from thrushes and Old World flycatchers in having unspotted juvenile plumage. However, DNA-DNA hybridization data (e.g. as summarized in classification of Sibley et al. 1988) strongly indicate that subfamily (as treated here) does not form a natural group: within a totally reconstructed Sylviidae, Sylvia closest (within same subfamily) to typical babblers in genera (e.g.) Pellorneum, Trichastoma, Malacopteron, Pomatorhinus, and Turdoides. Most other genera (including Cettia, Bradypterus, Locustella, Acrocephalus, Hippolais, Orthotomus, Eremomela, and Phylloscopus) rather more distantly related

(in separate subfamily with grassbirds Megalurus, babblers such as laughing-thrushes Garrulax, etc.). Other warbler genera still more distantly related and placed in separate families (but within same superfamily): Regulidae for kinglets and Cisticolidae for group now called 'African warblers' which includes Cisticola, Scotocerca, Prinia, and Apalis (C G Sibley). 2 other groups occasionally put in Sylviidae—Maluridae (fairy-wrens) and Acanthizidae (thornbills) of Australia—now placed far away, close to Meliphagidae (honey-eaters) (see Passeriformes, Volume V, p. 42).

Cettia cetti Cetti's Warbler

PLATE 2

[between pages 136 and 137]

Du. Cetti's Zanger Fr. Bouscarle de Cetti Ge. Seidensänger Ru. Широкохвостая камышовка Sp. Ruiseñor bastardo Sw. Cettisångare

Sylvia cetti Temminck, 1820

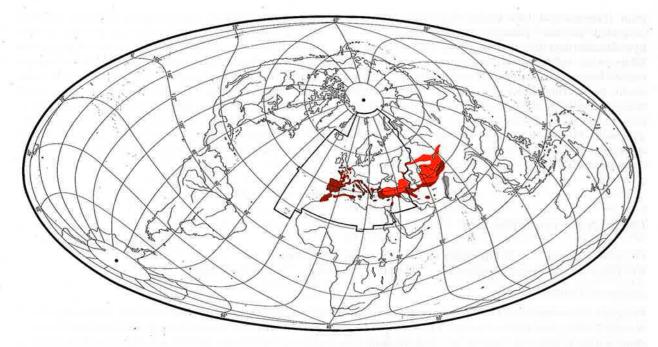
Polytypic. Nominate cetti (Temminck, 1820), north-west Africa and Europe east to Poltava (USSR), Crimea (possibly), western Turkey, and Crete; orientalis Tristram, 1867, central and eastern Asia Minor, Levant, and Caucasus area, east along northern shores of Caspian Sea to Karaganda area (northern Kazakhstan, USSR) and along southern shore to western Kopet Dag (Turkmeniya, USSR). Extralimital: albiventris Severtzov, 1872, Iran east from Lorestan and south from Elburz mountains, Turkmeniya east of middle Kopet Dag, north to southern Kazakhstan, east to Zaysan basin and Afghanistan.

Field characters. 13.5 cm; wing-span 15-19 cm. Head and body close in size to Reed Warbler Acrocephalus scirpaceus but wings 10% shorter and tail 20% longer, producing distinct structure recalling Sylvia rather than Acrocephalus; & averages 10% bigger than \$\mathbb{Q}\$. Mediumsized, quite robust warbler, with fine bill, domed head, short round wings, and relatively long, much rounded tail (often cocked). Plumage rather dark and dull: essentially rufous-brown above and greyish below, with dull white supercilium and dull white spots on brown under tail-coverts. Sudden loud outburst of song diagnostic. Sexes alike; little seasonal variation. Juvenile inseparable when full grown. 2 races in west Palearctic, scarcely separable in the field.

ADULT. Moults: June-September (complete), March-April (mainly body or nil). (1) European and north-west African race, nominate cetti. Upperparts and wings almost uniform chestnut-brown, crown, nape, and tail less chest-nut than rest; tone palest and brightest when sunlit, darkest and dullest in shadow or poor light (due partly to long, soft plumage). At close range, face shows off-white eye-ring and rather narrow, dull white or grey supercilium from nostril to behind eye; these contrast with dark brown lore but less so with mottled grey-brown cheeks. Chin and other central underparts dull white to grey, washed grey-brown on sides of neck and chest and suffused darker brown on flank, vent, and under tail-coverts; under tail-coverts tipped dull white, creating obvious mottling under

cocked tail. Underwing brown, with axillaries and coverts mottled grey-white, and flight-feathers looking silvery when lit. Duller with wear: upperparts less rufous, more olive-grey; supercilium less obvious; underparts paler (see also Plumages). Bill rather short, noticeably fine and flattened; dark brown, with flesh base to lower mandible. Legs strong; brown-flesh and shining brightly when lit. (2) Middle East race, orientalis. Upperparts less rufous than nominate cetti, more olive-grey, even when fresh; supercilium and underparts whiter. JUVENILE. Duller than adult above and below but inseparable except in comparison within family group.

Only west Palearctic member of essentially east Asian genus (bush warblers); easily identified by voice (see below), behaviour (see below), and marked preference for wet or damp areas with thickets. Although appearance becomes distinctive with experience, silent bird liable to initial confusion with brown species of Locustella and Acrocephalus warblers or even with nightingales Luscinia. Best structural character is prominent broad-feathered and rounded tail (with graduation visible on \(\frac{1}{3}\) of exposed length), often fanned, flicked, and cocked both on perch and in flight-but this structure and behaviour also displayed by Locustella. Best plumage characters at distance: (1) markedly uniform upperparts-with Locustella and Acrocephalus warblers (except Savi's Warbler L. luscinioides) showing some tonal contrast in good light and nightingales Luscinia exhibiting noticeably warmer tail; (2)

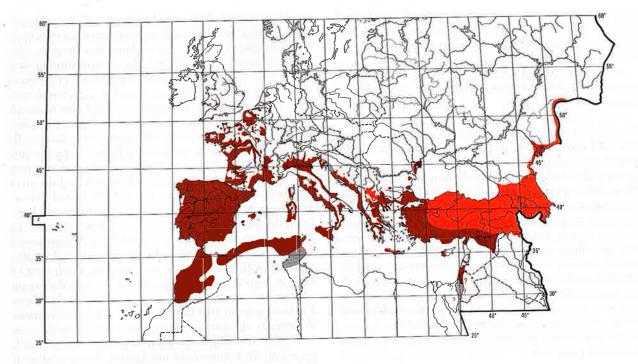


greyish underparts, less pale-centred than any confusion species. At close range, fine bill, rather domed, deep head, narrow, straight supercilium, and long, pale-tipped under tail-coverts form diagnostic combination. Flight rapid, bird dashing at low level between patches of dense cover with whirring beats of rounded wings and frequent tail-flirting (see above). Thus difficult to follow and best observed from nearby viewpoint overlooking favourite song-perches, to which bird periodically returns and on which it may momentarily sit openly. Movements within cover and on ground reminiscent of *Sylvia*, not *Locustella* or *Acrocephalus*: gait a short hop; carriage rather horizontal with tail held up; bird feeding purposefully on ground (like Dunnock *Prunella modularis*) often easiest to observe.

Song one of the most distinctive of west Palearctic warblers: a sudden, brief outburst of loud, clear, staccato notes, 'chee-cheeweecho-weecho-weechoo-chew(ee)'; given throughout the year (by resident birds at least), making listening a more productive means of locating birds than searching. In contrast to song, calls rather quiet: stuttered 'chich-ich-ich-ich-ich' is the most distinctive.

Habitat. In lower middle and now in some middle latitudes of west Palearctic, in temperate, Mediterranean, steppe, and (marginally) some desert zones. Lives basically in warm situations where thick shelter normally enables survival throughout year, even though occasional severe winters inflict heavy mortality, and emigration may be enforced from northern fringes. Ecologically a southern counterpart of the 2 nightingales *Luscinia*, but is more concentrated by watersides and swamps, in lower and

more fragmented bushy cover away from woodlands, although territory sometimes overlaps with that of those species. Since c. 1920 has successfully expanded over cooler oceanic lowlands fronting Bay of Biscay, English Channel, and North Sea, with winter temperatures liable to fall below o°C (Bonham and Robertson 1975). Sites here, however, are usually below 100 m, though in Cyprus mountain valleys are occupied up to c. 870 m (Bannerman and Bannerman 1971), in Spain up to 1450 m (Bannerman 1954), and in Haut Atlas of Morocco to 2100 m (Heim de Balsac and Mayaud 1962). Further east breeds more freely at high elevations, up to 1550-1700 m and even to 1900 m in Armeniya and to c. 2450 m in mountain riverbeds in northern Iran (Passburg 1959). Habitats in USSR are more varied than elsewhere, including meadows with isolated bushes, hedgerows protecting orchards, mountain streamsides flanked by impenetrable vegetation, and reedbeds or dense stands of grass (Dementiev and Gladkov 1954b). Generally favours patches, small copses, hedges, or borders of low and thick woody vegetation affording complete cover, often with steep front towards open ground, or track or pathway or watercourse composing linear territory. Mixtures of bracken Pteridium, honeysuckle Lonicera, coarse grass, or reed stems, with bramble Rubus, broom Sarothamnus, blackthorn Prunus spinosa, bamboo, papyrus, young willow Salix, poplars, or alder carr, are typically suitable forms of tangled low woody and mixed vegetation. Although habitat often flanks water, growth emerging from it is less favoured than cover over bare earth surfaces suitable for foraging. Where areas of reedbeds Phragmites are inhabited, prefers reed swamps, and wet or dry fen, not wet reeds or those along



