (1981), GLUTZ (1991), HUDEC (1983), KNYSH (1999), NAUMANN (1905), NIETHAMMER (1937), NOLL-TOBLER (1924), PTUSHENKO (1954), WIPRACHTIGER

Table XXI

The measurements (in mm) of 58 nests of the Marsh Warbler *Acrocephalus palustris*. Literature data cited below own materials [Arithmetic means are given in square brackets]

Measurement	N	Min.	Max.	Mean	SD	CV
Outer diameter	58	75	110	89.34	8.35	9.35
Opening diameter	58	45	62.5	52.99	3.68	6.94
Height	55	53	110	83.54	12.33	14.76
Depth	56	36	75	46.50	7.08	15.22

General:	Outer diameter	Opening diameter	Height	Depth
Own data:	75-110	45-62.5	53-110	36-75
Literature data:				
Poland (GOTZMAN & JABŁOŃSKI 1972)	85-115	45-55	80-110	40-50
South of British Is (HARTHAN 1938)*	76 (115)	45	100	45
former Czechoslovakia (HUDEC 1983)	75-150	45-65	50-130	40-75
(N=105)	[88]	[53]	[82]	[48]
"*Sylvia*-type"				
Poland (NAUMANN 1905)**	81	50	96	65
Kiev Province (NAUMANN 1905)**	109	55	67	39
Moscow Province (NAUMANN 1905)**	106	57	56	39
Twer Province (NAUMANN 1905)**	97-105	47-59	61-82	41-50
(N=4)	[100.7]	[54.7]	[74]	[45.7]
"*Acrocephalus*-type" (NAUMANN 1905)	100	64	127	54
former USSR (PTUSHENKO 1954) (N=?)	81-114	43-50	56-127	43-58
Ukraine: Sumy region (KNYSH 1999)	70-115	45-74	60-120	32-55
(N=61)	88.2x95.4	43.6x52.5	[86.1]	[43.6]
Volga-Kama Country (ZATSEPINA 1968)	65-110	45-65	65-110	30-60
(N=426)	[76]	[56]	[75]	[48]
Kharkov surroundings (KUSHNAREV 1987)	65-94	49-70	50-113	30-65
(N=70)	[79]	[59]	[66]	[50]

* calculated from inches and made even by CRAMP (1992)
** in the case of crosswise measurements of elliptic nests their means were calculated.

(1976) and ZATSEPINA (1968) listed alltogether at least 57 plants, and the list is surely not complete, because some authors named the most common (or most numerous) only. For example ZATSEPINA (1968), mentions saplings of 9 kinds of trees, but named only four of them. According to GLUTZ (1991), who summarized data from Belgium, Germany, and Switzerland, the most common plant supporting the nests is the nettle, *Urtica dioica*, (pure or mixed with other plants) which constitutes 82% of more than a thousand nests. Its share in local populations may be even higher – 94.6 % in N Bavaria (FRANZ 1981). On the other hand, KNYSH (1999) in the Ukraine found only 46.8% of nests in the nettle, this being similar to our data (Table XX). There are populations in which other plants dominate: in central Switzerland WIPRACHTIGER (1976) found 46.5% of nests in the dropwort, *Filipendula ulmaria*, BANNERMAN (1953 after BOND) mentioned 35.5% nests attached to the meadowsweet, *Spirea*, KUSHNAREV (1987) in the vicinity of Kharkov found 36% nests in the marsh-mallow

Althaea officinalis, and ZATSEPINA (1968) reported in the eastern part of European Russia 15.9% in the mountain ash, *Sorbus aucuparia* (the latter author does not mention nettle at all). Thus, GLUTZ (1991) is right in writing that not the plant species is important but the appearance of habitat, i.e. high plant tussock with many upright elements.

As shown in Table XX, the majority of authors indicate that the most common material for building the outer part of the nest are various parts of dry grasses, i.e. stalks, leaves, inflorescences, and sometimes rootlets (BANNERMAN 1953, GLUTZ 1991, HARTHAN 1938, HUDEC 1983, KNYSH 1999, PTUSHENKO 1954, WIPRACHTIGER 1976, WITHERBY et al. 1938). According to NOLL-TOBLER (1924) the nest is built of dry stems of cotton-grass and thin stems of rushes. On the other hand, DOWSETT-LEMAIRE (1981) writes that the nest is made "mainly of dead twigs of perennial plants of the previous season". This kind of material shares farther places in the lists of other authors. They mention also plant wool and bast (PTUSHENKO 1954), sheep wool (HARTHAN 1938), moss, cobweb, and animal hair (HUDEC 1983), strips of bast, nettle fibres, and fragments of thin stems, fragments of reed inflorescences and strips of leaves, rootlets, pieces of willow bark, cobweb, spider and insect cocoons, animal hair, and, in two cases feathers (KNYSH 1999). The longest grass stem found by the latter author as used for building, was 44 cm long, and fragment of hop stem – 70 cm. Besides natural materials, KNYSH (1999) found a piece of wadding in one nest, whereas DOWSETT-LEMAIRE (1981) found a large piece of white toilet paper. All authors write about the delicacy of materials used for lining the nest cup. Again, the most common are fragments of dry grasses, which, according to KNYSH (1999), are split into thin fibres, and fragments of grass or reed inflorescences. To the contrary, the latter material was never found by NOLL-TOBLER (1924). KNYSH (1999) mentions also thin stems, soft rootlets, moss sporophite petioles, and various animal hair. Lining materials listed by BANNERMAN (1953), HARTHAN (1938), HUDEC (1983), WIPRACHTIGER (1976) repeat at least partly the list given by KNYSH (1999); HUDEC (1983), however, mention also artificial fibre. Generally, every nest is built of 1-9 kinds of material – materials of walls are more diversified than those of the lining (KNYSH 1999).

Similarly to the great diversity of the nest site and material used for building, also the construction and shape of the Marsh Warbler's nests are diversified. DOWSETT-LEMAIRE (1981) writes that the nest structure depends on the type of vegetation it is built in: it may be suspended laterally to a few stems and not supported from below, but in bushes the nests are often set into a fork and not suspended. According to ZATSEPINA (1968) if the nest is built in a fork of a bush or a young tree, its bottom leans lightly against the branch. This situation is not accepted by NAUMANN (1905). He writes that the material of walls is strongly bound round supporting stems and then again woven into walls. According to PTUSHENKO (1954), the nest walls are attached to the supporting plant elements mainly by their upper parts. CRAMP (1992) writes about distinct handles which are woven from the rim round stems, whereas according to WITHERBY et al. (1938) the nests are fixed by "basket-handles". Similarly to the recent authors' data, both PTUSHENKO (1954) and ZATSEPINA (1968) record solid and thick nest bottom which is never transparent. The former author also indicates that the walls may be smooth but in some cases endings of materials may protrude outward 5-15 cm, and that the inner edge of ring at the rim is constricted making the opening diameter smaller than that of cup; to the contrary, GOTZMAN and JABŁOŃSKI (1972) write that rim constriction does not exist.

PTUSHENKO (1954) distinguishes three types of nests: round baskets (whose outer diameter is the greatest below the rim), cylindrical, and conical (in which the greatest outer diameter is at rim level). According to NAUMANN (1905 after PLESKE), there are two types of nests – those resembling the nests of *Sylvia* warblers, and those which are miniatures of those of the Reed Warbler's, and they differ among each other in their dimensions. Regardless of the name of category, it seems that all types mentioned above are represented in the nests under present study. PTUSHENKO (1954) writes that in spite of the irregular form of the outer contour, the shape of the opening is always round. It is not confirmed by our data, as in most nests the opening was more or less elliptic.

The measurements of nests cited by many authors are listed in the lower part of Table XXI. As in our material, the nest height is the most diversified variable in nests measured by HUDEC (1983),

PTUSHENKO (1954), KNYSH (1999), and KUSHNAREV (1987), whereas in the richest material presented by ZATSEPINA (1968) the diversity of the height is similar to that of the outer diameter.

XIII. GREAT REED WARBLER *Acrocephalus arundinaceus* (LINNAEUS, 1758)

The study material consists of 97 own nest record cards coming from various parts of Poland. The material also contains two nests from Kazakhstan (ZMMSU ex coll. APK) and one from Baygakum on Syrdaria (VVL). The nests from Poland belong to the nominative form *Acrocephalus a. arundinaceus* (LINNAEUS, 1758) whereas those from Middle Asia to *A. a. zarudnyi* HARTERT, 1907. The places of collecting are plotted on the map against the background of the breeding area of the species (Fig. 23).

Nest site

81 of all nests under study, belonging to the nominative form of the Great Reed Warbler, were attached to reed stems. The birds used fresh reeds, dry (last year) reeds, as well as mixed reeds, and in the latter case proportions between numbers of fresh and dry reeds varied. Two nests only were suspended on thick rush stems, one of them on fresh stems only and the other on mixed fresh and dry

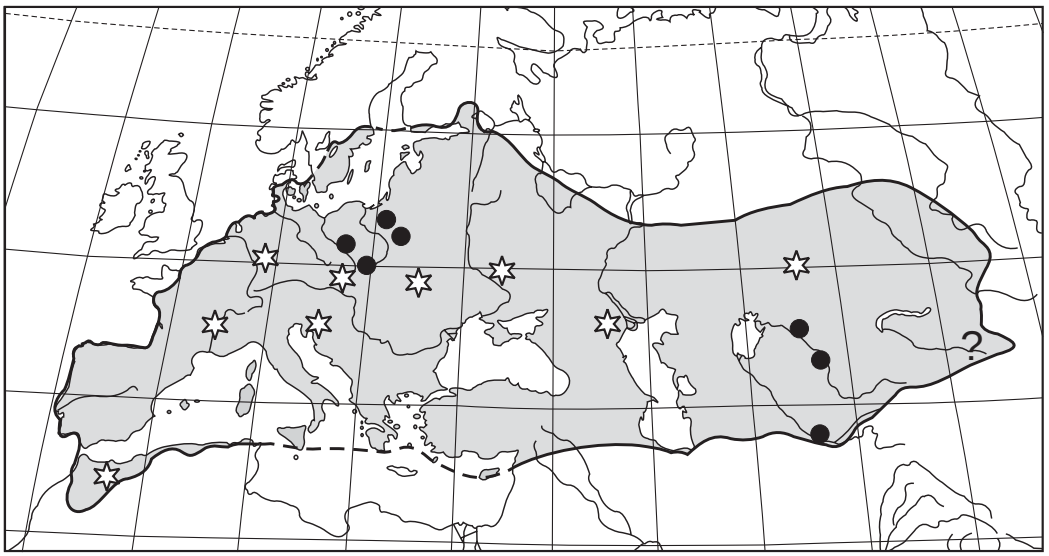


Fig. 23. Breeding distribution of the Great Reed Warbler *Acrocephalus arundinaceus* compiled from FLINT et al. (1968), GLUTZ (1991), CRAMP (1992), and URBAN et al. (1997), and simplified. On that background are shown the finding places of nests studied and described in the literature. Explanations as in Fig. 3.

stems. One nest, at the pond bank, was built on two reeds and two stems of an undefined plant, and another one in willow bush in a three-forked branch (Fig. 24).

The great majority of nests were sited in reed-beds, among them in not wide strips of reed-bed growing along the banks of a water body, usually above the water surface or, rarely, above ground near the bank. The height of nest site in 84 cases ranged from 13 to 180 cm, 51 cm on average (median = 47.5). The nests above the ground were sited slightly higher than those above water (Table XXII). The highest nest was built in a willow bush at the bank of an old river bed, whereas the lowest, containing six eggs, was attached to nine reeds, and there was nothing to indicate that it was previously built higher and then lowered. The highest nest built in fresh reeds was found at 130 cm

A

B

C

Fig. 24. The nests of the Great Reed Warbler *Acrocephalus arundinaceus*: A – not yet finished nest in typical habitat (fish pond in S Poland), B – a nest in three-forked branch of a willow bush (Biebrza marshes, NE Poland), C – complete nest built in reeds (ISEA collection).

Table XXII

Nesting heights (in m) of 84 nests of the Great Reed Warbler *Acrocephalus arundinaceus* in Poland

Nesting height	Nests situated above water		Nests situated above ground		Total	
	Number of nests	%	Number of nests	%	Number of nests	%
0-0.25	7	9.1	2	28.5	9	10.7
0.26-0.50	38	49.3	1	14.3	39	46.4
0.51-0.75	25	32.5	2	28.5	27	32.1
0.76-1.00	6	7.8	–		6	7.1
1.01-1.25	1	1.3	–		1	1.2
1.26-1.50	–		1	14.3	1	1.2
1.51-1.75	–		–		–	
1.76-2.00	–		1	14.3	1	1.2
Total	77	100.0	7	99.9	84	99.9
Mean	0.49		0.77		0.51	

Comparisons:	Number of nests	Height (cm)	Mean
Own data	84	13-180	51
Literature data:			
Poland (DYRCZ 1981)	138	10-100	50.4
Moravia (HAVLIN 1971)	135	10-210	43
Moravia (HONZA et al. 1993)	23		80
former Czechoslovakia (HUDEC 1983)	255		54.9
Slovenia (BOZIC 1999)	295	18-129	55.6
Germany (NIETHAMMER 1937)	–	50-275	–
Germany (DITTBERNER & DITTBERNER 1986)	19	9-175	62
Switzerland (DYRCZ 1981)	93	30-130	74.2
former USSR (PTUSHENKO 1954)	–	60-120	–

above the ground. The heighest nest built above water was found in mixed, fresh and dry, reeds at 110 cm.

The height of the nest site in the case of nests built in reeds seems to depend on the kind of stems (fresh or old) and on the period of the breeding season. In the case of 56 nests the kind of reed stems was noted, their dispersion in time being given in Table XXIII. Generally, nests built in fresh reeds are situated higher than those in old and mixed reeds, and the height rises in time. This is clearly seen from the lower part of Table XXIII illustrating 20-day intervals.

The number of plant elements supporting 85 nests ranged from three to eleven (Fig. 25); most nests were attached to five stems (Table XXIV). In the great majority of cases the supporting elements were more or less vertical and parallel to each other. In five cases only was it noted that some of the reed stems (one or two of all) were oblique and crossed with another ones.

One of the nests of *A. a. zarudnyi* was attached to two reeds only, and two others to four reeds each. The height of two nests was 90-100 cm and 110 cm above the water surface.

Nest material and construction

All the kinds of material used for building 80 nests of the nominative form are shown in Table XXV. They are generally so homogeneous that the lining was mentioned separately in 28 cases only. Is is interesting that the birds often use plant down (of the last-year reed mace, poplar and so

Table XXIII

Mean heights (in cm) of nest situation in the Great Reed Warbler *Acrocephalus arundinaceus* dependant on the period of the breeding season and on the kind of reed stems on which they were built i.e.: old (= last year, dry), mixed (= old and fresh), fresh (= green, living), but irrespective of the nest contents (not yet finished, eggs, nestlings, empty: fledglings gone)

Reeds	→31 May	1-10 Jun	11-20.Jun	21-30 Jun	1-10 Jul	11 Jul→
Old	2: 44.0	1: 29.0	2: 39.0	–	–	–
Mixed	2: 43.0	3: 50.0	10: 37.5	8: 59.7*	2: 56.0	1: 43.0
Fresh	–	5: 48.4	8: 36.9	2: 87.5	8: 61.5	2: 58.5

The same in 20-days intervals [ranges given in brackets]:

Reeds	19 May to 10 June	11 June to 30 June	1 July to 20 July
Old	3: 39.0 [15-73]	2: 39.0 [38; 40]	–
Mixed	5: 47.2 [30-62]	18: 47.4 [20-110]*	3: 51.6 [43-57]
Fresh	5: 48.4 [40-58]	10: 51.2 [25-130]	10: 60.9 [45-80]

* the nest containing young cuckoo sited 18 cm above water level was not taken in account because of the possibility of sinking

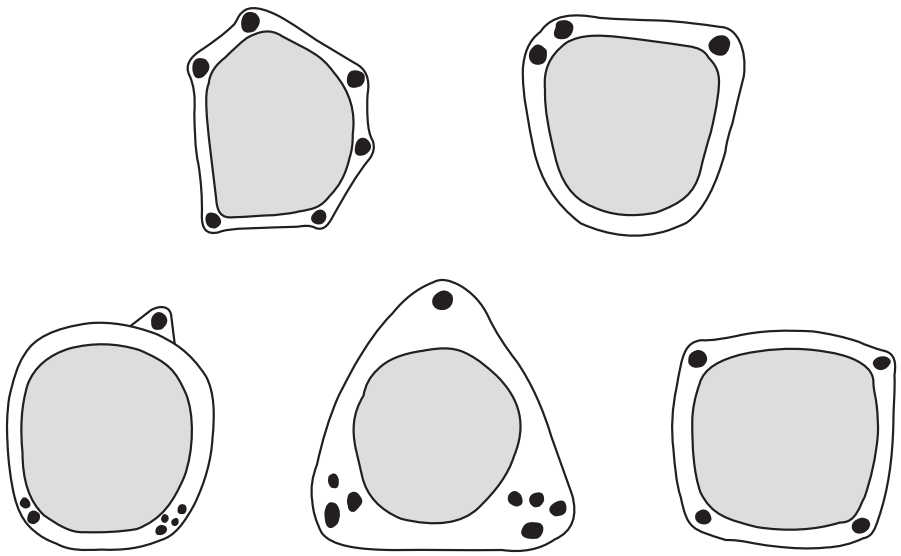


Fig. 25. A few examples of the distribution of reed stems (black dots) supporting the nests of the Great Reed Warbler *Acrocephalus arundinaceus*.

on), as well as of bird feathers in various numbers, for building the outer layer of the nest and its bottom; we never found feathers inside the nest, and only once reed mace down in the lining.

At least a part of the material used for the building of an external layer of the nest consists of wet last-year reed (and possibly other water plant) leaves, or their fragments (strips) only, gathered by birds from the water surface within the reed-bed. Fragments of fresh, green, reed leaves are encountered very rarely. The green duckweed was seen inside an unfinished nest, not yet lined. Green

Table XXIV

Number of reeds (or other vertical plant elements) to which 85 nests of the Great Reed Warbler *Acrocephalus a. arundinaceus* were attached

Number of elements	Nests situated exclusively in reeds		Nests situated in reeds and/or other plants	Total	
	Number of nests	%	Number of nests	Number of nests	%
3	5	6.2	1 *	6	7.1
4	20	24.7	1 **	21	24.7
5	22	27.2	1 ***	23	27.1
6	11	13.6	1 ***	12	14.1
7	13	16.0	–	13	15.3
8	5	6.2	–	5	5.9
9	4	4.9	–	4	4.7
10	–		–	–	
11	1	1.2	–	1	1.2
Total	81	100.0	4	85	100.1
				mean = 5.5 reeds	

* in the fork, among three thin branches of a willow *Salix* sp., 1.8 m above the ground
** in two reed and two other water plant stems
*** in thick bull-rushes

Table XXV

Material used to build 80 nests by the Great Reed Warbler *Acrocephalus arundinaceus* (in descending order)

Kind of material	Number of nests	%
A. Whole nests and/or bottom and outer layer (N=80):		
reed leaves (or strips of them)	78	97.5
reed inflorescences	69	86.25
plant down (reedmace, poplar, dandelion)	20	25.0
grasses + sedges (dry or fresh stalks, leaves, inflorescences)	8	10.0
bird feathers (duck, heron, corvid)	4	5.0
rootlets	3	3.75
duckweed	2	2.5
bird down (duck)	1	1.25
green leaf	1	1.25
green algae	1	1.25
sweet grass	1	1.25
piece of string	1	1.25
B. Inner lining (N=28):		
reed inflorescences	27	96.4
reed fibres	4	14.3
grass stalks	3	10.7
grass inflorescences	2	7.1
reedmace down	1	3.6
small green leaf	1	3.6

thread-like algae were used to link reed stems in the first stage of building. Both duckweed and algae indicate direct gathering the material from the water surface. Also, various feathers are collected from the water surface. Usually all these materials could be found in close vicinity of the nest. However, in the case of two nests built in loose clump of rushes the birds had to collect nest material in a reed-bed some dozen metres apart.

The process of nest building begins with the wrapping up of soft wet material round particular chosen reed stems. Each particular stem is then connected with a neighboring one along the circumference (never crosswise) using similar material. This wet material is compressed round reed stems when drying, and thus gives solid base for the nest. The nest is sometimes additionally supported by a reed leaf basis, constituting the base for a thick nest bottom. The walls are built in a similar way; thinner and narrower materials (fibres or stripes) are wrapped around the stems, whereas wider ones surround stems from outside only. The nest is built during a few days, and one may observe an incompleted nest in which, above the dry lower part, there is a wet part (1-3 cm wide) newly added. The upper rim of the nest is firmly woven, and the material is arranged in so a way that the opening diameter is distinctly smaller than the diameter of the cup. The nest cup is usually lined with more delicate and dry material such as reed inflorescences, which may also be seen in the rim. In one case only wet material inside a completely dry nest was found.

Stems supporting the nest are wrapped round by nest material at whole (or nearly whole) section of the nest height. Rarely, more distant stems are fastened with a few fibres only.