dykes or subject to cutting; coastal reedbeds seem to be favoured rather more than those inland (Bibby and Lunn 1982). Some densely settled habitats may be flanked by overspill sites on normally less favoured terrain such as edges of cornfields, dry scrub, dry reedbeds, and bushes fringing a shallow lake (Simms 1985). Combination of restless habits, intensely secretive nature, and necessity for compact territory which must offer year-round facilities limits choice of habitat, ruling out all types of open ground, from desert to grasslands and rocky or broken terrain, as well as canopied forest and settled or disturbed areas. Where wintering impossible, tends to shift only for shortest practicable distance to nearest habitable equivalent site. In Afghanistan, found after breeding season in valley scrub at 1800-2400 m (Paludan 1959). In India, winters at edge of inundated tamarisk jungle and in partially submerged bulrushes, swamps, reedbeds, and gardens (Ali and Ripley 1973a). Although not physically lacking in mobility is rarely seen to fly beyond shortest distances in lowest airspace.

Distribution. Marked increase and spread, especially to north and west, interrupted by cold winters. Map shows distribution in north and west before cold winter of 1084-5.

BRITAIN. First proved breeding 1972; marked spread

since, mainly in south-east England and then increasingly in south-west (Sharrock 1976; Lack 1986). Channel Islands: first proved breeding 1973 (probably bred 1971-2) (Long 1981; R Long). France. Marked spread. In 19th century almost confined to Provence; by 1927, gradual northward spread had reached Loire basin; northern Bretagne reached by 1960 and English Channel coast by 1961. Northern (and, presumably less often, even southern) populations affected by hard winters; heavy mortality during January 1985 led to disappearance from Alsace-Lorraine and reduction of populations in Orléanais and western France; in population crash after severe 1986-7 winter, almost disappeared from Camargue (map shows approximate distribution before severe winter 1984-5). (Mayaud 1929; Bonham and Robertson 1975; Yeatman 1976; Cruon et al. 1987; Spencer et al. 1988b.) BELGIUM. First recorded breeding 1964 (Lippens and Wille 1972). NETHERLANDS. First recorded 1968; proved breeding 1976, but undoubtedly bred earlier (Teixeira 1979). For subsequent decline, see Population. LUXEMBOURG. First recorded 1983 (Diederich 1984), but not yet known to have bred. WEST GERMANY. First recorded breeding Niedersachsen 1975 (AH). SWITZERLAND. First recorded 1965, annual since 1973; breeding recorded 1975-83, but not subsequently (Winkler 1984; RW). ITALY. Central and western Po valley colonized since c. 1970 (PB). MALTA. First proved breeding 1970, but probably established since at least early 1950s (Sultana and Gauci 1982). KUWAIT. Status uncertain; recorded most months, March-October (F E Warr).

Accidental. Ireland (first record 1967), Sweden (first record 1977), East Germany (first record 1975), Poland (first record 1988), Egypt.

Population. Britain. Increase from 1975, with decreases after cold winters, this effect less severe in milder southwest than in south-east and eastern England; peak of 313 pairs possibly breeding in 1984, declining to 173 in 1986, 187 in 1987 (Spencer et al. 1988b, 1989). Channel Islands: increased to estimated 30 pairs by 1978; since 1984 decreased to 4–5 pairs in 1988 (Long 1981; R Long). France. 10 000–100 000 pairs (Yeatman 1976). Netherlands. About 60 territories 1977. Drastic decline after 1978–9 winter; 10–20 occupied territories 1979–85 (SOVON 1987, 1988b; CSR); a few singing 33 1986–8, but no breeding records (CSR). Switzerland. Still no evidence of more than 1 pair 1 (RW). Greece. Probably 10 000–100 000 pairs; no changes noted (GIH).

Survival. Oldest ringed bird at least 7 years 4 months (Long and Long 1986).

Movements. Varies from migratory to sedentary in different parts of range.

WESTERN RACE, nominate cetti, mainly sedentary, with some northerly dispersal in autumn, and vertical displacement and southerly extension of range in winter. Some evidence of passage on French Atlantic coast late August and early September (Cruon et al. 1987). No evidence that any European birds reach North African coast, though possibly a rare migrant through Gibraltar (Cortés et al. 1980). In Mediterranean, basically sedentary, but with evidence of local movements; more widespread in winter than summer (Blondel 1966; Sultana and Gauci 1982; Muntaner et al. 1983; Thibault 1983). In Turkey, vertical displacement occurs in Taurus mountains, and birds apparently winter chiefly in west and south; longerdistance movements across southern Aegean Sea shown by not-infrequent occurrence as prey item of Eleonora's Falcon Falco eleonorae (Vittery et al. 1972; Beaman et al. 1975; Ristow et al. 1986). In North Africa, vertical displacement evident in Haut Atlas (Morocco), and birds are found on northern fringes of Sahara in winter, south of their normal breeding range (Heim de Balsac and Mayaud 1962; Ledant et al. 1981); thus at Gabès (southern Tunisia), regular in small numbers in winter (Castan 1063); in eastern Morocco, more widespread in winter than summer, and recorded on passage at Figuig, 32°10'N (Brosset 1961; Smith 1968); further south-west, however, no evidence of passage, either at Tafilalt (south-east Morocco), where population sedentary, or in adjacent region of western Algeria (Dupuy 1970; Monk and Johnson 1975; Destre 1984). Report of 2 birds at Kano (north-

ern Nigeria) probably a misidentification (Moreau 1972). During main period of range expansion in western Europe (see Distribution), there was evidence that juveniles dispersed in more or less northerly direction in autumn; first Jersey record was on 16 October 1960 and, of 34 birds ringed in Channel Islands up to end of 1974, most were juveniles in autumn (Bonham and Robertson 1975). Iuvenile ringed at Lokeren (Belgium), 16 July 1973, was recovered in Noord Brabant (Netherlands) 90 km northeast on 28 October of same year (Tekke 1974); juvenile ringed at Harchies-Hensies (Belgium) in August 1970 was found dead at Norwich (eastern England) in June 1973 (Bonham and Robertson 1975); juvenile ringed Jersey, July 1976, was recovered at Tring (Hertfordshire, England) the following June (Spencer and Hudson 1978). In extreme west, single birds reached Ouessant (north-west France) in late July 1968 and Cape Clear Island (southwest Ireland) on 24 August 1968, 600 km north-west of nearest known breeding site (Bonham and Robertson 1975). Studies of recent colonists in Dorset (southern England) indicate that though most 33 defend territories throughout the winter, some individuals of both sexes leave their breeding areas, returning the following April; extent of their movement not known, but arrival with 'falls' of Phylloscopus warblers suggests they may winter in continental Europe (D T Ireland). In Suffolk (eastern England), where winters are significantly colder on average, breeding grounds thought to be entirely vacated (J Sorensen). An early spring movement, smaller than in autumn (Bonham and Robertson 1975), is probably related to re-occupation of breeding territories by adults as well as colonization by 1st-year birds.

South-west Asian Race, orientalis, makes altitudinal movements, and limited movement southward. Midwinter records in central Turkey show tolerance of low temperatures (Porter et al. 1969; Vittery et al. 1972). In southern USSR, birds descend to foothills and plains in mountainous areas, though stragglers may remain well into November, and they reappear on higher ground after snow recedes; others apparently move further afield (Dementiev and Gladkov 1954b). In Israel, resident, but some disperse to non-breeding areas in winter; slight southward movement shown by occasional records from Elat and Sinai (Hovel 1987). 2 sight records in Egypt: 11 March 1979, 30 March 1982 (Baha el Din 1984; P L Meininger).

EASTERN RACE, albiventris (extralimital), migratory or chiefly migratory. Winters in southern parts of breeding range north to Tashkent, 41°16′N (southern USSR), and south to Iran, southern Afghanistan, and Pakistan, and perhaps in Iraq (Vaurie 1959; Dolgushin et al. 1972; C S Roselaar). Distance of movement of individual populations not known. Passage inconspicuous, with records almost always of single individuals; probably migrates at night. Recorded away from water in steppe and on bare mountainsides in passage periods. Main exodus from northern breeding areas occurs August-September; further south,

along Syr-Dar'ya river (southern USSR), birds linger until late November. (Dementiev and Gladkov 1954b; Dolgushin et al. 1972.) In south-west Tadzhikistan (USSR), common in wintering areas December-February (Abdusalyamov 1973). Main arrival in Pakistan in October (Ali and Ripley 1973a). In spring, one of the earliest migrants, leaving southernmost winter quarters in March, when common on passage in Kohat (northern Pakistan) (Ali and Ripley 1973a); reaches c. 45°N by 2nd week of March, and re-occupies breeding grounds 'at first sign of spring'; in north of range this may not be until late April or early May (Johansen 1954; Dolgushin et al. 1972).

AV, DFV

Food. Chiefly insects, also other invertebrates, taken mostly from or near ground (Bibby 1982; Bibby and Green 1983); diet not uncommonly includes aquatic invertebrates, perhaps more often in winter, presumably taken from water's edge or by reaching down to surface from raised stems, etc. According to Ferguson-Lees (1970a), seeds important in winter, but no data presented. In Kent (England), winter, seen feeding on open ground like Dunnock Prunella modularis, hopping over mud or flattened vegetation, pecking from side to side; also recorded darting and fluttering to pick prey from under leaves (e.g. nettles Urtica) and from bare twigs and branches (Hollyer 1975). Similar picking reported in summer (e.g. Simms 1985). Members of one pair seen using their large powerful toes to clasp fallen rotten branch of willow Salix and tugging out (with bill) insect larvae to feed nestlings; sometimes hammered branch like woodpecker (Picinae) (Harvey 1977). In Volga delta (USSR), winter, quick to appear where wild boars Sus have trampled reeds, and extracts invertebrates from damaged stems (Vinogradov and Reutski 1983).

The following recorded in diet in west Palearctic. Invertebrates: damsel flies (Odonata), bugs (Hemiptera, including Cicadellidae, Aphididae), earwigs (Dermaptera), adult and larval moths (Lepidoptera), caddis flies (Trichoptera), flies (Diptera), wasps (Hymenoptera), beetles (Coleoptera, including diving beetles Dytiscidae), spiders (Araneae), harvestmen (Opiliones), small snails (Gastropoda), earthworms (Oligochaeta). A few green seeds recorded in one stomach. (Witherby et al. 1938; Dementiev and Gladkov 1954b; Bibby 1982; Bibby and Green 1983; Vinogradov and Reutski 1983; Simms 1985.)

From analysis of 10 faecal samples collected at Le Mignon (western France), late July to early September, average number of items per sample as follows: 5 aphids (probably *Hyalopterus pruni*), 0.6 other bugs, 1.4 Diptera, 1.6 wasps, 1.8 beetles, 1.7 spiders, 0.7 others; at Passay, late August to early September, 10 samples yielded average of 0.2 damsel flies, 0.4 bugs, 1.5 Diptera, 1.3 wasps, 2.7 beetles, 2.1 spiders, 0.9 others. Of 142 items comprising flies, wasps, beetles, and spiders, 84% were less than 2-4 mm long, 15% 4-6 mm, 0.7% longer than 6 mm. (Bibby

and Green 1983.) In Crimea (south-west USSR), diet consists of various 'coastal' insects, worms, and molluscs. In Azerbaydzhan (south-west Caspian, USSR), adult and larval insects and molluscs; in February-March, larvae of aquatic insects, diving beetles *Dytiscus*, and snails (apparently *Hydrobia pusilla*) (Dementiev and Gladkov 1954b). In Talasskiy Alatau (Tien Shan, southern USSR), November bird contained numerous small water beetles (Hydrophilidae), I Dryopidae, 2 Coccinellidae, 2 Cicadellidae, and several other bugs (Kovshar' 1966). Stomach of bird from northern Kazakhstan, September, contained remains of beetles (Carabidae) and large number of Chironomidae (Dolgushin *et al.* 1972).

Diet of young apparently similar to that of adults, though soft-bodied insects predominate. In Dorset (England), 708 items from faeces of young in 9 nests comprised 25.8% (by number) spiders, 23.2% Diptera, 22.0% caterpillars, 10.0% beetles, 5.8% snails, 5.2% moths, 4.0% caddis flies, 1.6% harvestmen, 2.4% others (7 Hemiptera, 2 Hymenoptera, 1 earwig, 1 earthworm) (Bibby 1982). In Belgium, food brought to one brood included small green caterpillars (perhaps *Pieris*), also butterflies and moths, 'midges', hoverflies (Syrphidae), small worms, and probably also bugs (De Lust 1979).

Social pattern and behaviour. For important early work, see Trouche (1941-5) for southern France; for recent studies, see Hollyer (1975) for Kent (England), De Lust (1979) for Belgium, Le Sueur (1980) for Jersey (Channel Islands), and Bibby (1982b) for Radipole (Dorset, England). Account includes material supplied by D T Ireland for England and Wales, also notes by I Hollyer.

1. At least in southern England, ♂♂ and ♀♀ usually sedentary throughout the year (see below for details), but at Radipole minority of 33 and 99 (mates) regularly vacate breeding territories for winter, departing in September and returning April (D T Ireland). Recapture of marked birds shows that established 33 often hold same territories for several years. One 3 held same territory for 6 consecutive years (D T Ireland); in Kent, 1 & was resident for 5 years before being replaced by another for the same duration; another 5-year residency also recorded (J Hollyer), and one of 3 years (Le Sueur 1980). At Radipole, most ♀♀ sedentary, maintaining discrete 'territories' (within &'s territory: see Breeding Dispersion, below) throughout the year (D T Ireland, contra Bibby and Thomas 1984 who suggest 33 may displace their mates at end of breeding season). Retraps suggest that in Kent also, some PP stay in same area throughout the year (J Hollyer). In Volga delta (USSR), February, 3 reedbeds held 32, 84, and 104 birds per km2 (Vinogradov and Reutski 1983). Bonds. Mating system varies from monogamy to polygamy, but more often the latter, & practising successive polygyny with 2 or more PP such that broods overlap (Trouche 1941-5; Bibby 1982b). In study at Radipole of 125 territorial 33, 22 monogamous, 70 polygamous, of which 42 had 2 99, 22 had 3 ♀♀, 6 had 4 ♀♀; remaining 33 either unmated or status unknown (D T Ireland). Pair-bond, perhaps even in monogamy, never close, ♂ and ♀ associating little (see Heterosexual Behaviour, below), yet same bonds often renewed in successive years (see below). In both monogamous and polygamous mating systems, same &-Q combinations typically persist for 2nd broods. Occasionally, however, one & displaces another from territory in 9, range far from nest, but apparently stay within territorial limits of 3 (Le Sueur 1980). 3 sometimes takes young to unoccupied area up to 100-200 m from territory (D T Ireland); e.g. within 2 days of fledging, young in territory 450 m long moved into area c. 250 m from nest, and, over the next 20 days, of rarely strayed more than 75 m from them, only patrolling full length of his territory again after young independent and dispersed (Bibby 1982b). Before dispersing, one family party moved c. 800 m (Trouche 1941-5), i.e. presumably maximum displacement from nest before young disappeared. For site-fidelity of 33 and 99, see introduction to this paragraph. One & 'inherited' territory formerly occupied by his father and held it for 4 years (I Hollyer). ROOSTING. of roosts in territory, apparently c. 1-2 m above ground in dense scrub, but site varies from night to night and bears little relation to position of ♀ or nest (D T Ireland). In study by Trouche (1941-5), bigamous & sang every morning at dawn from the same perch near bramble Rubus thicket which housed nest and young, suggesting that he roosted close by. After 13 days there, he moved his dawn song-post, and presumed roostsite, c. 500 m, apparently in response to hatching of his other brood. For singing at night, see Song-display (below). Bathing recorded (Reboussin 1937; Géroudet 1963).

2. Skulking, keeping low in vegetation for long spells. In spite of habitat preference, however, not really shy (De Lust 1979). Captive birds (sexes not specified) much more secretive in spring than in autumn (Restall 1974). Independent young may show some curiosity about human intruders and approach giving apparent Rattle-calls (see 3b in Voice). & disturbed whilst singing immediately drops deeper into vegetation and shortly resumes song elsewhere. (Dementiev and Gladkov 1954b.) Detailed reactions described by Hollyer (1975) as follows. If agitated by human intruder, adopts Alarm-posture (tail fully cocked, wings drooped, head lowered); nervously flicks wings and tail and remains silent between bursts of Alarm-song (see 1c in Voice). Immediately after Alarm-song, often flies covertly, up to 250 m, through territory and sings again on re-alighting, sometimes giving 1st unit of song just before landing. Alarm-song (and Territorial-song: see 1a in Voice) can be stimulated by almost any sudden noise. Close approach of Sparrowhawk Accipiter nisus caused & to scream (see 5 in Voice), dive for cover and give Rattle-call (D T Ireland). For other alarm reactions, see Parental Anti-predator Strategies (below). Downward flicking and sometimes trailing of mostly fanned tail typical of active birds, especially \(\text{(Trouche 1941-5; Ferguson-Lees 1964). FLOCK} BEHAVIOUR. None recorded. SONG-DISPLAY. Territorial-song given by 3 in an upright posture with head thrown back, tail depressed and lightly trembled (Trouche 1041-5; Hollyer 1975). ♀ also sings occasionally (see Heterosexual Behaviour and Parental Anti-predator Strategies, below, for contexts; see also 1e in Voice). A typically delivers each song from a different perch, with long pauses between songs (see 1a in Voice for details). thus beats the bounds of his territory, periodically stopping to sing from depths of undergrowth, occasionally exposed perch (e.g. Dementiev and Gladkov 1954b, Burton 1979). & has favoured song-posts, separated by average of 100-250 m (De Lust 1979). In territory of c. 25 ha, 3 used up to 24 song-posts, of which o were preferred (Herremans 1976). Birds typically sing throughout year except for moult period in southern England, but song much depressed or absent in hard winter weather (D T Ireland). For intense winter Song-duel (2 33 singing 300 m apart all day), see De Lust (1979). At Minsmere (Suffolk), no song heard June-March, when birds thought to vacate area (J Sorensen). In south-west England, song intensity increases markedly in early March and reaches a peak by mid-April (D T Ireland). At Radipole, song (and patrolling) of