Three nests of Asiatic *A. a. zarudnyi* were built mainly of reed leaves and their strips or fibres, but in two of them thicker leaves probably of the sweet flag were added. In all of them, in an external layer, there was an addition of the plant down, and in one a little of green filiform algae. Their lining consisted of reed inflorescences or their petioles and fibres. All three nests were compactly built with solid ring at the rim. Compression of material woven round stems indicate that wet material was used.

Shape and sizes of the nest

The nests of the Great Reed Warbler are more or less cylindrical and belong to high and very high ones, while the latter category prevails: of 78 nests of the nominative form, in which both outer diameter and height were measured, in 65 (83.3%) the height exceeded the mean diameter (in the case of elliptic or irregular nests it is the arithmetic mean of the shortest and longest diameter). Its degree varies exceedingly: the height of the highest nest (21 cm) was more then twice as great as the longest diameter (10 cm), whereas in nine cases the height was equal to the shortest diameter (example: diameter – 11x9 cm, height – 9 cm). Nest contours seen from above are in greater part elliptic or irregular to a various degree (Fig. 25). Differences between diameters usually do not exceed 1.5 cm, but exceptionally noted was 3.5 cm. Only in seven cases diameters were equal to each other. This situation depends on the configuration of the reed stems. Three nests of the subspecies *zarudnyi*, studied in collections, were also high to very high, and regular as well as elliptic, but it is difficult to say to what degree this resulted from storing them in boxes.

46 of 74 nests (62.2%) belong to the category of deep and only 28 (37.8%) to very deep nests. The majority of them, however, range not very far from the categories' boundary.

The results of measuring 82 nests are given in Table XXVI. In nominative form the most characteristic is the diameter of the opening, having the smallest coefficient of variation. Most variable is the nest height, ranging from 80 to 210 mm. The data concerning three nests of *zarudnyi* differ to some degree: most similar is the mean depth, being only about four mm smaller, the mean of the opening diameter is eight mm smaller, whereas that of the outer diameter is nine mm larger. All of the individual measurements however lie within the limits of the nominative form, hence the differences mentioned above may be due to very small sample size only.

Table XXVI

Measurements (in mm) of nests of the Great Reed Warbler *Acrocephalus arundinaceus*. Literature data cited below own materials. [Arithmetic means are given in square brackets]

Measurement	N	Min.	Max.	Mean	SD	CV
A. a. arundinaceus from Poland:						
Outer diameter	79	82.5	125.0	99.30	8.27	8.32
Opening diameter	77	55.0	82.5	66.77	5.36	8.02
Height	78	80.0	210.0	120.44	22.14	18.38
Depth	75	38.0	80.0	63.80	8.66	13.57
A. a. zarudnyi from Central Asia:						
Outer diameter	3	95.0; 110.0; 120.0		108.33	–	–
Opening diameter	3	57.0; 60.0; 62.5		59.83	–	–
Height	3	95.0; 110.0; 125.0		110.00	–	–
Depth	3	50.0; 60.0; 65.0		58.33	–	–

Comparisons:	Outer diameter	Opening diameter	Height	Depth
Own data:				
arundinaceus	82.5-125	55-82.5	80-210	38-80
zarudnyi	95-120	57-62.5	95-125	50-65
Literature data:				
arundinaceus:				
Poland (GOTZMAN & JABŁOŃSKI 1972)	90-120	60-75	110-200	60-80
former Czechoslovakia (HUDEC 1983) (N=40)	70-120 [97]	50-75 [61]	90-130 [110]	47-80 [60]
Slovenia (BOZIC 1999)	85-130	–	80-380	60-80
S France (GLUTZ 1991) (N=29)	85-105x115 [95x104]	55x60-68x70 [60x65]	90-160 [120]	53-75 [67]
North Africa (URBAN et al.1997)	c.90	c.70	–	c.70
Ukraine: Eastern Galicia (NAUMANN 1905)	100-130	50-80	165-200	–
Ukraine: Kharkov Province (NABTOCHIY 1991) (N=12?)	88-105	60	81-129	61-98
Kalmukia (MUZAEV 1991) (N=53)	80-100	48-90	80-195	45-98
former USSR (PTUSHENKO 1954)	90-140	50-90	83-270	62-75
zarudnyi:				
Kazakhstan (KOVSHAR 1972)	105-120	60-70	200-300	55-70

Additional literature data and comments

The majority of authors mention reed as a plant most often used for supporting the nests. Although HAVLIN (1971) found the nests attached mainly to the reedmace stems, HUDEC (1983) summarizing the data from former Czechoslovakia, writes that 51.2% of 594 nests were built in reeds, another 46.2% in reedmace, and 1-4 nests in other plants (such as willow/herb, elder, hop, and willow bush). The high share of nests built in *Typha* contrasts with the statement by KLUYVER (1961) who writes that some females try to attach the nests to reedmace stems but usually without success. NIETHAMMER (1937) mentions, as exceptions, willows and other trees, PTUSHENKO (1954) generally bushes and trees growing on water banks, NAUMANN (1905) willows and alders, while

OLBERG (1952) mentions willow, MÜLLER (1973, 1979) bird cherry and URBANIAK and ZATWARNICKI (1979) described a nest attached to a forked willow branch and 2 nettle stems, which was built at a 2 km distance from the nearest reedbed. This distance to the reedbed, however, cannot be the only explanation for using tree branch, since bird cherry mentioned by MÜLLER (1979) grew 5 m off a well-developed stripe of reeds. In general, as in the author's own material, the commonest is type "A" of the nest site, the other i.e. type "D" being rare.

The heights of nest site cited by various authors differ to some degree. They are summarized in the lower part of Table XXII. In general the height of a nest site varies from 9 to 275 cm, but the majority of nests are situated between 30 and 60 cm. The highest sited nest are built in bushes, thus in places rather not typical to the species. According to HONZA et al. (1993), the height of a nest site may depend, among other things, on the plant species, because heavy nests are lower sited on fragile stems of reedmace and higher on strong reed stems. This confirms the data of HUDEC (1983). NIETHAMMER (1937) writes that growing up reeds raise up the nest. This is accepted by OLBERG (1952) and DYRCZ (1981). According to NEUMANN (1943), this raising may be very small if any, because the birds start building when the developing (raise) of lower parts of reed stems is finished. It seems, however, that the problem deals with nests attached to living (fresh) reeds only. NEUMANN (1942) observed that in the case of nests built in mixed, dry, and fresh reeds, the latter were loosely surrounded by nest material. In the authors' data, the mean height of 25 nests attached exclusively to fresh reeds raised at three successive 20-day intervals (Table XXIII). In spite of very small samples it suggests that the nests studied before June 20 were sited lower than those studied after June 21. On the other hand, it may reflect the tendency of birds to build the nests above the ground higher than above water surface (Table XXII), or individual preferencies. The raising of nests cannot be excluded, especially in the case of those built early in breeding season (end of May), and studied several weeks later, after leaving them by the young.

JĘDRASZKO-DĄBROWSKA (1991) measured the height of nest sites not above the water surface but above the bottom of the water body, since it could be important for the inclination of the nest during strong winds. Construction of the rim constrcting the nest cup (stated also by the present authors and emphazised by GOTZMAN and JABŁOŃSKI 1972) gives security to the eggs or chicks.

According to NIETHAMMER (1937) the nests are most often suspended on 2-4 reeds, which does not agree with the present authors' data, or with those obtained by HAVLIN (1971) and DYRCZ (1981). According to the former, the mean number of stems is 4.9, this corresponding with the latter who indicated that most nests were on 4-7 stems, similarly to our data. Extreme numbers of stems indicated by GLUTZ (1991) are 2 and 14, or 15 mentioned by BOZIC (1999).

Reed leaves or strips of them and inflorescences are mentioned as the most important and main nest material of the nominative form of the Great Reed Warbler from various places of its breeding area (among others PTUSHENKO 1954, KLUYVER 1955, GOTZMAN & JABŁOŃSKI 1972, HUDEC 1983, GLUTZ 1991, NABTOCHIY 1991, CRAMP 1992). According to KOZENA-TOUSKOVA (1973), reed fragments constituted nearly 69% of material in 11 nests analyzed by her in detail; however the number of its pieces in particular nests ranged from 5 to 837; the rest belonged to 24 other plant species such as *Carex*, *Agrostis*, *Baldingera*. On the contrary, according to NAUMANN (1905) the main nest material constitutes dry grass leaves and stalks mixed with fibres of *Urtica*, *Epilobium*, with the addition of reed fragments, plant down, from time to time green moss, insect follicles, etc. Among the other materials, are noted various meadow plants, moss, cobweb, fibres of willow and poplar bast, rootlets, *Potamogeton*, and a little of mud, as well as some artificial materials such as fragments of thread, string, pieces of plastic or gum (GLUTZ 1991, NIETHAMMER 1937, PTUSHENKO 1954). Many cited authors stress that the materials gathered from the water surface are wet which makes them soft and easier for weaving. KLUYVER (1955) writes that also when gathering dry material the bird soaks it in water before using it and that the use of wet material is inherent. The latter is supported by the data of the HEINROTHS (1965) who observed that the bird reared soaked a tissue paper in a cage. It seems that, besides making the nest material flexible for weaving (gathering it wet or soaking it), the birds choose material from the point of view of its colour, not contrasting with the

surroundings. This is suggested by HUBER (1939) who described an extraordinary nest made mainly of string; the bird used brownish pieces in spite of the fact that in the same heap there were also red, yellow and blue-green pieces in equal numbers.

The material used for lining the nest cup is less diversified. It is dry (gathered neither wet nor soaked) and delicate. According to NAUMANN (1905) and NIETHAMMER (1937) it mainly consists of grass and reed inflorescences and grass stalks, with rare addition of hair, plant down. GLUTZ (1991) mentions also small piece of a rag. It may be symptomatic that even in the above-mentioned extraordinary nest described by HUBER (1939) in the lining were found only reed fibres (besides swan's down, plant down, and a piece of paper). PTUSHENKO (1954) writes that lining in nominative form consists of small dry leaves, very thin stalks, rootlets, and single small feathers, and it differs from that in *zarudnyi*, in which it is more often made of fragments of reed inflorescences. This statement does not agree with the present authors' data where fragments of reed inflorescences were the main material of the lining (Table XXV). On the other hand, KOVSHAR (1972) found plant down as characteristic of the lining of the *zarudnyi*'s nests besides reed inflorescences.

The process of nest building was studied in detail by KLUYVER (1955). Wrapping long materials round stems supporting the nest and particular stages of building were at least in part confirmed by the present authors'data (see above).

The nests are generally described as deep, cylindrical cups (CRAMP 1992, URBAN et al. 1997, NAUMANN 1905, and others). In the lower part of Table XXVI are included the data cited by authors from various parts of the breeding area of the species. As in the present material, the most variable is the nest height: several authors have cited its upper limit as much higher than the present authors did (up to 38 cm in Slovenia). RUTHKE (1934) pointed out that such high nests, of normal other measurements, have a very thick base, reaching even 25 cm. The measurements of Asiatic form *zarudnyi* cited by KOVSHAR (1972) complete the authors' data very well, and confirm their supposition that the differences between subspecies are mainly due to the small number of the *zarudnyi* nests. It may be of interest that, according to GLUTZ (1991), the nests built among reedmaces are higher than those built among reeds and, and the outer diameter of nests built among reeds is greater. This statement confirms the conclusion concerning the nests of the Black-headed Gull, that outer measurements depend on the nests site conditions (BOCHEŃSKI 1962), and they do not reflect nest cup sizes.

XIV. ORIENTAL REED WARBLER *Acrocephalus orientalis* (TEMMINCK et SCHEGEL, 1845)

The description is based on 7 nests collected in Japan (BMNH), China (BMNH), N.Korea (ISEA), and the Russian Far East (ZMMSU, VVL). The places where the nests were collected are plotted against the breeding range of the species (Fig. 26).

Nest-site

Four of the nests were built in the reed-beds and attached to reed stems, two in willow shrubs (one of the shrubs grew inside the reed bed!) and one in *Artemisia*. In general, sites above the ground prevail over those above water. Even the nests built in reeds were found near the coast line above the ground or mud. The height above the ground (or water surface) was noted in 4 cases as 1.0, ca 1.0, 1.2 and 1.7 m. – this last was built in a *Salix* bush. The nest collected in Japan was built on 5 reeds above the reed leaves, whereas in the Korean nest seven thin reed stems as well as leaves were surrounded by nest material. The nest from China was attached to three reeds. Thus, the nests represent the type "A" of the nest site, but also types "D" and "C".

Nest material and construction

The material most often used for building the outside layer were grass stalks, various stems and reed inflorescences. This last were used in various amount. Plant down and cotton were also used, but not in all the nests and in various amounts. The rootlets and fibres were also noted in some nests. In one case a small fragment of a willow branch with a leave was noted. The inside was always lined

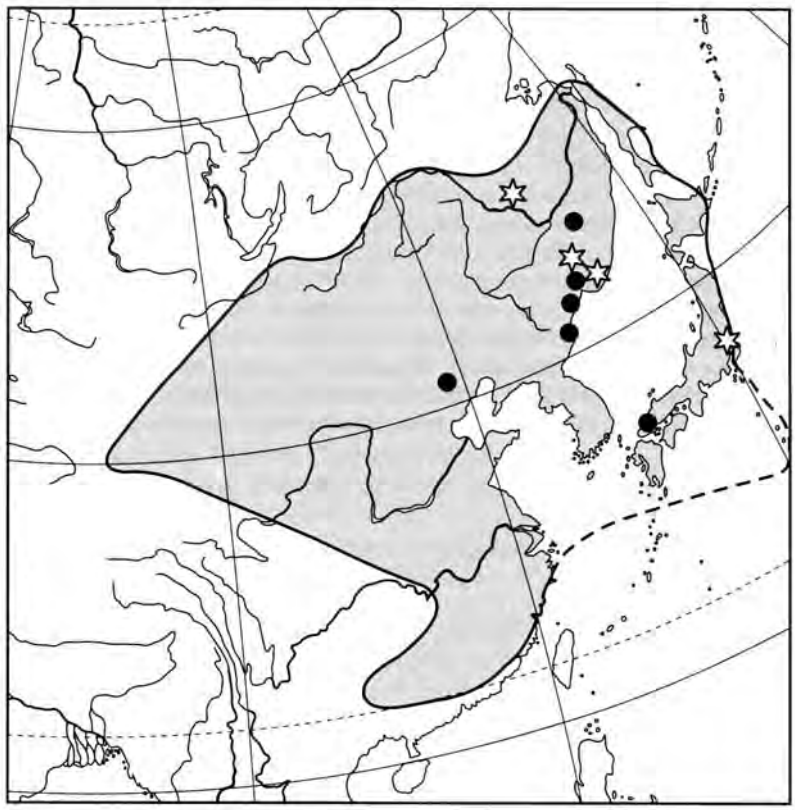


Fig. 26. Breeding distribution of the Eastern Great Reed Warbler *Acrocephalus orientalis* compiled from FLINT et al. (1968), CHENG (1976), and SONOBE (1982), and finding places of the mentioned nests. Explanations as in Fig. 3.

with very thin, elastic, long fragments of stalks, sometimes with fragments of reed inflorescences or their petioles.

All the nests under study were solid constructions, built of dry material, i.e. for example, long thin stalks – many of them surrounded supporting stems from the outside (Fig. 27). In some cases they are mixed with various amount of plant down. There were no traces indicating the using of wet or soaked long leaves or their strips to wind them round the supporting stems. Only delicate and soft fibres may rarely be wound. All the nests had a distinct, solidly woven ring at the nest rim, which always restricted the inside of the nest, so that the opening diameter was always to some degree smaller than the inner diameter of the cup below it. In two cases it was noted that the nest walls were slightly transparent (open worked).

Shape and size of nests

The measurements of the nests are given in Table XXVII. Those from Russian collections (ZMMSU,VVL) seem to be slightly deformed (flattened) by there having been stored in too small boxes; in one of them (from the Ussuriisk region) the outer part of the nest material was taken removed. If so, these nests could be in nature a little higher than is shown in Table XXVII. Nevertheless, the nests can be characterized as high to very high, although, most probably, in nature all of them were very high. They are also deep to very deep. They are round or slightly elliptic. One nest, collected on the Iman River and containing 6 eggs, had the inner diameter distinctly greater than the other nests, although nothing indicated that it was destroyed or deformed, because its ring at the rim was solid.

Additional literature data and comments

According to KOBAYASHI (1932-1940) the Oriental Reed Warbler in Japan "usually links its nests between several stems of reeds or bamboo-grass on the water-edge ... not infrequently ... between boughs of shrubs... usually 1-2 m above the ground". According to JAHN (1942) breeding in reeds or in shrubs or even in trees depends on local conditions. SAITOU (1976) mentions two kinds of reeds very similar to each other, i.e. *Phragmites communis* growing in submerged areas and *Rottboelia latifolia* in dry ground: in the former he found three times more nests than in the latter. Of the 107 nests which POLIVANOVA (1971) found on Khanka Lake, 76 were in deciduous forest on the shore and only 10 in reed-bed standing in water; the nests were built in 17 various plant species, including *Salix* – 25.3%, *Lonicera* – 14%, *Ulmus* – 9.3%, *Phragmites* – 9.3%, *Lespedeza* – 8.4%, *Crategus* – 8.4%, and *Syringa* – 6.6%. Generally, 72% of nests were in bushes, 15.8% in young trees, and the remaining 12.2% in reeds and worm-wood. These data, however, indicate that the type "D" of the nest site prevails. According to DYRCZ and NAGATA (2002), the average height of 71 nests in reed-beds was 125.2 cm above ground or water – they were attached to dead and fresh reed stems. Similar height is given by PANOV (1973) from Ussuriland, but all 5 nests described by him were found in *Salix* bushes. Another nest from Ussuriland was situated ca 50 cm above ground in a raspberry bush and hidden in nettle and cow-parsnip *Heracleum* (VOROBEV 1954). According to PTUSHENKO (1954), nests built in tall grasses are situated more than 50 cm above ground, whereas those built above water – 120-180 cm above the surface; they are attached to grasses, reeds, willows, and other shrubs. TACZANOWSKI (1891) also mentions reeds and willows but the

A B

Fig. 27. The nests of the Eastern Great Reed Warbler *Acrocephalus orientalis*: A – from North Korea (ISEA collection), B – from Japan (BMNH collection).

Table XXVII

Measurements (in mm) of seven nests of the Oriental Reed Warbler *Acrocephalus orientalis*. Literature data cited below own material. [Arithmetic means are given in square brackets]

Locality and collection	Outer diameter	Opening diameter	Height	Depth
Japan (BMNH)	95x100	55x60	110	80
China (BMNH)	90	55	100	60
North Korea (ISEA)	95x100	60x65	110	60
Ussurijsk (ZMMSU)	–	55x62	–	58
Chasan (ZMMSU)	100x115	58x65	70	50
Iman River (VVL)	100	60	80	55
Iman River (VVL)	110	75	80	60

Summarized:

Measurement	N	Min	Max	Mean	SD	CV
Outer diameter	6	90.0	110.0	100.42	7.32	7.29
Opening diameter	7	55.0	75.0	61.43	6.49	10.56
Height	6	70.0	110.0	91.67	17.22	18.78
Depth	7	50.0	80.0	60.43	9.38	15.52

Literature data:	Outer diameter	Opening diameter	Height	Depth
former USSR (PTUSHENKO 1954) (N=17)	[86]	[68]	[93]	[58]
Ussuriland (VOROBEV 1954)	–	60	–	60
Khanka Lake (POLIVANOVA 1971) (N=15)	[103]	[66.3]	[80.1]	[49]
Japan (KOBAYASHI 1932-1940)	80-120	55-65	70-90	55-70

height may reach as much as 210 cm (7 feet). According to POLIVANOVA (1971), the nests were sited between 0.2 and 2.5 m, and only rarely higher, but 63.6% were between 0.5 and 1.5 m; the lowest nests (i.e. below 1.0m) were built in reeds (100%), in willows (84%) and in *Lonicera* (60%). The numbers of reed stems supporting the nests cited by DYRCZ and NAGATA (2002) range from two and six (3.2 in average).

Nest materials found in an external layer include dry grasses, plant down, cotton, rootlets, stems, and inflorescences of *Calamagrostis*, and, in the nests built near human settlements, pieces of coloured thread as well as of white rag; the lining consists of horse and sheep hair (KOBAYASHI 1932-1940, PANOV 1973, PTUSHENKO 1954, VOROBEV 1954). In more than 70% of the nests studied by DYRCZ and NAGATA (2002) plastic strings were used as nest materials. POLIVANOVA (1971) writes that the material is collected up to 200-300 m from the nest, and depends on its availability. (For example, in the forest the bird may actively tear dry grasses out of the ground). None of the cited authors mentions that birds use wet material (collected from the water surface or washed) for building nests. The descriptions by VOROBEV (1954), PTUSHENKO (1954) and POLIVANOVA (1971) state that the elements supporting the nest are surrounded by nest material, which may also be wound round them. According to the latter author 80% of nests were attached with their upper parts to vertical twigs, and their bottoms hung among them – in the case of the remaining 20% the bottoms rested in a forked branch or even on a horizontal twig.