monogamous & declined steadily through breeding season, was interrupted when 1st brood fledged, recovered somewhat after brood independent, and virtually ceased mid-July (Bibby 1982b; see also Trouche 1939). Silence from mid-July to mid-August coincides with &-moult, after which singing and patrolling resume and juvenile 33 from 1st and 2nd broods are expelled. Le Sueur (1980) found that song-output increased markedly after fledging, but given the complexity of mating and breeding regimes, seasonal variation in different studies not unexpected. Usually, a few days of rather more concentrated song associated with nest-building for 2nd clutches (Bibby 1982b). 33 sing in spring from dawn to dusk (Hachez 1964a); see below for diurnal rhythm. Several reports of 33 singing at night (e.g. Kumerloeve 1966, Burton 1979, Henderson 1979), and widespread in Britain (D T Ireland); characterized by delivery from fixed perch and by song-structure (see 1b in Voice); typical day-song may also be given at night by juvenile 33 in September-November and by 1st-year 33 in May (D T Ireland). Nocturnal song suggested by Harvey (1980) to indicate bachelor status, but shown by Ireland (1984) to be given not uncommonly by 33 with mates incubating or brooding and thought to advertise vacant space in their territories for more QQ (D T Ireland); this consistent with lack of rival-response to playback of nocturnal song (J-C Roché). Nocturnal song usually given at continuously high rate from c. 01.30 hrs and finishes c. 15 min after dawn, followed c. 15-20 min later (in breeding season) by start of day-song. Song intensity then quickly reaches a peak (1-2 songs per min), and this level maintained for $2-2\frac{1}{2}$ hrs; then rapid decline towards midday. Little song in afternoon, but resurgence from 18.00 hrs until darkness. Song-rates can be depressed by cold nights and wide territorial spacing. In mild winter conditions, song heard for first 2 hrs after dawn, and then only occasionally for rest of day. (D T Ireland.) For diurnal rhythm in the Camargue during breeding season, see Trouche (1935, 1939). ANTAGONISTIC BEHAVIOUR. (1) General. 33 highly aggressive in defence of territory, assiduously patrolling boundaries, giving Territorial-song, and expelling intruders including conspecifics dispersing in autumn (Trouche 1941-5). Where sedentary, 33 and 22 defend respective territories (see above) throughout the year. Q usually takes no part in defence of 3's territory, but in spring, occasionally gives him some support in expelling intruding 33. (D T Ireland.) (2) Threat and fighting. Importance of song demonstrated by rapid occupation of territory if resident abandons it or dies (Trouche 1939). Tape-broadcast of song induced resident of to run towards source, singing loudly, in apparent alarm-posture: wings drooped and tail cocked (Herremans 1976). Attempt by & to settle in part of resident's territory led to owner delivering long bouts of song when formerly he had only sung briefly. Rivalry also indicated by frequent chasing. Eventually, intruder excluded resident from territory and bred with both PP which had already bred that season with former resident. (Trouche 1941-5.) In study of one territory, resident quickly evicted 4 strangers, 3 after 1 day, 1 after 2 days (Le Sueur 1980). Aggression may escalate into fighting. Following account by Tardieu (1979). Rival of perched face to face, 25 cm apart, in open view of, and quite oblivious to, observer 4 m away. Each bird sang repeatedly whilst slowly and continuously beating one wing at a time (with rather few changes from one to the other: Wing-waving display). Later, when one bird was alternating wings more often, the other suddenly pounced on it and the combatants tumbled to the ground and fought there for 1-2 min, grappling with their claws and pecking viciously. Then one freed itself and flew off, pursued by the other which, after 30 m, abandoned the chase and returned to its territory. The whole confrontation lasted 16 min. In similar display, birds perched on

in slow, hesitant 'windmill' fashion, while slowly circling each other; displayed thus for 4 minutes in silence until disturbed and flying off (Manns 1979). Individual 30 vary in tolerance of other Sylviidae; occasional aggression towards thrushes Turdus recorded; expulsions accompanied by 'chip' calls, once Churring-call (D T Ireland: see 2a and 4 in Voice). According to Vanvinckenroye (1969) in Limburg (Belgium), residents exclude almost all Sylviidae except Reed Warbler Acrocephalus scirpaceus from their territories. However, Trouche (1941-5) reported amicable cohabitation with most Sylviidae. In Kent, perhaps only in colonization phase, thought possibly to compete with Wren Troglodytes troglodytes (Hollyer 1975; I R Hepburn), but well-established birds appear to coexist amicably (I Hollyer). HETEROSEXUAL BEHAVIOUR. (1) General. Mate-choice discussed by Bibby (1982b). Some evidence that \mathcal{P} may favour bigger \mathcal{F} , perhaps selecting some associated quality, e.g. of the habitat bigger 33 able to claim. 33 evidently enhance their reproductive output by attracting more than 1 \(\text{\$\text{\$}} \) to breed in their territory. (2) Pair-bonding behaviour. Courtship can occur at any time of year between late September and March, but especially prevalent during March. Meetings of A and \(\text{from September} \) to about June, but especially March-May, commonly accompanied by simple Meeting-ceremony (much commoner than courtship-display): of ends or interrupts his normal song with 'chip' calls ('greeting song': see 1a and 2a in Voice) while ♀ gives a 'huit' call (D T Ireland: see 2b in Voice). Irrespective of mating system, 3 and 2 do not form strong bonds, associating only for courtship and copulation. A aftracts P by patrolling territory and giving Territorial- and Nocturnal-song (see above). In one study (Bibby 1982b), no new PP attracted after synchronized onset of breeding in late April. Courtship behaviour not fully described, but includes the following. (a) Soliciting-ceremony. In typical sequence, δ approached scrub in which \mathcal{P} was moving about quietly and keeping low. of gave one song phrase, then another ending with 'chip' calls ('greeting song'). Q responded with a 'huit' call. ♂ then moved near ♀ who continued calling softly in a submissive posture, flicking her wings and tail. S's song became much quieter and softer (see 1d in Voice) and was interspersed with groups of 'chip chip' calls. After displaying thus for c, 2 min, \mathcal{Q} usually moves off and \mathcal{J} either follows and sings/calls, or moves to another part of territory. (D T Ireland.) In probably similar encounter, the 2 birds, wings fluttering, crouched close together in low vegetation; one (presumably 3) was singing, the other answered with 'tsiet' calls (De Lust 1979: see 2b in Voice). Before nest-building, of frequently interrupts territorial activity to join \mathcal{P} ; one \mathcal{P} was also followed regularly, whilst collecting food for nestlings, by a new of who eventually mated with her (Trouche 1941-5). Soliciting-ceremony commonest March-May, but occurs September-June: may lead directly to copulation (D T Ireland: see below). (b) Chasingdisplay. Occurs regularly in April-May (Hollyer 1975; Harvey 1977, from which this account compiled). δ , following $\frac{1}{2}$ -1 m behind \mathcal{L} , pursues her at length (for $1-5\frac{1}{2}$ min) 3-50 m above ground but sometimes through dense cover. In one case, the 2 birds followed the same route 50-60 times. Participants zigzag rapidly with fluttering wings, and tail fully spread. 3 may give contact-calls (see 2a in Voice), but chase may be silent throughout. Chasing, of shorter duration and over a simpler course, reported September-October (Harvey 1977). (c) Wing-waving display. For description, see Antagonistic Behaviour. Heterosexual function claimed by W G Harvey. Trouche (1941-5) describes & initially displaying aggressively (no details) at Q with whom he subsequently mated, indicating that aggression may occur in a heterosexual context. (3) Courtship-feeding.

road appeared to take turns to wave alternate wings at each other

14 Sylviidae

None reported. (4) Mating. Observed once by D T Ireland: Soliciting-ceremony (see above) in bush led to of giving intense and continuous quiet song and calls. ♂ then mounted ♀ who gave a squeal (see 6a in Voice). After brief copulation, & moved to outside of bush, then shook and preened before moving away. (5) Nest-site selection and behaviour at nest. No information on nest-site selection, but presumably by \(\begin{aligned} \text{, who also builds nest,} \end{aligned} \) usually in silence, though occasionally said to sing (Trouche 1935). Meanwhile, & shows considerable interest by feverish activity, singing a little distance away, and by periodic visits to the nest. Once nest built, of shows little further interest (Bibby 1982b), though varying attentiveness attributed to 3 perhaps relates to the prevailing mating system. In study by Trouche (1941-5), laying and incubation induced bigamous of to become more distant from, and circumspect in, nest area; & continued singing but stopped calling. After onset of incubation, meetings between β and Ω were conducted in silence, whether away from the nest (when \$\times\$ left to feed or rest) or during \$\tilde{S}\$'s brief and occasional visits to the nest area. & heralds his approach to nest area with a burst of song (Ferguson-Lees 1964). In one study, 3 visited nest area (but not nest itself) about twice per hr, and, though incubating \mathcal{Q} sometimes called in response to his song. she never left the nest in response to his presence (Bibby 1982b). After hatching, & even more silent and discreet in nest area. One 3, who had 2 simultaneous broods, occasionally visited both \$\text{\$\Pi\$}, separately and briefly, away from nest or young. (Trouche 1941-5.) Q's return to nest always secretive, threading her way through the undergrowth, typically by a regular route (Trouche 1941-5; De Lust 1979; Le Sueur 1980). RELATIONS WITHIN Family Group. \mathcal{L} broods young for c. 6 days (Bibby 1982b). Nestlings start calling as ♀ nears nest with food (D T Ireland). Approaching ♀ wakened dozing young with a 'chup' call (D T Ireland: see 2a in Voice), once apparently with Rattle-calls (De Lust 1979). &'s role in feeding varies from nil to a modest amount (Bibby 1982b: see Bonds). Tonce seen approaching nest with food, then ate it himself (Le Sueur 1980). In Belgian study, 3, though taking no care of young, regularly accompanied ♀ back to nest, and the pair maintained regular contact by calls (De Lust 1979). ♀ maintains scrupulous nest-hygiene (Fig A) with



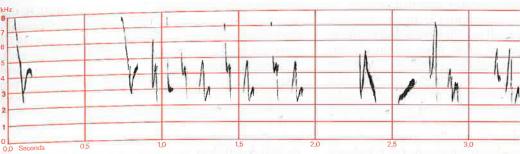
no help from & (Trouche 1941-5; De Lust 1979). Shortly before fledging, young preen regularly (De Lust 1979). May leave damaged nest prematurely (D T Ireland). On leaving nest, can flutter around, climb stems (etc.) with great agility (Dementiev and Gladkov 1954b). Brood initially stays together in one spot, only moving when summoned by \(\text{?}\) (Trouche 1941-5). Some & more active in feeding young at this stage (see Bonds). Young very noisy from the moment they leave the nest (D T Ireland), calling

excitedly and wing-shivering on approach of parent. Near independence, are more mobile and more dispersed from one another. (Trouche 1939, 1941-5.) By 30 days, young were fed little and were virtually independent; by 35 days, widely dispersed, silent, and liable to leave territory (Bibby 1982b). ANTI-PREDATOR RESPONSES OF YOUNG. In alarm, nestlings lie motionless (Dementiev and Gladkov 1954b), while recently fledged young fall silent (Trouche 1939). For calls of agitated nestlings, see Voice. Wariness of fledged young initially slight, but increases with age until independence (Trouche 1941-5). PARENTAL ANTI-PREDATOR STRATEGIES. (1) Passive measures. Q a tight sitter (Trouche 1941-5; De Lust 1979). When human approaches nest, she stares, crouches, and, at last moment, dives into undergrowth (Trouche 1941-5). Flushed ♀ crept about like a mouse on ground all around nest, then returned to nest while intruders still nearby (Ferguson-Lees 1964). (2) Active measures: against birds. No information. (3) Active measures: against man. Apart from vocal demonstration, no response is interpretable as active, though some possibly distractive. Q gives Rattle-call when intruder approaches nest containing young, of responding immediately with 'tsuk' call (De Lust 1979: see 3a in Voice). Once, when \$\varphi\$ returned to nest to find intruder ringing young, she sang harshly close by before retreating into the scrub and giving Rattle-call (D T Ireland). Alarmed & likewise calls and seeks concealment (Dementiev and Gladkov 1954b), though also reported towering and hovering (fluttering with shallow undulations), giving alarm-calls (Hugues 1916). & usually sings vigorously when nest area is approached (Chavigny 1934), notably during nestbuilding and incubation (Trouche 1939), and always when anyone was within c. 1 m of nest (Ferguson-Lees 1964). According to Dementiev and Gladkov (1954b), of then retreats, singing from time to time. (4) Active measures: against other animals. Mammalian predators elicit Rattle-calls and 'chip' calls from both sexes (D T Ireland).

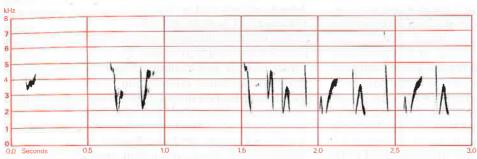
(Fig by D Rees from photograph in Blondel and Isenmann 1981.)

Voice. Freely used throughout the year, especially & song. For geographical variation, see below. Important studies by Trouche (1935, 1939) and Hollyer (1975); account incorporates scheme and descriptions provided by D T Ireland for southern England. For musical notation, see Stadler (1919). For additional sonagrams, see Bergmann and Helb (1982).

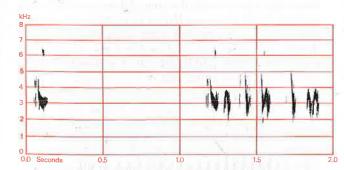
CALLS OF ADULTS. (1) Song. Widely studied. Given mainly by \mathcal{J} , also occasionally by \mathcal{L} . (1a) Territorial-song of 3. Highly distinctive. Described by Ferguson-Lees (1970a) as the most astonishingly loud song among small European birds: a sudden explosion of clear penetrating notes lasting typically 2.5-5 s (D T Ireland); ceases as abruptly as it begins and may not be repeated for several minutes. Audible up to 300 m (Trouche 1939). By day, 3 sings while patrolling territory, typically delivering each phrase from a different perch, with pauses of 1-4(-14) min between successive phrases (Hollyer 1975). At peak (dawn) intensity, c. 1-2 songs per min (D T Ireland). Phrase includes an exclamatory opening unit, thus: 'TCHI tchitchirititchirititchi' (Hachez 1964b); Fig I shows song with opening similar to this. In study in Camargue (France), last 2 notes, of which 2nd descends in pitch, were separated by short gap, and also sometimes repeated,



I P J Sellar France May 1977



II R Margoschis England May 1977

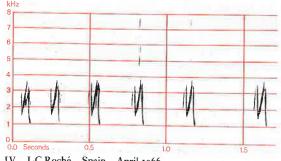


III J-C Roché Greece April 1963

thus 'TI tipitipitipi ti-pi(ti-pi)' (Trouche 1935, 1939, 1941-5, which see for variants). In Fig II, introductory unit (a quiet 'hui') thought to be call 2b of Q (R Margoschis: see below). Geographical variation occurs, each region having basic theme (Rucner 1975b; Bergmann and Helb 1982). In southern England, songs vary in composition (roughly 4 basic themes) and length (from very short to very long, commonly up to 10-15(-21) units, notably 'chwee' type) (D T Ireland). In Kent (England), song usually varies around 6 units of 'chwee' type, e.g. 'chuit-chuee-chuee-chuee-chuee' (Hollyer 1975). In Belgian study, song structure based on 'tsie' and 'wie' units (De Lust 1979, which see for details). For Cyprus, see Cyprus orn. Soc. (1969) Rep. 1971; for Elburz (Iran), see Schüz (1957); for Mallorca and north-east Spain, see Hollyer (1975). Within a region, there is much individual variation in length, structure, and timbre of song, but each d's phrase is stereotyped, allowing individual recog-

nition by human ear (e.g. Trouche 1941-5, Le Sueur 1980, Bibby 1982b). Sonagraphic analysis of 250 songs of different 33 showed that only 2 had identical song patterns; each of keeps the same song pattern for life. In so-called 'greeting song', given mainly March-May by & encountering ♀ (Meeting-ceremony) when patrolling territory, song followed abruptly by a series of 'chip' calls. Territorial-song, given from a fixed perch (i.e. bird not moving constantly from one to another) and much more continuously, e.g. 32 songs in 6 min 53 s at intervals of c. 13 (4-27) s (Burton 1979), maximum 10-11.8 phrases per min at c. 03.00 hrs (Henderson 1979; Ireland 1984). One song started with 'pwit', then, after a pause of $\frac{1}{2}$ s, 'pitchewitchewit' (Henderson 1979). In Greek recording (Fig III), song very similar: a dry scratchy 'pwit piti-chew-it-chew-it' (J Hall-Craggs), also less varied and rich than daytime song (P J Sellar). For function, see Social Pattern and Behaviour. (1c) Alarm-song of 3. A