The sizes of nests cited in the literature are given in the lower part of Table XXVII. Those cited by KOBAYASHI (1932-1940) from Japan do not differ from those of the present authors'. The mean outer diameter of the 17 nests from the Russian Far East cited by PTUSHENKO (1954) is smaller not

only than the mean calculated by the present authors but also than each particular measurement, which seems strange. It is even more surprising, on the background of the data from the Khanka Lake given by POLIVANOVA (1971), where the mean outer diameter was even larger than the present authors'. The mean diameters of the nest cup cited by PTUSHENKO (1954) and POLIVANOVA (1971) are similar to each other and larger than the present authors' but it is, however, not clear whether they measured the diameter of the nest opening or of the cup below it. Both values – the mean height and, especially, the depth of nests calculated by POLIVANOVA (1971) are the lowest. This may be at least in part connected with the nest sites in bushes.

XV. CLAMOROUS REED WARBLER *Acrocephalus stentoreus* (HEMPRICH et EHRENBERG, 1833)

The subspecies *brunnescens* JERDON, 1839 is represented by four nests which were collected in Turkmenistan (VVL) and one in Iran (ISEA), whereas the subspecies *siebersi* SALOMONSEN, 1928 is represented by three nests from Java (RMNH, BMNH). The places from which the nests come are plotted on the map (Fig. 28). The nests of those two forms, geographically very distant, are so different from each other that the authors describe them separately, although they belong to the same spe-

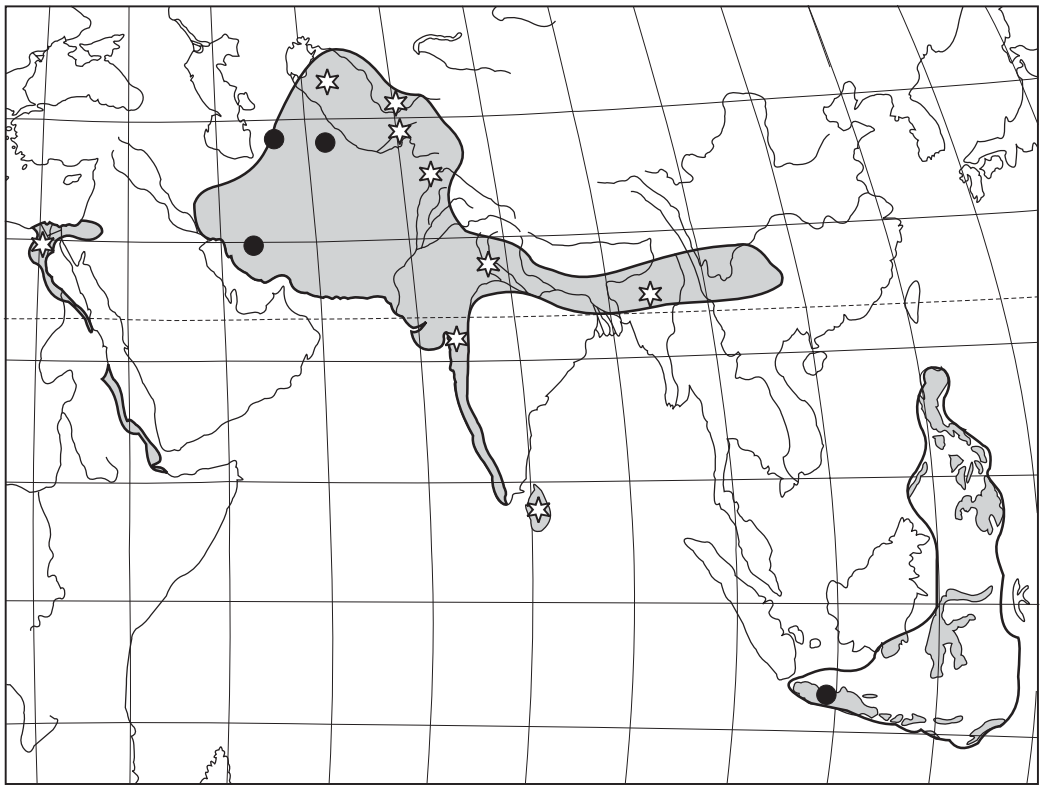


Fig. 28. Breeding distribution of the Clamorous Reed Warbler *Acrocephalus stentoreus* (subspecies listed by CLEMENTS 2000) compiled from ALI & RIPLEY (1973), CHENG (1976), HUE & ETCHECOPAR (1970), KOVSHAR (1972), URBAN et al. (1997). On that background are shown the finding places of nests studied and described in the literature. Explanations as in Fig. 3.

cies (CLEMENTS 2000; HOWARD and MOORE 1991). COURTNEY-HAINES (1991), however, places *siebersi* in the Australian Reed Warbler.

Acrocephalus s. brunnescens

Nest site

All five nests were built in the reed beds and attached to 3 or more reed stems at a height of 80 to 150 cm above the water. They belonged to the type "A" of the nest site.

Nest material and construction

The nests from Turkmenistan were built of natural material only, whereas in the case of the nest from Iran the bird also used man-made materials. The most characteristic, found in all nests, were strips of leaves and fibres of reeds and reed inflorescences, used mainly for making the nest rim and for lining. Various amounts of plant down were admixed in the bottom or in the lower part of walls. The outer layer of the nest from Iran was made mainly of long grasses (thin stalks and leaves). The bird also added something like scraps of wool, a few pieces of pale knitting wool, and rags. One rag was a coarse strip more than 20 cm long and 3 cm wide, woven round just below the rim (Fig. 29). The nest was generally soft, relatively loosely built, and nothing indicated the use of wet material for its building; it was prevented from slipping downwards by reed leaf. Its walls were also slightly transparent in some places. Reed stems supporting all the nests were surrounded and wound round by the nest material on the larger part of the nest height. In all nests there was a soft but distinctly woven ring at the rim, which made the opening diameter slightly smaller than the inner diameter of the nest cup below it.

Fig. 29. The nest of the Clamorous Reed Warbler *Acrocephalus stentoreus brunnescens* from Shiraz, Iran, collected by cpt. J. H. MACNEILE (and presented to ISEA collection).

Shape and size of the nest

Cylindrical nests of the Clamorous Reed Warbler are high to very high and deep to very deep. Their outer contours seen from above are round or nearly round (slightly elliptic). The same is true of the nest opening. Nest measurements are given in Table XXVIII. Most stable is the diameter of the opening.

Table XXVIII

The measurements (in mm) of the nests of the Clamorous Reed Warbler *Acrocephalus stentoreus*. Literature data cited below own material

Locality and collection	Outer diameter	Opening diameter	Height	Depth
A. s. brunnescens:				
Mary, Turkmenistan (VVL)	110	60	100	63
Mary, Turkmenistan (VVL)	105	60	110	63
Mary, Turkmenistan (VVL)	95x100	62	110	50
Kara-Kala,Turkmenistan (VVL)	95x110	60	115	70
Shiraz, Iran (ISEA)	100x105	65	120	70
A. s. siebersi:				
Java (RNH)	70x80	40x40	100	c.50
Java (RNH)	90x90	35x35	165	60
Java (BMNH)	95	48	85	50
Own data:				
brunnescens:	97.5-105	60-65	100-120	50-70
siebersi:	75-95	35-48	85-165	50-60
Literature data:				
brunnescens:				
Middle Asia (PTUSHENKO 1954)	94-102	60-64	195-230	59-64
Kazakhstan (KOVSHAR 1972) N=15	105-132	55-66	84-179	57-66
Tadjikistan (ABDUSALYANOV 1973)	93	57	120-169	60-70
stentoreus:				
NE Africa (URBAN et al. 1997)	110-130	c.60	–	c.60
meridionalis:				
Sri Lanka (PHILLIPS 1952)	c.100	c.50	95	45
Sri Lanka (HENRY 1955)	–	63	–	50

Acrocephalus s. siebersi

Nest site

All three nests were built amidst water plants (reeds or others) and thus belonged to the nest site type “A”. The number of stalks to which nests were attached varied considerably: 3-4, 5, 9. The height above water level was not given in the labels.

Nest material and construction

The material used for building was described in the case of two nests stored in Leiden (RMNH) only. They differed from each other. One of them was built exclusively of plant fibres, thicker in the

outer layer than inside, whereas in the other nest besides fibres, grasses and reed inflorescences were used. The walls, and especially the bottom, were thick. A distinctly woven ring at the rim was present in both nests. Reed stems supporting the nests were surrounded with nest material which wound round them in various ways.

Shape and size of the nest

All the nests belong to very high and very deep. The outer contour and the shape of the nest opening were round or nearly round. The measurements are given in Table XXVIII.

Additional literature data and comments

Most of the data concerns the subspecies *brunnescens*. In Kashmir, according to BATES and LOWTHER (1952), the nests were situated on (2)3 to 4 reeds, occasionally also in a young willow, usually 60 – 120 cm above the water level, whereas according to HUME (1889) the height of the nest site in reeds was about 45 cm (18 inches). Similar are the data of ALI and RIPLEY (1973) from India where the nests were attached to *Phragmites* and *Typha* stems 30 – 100 cm, but more often less than about 50 cm above water level. KOVSHAR (1972) found nests in Kazakhstan in reed beds at 105-150 cm (rarely up to 200 cm) above the water level. Similarly, IVANOV (1969) mentioned from Pamiro-Altay nests built mainly above water at between 15 and 200 cm. Five nests described by ABDUSALYAMOV (1973) from Tadjikistan were situated at 10-15 to 65 cm above water or ground. In Sri Lanka the nests of *meridionalis* (LEGGE, 1875) are situated about 60-90 cm above water, and "supported by five or six rush-stems" (PHILLIPS 1952), or "among reed stems" (HENRY 1955).

KOVSHAR (1972) gave the most detailed description of nest material of *brunnescens* from Kazakhstan and wrote that dead reed leaves being essential material used for building were often soaked. He also mentioned fresh green reed leaves torn by birds, rootlets and rhizomes of marsh plants, grasses, and plant down. According to that author, in the vicinity of human settlements the birds also used sheep wool and various rags; in lining he observed elastic fibres, horse-hair, and rarely, green fragments of reed inflorescences. Green slime found by KOVSHAR (1972) in some nests, especially round the supporting stems in the upper part of the nest, is very interesting. This slime "had to be gathered fresh, wet and sticky". ABDUSALYAMOV (1973) in Tadjikistan also reported sedges, and dry moss in lining. Materials cited by ALI (1969) from Kerala, ALI & RIPLEY (1973) and HUME (1889) from India, and BATES & LOWTHER (1952) from Kashmir are in general similar to those listed above. The nests of *meridionalis* are built of fine grasses, fibres, and strips of dead rush and lined with finer similar material and "rush flowers" (HUME 1889, PHILLIPS 1952, HENRY 1955). One must remember, however, that the name "rush" is also rarely used for reed.

According to ABDUSALYAMOV (1973), the bird starts nest building by selecting a few upright stems growing closely to each other and ties them together with soaked reed leaves. KOVSHAR (1972) stressed that the sides of the bottom were usually supported by the bases of leaves, and that the nest opening was nearly always constricted in relation to the nest cup, as the rim was woven of more elastic material than the walls, which were more or less smooth. The photograph of nest published by BATES and LOWTHER (1952) indicated that the nest material was wound round the twigs of the bush in which it was built. This photograph also showed that the nest to some extant resembled those of the Marsh Warbler and the Great Reed Warbler. ALI & RIPLEY (1973) characterized the nest as a neat, deep, and massive cup, whereas HUME (1889) citing Mr. DOIG described them as "loosely put together". It may be interesting that the nest from Iran is also loosely woven.

CRAMP (1992) discussed *brunnescens* together with nominative *stentoreus* from NE Africa, probably because of their similarity. A very brief description of African nests by URBAN et al. (1997) confirms in general this similarity. Data given by SMYTHIES (1953) from Burma, in spite of the fact that the author wrote about "*brunnescens*", when deal with another subspecies i.e. *A. s. amyae* STUART BAKER, 1922 (CLEMENTS 2000, PTUSHENKO 1954, COURTNEY-HAYNES 1991). Nest material in Burma consists of "rush blades and bark" (see the remark above), while the nest itself is a "large edition of the nest of the British reed warbler" (SMYTHIES 1953).

The measurements of the nests of *brunnescens*, *stentoreus* and *meridionalis*, cited by several authors, are given in the lower part of Table XXVIII. They show that especially the nest height is much more diversified than in the present authors' data (some nests may be much higher). In African nests (URBAN et al. 1997) the outer diameter is distinctly larger than in *brunnescens*, but the opening diameter and the depth lie in the same limits. The same is true for the opening diameter and depth in *meridionalis*. On the other hand, the outer and opening diameters in the three nests of *siebersi* from Java are distinctly smaller; the opening diameter does not even overlap that measurement in other subspecies of the Clamorous Reed Warbler discussed above.

XVI. AUSTRALIAN REED WARBLER *Acrocephalus australis* GOULD, 1838

Two nests of the Australian Reed Warbler from SE Australia, borrowed from the South Australian Museum in Adelaide were studied in detail. The other two nests of the same collection were measured by Dr Ph. HORTON. All of them belong to the subspecies *australis*. The places they come from are plotted on the map (Fig. 30).

Nest site

Though, according to HORTON (in litt.), the nest from Narykita Swamp was "placed 4 ft up in bulrushes in shallow water", it was attached to two reed stems between leaves. The data on the second nest are unknown. One of the nests measured by HORTON (in litt.) was attached to 5 reed stems;

Fig. 30. Breeding distribution of the Australian Reed Warbler *Acrocephalus australis* on the Australian continent after SCHODDE and MASON (1999) and the finding places of nests studied and described in literature. Explanations as in Fig. 3.

concerning another one it is known only that it was built 60 cm above water level. All of them belonged to the type "A" of the nest site.

Nest material and construction

Generally, the two borrowed nests were similar to each other. Their outer layer was made of long fragments of reed leaves, some narrower leaves (of grasses?), reed inflorescences, and fibres. In one of the nests a piece of string was hanged from its bottom. The ring at the rim consisted of reed inflorescences, and the lining of long, thin, and elastic petioles of reed inflorescences only. The consistence of the nest, especially its lower part, may suggest that part of the material was wet when it was used for building. Part of the long materials of the outer layer from the outside surrounds the reed stems supporting the nest, but only some of them are wound round the stems. The ring at the nest rim is distinctly woven and makes the nest opening slightly smaller (narrower) than the inside of the cup. Nest walls may be a little transparent near the supporting reed stems.

Shape and size of the nest

The nests of the Australian Reed Warbler belong to the categories of high to very high and deep to very deep. They are more or less cylindrical in shape (Fig. 31). The contours of two nests described in details, seen from above, were elliptic: their shorter diameters constituted ca 72 and 80% of the longer ones. The same is true of the shape of the nest opening. Their sizes are given in Table XXIX.

Additional literature data and comments

Breeding of the nominative race from eastern Australia is best known. According to COURTNEY-HAINES (1974), HILL (1967) and NORTH (1901-1904), the nests are usually attached to two or several vertical reed stems (it concerns *Arundo donax* – the first author writes that he never found nests in delicate *Phragmites australis*), and also to stems of reed-mace *Typha orientalis* named "bulrush", bulrush (i.e, *Scirpus*), bamboo, dock, and occasionally attached to upright twigs or built in forks of waterside bushes and trees such as willow, paper-bark tree, elm, and mulberry, which may be at some distance from water. Hence, the nests representing the the nest site type "D"

Fig. 31. Two nests of the Australian Reed Warbler *Acrocephalus australis* from SE Australia (SAM collection).

Table XXIX

Measurements (in mm) of four nests of the Australian Reed Warbler *Acrocephalus a. australis*. Literature data cited below own material. [Arithmetic means are given in square brackets]

Locality and collection	Outer diameter	Opening diameter	Height	Depth
Narykita Swamp, SE Australia (SAM)	70x88	48x58	75 (-95)	53
SE Australia (SAM)	65x90	42x60	70 (-100)	c.55
Clayton Creek, NE South Australia (SAM)*	80	40	185	60
South Australia (SAM)*	90	50	115	65
Own data means (N=4)	[81.6]	[48.5]	[123.7]	[58.3]
Literature data:				
NOTRH (1901-1904)**	75.0	43.7	100.0	50.0
COURTNEY-HAINES (1974) nest A**	70.0	45.0	70.0	54.0
nest B**	64.0	38.0	125.0	51.0
COURTNEY-HAINES (1991) (N=?)	[76.0]	[51.0]	[110.0]	[53.0]

* Nests measured by dr Philippa HORTON of South Australian Museum
** Calculated from data given in inches

may also be encountered. The nest may be attached to drooping branches of trees overhanging or trailing in the water (NORTH 1901-1904). According to COURTNEY-HAINES (1991), "it is not unusual for nests to be built on top of cock nests" – such a situation has not been noted in other reed warblers. He writes also that one or more reed leaves prevent nests from slipping downwards, and nests entirely devoid of supports of this kind are rare. This is also shown in a photograph (Fig. 31). The height of the nest site is 60-90 cm (NORTH 1901-1904) and 90-152 cm (COURTNEY-HAINES 1991) above the water level.

Besides fragments of reed leaves, leaves of grasses and reed inflorescences found in two nests described by the present authors and mentioned by NORTH (1901-1904) and COURTNEY-HAINES (1974, 1991), both authors also listed other materials, including decaying water weeds, plant-down, reed-mace catkins and, rarely single feathers. NORTH (1901-1904) also observed pieces of thick soft string, as in one of the nests analyzed by us. COURTNEY-HAINES (1974, 1991) emphasizes that the materials used for building are both dry and wet, and so more easily woven and modeled. The wet pieces of reeds are "usually impregnated with mud", and the birds were observed "dipping dry building material into muddy water" before using it. In general, according to NORTH (1901-1904), nest material varies considerably, depending on the nest site, but part of the material of the outer layer is firmly woven around the supporting stems.

Both NORTH (1901-1904) and COURTNEY-HAINES (1974, 1991) described the Australian Reed Warbler's nests as deep cup-shaped or cone-shaped structures. According to the latter author the nests built in reeds are ball-shaped as their outer diameter at the rim is smaller than in the centre, and those built in bulrush (*Typha* ? – see above), are cone-shaped. He also mentioned cock nests being rather ball-shaped. The measurements given by both authors are cited in Table XXIX below the present authors' own data. Both authors emphasized that the inner diameter of the cup (below the nest rim) is greater than that of the opening – the difference given by NORTH (1901-1904) is 1/4 of

inch, i.e. about 6 mm. According to COURTNEY-HAINES (1991) the "nests are approximately of the same size as those of the Great Reed Warbler". This is not true, and even his own measurements (see Table XXIX) indicate that they are distinctly smaller than the nests of that European species.

COURTNEY-HAINES (1991) wrote about the nest of western Australian subspecies, *A. australis gouldi* DUBOIS, 1901, that it is identical to that of the nominate race, whereas the third subspecies *A. a. carterae* MATHEWS, 1912, listed by him from the Australian continent, is know only from a single type specimen (nests are not known).

XVII. NIGHTINGALE REED WARBLER *Acrocephalus luscinius* (QUOY et GAIMARD, 1830)

According to CLEMENTS (2000) only the birds inhabiting various Mariana Islands belong to the three subspecies of the Nightingale Reed Warbler. Some authors (WOLTERS 1980; HOWARD and MOORE 1991; COURTNEY-HAYNES 1991) include also in *luscinius**, as a subspecies, *A. syrinx* of the Caroline Islands, treated by the present authors, after CLEMENTS (2000) separately as a valid species. The following description, dealing only with the nominative form from the Saipan Island, is taken from the paper by MOSHER and FANCY (2002). The situation of the Saipan (Mariana Islands) in relation to other Pacific archipelagoes inhabited by reed warblers is given in Fig. 32.

Nest site

The Nightingale Reed Warbler is not strictly connected with water habitats; it inhabits reed marshes, elephant tall grass in moist gullies at the top of the mountains, thicket vegetation, dense low forests on rocky grounds on the shore, forest openings, edge of woodlands, and vegetation along streams in wooded canyons (MARSHALL 1949, CRAIG 1992). However, the detailed studies of MOSHER and FANCY (2002) indicate that most nests were built in trees (of them 79 nests i.e. 94% in introduced to the Saipan Island tangantangan tree *Leucaena leucocephala*) at a height from 2.3 to 10.0 m; the nests situated in mangrove and reed wetlands constituted a minority. Hence, the most common is the type "E" of the nests site, while the type "A" (and possibly "C") are rare.

Nest material and construction

MOSHER and FANCY (2002) found that the commonest nest material, used by birds in the outer layer of all examined 73 nests, both in tangantangan forest and in mangrove wetland were, dry vine stems. Besides them there were used dry grass blades and dry bark strips (more frequently in forests), also branchlets of *Casuarina equisetifolia* in wetlands. In the external layer of ten percent of nests in forests a spider web was observed. It is worth noting that the outer layer of one nest found in a reed-bed was constructed also of dry vine stems besides dry, coarse, reed blades. The nests in tangantangan forests were lined mainly with the petioles of that plant, those in mangroves with *Casuarina* branchlets, whereas the nest which was built in reed-bed – with reed panicles.

According to COURTNEY-HAINES (1991), the nests "are of typical acrocephaline architecture". Descriptions and photographs by MOSHER and FANCY (2002) indicate that this is not quite true, because even in the nest hanging among vertical reed stems two other stems supported the bottom; the nests placed in tangantangan trees, both in forks and attached to the trunk and branches, had bottoms supported by at least one branch (Fig. 33) – typical continental reed warbler nests have free hanging bottoms. On the other hand, a typical acrocephaline character is seen in the surrounding of vertical or oblique supporting elements by the nest material. In photographs it is seen that single soft strips or fibres are woven round the supporting elements, but nothing indicates the use of wet material. According to MOSHER (in litt.) the birds were never observed collecting or carrying wet nest material or washing it.

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* According to DAVID and GOSSELIN (2002) the species name should be masculine.

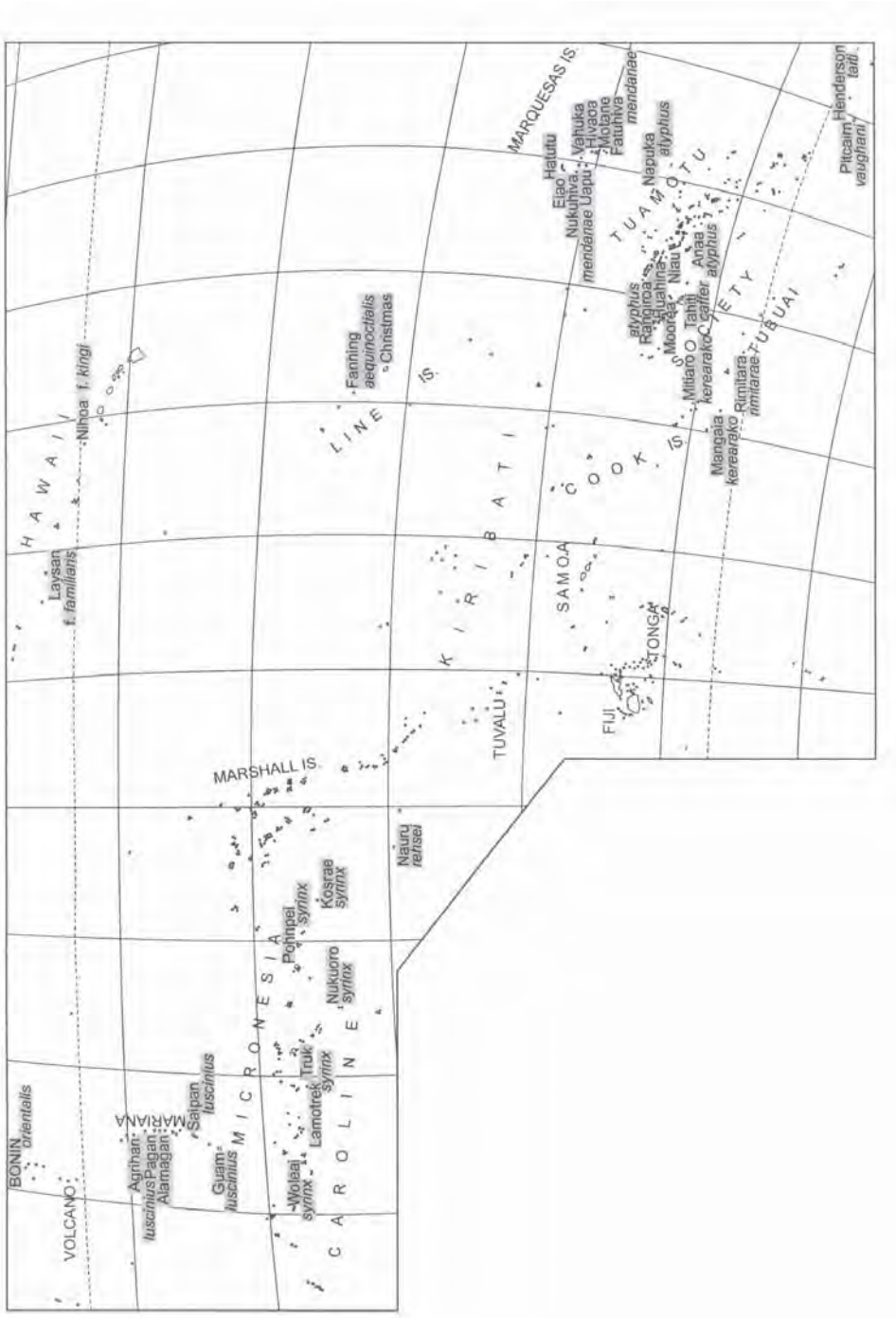


Fig. 32. The map of the Pacific Ocean indicating archipelagoes or islands inhabited by particular reed warbler species (marked in grey). Latin species names are given in italics beside the island's names.

Fig. 33. The nests of the Nightingale Reed Warbler *Acrocephalus luscinius* photographed by dr S. M. MOSHER on Saipan Island, published in the paper by MOSHER & FANCY (2002) in The Wilson Bulletin, 114 (1): 1-10. Author's and Editor's courtesy.

Shape and size of the nest

MOSHER and FANCY (2002) write about two forms of nests, i.e., tightly compact and larger tightly woven, which seems to depend on the nest site. The nest opening is circular or elliptic and in some nests only the ring at the rim slightly narrows the nest cup. The measurements of 66 nests are cited in Table XXX. They indicate that the nests belong to high and very high (the latter seem to be in the minority), and to deep ones. Most variable is the nest hight, and the most stable the diameter of the opening.

Table XXX

Measurements (in mm) of 66 nests of the Nightingale Reed Warbler *Acrocephalus luscinius* from the Saipan Island, published by MOSHER and FANCY (2002). We added only the values of coefficient of variation (CV)

Measurement	Nests built in tangantangan and mangroves						One nest built in reeds
	N	Min.	Max.	Mean	SD	CV	
Outer diameter	65	83	127	106	10	9.4	117
Opening diameter	65	46	86	65	6	9.2	56.5
Height	65	57	177	90	20	22.2	98
Depth	65	29	58	45	7	15.6	43

XVIII. CAROLINE ISLANDS REED WARBLER *Acrocephalus syrinx* (KITTLITZ, 1835)

16 nests were very briefly studied at BMNH, where they are labelled as "*A. luscinia*". All of them came from the Caroline Islands (Fig. 32) therefore they belong to the Caroline Islands Reed

Warbler, regarded now as a distinct species. Four of them were measured. The labels do not contain data on the nest site.

Nest construction, shape and size

All nests are firmly woven hard structures, more or less resembling a sphere with an upper pole cut (Fig. 34). They have a distinct ring at the rim, which makes their openings narrower than the inside of the nest cup. There are no marks indicating the weaving of nest material around vertical plant elements supporting the nests. The measurements are given in Table XXXI. Even in this small sample, both height and depth of the nest were highly variable.

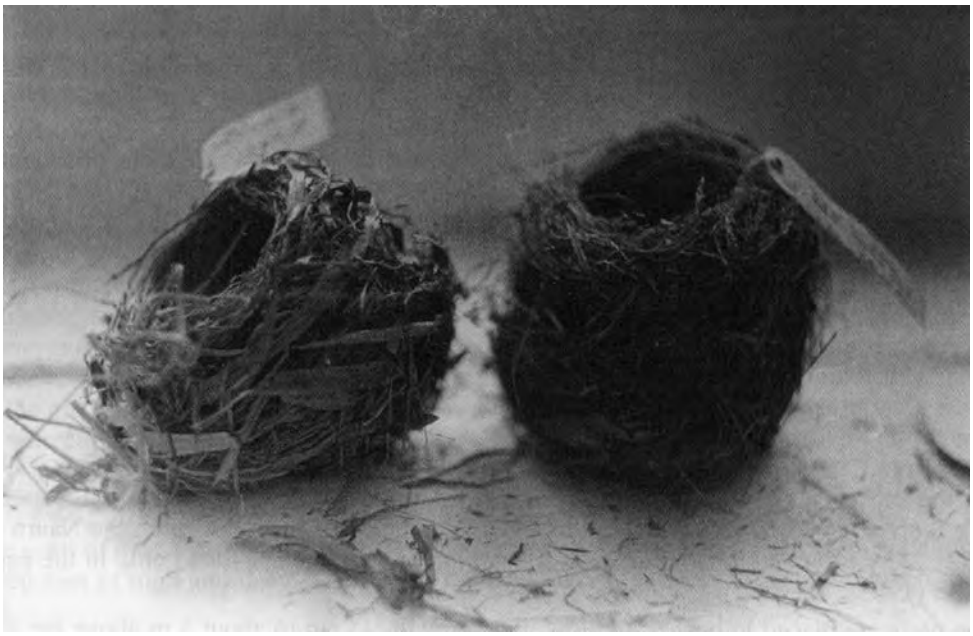


Fig. 34. Two nests of the Caroline Islands Reed Warbler *Acrocephalus syrinx* (BMNH collection).

Table XXXI

Measurements (in mm) of four nests of the Caroline Islands Reed Warbler *Acrocephalus syrinx*. Literature data cited below own material. [Arithmetic means are given in square brackets]

Collection	Outer diameter	Inner diameter	Height	Depth
BMNH	80x100	43x50	88	60
BMNH	82x94	50x55	84	55
BMNH*	92x107	53x60	50	35
BMNH*	110x117	51x60	47	40
means	[97.75]	[52.75]	[67.25]	[47.5]
BRANDT (1962) (N=15)		[56.0]		[45]

* Nests measured by mgr J. WÓJCIK are, according to her description seriously disfigured (flattened).

Additional literature data and comments

Literature data indicate that most nests are situated above ground, and only exceptionally above a water surface. They are built mainly in various forested areas, even in the canopy of a montane rain forest, in such trees as bread-fruit, mango, ivory-palm and coconut-palm trees, in various bushes, but also in open habitats such as stands of tall grass or cane swamps; however nests attached to canes are not common (BRANDT 1962, HARTERT 1900, PRATT et al. 1987). Thus, the nest site spectrum is large and contains the types "E" (the most common), "D", and "F", but also "A". It seems that the nest site depends, at least to some degree, on the local habitat conditions existing on particular isles.

HARTERT (1900) emphasized that the nests "are not hanging up on reeds or twigs, like those of our *Acrocephali*". According to BRANDT(1962), "the nest was often in the centre of a cluster of branches so that it was supported on all sides". These remarks confirm the authors' statement that the nest material is not woven round elements supporting the nest. Unfortunately, BRANDT (1962) did not describe the way the nests were attached to canes. The height of nest site above the ground varied from 1.8 to more than 12 m.

BRANDT (1962) described the nests as "crude, bulky affairs" having thick walls, built of grasses, stems, and leaves, with cups lined with fine grass. It can be presumed that the leaves used for building the external layer were long and belonged to monocotyledonous plants because the author mentioned that some of them were up to 12 mm wide. According to HARTERT (1900), the nests are strongly woven together, made of fibres of coconut palms and other fibres, and they are very deep, this making them similar to the nests of other reed warblers.

XIX. NAURU REED WARBLER *Acrocephalus rehsei* (FINSCH, 1883)

The Nauru Reed Warbler was treated by WOLTERS (1980) and HOWARD and MOORE (1991) as one of the subspecies of the Nightingale Reed Warbler. However, according to MORONY et al. (1975), SIBLEY (1996) and CLEMENTS (2000), it is a valid endemic species on the Nauru Island (Fig. 32). Very brief and incomplete data concerning its nest site are found only in the paper by PEARSON (1962). They are as follows:

The nests are placed in bushes and low undergrowth, 45 cm to about 3 m above the ground. PEARSON (1962) found the nests in forked branches of hibiscus and lime trees. The nests belong to the types "C" and "D" of the nest site. It is difficult to decide whether the type "E" is also represented. PEARSON (1962) stressed that one nest in a low semi-wooded shrub was "bound to upright stems in the usual Reed-Warbler fashion". This sentence may suggest that the stems were surrounded by nest material which, possibly, was wound round them, and that the nest hung among the stems. It may also suggest that in the remaining nests the bottoms rested in forks.

XX. MILLERBIRD *Acrocephalus familiaris* (ROTHSCHILD, 1892)

One nest of the extinct nominative form collected on the Laysan Island of the Hawaii Archipelago (BMNH) was seen. According to WOLTERS (1980), SIBLEY and MONROE (1990), COURTNEY-HAINES (1991), MORIN et al. (1997), and CLEMENTS (2000) the species *familiaris* consists of two subspecies: *familiaris* (ROTHSCHILD, 1892) from the Laysan Island extinct in the twenties and *kingi* (WETMORE, 1923) from the Nihoa Island (Fig. 32). On the other hand, MORONY et al. (1975) as well as HOWARD and MOORE (1991) mention only *A. kingi* as a valid species. Perhaps it is due to the fact that they list living species only.

Laysan Millerbird *A. f. familiaris*

The description is based mainly on a short description and photographs taken in 1902 by FISHER (1903) and the literature data gathered by MORIN et al. (1997):

Nest site

The label of the nest stored at the Tring Museum does not contain data concerning its site. COURTNEY-HAINES (1991, on the basis of MUNRO's 1960 data) wrote that one nest was located on the top of a shrub. FISHER (1903), who saw "many nests", writes that it "is built usually in the midst of a big tussock of grass". According to MORIN et al. (1997), the nests were sited "a couple of feet above ground in tall bunchgrass *Eragrostis variabilis*". Two nests photographed by FISHER (1903) were built among several stems of plants similar to thick grass or reeds, perhaps no higher than one or 1.2 m above ground. They therefore belonged to the type "A" of the nest site.

Nest material and construction

The nest stored at the Tring Museum was not in good condition, so it is only briefly described. It was loosely built, shallower (not so deep) than most of the other nests of reed warblers. No traces of binding round supporting plant elements were seen. COURTNEY-HAINES (1991) described nests as constructed of grass, down, and feathers, and one of them was "lined with feathers of *Diomedea immutabilis*, which formed a fringe around the rim of the cup and almost covered it". According to MORIN et al. (1997), the nests were made of fine rootlets, twigs, dried grass stems and blades, down feathers, and white sea bird (presumably *Diomedea immutabilis*) feathers, and lined with fine rootlets, strips of grass, white feathers, and occasionally some down. FISHER (1903) emphasized that white albatross feathers were "strictly characteristic of all the nests found". MORIN et al. (1997) also cited ROTHSCHILD's report of a nest built "chiefly of down and feathers of sea birds". The nests had to be deep and soft – the latter character agrees with the nest under the present authors' study. In one of the above-mentioned photographs it can be seen that one grass stem was surrounded by nest material (the picture is too small and not sharp enough to state whether fibres are wrapped round the stem), whereas in the other photograph only single strips or fibres loosely surround the stem.

Shape and size of nest

The nests of the Laysan Millerbird were cup shaped and rather small. Perhaps they belonged to the categories of high and deep. Their measurements based on literature data are given in Table XXXII.

Table XXXII

Measurements (in mm) of the nests of *Acrocephalus f. familiaris* and *A. f. kingi*, cited after SINCOCK and KRIDLER (1977), COURTNEY-HAINES (1991) and MORIN et al. (1997). [Arithmetic means are given in square brackets]

Locality and Author	Outer diameter	Opening diameter	Height	Depth
A. f. familiaris of Laysan				
FISHER (1903)	88.8	44.4	–	44.4
COURTNEY-HAINES (1991: after MUNRO 1960)	76	51	–	38
A f. kingi of Nihoa				
MORIN et al. (1997) (N=18)	92-110 [100.4]	48-58 [52.5]	70-105 [86.6]	44-65 [52.7]
BERGER (1972)	76x102	–	–	–
SINCOCK & KRIDLER (1977)	103.6 114.0	52 57	– –	– –

Nihoa Millerbird *A. f. kingi*

No own data. The following description is taken mainly from MORIN et al. (1997) and also from BERGER (1972) and SINCOCK and KRIDLER (1977):

Nest site

The Nihoa Millerbird prefers to nest in dense shrubs, mainly *Chenopodium oahuense* but also *Sida fallax* and *Solanum nelsoni* (BERGER 1972, SINCOCK and KRIDLER 1977, CONANT 1983). The average height of the nest above the ground is 33 cm (N = 35, CONANT 1983). The nests represent type "C" of the nest site.

Nest material and construction

The nest is composed of stem fragments and strips of dead grass (e.g. *Panicum torridum*), rootlets, and some feathers, which were present in all nests. The feathers were mainly of the Great Frigatebird *Fregata minor*, but also of the Nihoa Millerbird; white feathers predominated (BERGER 1972, SINCOCK and KRIDLER 1977).

Shape and size of nest

The nest is cup-shaped. According to SINCOCK and KRIDLER (1977) it is neat and round. It belongs to the categories of high and deep to very deep nests. The measurements are cited in Table XXXII.

Differences between the two subspecies

MORIN et al. (1997) found a difference in the nest site – the Laysan Millerbird nested much higher in bunchgrass, whereas the Nihoa Millerbird in dense shrubs low above the ground. The difference is connected with great differences in the plant cover of the islands. It also seems, that the nests of the nominative form were generally smaller then those of *kingi* (cf. Table XXXII), but this statements is based on a scarce number of measurements of the extinct nominative form.

XXI. POLYNESIAN REED WARBLER *Acrocephalus aequinoctialis* (LATHAM, 1790)

According to PRATT et al. (1987) the Polynesian Reed Warbler is endemic to the Line Islands in the South Pacific where it inhabits dense brush. There are two subspecies: *A. a. aequinoctialis* (LATHAM, 1790) from the Christmas Island and *A. a. pistor* TRISTRAM, 1883, from Fanning Island and Washington Island (extinct ?) (Fig. 32). The following data are based on the literature only.

Nest site

The bird nests in low trees or bushes, particularly beech heliotrope (PRATT et al. 1987). The nests of the nominate form described by GALLAGHER (1960) as well as all 15 nests found by SCHREIBER (1979) on Christmas Island were built in this kind of plant (*Messerschmidia argentea*) "in the tallest, most mature forms with open branching areas below the canopy" and situated "just below the canopy in a 3- or 4-branch fork" (Fig. 35). HOLOYAK and THIBAULT (1984 after TRISTRAM) also mention a nest built in *Pandanus*. Thus, all nests represent the type "E" of the nest site. The height of the nest site above the ground ranges, according to SCHREIBER (1979), from 1.8 to 8.1 m (mean 5.3 m), most being between 6 and 7 m. The heights cited by HOLOYAK and THIBAULT (1984 after BECK) were between less than 1.5 m and 7 m, whereas according to GALLAGHER (1960) between 2 and 5 m. The diameters of 5 heliothrope branches on which the nests were built ranged from 12 to 25 mm, whereas those of branches supporting nest sides – from 6 to 18 mm (SCHREIBER 1979).

COURTNEY-HAINES (1991) describes a nest of *A. a. pistor* from the Fanning Island as "situated in the fork of a *Pandanus* pine, and held securely in place by three stems".

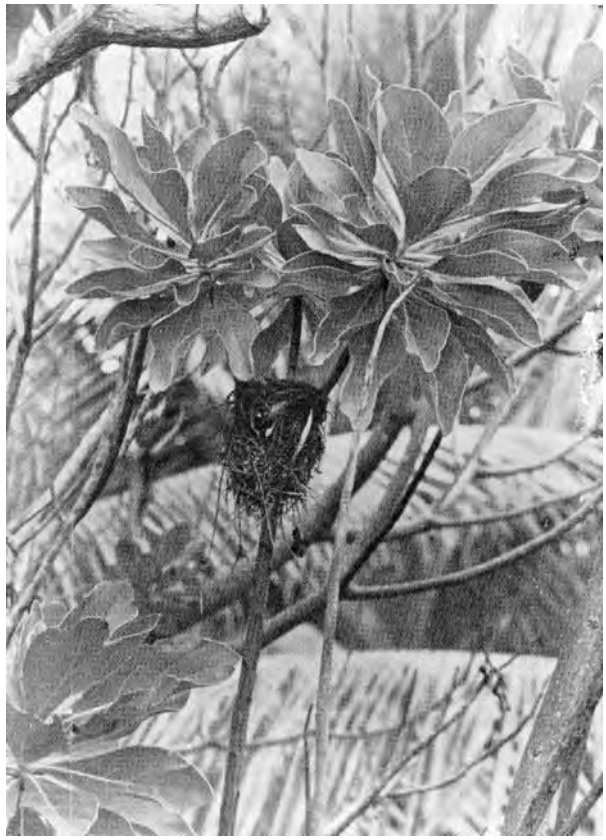


Fig. 35. The nest of the Polynesian Reed Warbler *Acrocephalus aequinoctialis* photographed on Christmas Island by Dr R. W. SCHREIBER, published by Bulletin of the British Ornithologists' Club, 99 (4): 120-124. Editor's courtesy.