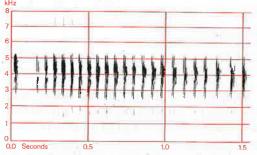
very harsh and often rapidly repeated variant of Territorial-song, often accompanied by harsh 'chip-chip' calls (D T Ireland: see call 2a). Also described as 'chuitphuit', followed by slurred 'phuit' units; an introductory 'chip' sometimes given just before perching, rest of song following once perched, and frequently heard when bird is closely watched (Hollyer 1975). See also 1e (below) for song of alarmed Q. (1d) Courtship-song and Subsong. A quiet, soft, almost continuous variant of Territorial-song, given by of in presence of \(\bigcap_1 \), usually September-March. May be interspersed with soft 'chip' calls (D T Ireland). This probably the variant called Subsong by Witherby et al. (1938b). According to Hollyer (1975, which see for rendering), Subsong can be very forceful and carrying. Autumn song, described as quiet and listless (Dementiey and Gladkov 1954b), presumably also of Subsong type. See also Calls of Young. (1e) Song of Q. Occasionally reported and in varying circumstances, but not common. Heard only once by D T Ireland—a harsh song given close to listener when nestlings being ringed-and thought to be restricted to disturbance of this kind. However, also apparently associated with mating (Le Sueur 1980), and nest-building (Trouche 1935), 2 songs of 1 \(\text{Q}\) (D T Ireland: see call 2a, also song-variant 1d.) (1b) Nocturnal-song of S. By contrast with daytime described as follows: 1st was a phrase of 4 uncommonly sweet notes, delivered 5 times in 10 min; 2nd began with a harsh unit followed by 7 sweet ones like final cadence of song of Willow Warbler Phylloscopus trochilus (Le Sueur 1980). (2) Contact-alarm calls. Apparently the same calls sometimes attributed to contact and alarm, and similar calls, differing in emphasis and rate of delivery, undoubtedly represent a continuum of self-advertisement, excitement, and alarm. (2a) Commonest call, given mostly by 3 but also at times by \(\begin{aligned} \text{, perched or in flight. Described as} \end{aligned} \) a fairly harsh staccato 'chip' (D T Ireland), a hard 'chich' (Harvey 1977) or 'tschiek' (J Hall-Craggs: Fig IV, which



IV J-C Roché Spain April 1966

shows call tending towards a disyllable). Q gives 'chip' in response to or, near nest, a louder harsher 'tschik' (D T Ireland). Basic call often likened to contact-call of Great Spotted Woodpecker Dendrocopos major (e.g. Bergmann and Helb 1982). Various calls ('pit', 'ti', 'ki', 'tick', etc.)

listed by Trouche (1935, 1939) apparently belong in this category, perhaps also soft 'twic' given by & in Chasingdisplay (Harvey 1977). This, and 'chup' given by Q approaching nest to waken dozing young (D T Ireland), are possibly variants. Typical ('chic') call is often heard from bird moving through undergrowth (Hollyer 1975), or from of when mildly agitated (e.g. by intruding warblers Sylviidae), or when locating ♀ in territory (D T Ireland). With increasing excitement, calls strung together in a loose series (Bergmann and Helb 1982), tending towards call 3b. (2b) A soft 'huit' or 'wheet' commonly given by ♀ in presence of & (D T Ireland). 1st unit ('whi' or 'hui': J Hall-Craggs) in Fig II apparently this call. On Balearic Islands, plaintive 'phiu' from birds hopping around nest (Munn 1931) perhaps this call or variant. Also possibly in this category: 'tsiet-tsiet' by ♀ in response to ♂'s song in close sexual encounter (De Lust 1979); 'psweet' (Hollyer 1975). (2c) Repeated 'treep', much like Water Rail Rallus aquaticus, given by ♀ in winter (D T Ireland). (3) Alarm-calls. (3a) A loud 'tsuk tsuk' when human intruder in territory (De Lust 1979). Call of bird at nest or with young a 'dar-dar-duc-duc', also in agitation a 'swik' with quality of House Sparrow Passer domesticus (Hollyer 1975). Harsh clicking call, somewhat like Blackbird Turdus merula, of ♀ alarmed near nest (Sultana and Gauci 1982) presumably the same. All may well be harder variants of call 2a. In one bird, a very soft 'tsuptsuptsup', sometimes on its own but more often after song, and thought probably to signal alarm (De Lust 1979), may be a subdued variant. (3b) Rattle-call. A prolonged metallic rattle (Fig V), not unlike that of Wren Troglodytes trog-



V PS Hansen India February 1986

lodytes but slower and sounding higher (J Hall-Craggs), given throughout the year by both sexes (perhaps more often Q: De Lust 1979) in highest-intensity alarm (Trouche 1935, 1939; Hachez 1964a). Likened to winding a mechanical alarm-clock (D'Alessandri 1976); described as approximately 't-k-t-k-t-k-t-k...' (J Hall-Craggs), a rapidly repeated staccato 'tit' (Hollyer 1975, for juvenile); in albiventris a 'tich-ich-ich' (Dementiev and Gladkov 1954b). (4) Churring-call. A quiet but harsh staccato 'chhrrr', reminiscent (like call 3b) of T. troglodytes, given in breeding season by a 3 chasing off bird of another

species (D T Ireland); also 'tschirr' (Bergmann and Helb 1982, which see for sonagram), 'crrr' (Reboussin 1937). (5) Distress-call. A high-pitched strangled scream once given by of diving into bush when alarmed by Sparrowhawk Accipiter nisus (D T Ireland). (6) Other calls. (6a) A short, quiet pig-like squeal, given by ♀ as ♂ mounted her; almost identical to call 5 (D T Ireland). (6b) A high-pitched 'peep' given by incubating ♀ immediately after song-phrase of nearby mate (D T Ireland).

CALLS OF YOUNG. At 5-6 days, a soft high-pitched 'pseee pseee'. At 10-12 days, a soft version of \$\textit{2}\$'s 'huit' (call 2b, above) given when approaching nest, and a soft 'truup' or 'treep' (compare call 2c) when away from nest; when agitated, a harsh staccato 'treep'. Fledged young give a harsh clipped 'trrip trrip', continuously if not disturbed; on approach of parent, intensity and rate of calling increase, and high-pitched 'psee' calls are liberally interspersed. (D T Ireland.) In the Camargue, Trouche (1939, 1941-5) distinguished 2 soft sibilant sounds: a descending 'isse' and, more commonly, a 'siii' of uniform pitch; these 2 calls given by different individuals in the same brood, especially towards 3 weeks old; ceased when alarmed or satiated. Fledglings also give a clipped 'pit', developing into 'pit-trri' in 5th week, and this, along with a few rattle sounds, probably precursor of adult Rattle-call (3b, above). (Trouche 1939, 1941-5.) Juvenile 33 give subdued listless song from late August until early October, thereafter full Territorial-song whose pattern, once established, is retained for life (D T Ireland).

Breeding. SEASON. West and south-west Europe (including Britain), also Greece and southern USSR: main laying period mid- to end of June (Dementiev and Gladkov 1954b; Makatsch 1976). SITE. In thick vegetation, e.g. supported on stems of reed Phragmites or nettle Urtica, among twigs, or occasionally in stouter branches of dense tangled scrub; in zone where ground vegetation tangled with woody stems (Bibby 1982b). Mainly at 30-45 cm above ground level, rarely to 2 m (Meiklejohn 1931; Munn 1932). 1st-brood nests, $(36 \pm SD12.4 \text{ cm}, n=9)$, significantly lower than 2nd-brood nests $(68 \pm 24.9 \text{ cm}, n = 5)$ (Bibby 1982b). Nest: bulky, untidy cup, with base of leaves and stems, finer stems and roots above; lined with feathers, hair, reed flowers, and other fine material. Mean dimensions of 6 nests: height 91.5 mm (81-104), width 87.0 mm (84-91), cup width 51.2 mm (49-54), cup depth 51.3 mm (47-56) (Worobiew 1931). Building: by ♀ (Le Sueur 1980, which see for details and timing of construction). EGGs. See Plate 29. Sub-elliptical, smooth and glossy; chestnut-red to deep red, sometimes paler; occasionally with band of darker colour at broad end. Nominate cetti: 18.0×13.0 mm $(16.5-19.8 \times 12.45-14.5)$, n=178; calculated weight 1.8 g. C. c. albiventris: 18.7×14.5 mm $(17.2-20.0 \times 13.9-15.6)$, n=52. (Schönwetter 1979.) Weight of fresh eggs, nominate cetti: 2.07 ± SDo·10 g (means of whole clutches: 4 of 4 eggs, 5 of 5 eggs) (Bibby 1982b). Clutch: (2-)4-5. Of 9 clutches, England: 4 eggs, 4; 5, 5; mean 4.55; clutch size from polygynous matings (4 eggs, 1; 5 eggs, 5; mean 4.83) significantly larger than from monogamous matings (4 eggs, 3) (Bibby 1982b). Of 11 clutches, Volga (USSR): 4 eggs, 5; 5 eggs, 6; mean 4.54 (Worobiew 1931). Eggs laid daily; in early morning (Le Sueur 1980). 2 broods in southern England (Bibby 1982b), Channel Islands (Le Sueur 1980), southern France (Trouche 1941-5), Portugal (Ferguson-Lees 1964), and Malta (Sultana and Gauci 1982), but not proved throughout range. Replacements laid after egg loss, including of 2nd brood; in 2 successive years, southern England, one Q laid 3rd clutch (successfully fledging young) after losing first 2 clutches to weather and predation (D T Ireland). Intervals between broods, from 1st egg to 1st egg, 46, 48, and 57 days (Bibby 1982b). INCUBATION. 16 days (n=4) (Bibby 1982b). 16-17 days (n=2) (Le Sueur 1980). Up to 17 days (n=28) (Sultana and Gauci 1982). One record of 13 days (Becker 1975). Begins when clutch complete. By \(\times \) only. During 34 daylight hours, one ♀ sitting for spells of 11.8 ± SD4.84 min (n=107) and absent for spells of $6.3 \pm SD_{2.05}$ min (n=110); sitting spells slightly longer early and late in day but absences less variable; nest unattended for 34.8% of time, or c. 5.6 hr in 16 hr day. (Bibby 1982b.) Young. Nestlings fed and brooded wholly or largely by ♀. FLED-GING TO MATURITY. Fledging period 14-16 days (Le Sueur 1980; Bibby 1982b; Sultana and Gauci 1982). Brood remains together and fed by parents for at least 15 days, virtually independent by 30 days, with young separating by 35 days (Bibby 1982b). Age of first breeding 1 year (D T Ireland). Breeding Success. In southern England, of 41 eggs in 1st clutches, 98% hatched; of 14 1st clutches, at least 12 produced fledged young, 1 produced none, 1 uncertain; of 4 2nd clutches, none produced fledged young (Bibby 1982b).