Nest material and construction

SCHREIBER (1979) writes that three occupied nests were deep and had complicated bases. In two photographs of the nests in his paper the following details of the nest construction are visible: the ring at the nest rim is distinctly woven, the branches supporting nest sides are surrounded by nest material, especially in lower parts of the nest walls (however, wrapping of branches by nest material is not visible), the loose endings of material (stalks, fibres, etc) do not protrude externally. This picture is confirmed by COURTNEY-HAINES (1991 citing the TRISTRAM'S description) who writes that "the nest is neatly constructed of long grasses and rootlets into which odd feathers and tufts of small herbage were attractively worked [and] tree stems were completely concealed within the fabric of structure. The interior [was] lined and formed exclusively with very fine rootlets". About the same nest HOLOYAK and THIBAULT (1984) wrote that it was made of feathers and grasses. GALLAGHER (1960) listed creeper, grass, roots and down as nest material.

According to SCHREIBER (1979) "the most common plant material are grasses (*Digitaria* sp., *Eragrostis* sp., *Lepturus* sp.), with macerated coconut *Cocos nucifera* frond/bark/fibre and *Cassytha filiformis* also present; coconut husk tendrils were used in the cups of all the nests examined. A nest found within 100 m of human housing contained primarily string and other man-made material such as plastic".

SCHREIBER (1979) suspects that besides breeding nests the birds build 'play' nests which are simpler and more shallow.

Shape and size of the nest

The nests of the Polynesian Reed Warbler belong to the categories of high to very high and deep to very deep nests. The measurements of five nests from Christmas Island given by GALLAGHER (1960), SCHREIBER (1979) and HOLOYAK and THIBAULT (1984 after BECK and TRISTRAM) are shown in Table XXXII. They indicate great fluctuations, especially as concerns the outer diameter and height. Inner measurements of the nest cup are less variable and seem to depend on the nest contents: chicks may distend them.

The measurements of the nest of *A. a. pistor* from the Fanning Island, cited by COURTNEY-HAINES (1991, after TRISTRAM 1883) – 7.6 cm in depth and 7 cm in diameter – are strange in comparison with those given in Table XXXII, as it is not clear whether they refer to the nest exterior or the inside (some authors write "external depth" in place of height).

Table XXXIII

Measurements (in mm) of nests of the Polynesian Warbler *Acrocephalus a. aequinoctialis* from Christmas Island, cited by GALLAGHER (1960), SCHREIBER (1979) and HOLYOAK and THIBAULT (1984 after BECK and TRISTRAM). [Arithmetic means are given in square brackets]

Author		Outer diameter	Opening diameter	Height	Depth
Series (GALLAGHER 1960)	(N=?)	–	[ca58]	[90]	[65]
Single nests (SCHREIBER):	1	80x92	40x50	70	48
	2	85x95	42x50	100	53
	3	95x105	40x50	85	50
	4*	140	49x64	110	55
	5**	72x95	52x58	135	41
(BECK):	6	80	47	–	47
(TRISTRAM):	7	70	–	75	–

Summarized:

Measurement	N	Min.	Max.	Mean	SD	CV
Outer diameter	7	70	140	92.78	22.74	24.50
Opening diameter	6	42.5	56.5	48.67	5.71	11.72
Height	6	70	135	95.83	24.38	25.44
Depth	6	41	55	49.00	4.94	10.08

* 2 nestlings
** 4 nestlings left the nest

XXII. TAHITI REED WARBLER *Acrocephalus caffer* (SPARRMAN, 1786)

The Tahiti Reed Warbler (known also as Long-billed Reed Warbler) is endemic to the Society Islands (Fig. 32). The data on its nesting habits are very scanty.

Concerning nesting habitats PRATT et al. (1987) write that they are bamboo thickets and second-growth forests in river valleys. According to THIBAULT (1975), it "nests in bamboo thickets, less often in *purau*, at heights of up to 30 feet [9 m] or more above the ground". HOLYOAK and

THIBAULT (1984) also mention hibiscus as a nest supporting plant. Thus, most probably, the nests belonged to the types "D" and "E" of the nest site.

The nest itself is a cup-shaped, bulky, elaborately constructed structure, built of various dry plant materials (THIBAULT 1975). According to HOLYOAK and THIBAULT (1984), it is "a big cup made of plants, grasses, rootlets and moss. Mean measurements of two nests: height 17 cm, inner diameter 9 cm, depth 12 cm". The proportions indicate that the nests belong to the category of very deep.

XXIII. TUAMOTU REED WARBLER *Acrocephalus atyphus* (WETMORE, 1919)

Six subspecies of the Tuamotu Reed Warbler inhabit various isles of the Tuamotu Archipelago (Fig. 32). The data presented here are based on the paper by HOLYOAK & THIBAULT (1984) which deals mainly with a series of nests of *A. atyphus ravus* (WETMORE, 1919), with only one nest from the Makatea Island which, according to COURTNEY-HAINES (1991) and CLEMENTS (2000), represents *A. atyphus eremus* (WETMORE, 1919), and with very short data by HOLYOAK (1973) from the Rangiroa atoll – according to CLEMENTS (2000) NW part of the Tuamotu is inhabited by the nominate form *A. a. atyphus* (WETMORE, 1919).

Nest site

The Tuamotu Reed Warbler nests are sited above the ground in "woodland and brush country" (COURTNEY-HAINES 1991). According to HOLYOAK and THIBAULT (1984), the nests of *ravus* are situated in bushes, e.g. *Pemphis acidula*, trees such as *Tournefortia*, *Guettarda* and *Pandanus*, and sometimes in coconut palms. Thus, they represent the types "D", "E", and, more rarely, type "F" of the nest site. The nests are usually 1.5 to 5 m above the ground, but may also be 10 m, built in forked branches. The nests of the nominate *atyphus* on Rangiroa were built among trailing vine growth in bushes (one of them in a forked branch of a bush) 4-8 m above the ground (HOLYOAK 1973).

Nest material and construction

The nests of *ravus* were built of twigs, dry leaves of creepers, coconut fibres (seen in almost all nests) and dry grasses. The cup bottom consists of carefully arranged delicate fibres and dry grasses, and is sometimes lined with small green leaves of *Pemphis*. The nest of *eremus* was made similarly. Writing about the nest sites in bifurcation of branches HOLYOAK and THIBAULT (1984) do not mention wrapping materials round supporting twigs nor the ring woven on the nest rim. HOLYOAK (1973) described one nest of the nominate *atyphus* as "a substantial, deep, cupe-shaped structure built of grass stems, long leaves and the fine stems of vines, with lining of slender vine stems".

Shape and size of nests

HOLYOAK and THIBAULT (1984) write that the nests are "deep cups", but the measurements (Table XXXIV) indicate that their shape is rather hemispheric, the same being true for the inside of the cup. The authors do not write about narrowing of the nest opening in relation to the inner diameter below the rim, which is characteristic of many other reed warblers.

Table XXXIV

Measurements (in mm) of the nests of two subspecies of the Tuamotu Reed Warbler *Acrocephalus atyphus*, cited by HOLYOAK (1973) and HOLYOAK & THIBAULT (1984)

Islands/subspecies		Outer diameter	Opening diameter	Height	Depth
Rangiroa atoll:	*atyphus*	–	–	120	–
SE Tuamotu Archipelago:	*ravus* (series)	90-130	55-80	60	45
Makatea:	*eremus*	110	55	60	35

XXIV. RIMITARA REED WARBLER *Acrocephalus rimitarae* (MURPHY et MATHEWS, 1929)

Only one nest from the Rimitara Island (Fig. 32) was described by HOLYOAK and THIBAULT (1984), who consider the Rimitara Reed Warbles as a subspecies of *A. vaughani*, similarly to WOLTERS (1980) and HOWARD and MOORE (1991). However, according to SIBLEY (1996) and CLEMENTS (2000) it is a valid species.

The nest described by HOLYOAK and THIBAULT (1984) was situated in a forked branch of a tree, 6-7 m above the ground and therefore represented the type "E" of the nest site.. It was built of various grasses and fibres (among others that of coconut). Unfortunately the authors did not mention whether some materials were wrapped round supporting twigs or only surrounded them. The measurements of nest were as follows: outer diameter – 9 cm, inner diameter (opening ?) – 5 cm, and height – 10 cm. It therefore belongs to the category of very high nests.

XXV. PITCAIRN REED WARBLER *Acrocephalus vaughani* (SHARPE, 1900)

The following description of nests of the Pitcairn Reed Warbler is based on scanty literature data (WILLIAMS 1960), then repeated by HOLYOAK and THIBAULT (1984) using latin names and metric scale. Only the birds living on the Pitcairn Island are now taken into account (Fig. 32). Those from the Rimitara and Henderson Islands are treated by WOLTERS (1980), HOWARD and MOORE (1991), COURTNEY-HAINES (1991), as well as by WILLIAMS (1960) and HOLYOAK & THIBAULT (1984), often with some other forms, as a subspecies of *A. vaughani*. However SIBLEY (1996) and CLEMENTS (2000) regard them as a distinct species.

Nest site

The nests of the Pitcairn Reed Warbler are built always in land habitats in various sites. According to WILLIAMS (1960), most common are the nests sited among branches of *Eugenia jambos*, artificially introduced to the island. They may also be found among the top branches of a mango tree, or in the hollow at the base of leaf of *Cordylina terminalis*. The nests represent the type "E" and probably type "D" of the nest site. The height above the ground also varies: between a metre or so ("a few feet") up to about ten metres, but usually below 5 metres.

Nest material and construction

WILLIAMS (1960) briefly noted that the nests were "made of grass or banana fibres". HOLYOAK and THIBAULT (1984) on the basis of one nest collected by BECK, and stored in the American Museum of Nat. Hist., wrote about banana fibres and various dry plants. None of them gave details of construction such as compactness, ring at the rim, or woven nest material round supporting elements.

Shape and size of the nest

According to WILLIAMS (1960) the nests were cup-shaped, whereas HOLYOAK and THIBAULT (1984) write about a deep cup. Nest measurements are given in Table XXXV. They indicate that at least one nest, described by HOLYOAK and THIBAULT (1984) was typical of the category of very high, and deep to very deep nests.

XXVI. HENDERSON ISLAND REED WARBLER *Acrocephalus taiti* OGILVIE-GRANT, 1913

Only one old nest from the Henderson Island (Fig. 32), deformed to some degree, seen perhaps in a collection, was described by HOLYOAK and THIBAULT (1984) as a subspecies of *A. vaughani*. This form is also considered as a subspecies by WOLTERS (1980), HOWARD and MOORE (1991), and COURTNEY-HAYNES (1991), only SIBLEY (1996) and CLEMENTS (2000) regarding it as a valid spe-

Table XXXV

Measurements (in mm) of the nests of the Pitcairn Reed Warbler *Acrocephalus vaughani*, cited by WILLIAMS (1960) and HOLYOAK & THIBAULT (1984)

Author	Outer diameter	Opening diameter	Height	Depth
WILLIAMS (1960)	c.100	–	–	50
HOLYOAK & THIBAULT (1984)	80-100	50x90	140	50-60

cies. The following description is based mainly on papers by GRAVES (1992) and BROOKE and HARTLEY (1995).

According to GRAVES (1992), one nest found by him was built "in a fork of a thin and nearly horizontal lower branch of *Thespesia argentea*, 4 m above ground". Later on BROOKE and HARTLEY (1995) found 27 nests placed in nine various kinds of trees at height of 1.7-7.0 m (mean: 3.6 m). Most nests (7) were built in *Xylosma suaveolens* trees. There are, however, no more details concerning nest site. However we encount them to the type "E" of the nest site.

According to HOLYOAK and THIBAULT (1984), the nest is "a deep cup, similar to the nests of other forms [subspecies of *vaughani*? – Z.B.], built of dry leaves and plant fibres". Two nests observed by GRAVES (1992) were bulky, composed of thin rootlets and *Cocos* fibers and lined with finer material. A general description by BROOKE and HARTLEY (1995) is similar.

The measurements of a single nest cited by GRAVES (1992) and five nests cited by BROOKE and HARTLEY (1995) are assembled in Table XXXVI. There are such serious differences between these data in the case of the outer diameter and the height, that the possibility of a mistake by GRAVES (1992) should be taken into account, or the nest should be treated as an untypical, extraordinary, specimen. Its outer diameter outsizes nearly twice the mean calculated by BROOKE and HARTLEY (1995); comparison of its outer diameter and that of the nest cup indicates extremely thick walls, not observed in any other reed warblers; no relation between its outer diameter and height pointing to the category of flat nests was observed in reed warblers this being in controversy with its description as "bulky" (GRAVES 1992). The height of that nest is distinctly lower than the mean height cited by BROOKE and HARTLEY (1995), even if the lower limit of standard deviation is taken into account. Means calculated by BROOKE and HARTLEY (1995) indicate that nests studied by them were very high.

Table XXXVI

The measurements (in mm) of the nests of the Henderson Island Reed Warbler *Acrocephalus taiti*, cited by GRAVES (1992) and BROOKE & HARTLEY (1995). [Arithmetic means are given in square brackets]

Author	Outer diameter	Opening diameter	Height	Depth
GRAVES (1992) single nest	210x200	55	80	45
BROOKE & HARTLEY (1995), (N=5)	[114 6.2]	[59 8.4]	[132 12.8]	[52 7.3]

XXVII. MARQUESAN REED WARBLER *Acrocephalus mendanae* TRISTRAM, 1883

4 nests collected by D. T. HOLYOAK at Nukuhiva, Marquesas Islands (BMNH) are described. They are labelled as *Acrocephalus* "*caffra*". However, according to PRATT et al. (1987) and

CLEMENTS (2000), *A. caffer* inhabits Society Islands only, whereas at Marquesas (Fig. 32) live eight subspecies of *A. mendanae*, and among them, at Nukuhiva *A. m. percerni*s (WETMORE, 1919)

Nest site

According to the labels noted by the collector, all nests were situated among thin, forked branches of thin trees or saplings in the forest (Fig. 36). They were built at a height of 10 to 25 ft (3 to 8 m) up. Thus, they represent the types "E", and possibly the type "D" of the nest site.

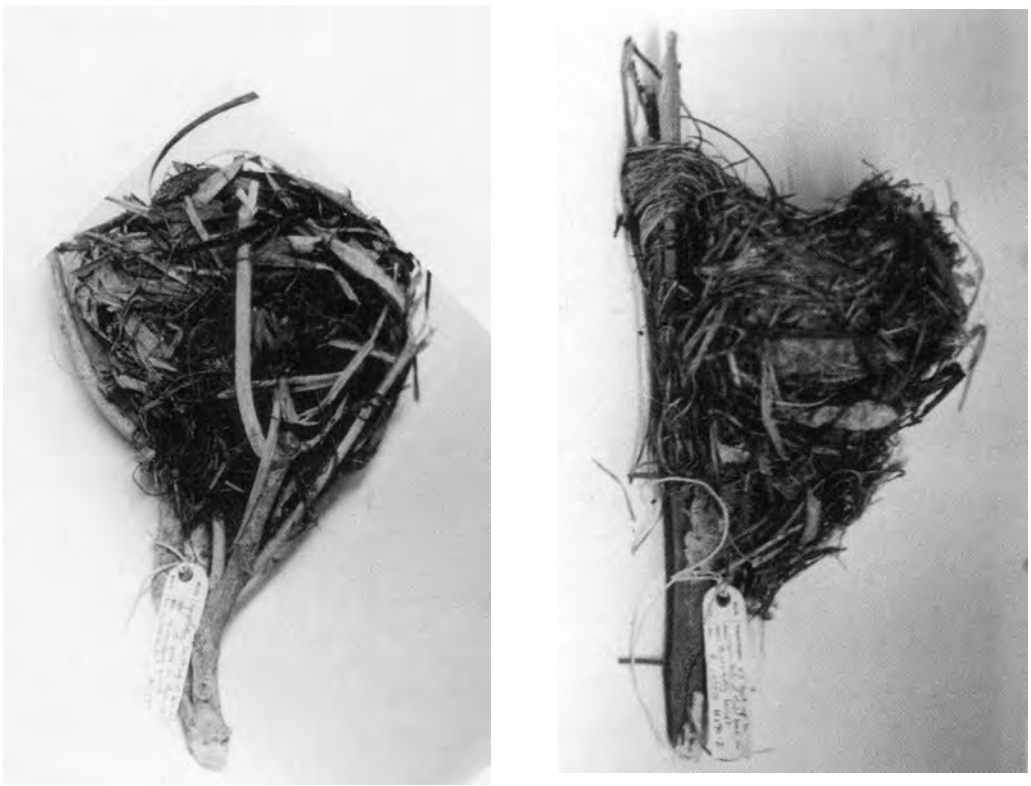


Fig. 36. The nests of the Marquesan Reed Warbler *Acrocephalus mendanae* collected by Dr D. T. HOLYOAK on Nukuhiva Island (BMNH collection).

Nest material and construction

Large, massive nests, built of large amount of material. The material was diversified. In the outer part it contained long leaves of monocotyledonous plants, pieces of bast, rotten leaves, pods and a ca 5 cm long piece of a rough texture or a kind of net. The majority of those elements were arranged horizontally round the nest. The nest cups were lined with delicate materials, i.e., thin stems or so, arranged round the cup. Two of the nests are destroyed, flattened, and seemed to be slightly incomplete. The two remaining nests have solid, well woven, rims. One of them was built between two thin twigs, both twigs being surrounded with nest material. The other nest was built among several twigs, of which only two were surrounded by the nest material; one of those sticks was evidently wound round with long strips of nest material.

Shape and size of the nests

The nests belong to the categories of high and very high as well as deep nests with thick walls and especially thick bottom. Their outer contour and the shape of the opening are elliptic (it is difficult to state if it is natural, or the nests were deformed to some degree after collection). The measurements of two nests stored at the Tring Museum are given in Table XXXVII.

Additional literature data and comments

It is highly probable that the descriptions by HOLYOAK (1975) and HOLYOAK and THIBAULT (1984) deal in part with the same specimens as above, since HOLYOAK (1975) mentions five nests collected by him. Nevertheless, the papers contain more details, based on a greater number of nests. They were situated 1.5 to 25 m high above the ground (the majority between 3 and 12 m), in trees and bushes (among others in *Eugenia rariflora*, *Pandanus*, *Cordia lutea*, *Metrocideros collins* and *Ficus prolixa*). They were attached with fibres, stalks, and moss to the forked branches. The nests described above were built of diversified material but generally they were similar to each other. According to HOLYOAK (1975), the nest material used for building this type of nest also included grasses, coconut fibres, cobweb, and plant down. However, he also described another type, built mainly of moss and hepatices and lined with fibres and plant down. According to HOLYOAK and THIBAULT (1984), the plant material used for building depends on the surrounding habitat; leaves, coconut fibres, bast, and rootlets may occasionally be completed by cotton, ship wool, horse-hair and feathers, which may be found both in outer and inner layers. The measurements cited by HOLYOAK (1975) and HOLYOAK and THIBAULT (1984) are added to Table XXXVII. Their depths, smaller than those measured in the collection, are difficult to explain.

Table XXXVII

Measurements (in mm) of two nests of *Acrocephalus mendanae percernis*, collected at the Nukuhiva I. Literature data cited below own material

Collection/Author	Outer diameter	Opening diameter	Height	Depth
BMNH, N.270.2	100x120	50x75	150	60
BMNH, N.270.3	100x150	50x85	120	65
Literature data:				
HOLYOAK (1975)	–	45-55	120-200	35-55
HOLYOAK & THIBAULT (1984)	120-140	45-60	100-120	35-60

XXVIII.COOK ISLANDS REED WARBLER *Acrocephalus kerearako* HOLOYAK, 1974

The Cook Islands Reed Warbler is represented by two subspecies i.e. *A. k. kerearako* HOLYOAK, 1974, living on Mangaia Island, and *A. k. kaoko* HOLYOAK, 1974, on Mitiaro Island (Fig. 32). Present data are based on the paper by HOLYOAK and THIBAULT (1984) – the authors described the nests from Mitiaro (i.e. of *A. k. kaoko*) only, because on the Mangaia no nest was found.

Nest site

The nests are built in various places, always above the ground, in trees such as *Casuarina*, or in bushes, some of them in forked branches. All of them represent the types “E” and “D” of the nest site. They are situated at a height between ca 1 m and 8 m.

Nest material and construction

The nest material consists of thin dry stems and various fibres. The coconut fibres constitute the major part of the nest mass; they are woven round the nest rim (creating the ring ?). The nest bottom [inside ?] is made of the same kinds of material, but more delicate. Materials of the outer layer surround branches supporting the nest (it is not clear whether or not long materials are woven round the branches).

Shape and size of nests

According to HOLYOAK and THIBAULT (1984), four nests collected were very deep cups with elliptic openings. Their measurements are as follows: outer diameter 80-105 mm, inner diameter ca 50 mm (it is not explained whether it is the mean of long and short diameter of ellipse or one of them only), the depth of cup 50-75 mm. The proportions indicate that the nests most probably belonged to the category of very deep nests.

XXIX. GREATER SWAMP WARBLER *Acrocephalus rufescens* (SHARPE et BOUVIER, 1876)

The description of nests of the Greater Swamp Warbler is based on literature data only. It deals with two subspecies i.e. *A. r. rufescens* (SHARPE et BOUVIER, 1876) and *A. r. ansorgei* (HARTERT, 1906), which is considered as synonymous with *niloticus* (NEUMANN, 1908). Nevertheless, the data come from several places of the breeding area of the species (Fig. 37).

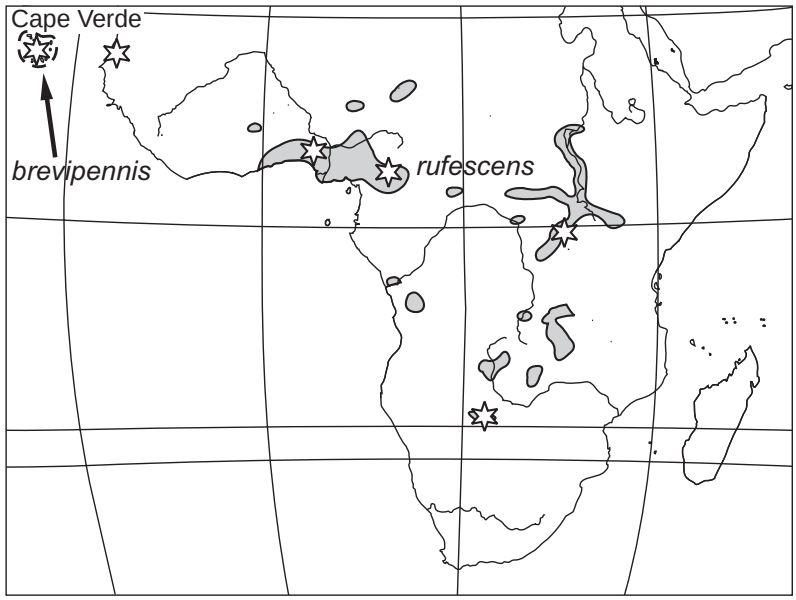


Fig. 37. Breeding distribution of the Greater Swamp Warbler *Acrocephalus rufescens* in Africa, after URBAN et al. (1997). On that background are shown the finding places of nests described in the literature. The Cape Verde Islands are added as a breeding place of the Cape Verde Warbler *Acrocephalus brevipennis*. Explanations as in Fig. 3.

Nest site

The nests were built in reeds and papyrus *Cyperus papyrus* standing in water (WINTERBOTTOM 1971; URBAN et al. 1997), or in *Typha* (DE NAUROIS 1985). SERLE (1953) mentioned also "other aquatic plants", a single upright shoot of a tree growing in the marsh and the tall *Pennisetum* and other grasses, whereas STEYN (1996) recorded in the Okawango Delta a nest in the matted outer

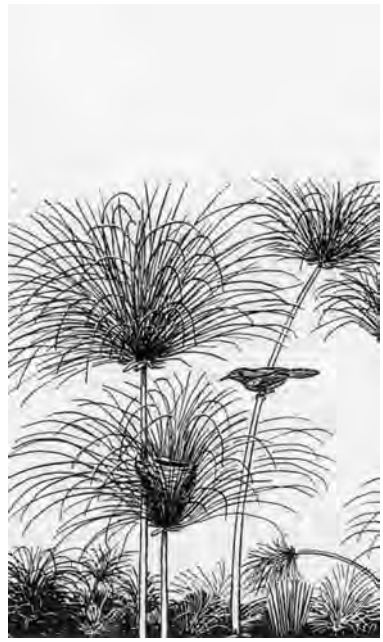
branches of a swamp fig. COURTNEY-HAINES (1991) wrote that *niloticus* built its nests also in elephant grass. According to URBAN et al. (1997), the nests were built 2-2.5 m above the surface of deep water. This agrees with the data of SERLE (1953), and it is repeated by COURTNEY-HAINES (1991) in relation to *A. r. rufescens*. As to *ansorgei* (= *niloticus*) the latter author cites CHAPIN (1953) who described a nest built in papyrus 3.35 m high. The nests were attached to one or more vertical plant elements. Thus, the most common type of the nest site is "A", although the type "E" (or "D") may also be rarely encountered.

Nest material and construction

The outer layer of the nest material consists of dry grass blades and plant stems, of reed, papyrus or grass strips (COURTNEY-HAINES 1991; SERLE 1953; URBAN et al. 1997; WINTERBOTTOM 1971). CHAPIN (1953) also mentions strips of leaf sheaths of the cane-like grass. The strips may be very long (URBAN et al. 1997), or parchment-like (SERLE 1953). In the photograph of the DE NAUROIS (1985) paper (Fig. 38) can also be seen single plant fibres (perhaps parts of stripes) used for attachment of the nest to stems supporting it. The inner layer, i.e. the lining of a cup, is made of finer strips of vegetation and sometimes a few feathers (URBAN et al. 1997), or of small grass strips and fine plant stems (SERLE 1953). Hence, the nest material depends to some degree on local possibilities.

The majority of the Greater Swamp Warbler's nests are of the reed warbler's type (COURTNEY-HAINES 1991; STEYN 1996), i.e., they are suspended between upright stems, being at-

A



B

Fig. 38. The nests of the Greater Swamp Warbler *Acrocephalus rufescens* A – the nest built in reed maces photographed by Dr R. DE NAUROIS in Niayes de M'Boro, NW Senegal (after DE NAUROIS, 1985 – courtesy of the Editor of "Alauda"). B – nest site in papyrus bed in Congo (after CHAPIN 1953 – courtesy of the American Museum of Natural History).

tached by nest material wound round them. However, the photograph (Fig. 38A) in the paper by DE NAUROIS (1985) shows that plant fibres of the nest wall do not wind supporting stems on the whole height of the nest as in the Reed Warbler in Europe, but in several places only. It also shows, that the walls are fairly thick, and not transparent; they end with a firmly woven ring at their rim. According to SERLE (1953), the outer layer is rather loosely woven, while the inner one is more compact.

COURTNEY-HAINES (1991) stressed that in the *niloticus* subspecies there are two types of nests. One of them, built in elephant grass, is similar to that described above. The other type was described by CHAPIN (1953): the nest was placed in the middle of a papyrus head (supported from below) and attached by its rim to one stem of another plant only (Fig. 38 B). However, it is not known how common is that type in papyrus thickets.

Shape and size of nests

The nests are characterized as regular, deep cups (SERLE 1953, URBAN et al. 1997, WINTERBOTTOM 1971), which in *rufescens* are often quite bulky (CHAPIN 1953). Their proportions indicate that they belong to the categories of deep and high nests. Some nests may also belong to the lowest portion of very high nests, because they have a very thick bottom. The photograph published by DE NAUROIS (1985), as well as the drawing by CHAPIN (1953), may indicate that the nests are cone-shaped, being widest in the upper part near the rim, and narrower in the lower parts, and it does not depend on the type of nest site. Nest dimensions are assembled in Table XXXVIII.

Table XXXVIII

Measurements (in mm) of the nests of the Greater Swamp Warbler *Acrocephalus rufescens* cited by SERLE (1953) and URBAN et al.(1997) [in the case of data of the latter nest heights, not given by the author, are calculated from their depth and bottom thickness]

Data source	Outer diameter	Opening diameter	Height	Depth	Bottom thickness
SERLE (1953) (N=?)	85-90	55-60	75-95	55-60	–
URBAN et al. (1997)	81	49	[90]	45	45
	83	52x61	[108]	48	60

XXX. CAPE VERDFE SWAMP WARBLER *Acrocephalus brevipennis* (KEULEMANS, 1866)

The data on the nesting of the Cape Verde Swamp Warbler come from the literature descriptions only. Its distribution is restricted only to the Cape Verde Isles (Fig. 37).

Nest site

The nests are situated above the water surface or above ground, in reed-like plants, i.e. in giant reed *Arundo*, and sugar-cane *Saccharum*, as well as in bushes such as manioc or coffee and in the canopy of orange and eucalyptus trees (ALEXANDER 1898 a, b, BOURNE 1955, BANNERMAN & BANNERMAN 1968, DE NAUROIS 1985, CRAMP 1992, CASTELL 1999). They represent the types "A", "D" and "E" of the nest site. The nests are suspended between two or three stems of a sugar-cane or two or more twigs of a bush or young tree (ALEXANDER 1898 a,b), however CASTELL (1999) emphasizes that each of five nests found by him was suspended between two reeds, at 1.3 to 2.3 m above ground. The height above water or ground surface, depending on the kind of plant, is summarized by CRAMP (1992) as between 0,6 and 5 m. According to BOURNE (1955), nesting in trees and bushes is the adaptation to the "thrush" niche, and differs on particular isles of the archipelago: on S.

Thiago Island the bird breeds in plants densely growing on irrigated areas and only forages in other habitats, whereas on Island Brava it is "living and feeding in the trees and bushes of the town like a typical thrush."

Nest material and construction

ALEXANDER (1898 b) writes that the nests are built of strips of dry blades of maize, dry grass, and "fibrous rind from the trunk of the banana-tree" and lined with fine grass and bents. It is bound to a few vertical or semi-vertical plant elements, i.e., stems or twigs (BOURNE 1955, BANNERMAN & BANNERMAN 1968). Those supporting elements are "passing upwards through the rim" (BOURNE 1955). The distinct ring as well as protruding out material endings from the ring and walls are seen in two photographs of nests published by CASTELL (1999). There is, however, no data about the usage of wet material, nor about the weaving of materials round supporting elements; however the latter is possible because ALEXANDER (1898 b) writes about binding the nest.

Shape and size of the nest

According to ALEXANDER (1898 b) the the nest is of a deep cup-shaped form, while BANNERMAN and BANNERMAN (1968) write that it resembles that of the Great Reed Warbler *A. arundinaceus* which is repeated by CRAMP (1991). None of the authors gives the measurements of the nest, however, according to CASTELL (1999), its size is between *A. scirpaceus* and *arundinaceus*.

XXXI. LESSER SWAMP WARBLER *Acrocephalus gracilirostris* HARTLAUB, 1864

The present authors did not see the nests of the Lesser Swamp Warbler, which is widely distributed in Subsaharan Africa (Fig. 39). The following data are based on descriptions and photographs published in various papers. They deal with the nest of *A. g. leptorhynchus* (REICHENOW, 1879), de-

Fig. 39. Breeding distribution of the Lesser Swamp Warbler *Acrocephalus gracilirostris* in Subsaharan Africa, after URBAN et al. (1997). On that background are shown the finding places of nests described in the literature. Explanations as in Fig. 3.

scribed by CHAPIN (1953) from Congo and, most probably, with those of the nominative form from South Africa.

Nest site

The nest is always built above the water in dense plants. Their list includes reeds, rushes, papyrus, *Arum* lilies, giant *Cyperus* head, shrubs, and a small flooded wattle tree (CHAPIN 1953; ROBERTS Birds of South Africa 1958; STEYN 1971, 1996; URBAN et al. 1997; WINTERBOTTOM 1971). Thus, the sites belong to the types "A" and "D". The height of the site above water varies slightly in particular reports, which may depend on the region of Africa from which come the data; it is between about 20 cm (eight inches – ROBERTS Birds of South Africa 1958) and 1.8 m above water (URBAN et al. 1997). The nest is attached to a few vertical plant elements (stems or others). The mentioned number of nest supporting elements is two, three or a few. A very interesting and outstanding feature cited in ROBERTS Birds of South Africa (1958) is that the nest is sited "very often near or under a larger bird's nest or even near an observation hide". According to STEYN (1996) those are nests of herons.

Nest material and construction

The material used to build the outer layer of nest consists of dried grass blades and bents (WINTERBOTTOM 1971) or of dry reed strips, coarse grass, and sometimes water weed (URBAN et al. 1997). In the nest photographs (STEYN 1971: p. 235 and 1996: p. 170) those strips look as if they were several mm wide (Fig. 40). They surround supporting stems from the outside and some pieces of material (narrower strips or fibres) are also wound round them. There appears to be a firmly woven ring a the rim as in typical reed warblers. According to STEYN (1996), nest material is often wetted by birds before being used. There are no more or less stiff endings of stalks protruding from the nest walls, but some soft material may hang down from the bottom. The nest cup is lined with fine strips, fine grass, and sometimes a few feathers (STEYN 1996, URBAN et al. 1997).

Shape and size of the nest

The nest of the Lesser Swamp Warbler is a cone-shaped structure and belongs to the category of very deep. None of the authors give the nest height, but the photograph published by STEYN (1996: page 170) (Fig. 40) indicates that it belongs to the category of very high nests. The approximate measurements cited by URBAN et al. (1997) are as follows: outer diameter – c. 100, cup diameter – c. 50 (it deals perhaps with the opening of the nest, as the cup itself may be slightly wider) and cup depth c. 85 mm.

XXXII. MADAGASCAR SWAMP WARBLER *Acrocephalus newtoni* (HARTLAUB, 1863)

The description is based on one nest collected on Lake Alaotra, NE Madagascar (Fig. 41) and presented to the ISEA collection by Dr O. LANGRAND.

Nest site

According to a letter of Dr LANGRAND "the nest was built in reeds *Phragmites communis*, about 60 cm above the level of water; the access to the nest was only possible by dugout canoe." Generally, the bird is known to breed in wetlands of Madagascar. "It builds its nest in reeds and papyrus *Cyperus papyrus* (*madagascariensis*) in wet if not inundated environment" (LANGRAND in litt.). Thus, it belongs to the type "A" of the nest site.

Nest material and construction

The nest under study is a relatively firmly built structure with thick walls (ca 20 mm), at the rim ending with a ring, which narrows ca 10 mm the nest opening in relation to the inner diameter of the nest cup. In spite of the fact that "the nest was built in reeds" (see: above), it does not exhibit any

Fig. 40. The nest of the Lesser Swamp Warbler *Acrocephalus gracilirostris* (drawing by M. FINIK from the photograph taken by Dereg LONGRIGG and published by STEYN 1996).

traces of weaving nest material round the reed stems supporting it (Fig. 42), as in typical reed warblers. There are also no traces of use by birds of wet material for building. The outer layer is built mainly of dry grass stems, straight or bent up to several times in various angles, and of long dry grass leaves, also bent. There are also some fragments of stalks and a few small rootlets. Stems and stalks are generally thin. A few pieces of bark and plant fibres appear macerated, but used by birds as dry. In its outermost part the material is more loosely woven than in the deeper one, and stiff endings of stems or stalks may slightly protrude outwards; there are also numerous spider (or insect) cocoons and plenty of cobweb. The cup is lined mainly with the very thin elastic parts of stems without nodes, circuitously arranged; besides them one small feather was found.

Shape and size of the nest

The nest resembles a sphere with the upper part cut (Fig. 42) because the largest outer diameter is ca 1 cm below the rim. Its outer contour, as well as the opening's outline, are slightly elliptic. The measurements are given in Table XXXIX.

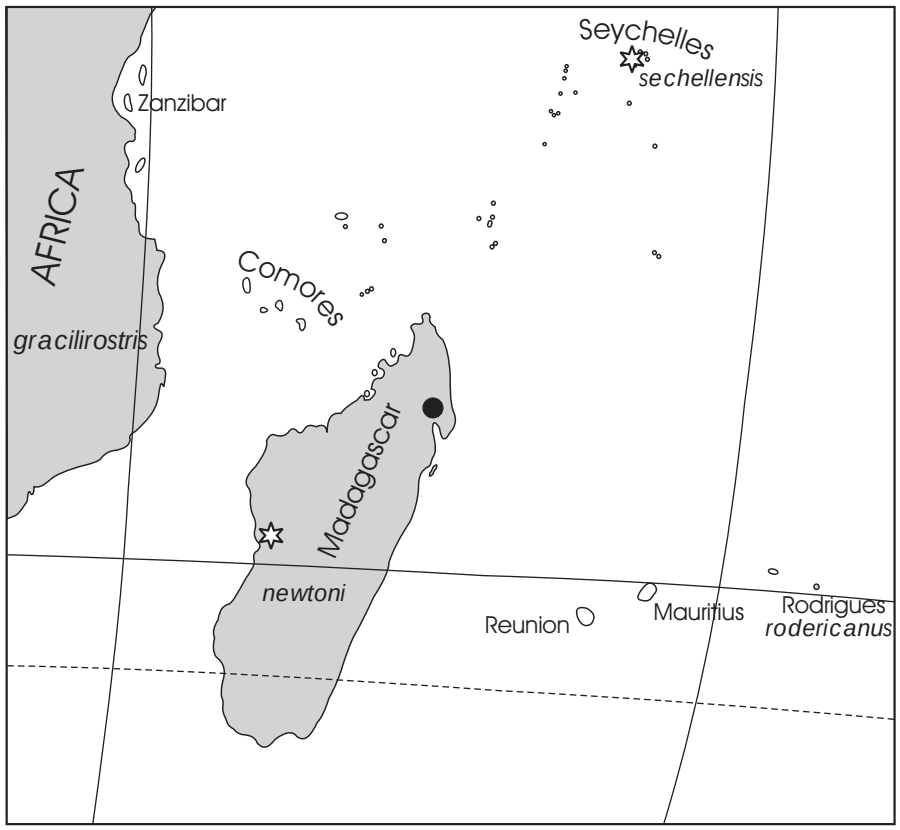


Fig. 41. Western part of the Indian Ocean and islands inhabited by reed warblers. Latin species names are given in italics below the island's names.

Fig. 42. The nest of the Madagascar Swamp Warbler *Acrocephalus newtoni* collected on the Lake Alaotra, Madagascar, by Dr O. LANGRAND (and presented to ISEA collection).

Table XXXIX

Measurements (in mm) of the nests of the Madagascar Swamp Warbler *Acrocephalus newtoni*. Literature data cited below own matertrial

Nest / source		Outer diameter	Opening diameter	Height	Depth
Lake Alaotra (ISEA)		115x105	55x50	65	38-40
Literature data:					
RAND (1936)	1.	90	50	110	50
	2.	100	50	100	55

Additional literature data and comments

Descriptions of the nest of the Madagascar Swamp Warbler are scarce. Contrary to the nest described above, both RAND (1936) and MILON et al. (1973), and, probably repeating their data, COURTNEY-HAINES (1991) write that the nests are situated in the fork of a tree or bush, at a height of 0.75 to 1.5 m above the water. Therefore, the type "D" of the nest site may also be encountered. The detailed descriptions of two nests by RAND (1936) indicate that the nest material, as well as its arrangement, are generally similar to those in the discussed nest, though they vary slightly between each other. The most conspicuous similarity seems to be the loose arrangement of the outermost part of the walls and bottom, while the greatest difference is the use in the nests described by RAND (1936) of plant down, moss, and especially feathers in the lining; these feathers are arranged in such a way that their free ends, curling up over the nest opening, conceal the eggs.

When the nest is situated in the fork, especially in the deep one, it is not necessary to tie it to sticks (or other vertical supporting elements) with nest material. This may be the reason why in the nest under study there are no traces of such tying, though the details of its setting remain unknown.

The values of height and depth of the nests cited by RAND (1936) are higher than those in the present authors' nest under study. The state of brood in this nest remains unknown. (It is quite possible that the nest was collected after its being left by chicks, which could flatten it slightly; and, on the other hand, some loose material at the bottom could be left in situ when the nest was collected.) Nevertheless, the great majority of characters concerning the material, shape, and construction are common to all three nests.

XXXIII. THICK-BILLED WARBLER *Acrocephalus aedon* (PALLAS, 1776)

Six nests come from East Asia i.e. one from the vicinity of Irkutsk, one from Buryat Rep. (both stored in ZMMSU), one from Khabarovski Kray, one from the river Iman, and two from the surroundings of the lake Khanka (coll. VVL). The first two nests therefore belonged to the nominative *A. a. aedon* (PALLAS, 1776) and the four remaining specimens to *A. a. rufescens* (STEGMANN, 1929). The places of their collection are plotted against the background of the breeding distribution of the species (Fig. 43).

Nest site

Data concerning nest sites were noted only in three labels of *A. a. rufescens*. Those nests were built at a height of 0.8, 1.0, and 1.4 m. above the ground. They were built on *Spirea*, an unknown shrub, and a pear shrub respectively, and thus belonged to the type "D" of the nest site.