Plumages (nominate cetti). ADULT. In fresh plumage, upperparts rufous-brown, forehead, crown, hindneck, and upper mantle often with olive-brown tinge, rump and upper tail-coverts brighter rufous-cinnamon. Rather short and narrow supercilium greyish-white, sometimes faintly spotted dusky grey; above lore, often slightly greyer, not reaching nostril; at rear, distinct to above middle of ear-coverts, fainter and gradually merging into sides of neck further backwards. Rather faint stripe on lore dusky grey, partly mottled cream; eye-ring off-white, broken in front and behind. Ear-coverts brown-grey, mottled rufousbrown on upper coverts and off-white on lower. Side of neck light brown-grey, rufous-brown or olive-brown towards hindneck, greyer towards throat. Lower cheek, chin, and throat off-white, often faintly mottled grey on cheek and sometimes tinged pale grey or cream on chin and throat. Chest and side of breast light brown-grey, sometimes almost white on central chest; belly off-white; upper flank light brown-grey, gradually darkening to olive-brown on lower flank, vent, and under tail-coverts; tips of under tail-coverts fringed off-white. Tail dark rufousbrown, less bright and rufous than upper tail-coverts; inner webs often blackish-brown, except on central pair (t1). Flight-feathers blackish-brown or dark grey-brown, outer webs with broad but

ill-defined rufous-brown fringes (except on p9-p10 and emarginated parts of other primaries). Tertials and upper wingcoverts rufous-brown, similar to mantle and scapulars or slightly brighter rufous; inner webs of tertials and greater upper wingcoverts and entire longest feather of bastard wing duller and darker brown or black-brown. Under wing-coverts and axillaries light brown-grey (like upper flank) or almost white; shorter under primary coverts (including those at leading edge of wing) offwhite. In morn plumage, upperparts dark olive-brown, or (when heavily worn) almost greyish-olive, especially on crown and hindneck, rufous remaining on rump and upper tail-coverts only; side of head and neck brown-grey with some paler grey or cream mottling, supercilium sometimes reduced to row of off-white spots, but broken off-white eye-ring usually still distinct; chin, throat, and belly more extensively white; yent pale buff; side of breast, flank, vent, and under tail-coverts paler and greyer; wing and tail duller, browner, less rufous. Much individual variation, in part due to differences in abrasion: some birds more rufous above, others more greyish olive-brown; some with more olivebrown side of head, side of breast, and flank, others more grey. Sexes similar; 2 reported to be less rufous than 3 (Vanvinckenroye 1969), but perhaps due to differences in abrasion. NESTLING. Down rather long but scanty, on upperparts only: dark mouse-brown or almost black (Witherby et al. 1938b). JUVENILE. Closely similar to adult; upperparts duller and less rufous; white of underparts more creamy, more grey of featherbases showing through; side of body browner; feathering of underparts slightly shorter and looser, especially vent and under tail-coverts; wing and tail fresh when those of adult are worn or moulting. See also Bare Parts. FIRST ADULT. Like adult and often indistinguishable (but see Bare Parts). Tail-feathers narrower than those of adult, primaries and tail more worn than those of adult at same time of year, but these characters useful only when a number of birds can be compared, and with some experience. For tail-bars, see Mead (1965).

Bare parts. ADULT. Iris sepia-brown, dark brown, or blackbrown. Bill dark purplish-horn, dark horn-brown, or blackbrown, base of lower mandible pinkish-horn, pale flesh-brown, or grey-brown; cutting edge of upper mandible horn-brown, gape yellow, mouth flesh or shading from pink to orange-yellow. Leg and foot flesh-brown, reddish-brown, or violet, soles dusky yellow, grey, or pinkish; paler flesh in autumn and winter than in spring and summer, and of apparently slightly darker than 9; claws grey. NESTLING. Bill, leg, and foot flesh-pink; bill-flanges pale yellow, mouth yellow-orange; tongue with 2 black spots at base, 1 at tip. JUVENILE, FIRST ADULT. Iris grey-brown or dark brown. Bill dark horn-brown, base of lower mandible flesh-pink; cutting edge of upper mandible whitish-yellow at fledging. Black or grey spots on tongue still present at fledging; black tip present until late in autumn, black or grey spots at base until at least December. Leg pale whitish-grey (just fledged) or pink-flesh. (Harber 1964; Suffern and Ferguson-Lees 1964; Vanvinckenroye 1969; Herroelen 1974; Williamson 1968a; Becker 1975; Mester 1975; Lindell 1979; De Lust 1979; Busse 1984.)

Moults. Adult Post-Breeding. Complete; primaries descendent. In Britain, starts with p1 about mid-July to mid-August, completing September (n=11); secondaries start when p5 dropped; tertials moult irregular; tail-feathers perhaps simultaneous (Ginn and Melville 1983; Bibby and Thomas 1984). In Belgium, mid-June to August (Herroelen 1974). In western France, starts late June to early August (in δ , on average 3 July, n=15; in \mathfrak{P} , 8 July, n=20); duration \mathfrak{e} . 60 days; completed

late August or early September. In Portugal, starts mid-June to mid-July (both sexes on average 30 June, n = 27); duration c. 60 days. (Bibby and Green 1983; Bibby and Thomas 1984.) On Malta, & nearing completion 10 and 25 August, fully completed 22 and 26 August; one 2 not yet started 4 August, one in advanced moult 20 September, others completed 23 and 27 September, hence Q apparently later than & (Sultana and Gauci 1973b). In southern Yugoslavia, moult almost completed in one from 13 September (Stresemann 1920). In 2 of orientalis from eastern Turkey, body moult started 6 July but not flight-feathers or tail (ZFMK). In USSR, no moult of albiventris by 2nd half of July or orientalis by mid-August (Dementiev and Gladkov 1954b). ADULT PRE-BREEDING. Partial in some birds (extent not always established), no moult at all in many others. In Britain, some birds moult head, body, wing-coverts, variable number of tail-feathers (apparently starting with t1), and perhaps tertials March-April (Ginn and Melville 1983). In Balkan countries, usually no moult (Stresemann 1920). In USSR, orientalis in vigorous body moult mid-March to early April, occasionally ti also replaced (Dementiev and Gladkov 1954b), but no prebreeding moult in albiventris according to Williamson (1968a). POST-JUVENILE. Partial: head, body, at least sometimes also inner 2 tertials (Ginn and Melville 1983). In Britain, mid-July to mid-September (Ginn and Melville 1983), but moult starts soon after fledging (e.g. late June in Yugoslavia, when tail not yet full-grown: Stresemann 1920), and, as fledging period protracted, period during which moulting birds encountered usually longer than stated for Britain: June-September in Yugoslavia (Stresemann 1920), July-November in Belgium (Herroelen 1974), but mid-July to early September on Malta (Sultana and Gauci 1973b).

Measurements. Nominate cetti. Ages combined. Southern Europe (west of Yugoslavia) and Algeria, all year; skins (RMNH, ZFMK, ZMA). Bill (S) to skull, bill (N) to distal corner of nostril; exposed culmen on average 3·3 shorter than bill (S).

WING &	61.9 (2.19; 35)	58–66 ♀	54.0 (1.59; 13)	52-57
TAIL	58.5 (2.80; 31)	54-63	51.3 (3.15; 13)	48-56
BILL (S)	14.4 (0.60; 33)	13.6-15.6	13.7 (0.49; 13)	12.8-14.4
BILL (N)	7.7 (0.37; 28)	7.2-8.5	7.3 (0.52; 12)	6.6-7.9
TARSUS	22.1 (0.88; 26)	20.7-23.6	19.4 (0.60; 13)	18-4-20-2
Sex differences significant.				