Nest material and construction

The material used for building the ring and outer layer of the walls consisted of dry grass stalks and herbaceous stems (in one case together with fruits). Some long stalks and stems were bent even several times. Some of their endings protruded outwards. These protruding endings may loosely

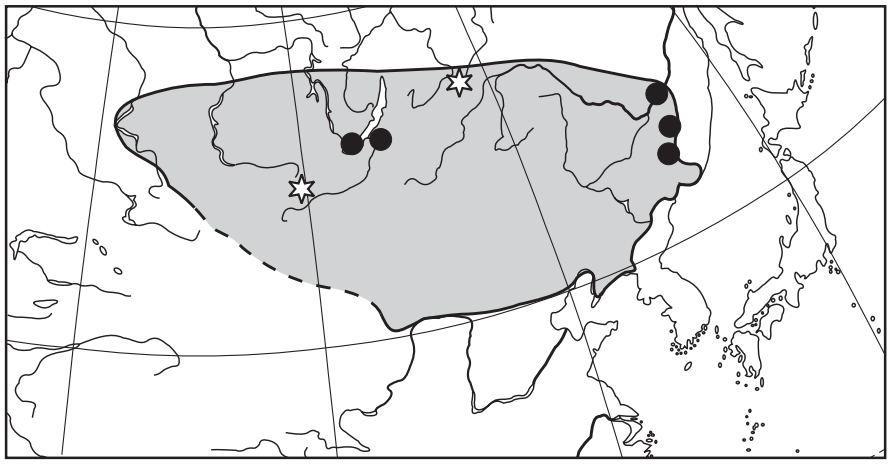
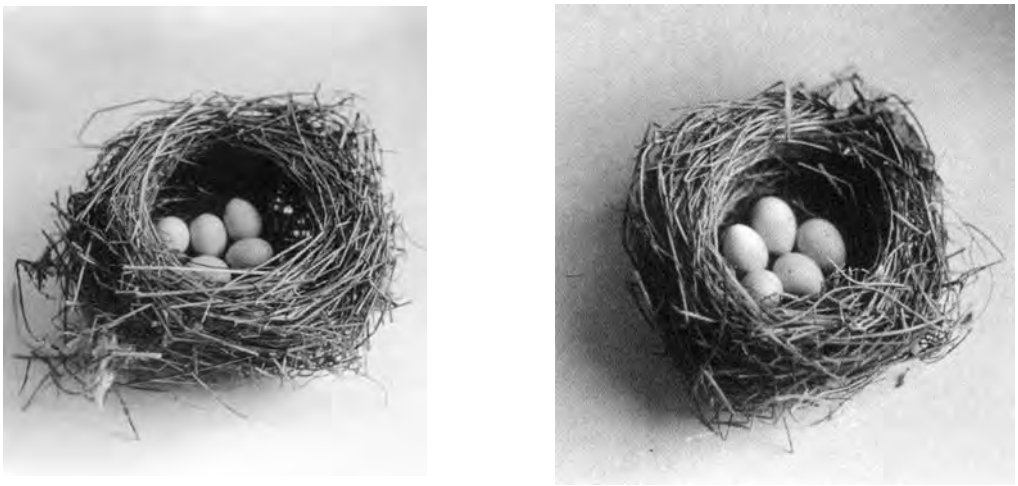


Fig. 43. Breeding distribution of the Thick-billed Warbler *Acrocephalus aedon* after FLINT et al. (1968) and KOVSHAR (1972), simplified. On that background are shown the finding places of nests described in the literature. Explanations as in Fig. 3.

surround a little stems or branches supporting the nest, but in one case only a branch was evidently wound with the nest material. In one case also a leaf of the plant supporting the nest was plaited into the nest wall. The lining of the nest cup consisted of delicate stalks (some of them together with inflorescences). The nests are compact and massive with a distinct ring at the rim, which restricts the inner diameter of the nest cup. In four cases the ring was very strong, and thick, while in the remaining two it was less conspicuous. In spite of the relatively large amount of the nest material, half of the nests had walls or a bottom slightly transparent in some places (Fig. 44).

Shape and size of the nests

All the nests under study were fairly high and deep – indicating that their walls may be thicker than the bottoms. Three nests had slightly elliptical outer contours; the greatest difference of the di-



A B

Fig. 44. Two nests of the Thick-billed Warbler *Acrocephalus aedon*: A – from the vicinity of Irkutsk (transparency of the bottom is seen), B – from Buryat Republic (both nests – ZMMSU collection).

ameters was 10 mm (110 x 120 mm). The opening inside the ring was round in four cases, and in two others elliptic. The measurements are given in Table XL. They are similar in the two subspecies.

Table XL

The measurements (in mm) of the nests of the Thick-billed Warbler *Acrocephalus aedon* (approximate sizes in brackets). Literature data cited below own material

Specimen and collection	Outer diameter	Opening diameter	Height	Depth
A.a.aedon:				
Irkuck surroundings (ZMMSU)	115x120	65x70	75	40
Buryat Rep. (ZMMSU)	110x105	65x65	60	45
A.a.rufescens:				
Ussuri, Khabarovski Kray (VVL)	110x120	50x70	65	50
River Iman (VVL)	110	65	(75)	45
Lake Khanka (VVL)	110	75	(90)	55
Lake Khanka (VVL)	100	70	85	55
Mean:	[110]	[67.1]	[75]	[48.0]
Literature data:				
PTUSHENKO (1954) (*a.aedon*)	120	70	80-100	60-75
TACZANOWSKI (1891)	c.100	c.60	100(-200)	60-80

Additional literature data and comments

Literature data are rather scarce. The nests of the Thick-billed Warbler are generally built in shrubs. PTUSHENKO (1954) listed birch, willow thickets, and *Spirea*. The latter plant is also mentioned by TACZANOWSKI (1891). COURTNEY-HAYNES (1991) writes that it occurs even if there are reed-beds in the vicinity, and that the nests are situated usually "60-90 cm above the ground in the fork of a small tree". According to PTUSHENKO (1954), the nests of the *rufescens* subspecies are built at similar height (50-100 cm), whereas those of the nominative form are situated higher (100-150 cm). This difference does not correspond to the authors' data because one nest from Lake Khanka (belonging to *rufescens*) was built at the height of 140 cm. In the case of *aedon*, PTUSHENKO (1954) also describes nests resembling those of the Reed Warbler, firmly attached to several thin sticks, which are wound with the nest material. Such nests were also mentioned by TACZANOWSKI (1891). To the contrary, COURTNEY-HAYNES (1991) emphasizes that the nest is quite unlike nests of typical reed warblers, being untidily fashioned on the outside. Of *rufescens* nests PTUSZENKO (1954) writes only that they are negligible.

Nest material listed by PTUSHENKO (1954) and COURTNEY-HAYNES (1991) is similar to that described by the present authors; the only addition by PTUSHENKO (1954) is horse-hair, and by COURTNEY-HAYNES (1991) small rootlets in the lining of some nests. TACZANOWSKI (1891), however, emphasizes that there are no feathers or down in the material. The measurements of the nests of nominative form cited by PTUSHENKO (1954) differ slightly from those of the nests studied by thee present authors: they are higher and deeper. The same is true of the data of TACZANOWSKI (1891), but according to him the height reaches 20 cm when it is measured together with a "tail" below the nest bottom. Such a "tail" had not been preserved in the nests stored in collections. To the contrary, according to COURTNEY-HAYNES (1991), the nests are shallower than those of typical reed Warblers. Perhaps COURTNEY-HAYNES (1991) based his description on the nests of *rufescens* only.

It seems that the differences between the nests of the two subspecies are too vague for treating the subspecies separately.

XXXIV. SEYCHELLES BRUSH WARBLER *Acrocephalus sechellensis* (OUSTALET, 1878)

The nests of the endemic Seychelles Brush Warbler were not seen by the authors and the data on the nest building is rather scanty. It was known from the Cousin Island only and seriously endangered. To conserve the species parts of this population were translocated in 1988 and 1990 to two neighboring islands, Aride and Cousine (Fig. 41), where they formed a healthy breeding populations (KOMDEUR 1994). The literature data concerning the nests deal both with parent and translocated populations.

Nest site

According to GAYMER et al. (1969) and PENNY (1974) the nests are usually sited in vertically forked branches in the canopy of dense trees and bushes or just below the canopy. The same is true in the case of 25 nests of birds introduced to Cousine Island (KOMDEUR 1996). Kinds of plant are not given. Only VESEY-FITZGERALD (1940) writes about a bamboo. The nest sites belong to the type "D". The height above the ground is described as 7 to 10 feet i.e. ca 2.10 to 3.05 m (GAYMER et al. 1969, VESEY-FITZGERALD 1940).

Nest material and construction

VESEY-FITZGERALD (1940) described nest material generally as "dry grass-blades and vegetable fibre". According to PENNY (1974), the nests were made of coconut fibres and grass, and lined with finer material. The latter author also mentioned that in the vicinity of human settlements some other materials were observed, such as cotton rags, wood shavings, and in one case even a whole polythene bag. Nest materials as well as construction can be seen in photographs. Thus, in a picture published in the book "NA TROPACH SEKRETÓW PRZYRODY" (1999) nest material of the outer layer consisted mainly of soft strips of a brown bast and/or grass leaves, which, similarly to *A. palustris*, were wound round supporting twigs. Some of their endings hung loosely. There were also some stiff stems, their endings protruding outwards (one of them as about as long as the nest diameter).

The photograph of two nests published by KOMDEUR (1996) indicate that vertical or slant supporting elements were surrounded by nest material (some of them with a few "fibres" only), and a part of the material is wound round them (Fig. 45). The outer layer was made of thicker materials, some of which were stiff with protruding endings. Inside the nests "thin stalks" were seen. The walls of both nests were thick and not transparent. In both nests there was also a distinct ring at the rim, which perhaps slightly narrowed the opening of the cup.

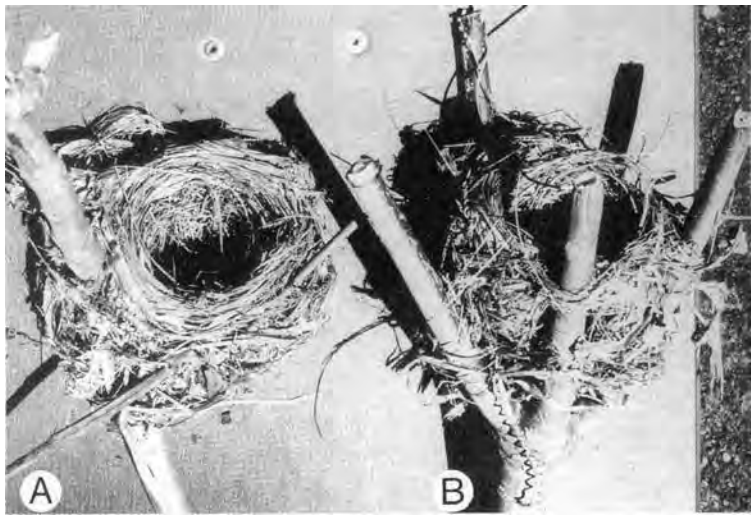


Fig. 45. The nests of the Seychelles Warbler *Acrocephalus sechellensis* collected on Cousine Island (reproduced after KOMDEUR 1996 – courtesy of the editor of Behavioral Ecology, 7 (3): 326-333.

Shape and size of the nest

VESEY-FITZGERALD (1940) described a nest as a little oval cup, whereas according to GAYMER et al. (1969) it is a quite large open cup, somewhat untidy in appearance and, according to PENNY (1974), it is neat, strong, and solid.

The measurements of one nest given by VESEY-FITZGERALD (1940) were "3 in. in diameter and 1.25 in. deep". They were next cited by GAYMER et al. (1969) as "the internal measurements [...] as 8 x 3 cm deep". It is not, however, quite sure whether "3 in. in diameter" concrns the diameter of the nest opening, and, moreover, the calculation is not precise, because 3 inches are equal 7.6 cm.

XXXV. GENERAL COMMENTS

As mentioned in the Introduction, nest construction was used as a diagnostic character in the systematics of various groups of birds. It was mainly done at the order or family level. Thus, MAYR and BOND (1943) proposed the classification of Hirundinidae, which next was generally confirmed and supported by molecular data (WINCLER & SCHELDON 1993). LACK (1956) did the same for the swift family; forty years later LEE et al. (1996) discussing Apodinae nests structure on the background of DNA relations stated that "nest characters are not philogenetically reliable in swiftlets" – this statement was however criticized by ZYSKOWSKI and PRUM (1999) as based on a small number of nest characters (only four). The latter authors based their phylogenetic analysis of the nest architecture of Furnariidae on 24 characters. MOREAU (1960), CROOK (1963) and COLLIAS & COLLIAS (1964) used nest building for the systematics of Ploceidae. Systematic implications based on the nest structure in Remizidae were proposed by BOCHEŃSKI (1998).

The nests of particular species belonging to the same genus are usually similar to each other. Nevertheless groups proposed by BOCHEŃSKI (1968) within the genus *Turdus* were then confirmed by chromosomal data (PANOV & BULATOVA 1972). In the case of African *Agapornis* parrots EBERHARD (1998) stated that nest similarities are parallel to DNA data.

So far, only HAFFER (1991) has used nest structure as one of the characters to divide the total cluster of species within the genus *Acrocephalus* into two general groups. BRUNER was another author (unpublished BRUNER's paper after PRATT et al. 1987) who stated that *A. mendanae* is not a subspecies of *A. caffer*, because the two forms differ, among others, in nesting habits. Unfortunately, BRUNNER's unpublished paper could not be obtained.

A comparison of data concerning the nests of particular species (Table XLI), based on 38 characters, taken from the descriptive part of this paper was prepared. Not all characters are clear-cut, and observed in all specimens of a given species. It can be presumed that some characters have been overlooked by some authors or treated as "not important" and not included in their descriptions. A typical example is the use of wet materials for building the external layer of the nest by the Great Reed Warbler and some other species. In the case of the Great Reed Warbler it was not mentioned even by PTUSHENKO (1954) or KOVSHAR (1972), in spite of the fact that its nesting habit is the best known within the genus. It is possible that the nests described by some authors were observed when they were already finished and/or dried, i.e. not early in the morning at the time of building. Possibly, species that do not breed directly above water and weave soft nest material round the supporting elements, such as the Marsh Warbler or Blyth's Reed Warbler, use material soaked by rain or morning dew, but this was never noted. That is why one of the listed characters is "wet material not noted" instead of "not used". Similarly, there are not sharp divisions among the three classes of the nest site heights: up to one meter, several dozen centimeters to three meters, and a few meters up to even 20 m (accounting for exceptionally higher places in species belonging to the two former classes).

List of characters compared in Table XLI:

1 – nest situated above water (or above ground, but very close to water);

2 – nest situated above ground; the vicinity of water not necessary (may be accidental);

3 – nest situated in a sedge tussock protruding from shallow water of the marsh (nest not directly above water surface);

4 – nest attached to stems of emergent water plants (e.g. various kinds of reed, reed-mace, rush, papyrus, etc) growing in water or very close to it;

5 – nest situated among herbaceous land plants (e.g. nettle, wormwood, corn, elephant grass, also reeds growing on a wet ground at various distance from open water), which may be mixed with grasses, or at the foot of a bush;

6 – in small or large bushes (e.g. willow or tamarisk), also in small trees growing on land or in water;

7 – nests in trees, a dozen or more meters high;

8 – nests in palm trees;

9 – nest situated usually lower than 1 m above ground or water level – higher situations are exceptional;

10 – nest situated usually between a few dozen cm and 3 m above ground or water level – higher situations are exceptional;

11 – nest situated several meters (even more than 20 m) above ground;

12 – soft, not bent, material (reed leaves, their strips, various fibers, dry inflorescences, etc.) prevails in the construction;

13 – besides soft material, in outer layer of the nest there are many stiff stalks and stems, the longer of them being bent even a few times;

14 – ends of materials (stiff stalks or soft strips or fibres) protruding or hanging off the outside surface of the nest walls;

15 – wet material collected from the water surface (or purposely washed by birds) is used for building the external layer of the nest;

16 – wet material was not noted;

17 – mud or slime (collected by birds together with wet plant fragments) is used in nest construction;

18 – various kinds of plant down are usually found in nest construction

19 – moss in various amounts is found in the majority of nests;

20 – bird feathers of various length are used as nest material, mainly for lining, but also in the construction of the external layer;

21 – animal hair or wool (mainly in lining, but in some cases also in the external layer) is encountered in a number of nests;

22 – insect or spider cocoons and/or cobweb is used for building the external layer and/or the ring;

23 – thick walls of nest are not transparent (open-worked);

24 – nest walls may be transparent (open-worked) to a various degree;

25 – a firmly woven ring at the rim of the nest is present, which makes the opening narrower than the inside of the nest cup;

26 – ring at the rim is weakly woven or lacking;

27 – nest bottom always hangs among more or less vertical elements to which the nest is attached;

28 – nest is "pressed" among dense sedges, grasses and so on, so that its bottom rests, at least on its sides, on oblique parts of stems which are pushed aside;

29 – nest bottom does not hang but rests in fork (or something similar);

30 – soft (mainly wet) nest material is woven tightly round vertical elements supporting the nest;

31 – soft material surrounds supporting elements but is not woven around them;

32 – some stiff ends of nest material, protruding from tits walls may cross outside vertical elements surrounding the nest;

33 – some nests may be tied to elements standing relatively far away by means of "basket handles" (also named "ears");

34 – nest proportions resemble hemisphere (nest height is approximately as great as half of the outer diameter);

35 – nest is high (its height is greater than a half - up to the total length of the outer diameter);

36 – nest is very high (its height exceeds the outer diameter);

37 – nest is deep (its depth is larger than half – up to the total of diameter of the nest opening);

38 – nest is very deep (its depth exceeds the diameter of the nest opening).

It is interesting to see how the nest building corresponds with phylogenetic relations and systematics. To answer this question a comparison of the numbers of characters that differ in particular forms taken from Table XLI to the total numbers of compared characters (unknown characters of both compared taxa were not included). This was carried out in spite of the fact that values of particular characters were not the same.

The first problem is whether nest building reflects particular subgenera distinguished in the genus *Acrocephalus.* As mentioned earlier, HAFFER (1991), on the basis of nests, divided all acrocephalines into two groups. One of these, having untidy nests, includes the subgenus *Calamodus* with four species, i.e. *schoenobaenus*, *sorgophilus*, *bistrigiceps*, and *paludicola*. The second subgenus *Lusciniola* includes one species – *melanopogon*. COURTNEY-HAINES (1991) on the basis of the general type of feather coloration, joins these two subgenera into "streaked reed warblers". Two recent papers, based on molecular data (LEISLER et al. 1997 and HELBIG & SEIBOLD 1999), do not contain all acrocephaline species. In the case of "streaked reed warblers" they omit *sorgophilus*, but in both papers the remaining four species are generally closely related, included into one subgenus/genus *Calamodus*, and according to LEISLER et al. (1997) "the retention of the genus *Lusciniola* for *melanopogon* is unjustified". Moreover, in the cluster analysis using morphological characters (LEISLER et al. 1997) *melanopogon* is closest to *paludicola*. On that background the nest similarity based on data from Table XLI is absolutely controversial, because the percentages of characters separating *melanopogon* from *bistrigiceps* and *melanopogon* from *paludicola* are 43% and 54% respectively (the latter is the highest found in this study). Those differentiating *melanopogon* from *orientalis* and *melanopogon* from *arundinaceus,* belonging to the subgenus *Acrocephalus*, are more than two times lower (21% and 13%).

The subgenus *Phragmaticola* contains only one species, *aedon*. Its nests were compared with those of the members of the subgenera *Calamodus*, *Notiocichla*, *Acrocephalus* and *Calamocichla*. *Bistrigiceps* and *melanopogon* were chosen from the subgenus *Calamodus* because these species were included earlier in two different subgenera (HAFFER 1991) or even genera (WILLIAMSON 1960, MORONY et al. 1975). The nests of *aedon* differ from those of *bistrigiceps* in 9 characters of 35 (i.e. 25.7%) and from *melanopogon* in 15 out of 35 (42.9%). The nests of *scirpaceus fuscus* from subgenus *Notiocichla* were chosen because of their Asiatic distribution; they differ from the nests of *aedon* in 15 characters out of 32 (46.9%). The subgenus *Acrocephalus* is represented by two species: *orientalis* and *arundinaceus*. The former, inhabiting as *aedon* to the Far East, differs in ten characters out of 35 (28.6%), whereas the latter, living west of *aedon*, differs even in 18 characters out of 35 (51.4%). Two specied were compared in the subgenus *Calamocichla*, i.e., *rufescens* from West Africa, and *newtoni* from Madagascar. They differ from each other in eleven out of 33 characters, thus in 33.3% whereas from *aedon* they differ in 39.4% and 41.2% respectively. There are two possible explanations of the results. The smallest differences are between *aedon* and two species living generally in the same area (*bistrigiceps* and *orientalis*) – differences between representatives of subgenera living in geographically distant areas are usually larger. On the other hand, the differences may depend on the amount of data on the compared species. The results of the comparison with *fuscus* (based on relatively sparse data) suggest that the first explanation is more probable.

Table XLI

Characters connected with the nest site, material, construction and proportions in the discussed reed warbler forms of the *Acrocephalus* based on own materials and literature data (for the descriptions of particular characters see text). The sequence of species follows CLEMENTS (2000). Legend: **1** – character present in all or in most nests (typical), 1 – character present in a part of nests only, 1? – charater not surely pointed but deduced, 0 – character absent, 0? – absence deduced, ? – nothing known about character

Species / Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
melanopogon	**1**	**1**	0	**1**	**1**	1	0	0	**1**	0	0	**1**	0	0	**1**	0	0	**1**	0
paludicola	**1**	1	**1**	1	1	0	0	0	**1**	0	0	**1**	1	1	?	1	0	**1**	1
schoenobaenus	**1**	**1**	**1**	1	1	1	0	0	**1**	1	0	1	**1**	1	0	**1**	0	1	**1**
bistrigiceps	0	**1**	0	0	**1**	1	0	0	**1**	0	0	**1**	**1**	**1**	0	**1**	0	0	0
agricola	1	1	0	**1**	1	1	0	0	**1**	0	0	**1**	0	0	**1**	0	0	**1**	0
concinens	0	**1**	0	**1**	**1**	1	0	0	**1**	0	0	**1**	0	0	?	**1**	0	**1**	1
scirpaceus scirpaceus	**1**	1	0	**1**	1	1	0	0	**1**	1	0	**1**	0	0	1	0	0	1	1
scirpaceus fuscus	**1**	0	0	**1**	0	1	0	0	1	**1**	0	**1**	0	0	1	0	1	1	0
baeticatus	**1**	1	0	1	1	1	?	0	**1**	1	0	**1**	0	**1**	?	**1**	0	1	0
dumetorum	0	**1**	0	0	**1**	**1**	0	0	**1**	0	0	1	1	1	0	**1**	0	1	0
palustris	1	**1**	0	0	**1**	**1**	0	0	**1**	1	0	**1**	**1**	**1**	0	**1**	0	1	1
arundinaceus arundinaceus	**1**	1	0	**1**	0	1	0	0	**1**	1	0	**1**	0	0	**1**	0	0	1	1
arundinaceus zarudnyi	**1**	0	0	**1**	0	0	0	0	**1**	0	0	**1**	0	0	**1**	0	1	1	0
orientalis	1	**1**	0	**1**	1	**1**	0	0	1	**1**	0	0	**1**	0	0	**1**	0	1	0
stentoreus brunnescens	**1**	0	0	**1**	0	1	0	0	**1**	**1**	0	**1**	0	0	1	0	1	**1**	1
stentoreus siebersi	**1**	0	0	**1**	0	0	0	0	?	?	?	**1**	0	0	?	?	0	0	0
australis	**1**	1	0	**1**	1	1	1	0	**1**	1	0	**1**	0	0	**1**	0	1	1	0
luscinius	1	**1**	0	1	1	**1**	**1**	0	0	1	**1**	0	**1**	**1**	0	**1**	0	0	0
syrinx	1	**1**	0	1	1	1	1	1	0	1	**1**	**1**	0	0	?	**1**	0	0	0
rehsei	0	**1**	0	0	0	**1**	0	0	**1**	**1**	0	?	?	?	?	**1**	?	?	?
familiaris familiaris	0	**1**	0	0	**1**	0?	0	0	?	**1**	0	**1**	0	?	0?	**1**	0	0?	0
familiaris kingi	0	**1**	0	0	0?	**1**	0	0	**1**	0	0	**1**	?	?	0?	1	0	0?	0
aequinoctialis	0	**1**	0	0	0	**1**	**1**	0	0	1	**1**	**1**	0?	0	?	**1**	0	?	0?
caffer	0	**1**	0	0	0	**1**	**1**	0	0	?	**1**	**1**	?	?	?	**1**	0	0	**1**
atyphus	0	**1**	0	0	0	**1**	**1**	1	0	**1**	1	**1**	1	?	?	1?	0	0	0
rimitarae (N=1)	0	**1**	0	0	0	0	**1**	0	0	0	**1**	**1**	0	?	?	**1**	?	?	0?
vaughani	0	**1**	0	0	0	?	**1**	0	0	1	**1**	1	?	?	?	1	?	?	?
taiti	0	**1**	0	0	0	1	**1**	0	0	1	**1**	1	0	?	?	1	?	?	?
mendanae	0	**1**	0	0	0	**1**	**1**	0	0	1	**1**	**1**	0	0	0	**1**	0	1	**1**
kerearako	0	**1**	0	0	0	**1**	**1**	0	0	**1**	**1**	**1**	?	?	?	**1**	0	?	?
rufescens	**1**	1	0	**1**	1	1	0	0	0	**1**	0	**1**	0	0	?	**1**	0	0	0
brevipennis	**1**	**1**	0	**1**	0	1	1	0	1	1	1	**1**	0	1	?	**1**	0	?	?
gracilirostris	**1**	0	0	**1**	0	1	0	0	1	**1**	0	**1**	0	1	**1**	0	0	0	0
newtoni	**1**	0	0	**1**	0	**1**	0	0	**1**	**1**	0	**1**	**1**	1	0	**1**	0	**1**	**1**
aedon	0	**1**	0	0	0	**1**	0	0	**1**	**1**	0	0	**1**	**1**	0	**1**	0	0	0
sechellensis	0	**1**	0	0	0	**1**	1?	0	0	**1**	0	**1**	1	1	0	**1**	0	0	0

Table XLI (continued)

Species / Character	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
melanopogon	0	0	1	**1**	0	**1**	0	**1**	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	**1**
paludicola	1	0	0	0	**1**	0	**1**	0	**1**	1	0	0	**1**	0	**1**	**1**	0	**1**	1
schoenobaenus	**1**	1	1	**1**	1	**1**	0	0	**1**	1	0	**1**	**1**	0	1	**1**	**1**	**1**	0
bistrigiceps	1	1	0	**1**	1	**1**	1	1?	1	0	0	**1**	?	1	**1**	**1**	1	**1**	1
agricola	**1**	0	0	**1**	0	0	**1**	**1**	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	1
concinens	1	1	0	?	?	?	?	**1**	0	0	?	**1**	0	?	?	?	?	?	?
scirpaceus scirpaceus	1	1	1	**1**	1	0	**1**	**1**	0	0	**1**	**1**	0	**1**	0	**1**	**1**	**1**	**1**
scirpaceus fuscus	0	1	1	?	?	**1**	0	**1**	0	0	**1**	**1**	0	?	0	**1**	**1**	**1**	1
baeticatus	0	0	0	**1**	?	**1**	0	**1**	0	?	**1**	**1**	0	**1**	0	0	**1**	**1**	**1**
dumetorum	1	1	1	**1**	0	**1**	1	**1**	0	0	1	**1**	0	1	0	**1**	1	**1**	0
palustris	1	**1**	**1**	0	**1**	0	**1**	**1**	0	1	**1**	**1**	0	1	0	**1**	**1**	**1**	**1**
arundinaceus arundinaceus	1	0	1	**1**	0	**1**	0	1	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	**1**
arundinaceus zarudnyi	1	0	1	**1**	0	**1**	0	**1**	0	0	**1**	1	0	0	0	1	**1**	1	**1**
orientalis	0	0	0	**1**	1	**1**	0	**1**	0	1	1	**1**	0	0	0	**1**	**1**	**1**	**1**
stentoreus brunnescens	0	1	0	**1**	1	0	**1**	**1**	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	**1**
stentoreus siebersi	0	0	0	**1**	0	**1**	0	**1**	0	0	**1**	**1**	0	0	0	**1**	**1**	**1**	**1**
australis	0	0	0	**1**	1	**1**	0	**1**	0	0	**1**	**1**	0	0	0	1	**1**	1	**1**
luscinius	0	0	**1**	**1**	0	1	1	0	0	**1**	1	**1**	0	0	0	**1**	1	**1**	0
syrinx	0	0	0	**1**	0	**1**	0	?	0	1?	0	0	0	0	1?	**1**	0	**1**	**1**
rehsei	?	?	?	?	?	?	?	1	0	**1**	?	**1**	?	0	?	?	?	?	?
familiaris familiaris	**1**	0	0	1?	?	0	**1**	?	0	?	0	**1**	0	0	0	1?	0	**1**	0
familiaris kingi	**1**	0	0	?	?	?	1?	?	0	?	?	?	0	0	?	**1**	0	**1**	**1**
aequinoctialis	**1**	0	?	1?	?	**1**	0	?	0	?	0	**1**	0	0	0	**1**	**1**	**1**	**1**
caffer	0	?	?	?	?	?	?	?	0	?	?	?	0	0	0	?	?	0	**1**
atyphus	0	?	?	?	?	?	?	?	0	?	?	?	0?	?	**1**	**1**	0	**1**	0
rimitarae (N=1)	0	?	?	?	?	?	?	?	0	?	?	?	0	0?	0	0	**1**	?	?
vaughani	?	?	?	?	?	?	?	?	0	?	?	?	0	0	0	0	**1**	**1**	**1**
taiti	?	?	?	**1**	0	?	?	?	0	?	0	?	0	0	0	1	**1**	1?	1?
mendanae	1	1	1	**1**	0	**1**	0	?	0	?	**1**	**1**	0	0	0	**1**	**1**	**1**	0
kerearako	?	?	?	?	?	1?	0	?	0	?	?	**1**	0	0	0	?	?	0	**1**
rufescens	1	?	0	**1**	0	**1**	0	?	0	1?	1	1	0	0	0	**1**	**1**	**1**	0
brevipennis	?	?	?	1?	?	**1**	?	1	0	0?	1?	**1**	0	0	0?	**1**	?	**1**	?
gracilirostris	1	?	?	1?	?	**1**	0	1	0	0?	**1**	**1**	0	0	0	0	**1**	0	**1**
newtoni	**1**	0	**1**	**1**	0	**1**	0	?	0	?	0	0	?	0	0	**1**	**1**	**1**	**1**
aedon	0	**1**	0	1	**1**	**1**	1	?	0	?	1	?	**1**	0	0	**1**	0	**1**	0
sechellensis	0	0	0	**1**	0	**1**	0	?	0	?	**1**	**1**	1?	0	1?	1?	?	?	?

In a few cases a comparison was made of nests of subspecies representing the same species. In the Great Reed Warbler the nests of *arundinaceus* and *zarudnyi* differ only in four characters out of 38 (10.5%). Of two subspecies of the Millerbird, the nests of the extinct in the first half of the twentieth century nominate *familiaris* from Laysan Island differ from those of *familiaris kingi* from Nihoa in four characters (of 27 = 14.8%). In *scirpaceus* the difference between the nests of the nominate form and *fuscus* is 20%, only slightly less than the difference between *stentoreus brunnescens* and *siebersi* (24.2%).

The results mentioned above suggest that in many cases the percentage differences between taxa may reflect their phylogenetic relations. There are, however, some exceptions, such as the differences between *melanopogon* and *paludicola* (the same subgenus – 54%), and between *melanopogon* and representatives of two other subgenera, i.e., *arundinaceus* (13%) and *baeticatu*s (14.7%). It is not known whether this indicates the need of further studies of the *melanopogon* systematic position. The situation is not exceptional, because, according to HOUDE et al. (1997), their results concerning relations between particular families of Gruiformes are inconsistent with DNA data.

Acrocephalus stentoreus, treated by some authors together with its subspecies as a part of *arundinaceus* (e.g. by BAKER 1951, PTUSHENKO 1954) was then separated, although according to others it includes many forms living in Africa, South, East, and South-Eastern Asia, Asia Minor and Australia (WOLTERS 1980, HOWARD & MOORE 1991). One of such forms is *orientalis* – the history of its being treated as a subspecies of *stentoreus* and *arundinaceus*, and finally as a valid species – was briefly presented by STRESEMANN and ARNOLD (1949). The present study limited to the most widely distributed subspecies of *stentoreus*, i.e., *brunnescens*, and to *siebersi* from Java. A comparison of the nests of *arundinaceus* (including *zarudnyi*), *brunnescens*, and *orientalis*, indicates that they are similar to each other in size, and that they have several structure characters in common, but there are also characters typical of each particular form. For example, the location of nests above ground or mud, or the use of stiff stalks and stems, sometimes bent, is typical of *orientalis*. This confirms the results of STRESEMANN & ARNOLD (1949), and also partially of HAFFER (1991), who place them all in one superspecies. LEISLER et al. (1997), on the basis of DNA data placed them, together with *australis* and *vaughani* into one *arundinaceus*-complex.

STRESEMANN & ARNOLD (1949), WOLTERS (1980), and HOWARD & MOORE (1991) include all Indonesian and Australian forms in *A. stentoreus* as its subspecies. COURTNEY-HAINES (1991) and CLEMENTS (2000) assign some of them to the species *A. australis*. The present authors were able to compare only the nests of *A. australis* with those of *A. stentoreus brunnescens* and *siebersi* from Java.In general, all three forms are similar, although some differences are apparent. The nests of *brunnescens* differ from *australis* in seven characters out of 38 (18.4%), and from *siebersi* in eight characters of 33 (24.2%). The difference between *australis* and *siebersi* is similar (seven characters out of 33, i.e., 21.2%). The nests of *brunnescens*, however, are distinctly larger than those of the remaining two forms, which, on the other hand, are similar to each other. This refers especially to the outer diameter and the diameter of the nest opening (Tables XXVIII and XXIX, and Fig. 46). The sizes of nests of the nominate form *stentoreus* from N Africa are similar to those of the Asiatic *brunnescens*, and those of *meridionalis* from Sri Lanka are also similar or slightly smaller (Table XXVIII: approximate, not precise data). Of the structural characters, the most important similarity of *australis* and *siebersi* is the presence of a solid, firmly woven, ring at the rim, which in *brunnescens* is much less pronounced. Hence, the nests of *siebersi* are more similar to those of *australis* than to those of *stentoreus* (*brunnescens*). Regrettably, no data was obtained concerning the nests of the other Indonesian subspecies. The similarity of *siebersi* and *australis* mentioned above may suggest that COURTNEY-HAINES (1991) is right in assigning only forms from Africa, continental Asia, and Sri Lanka to *stentoreus* while including all insular forms from Indonesia, New Guinea and so on in *australis*. It is, however, also possible that the relation among them is not so close (not at subspecies level).

Fig. 46. Comparison of nests of the the Australian Reed Warbler *Acrocephalus australis* (left) and Clamorous Reed Warbler *Acrocephalus stentoreus brunnescens* (right).

HAFFER (1991) included *A. baeticatus* and *scirpaceus* together with *cinnamomaeus* in one superspecies of the subgenus *Acrocephalus*. DOWSETT-LENAIRE and DOWSETT (1987) proposed to include the three forms into one species *scirpaceus*. They based their proposal conception on vocal and other evidence, not taking into account nesting biology. KNOX et al. (2002) also acknowledge this. CLEMENTS (2000) includes *cinnamomaeus* in *baeticatus* as a subspecies, so it is used here quite formally, bearing in mind that for some authors (WOLTERS 1980, and others) it represents a valid species. The authors were unable to find data pertaining to its nests, therefore systematic rank cannot be discussed in the present paper. Data concerning the Reed Warbler is based on a series of nests studied in nature, collections, and rich literature, whereas information on the African Reed Warbler is based on several papers only (STEYN 1996, and others). Nevertheless, the nests of *baeticatus* differ in nine characters (out of 34 = 26,5%) from those of *scirpaceus*. The most important aspect seems to be the location of *baeticatus* nests above ground, and among various land plants. Another differentiating character is that endings of the nest material often protrude or hang off the outside surface of *baeticatus* nest walls. Thus, the differences are too great and the nests cannot belong to one species.

The other question is the systematic position of a few forms inhabiting the Far East, i.e. *bistrigiceps*, *agricola*, *concinens*, and *tangorum*, and the relations among them. The most controversial seems to be the position of *tangorum*, which is included in *bistrigiceps* by WILLIAMSON (1960), HOWARD & MOORE (1991), and CLEMENTS (2000). It is also treated as a subspecies of *agricola* (PTUSHENKO 1954, COURTNEY-HAINES 1991), as well as a valid species (SIBLEY 1996). DNA studies of LEISLER et al. (1997) and of HELBIG & SEIBOLD (1999) indicated also the validity of this species; however, according to the former authors, it is closely related to *concinens*, whereas according to the latter – to *agricola*. The present authors have not seen the nests of *tangorum* or a description of its nests in literature, so the problem cannot be discussed here. As to the other three species, data concerning the nests of *concinens* is very incomplete, because out of the 38 characters listed in Table XLI eleven are not known. When the unknown characters and those common for all three species are eliminated, we get three characters which are the same in the nests of *bistrigiceps* and *concinens* (among them the so far not recorded use of wet material and also hair and animal wool found in the lining). On the other hand, five characters are common for *concinens* and *agricola*. The most important seems to be the attachment of nests to vertical plant stems, non-use of stiff materials, and the presence of plant down. As to the differences, there are six characters out of 25 (24.0%) differentiating the nests of *concinens* and *bistrigiceps*, and only four characters out of 26 (15.4%) separating *agricola* and *concinens*. Thus, the nests of *concinens* are

more similar to those of *agricola*. This reflects the close phylogenetic relationship of these two species indicated by DNA studies (LEISLER et al. 1997).

Data concerning nest building in the Pacific species are incomplete to a various degree, and in some cases many characters used for comparisons remain unknown for particular species (see Table XLI). This is often connected to the number of described specimens of given species (only one nest in the case of *rimitarae*), and also with imprecise literature descriptions of nests. Most complete data concern nest site selection. Pacific reed warblers build their nests mainly in various kinds of forests, usually in canopy, and in various shrubs. The acrocephalines are, however, according to STEADMAN and ROLETT (1996), less dependent on forest than other terrestrial island passerines. This may be associated with the fact that forest is not their primary, aboriginal habitat. Moreover, Pacific species choose nest sites not known in continental (Eurasian, African, and Australian) forms, i.e., very high in trees (even more than a dozen meters), or in palm trees and *Cordylina* (which may be treated as "miniature palm"). On the other hand, typical nest sites (among vertical stems of emergent water plants, among twigs, etc) are also observed in some Pacific insular species, but they constitute absolute minority and have been recorded on some isles only. The vegetation of particular isles should yield an explanation of this phenomenon. MUELLER-DOMBOIS and FOSBERG (1998) mention reed marsh only from Guam (Marianas); MOSHER and FANCY (2002) found this habitat also on Saipan (Marianas), but only one nest of the Nightingale Reed Warbler inhabiting that island was observed by these authors among reeds.

SIBLEY (1996) and CLEMENTS (2000) list twelve endemic *Acrocephalus* species inhabiting Pacific islands (not taking into account, among others, Bonin, Indonesia, the Philippines, the Bismarck Archipelago, and the Solomons, inhabited by various subspecies of Eurasian and Australian species). Not so long ago WOLTERS (1980), and COURTNEY-HAINES (1991) mentioned only six species, and HOWARD & MOORE (1991) only seven, treating all remaining taxa as subspecies of three of them, i.e., *luscinius*, *caffer*, and *vaughani*. In the case of *luscinius* this concerns two species, i.e., *syrinx* and *rehsei*. The former species differs in 11 characters from *luscinius*, which constitute more than 30% of the 36 compared characters. For the latter species it is four characters out of 17 compared, i.e., 23.5%. The difference between *caffer* and *mendanae* is four out of 22 compared characters, which constitutes 18.2%. The result may confirm the statement of BRUNER (after PRATT et al. 1987) that *mendanae* is a separate species. It also implicates a similar situation in the case of *luscinius*. The differences between three forms formelly included in *vaughani* (i.e. *rimitarae*, *taiti*, and *kerearako*) and the latter are only 5.0% to 5.5%. This may be due to a very large number of unknown characters (18-20), to habitat similarities of islands they inhabit, and also to their close phylogenetic relations, even on the subspecies level (see COURTNEY-HAINES 1991). The problem remains open to genetic studies solve it.

According to BAKER (1951) reed warblers inhabiting Polynesia and Micronesia represent "an invasion of a continental form of *Acrocephalus arundinaceus*" from Asia. This involves, of course, *A. orientalis*, because BAKER (1951) treated it as one of the subspecies of *arundinaceus*. According to this author, "this species resembles the oceanic populations in size, general colouring, shape of bill, and wing and tail structure". BAKER (1951) did not mention other plain-coloured species from East Asia (*concinens* and *aedon*) when pointing out these criteria. Another argument of his was the breeding of "*arundinaceus orientalis*" on Bonin. The present study compared data on nesting of oceanic and continental species but the characters presented in Table XLI do not show any special similarities indicating which continental form is the ancestral of the oceanic ones.

The authors suppose that the invasion of Oceania took place by way of accidental irruption (one or probably more) caused by winds. Its haphazard character may be seen from the geographical distribution of acrocephaline species on the Pacific (Fig. 32). Representatives of the genus *Acrocephalus* inhabit several dozen islands, but often not all the islands of a given archipelago, even if they do not generally differ in vegetation. There are, however, whole archipelagoes, for example, the Marshals (BAKER 1951) and Tonga (STAEDMAN 1998), where they are absent, and plenty of isles on which birds were not studied. Also some isles have been inhabited in the past, but

acrocephalines died out or were extirpated (for example nominative *familiaris* on Laysan – MORIN et al. 1997, or *luscinius* on Titian, Mariana Is. – STAEDMAN 1999). Therefore, the lack of representatives of the genus on many isles may be wrongly interpreted because they simply never irrupted there.

MUELLER-DOMBOIS and FOSBERG (1998) write that typhoons combined with tornados in the western Pacific contribute to air flotation of some seeds from SE Asia to Hawaii. They also present a map of January jet streams moving across the Pacific at an altitude of 10000-12000 m. One may imagine that this to be the way of colonization by some snatched-up ancestor stock of the recent Millerbird, since in SE Asia there are winter quarters of a few *Acrocephalus* species. However, it concerns only the Hawaii and *A. familiaris*, assuming that a height of 10000 m or more is acceptable from the viewpoint of avian physiology. Thus, if this supposition is correct it would indicate more than one irruption.

Nesting in low trees and in bushes is encountered in continental species with various frequency, so that it was not completely unknown for the members of flocks which settled down in the Pacific isles. They had to adapt to nesting in the canopy of high trees and in palms. Most probably it was a matter of "to be or not to be" – they appeared in a new habitat, for them atypical, and faced a situation in which they had to adopt atypical nesting places and survive, or rapidly become extinct.

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