WING. Live birds, unless otherwise noted. (1) Dorset (Britain), adult; western France, (2) adult, (3) juvenile; Portugal, (4) adult, (5) juvenile (Bibby and Thomas 1984). (6) Camargue (France), (7) Balearic Islands (Mester 1975). (8) Mallorca, skins (ZFMK). (9) Corsica, Sardinia, and Sicily, skins (Rokitansky 1934; Vaurie 1954c; RMNH, ZFMK, ZMA). (10) Naples area (Italy) (G L Lövei). (11) Malta (Sultana and Gauci 1973b). (12) Yugoslavia, Greece, and European Turkey, skins (Stresemann 1920; Niethammer 1943; Makatsch 1950; Rokitansky and Schifter 1971; RMNH, ZFMK, ZMA). (13) Cyprus (Flint and Stewart 1983).

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ð 64·4 (1·65; 10) —
                          ♀ 56.7 (0.90; 11) —
   63.5 (1.41; 8) -
                            57.1 (1.06; 18) —
  62.5 (1.21; 152)
                            55.9 (1.25; 138)
  63.3 (1.03; 15) -
                            56.5 (1.45; 70)
  61.7 (1.18; 67) -
                            55.5 (1.19; 209)
                            55.8 (1.22; 1179) 50-61
  62.2 (1.21; 609) 59-66
  59.9 (1.51; 106) 57-64
                            53.4 (1.13; 79) 51-61
  61.9 (2.53; 5) 58-65
                             52.0 ( — ;
  61.6 ( - ; 22) 58-66
                            53.8 (1.41; 6) 52-56
  62.5 (2.07; 12) 59-66
                            55.7 (1.85; 17) 54-62
                             - ( - ; 19) 51-57
   -(-'; 24) 58-64
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(12) 64.5 (1.69; 51) 60-68 57.5 (1.34; 12) 55-60 62.2 (-; 108) 57-68 56.0 (-; 105) 51-61
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C. c. orientalis. Wing. (1) Asia Minor and Levant (Jordans and Steinbacher 1948; Vaurie 1954c; Kumerloeve 1961b, 1969a; Rokitansky and Schifter 1971; ZFMK, ZMA). (2) West of Zagros mountains at border of Iraq and Iran (Vaurie 1954c).

(1) 3 64.0 (1.42; 11) 62-67 ¥ 61.0 (2.35; 4) 59-65 (2) 67.0 (-; 6) 63-69 -(-; -) -

C. c. albiventris. Wing. (1) Zagros mountains, Khorasan (Iran), and Afghanistan (Paludan 1938, 1959; Vaurie 1954c); (2) Pakistan (Ali and Ripley 1973a).

Weights. Nominate cetti. (1) Dorset (Britain); (2) western France, autumn; (3) Portugal, autumn (Bibby and Thomas 1984). (4) Bretagne (France), August; south-east France, (5) April-August, (6) September-November (G Olioso). (7) Camargue (France), (8) Balearic Islands, all year (Mester 1975). (9) Malta, all year (Sultana and Gauci 1973b). Naples area (Italy): (10) April, (11) October-February (G L Lövei). (12) Scattered data from Europe combined, April-July (Niethammer 1943; Vanvinckenroye 1969; Rokitansky and Schifter 1971; Becker 1975; Lindell 1979). (13) Cyprus (Flint and Stewart 1983).

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♂ 16·0 (0·77; 9) — ♀ 12·2 (0·77; 11)
             14.9 (1.33; 169) -
                                          11.8 (0.93; 163)
             13.9 (0.88; 82)
                                          10.6 (0.60; 279)
(3)
             16.3 (1.44; 8) 14-18
                                         12.2 (0.41; 6) 11.5-12.5
             15.9 (0.89; 16) 14-17.5
                                          13.0 (1.22; 5) 12-15
(5)
                                          11.8 (0.89; 16) 10.5-13
             15.1 (0.74; 15) 13.5-16
(6)
                                         11.5 (0.81; 8.73) 8.5-14.5
             15.2 (0.95; 464) 12.8-18.5
(8)
             12.8 (1.14; 72) 10.1-15.5
                                          9.9 (0.87; 63) 8.3-12.5
                                          11.5 ( -; 19) 10.3-13.4
(9)
             14.7 ( - ; 24) 12.5-16.9
             15.8 (1.16; 10) 12.8-16.8
                                          12.3 (1.54; 11) 10.9-16.0
(11)
                                          11.7 (0.58; 7) 11.0-12.5
             15.4 (1.38; 4) 14.0-17.0
             15.3 (1.60; 5) 13.0-17.0
                                          12.3 (0.99; 5) 11.5-14.0
(12)
             13.3 ( -- ; 108) 10.1-17.0
                                          10.5 ( - ; 105) 9.1-15.3
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December, &&: northern Greece, 18 (Makatsch 1950); Sicily, 15 (Rokitansky 1934). Range of many birds Belgium: 10·5-20 (Herroelen 1974). In western France, insignificant decrease of 0·03 per day during moult (Bibby and Green 1983). South-east France, winter: \$\Phi\$ 11·5, 12·0, 12·5 (G Olioso).

C. c. orientalis. Asia Minor, July: & 18.4, Q 10 (Kumerloeve 1969a; Rokitansky and Schifter 1971). East-central Turkey, September: 14.4 (30) (Harrison et al. 1973).

C. c. albiventris. Iran, Afghanistan, and Kazakhstan (USSR), combined, May-October: 3 15:4 (0.86; 8) 14:4-16:8, \$\Pi\$ 12:0 (0.62; 5) 11:8-13:0 (Paludan 1938, 1959; Dolgushin et al. 1972).

Structure. Wing short, rather broad at base, tip rounded. 10 primaries: p6 and p7 longest (p7 occasionally 0.5 shorter), p8 0.5-3 shorter, p9 6.5-12, p5 0-2, p4 1.5-4, p3 2.5-5, p1 5.5-9 (n=20) (RMNH, ZMA; see also Mead 1977). P10 reduced, 4-5 mm wide, tip rounded; 19-25 (\$\Pi\$) or 22-28 (\$\Bar{\infty}\$) shorter than p6, 10.3 (20) 9-12 longer than longest upper primary covert. Outer web of p6-p8 emarginated (p8 sometimes faintly), frequently also

p5 and p9 (emargination on p9 usually hidden below tips of upper primary coverts), exceptionally p4; in 26 birds from France, p5-p8 emarginated in 46%, p6-p8 in 54% (G Olioso); see also Scott and Svensson (1972). Longest tertial reaches secondary-tips. Tail rather short (but long compared with wing length, projecting well beyond short, rounded wing-tips), tip rounded; 10 feathers, broad and with rounded tips, rather soft; ts 7-12(-17) shorter than t1, on average 10.5 shorter (n=20); feathers c. 10-14 (t1) or c. 8-12 (t5) wide, in part depending on age, sex, and abrasion (widest in fresh adult of, narrowest in worn 1st adult 2). Bill straight, short, fine; rather narrow at base, laterally compressed at tip; tip of culmen slightly decurved. Nostril oval, partly covered by narrow membrane above. Some inconspicuous, short, fine bristles near base of upper mandible. Tarsus and toes rather short but strong; middle toe with claw 16.9(5) 16-17.5; outer toe with claw c. 76% of middle with claw, inner c. 73%, hind c. 89%. Claws short, fine, slightly decurved.

Geographical variation. Largely clinal: size increases and pigmentation decreases from west to east. Only westernmost race (nominate cetti) and easternmost albiventris are distinct, but intermediate orientalis recognized as smaller than albiventris and paler than nominate cetti (Vaurie 1954c). Boundaries between nominate cetti and orientalis in west and between orientalis and albiventris in east difficult to define; for west, Vaurie (1954c, 1050) followed here, supported by specimens examined (RMNH, ZFMK, ZMA); for east, Dolgushin et al. (1972) and Stepanyan (1978) followed. C. c. orientalis paler rufous-brown on upperparts than nominate cetti, less saturated rufous, slightly more olive (even when fresh), greyer when worn; underparts much more extensively off-white; supercilium wider and whiter; earcoverts, side of neck, side of breast, flank, and under tail-coverts paler and less extensive brown-grey, hardly olive or rufous; wing and tail on average a few mm longer. Some birds from Balearic Islands and north-west Africa almost as pale as orientalis (ZFMK, ZMA: see also Stresemann 1920 appendix), and these sometimes separated as salvatoris Von Jordans, 1914. Birds from Balkan area to Crete and western Turkey similar in size to orientalis, but colour near nominate cetti; sometimes separated as reiseri Parrot, 1910 (see, e.g., Matvejev and Vasić 1977), or muelleri Stresemann, 1919, but only a few birds have wing, tail, and bill longer than nominate cetti and most birds are indistinguishable in colour and size. C. c. albiventris is large; even paler on upperparts than orientalis, more diluted olive-brown; underparts largely white, light greyish-brown restricted to flank and under tail-coverts (Vaurie 1954c).

Recognition. Differs from unstreaked species of Locustella and Acrocephalus in short, rounded wing (with many primaries emarginated and long p10) and in rounded tail with only 10 feathers (12 in other species). In summer, when moulting, sometimes less easy to identify: in particular, moulting Savi's Warbler L. luscinioides is similar in colour and tail shape, and some tail-feathers may be missing; differs then from L. luscinioides in whiter and more distinct supercilium and eye-ring, rufous rump and upper tail-coverts (upperparts not uniform), greyer flank and chest, presence of emarginations on primaries, and (if present) long p10.