

SOOTY GRASSQUIT *Tiaris fuliginosa*

The species was first recorded for Paraguay at the RNBM on 12 September 1992 (Brooks *et al.* 1993). Since then, a male was observed calling at the same place (24°08'58"S, 55°25'22"W) on 26 September 1994 (AMN), and another male was seen in November 1994 at 24°08'03"S, 55°31'44"W (R. Clay).

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References:

- Acevedo, C., Fox, J., Gauto, R., Granizo, T., Keel, S., Pinazzo, J., Spinzi, L., Sosa, W. & Vera, V. 1990. *Áreas prioritarias para la conservación en la región oriental del Paraguay*. Centro de Datos para la Conservación, Asunción.
- Brooks, T. M., Barnes, R., Bartrina, L., Butchart, S. H. M., Clay, R. P., Esquivel, E. Z., Etcheverry, N. I., Lowen, J. C. & Vincent, J. 1993. Bird surveys and conservation in the Paraguayan Atlantic forest. *BirdLife International Study Rep.* 57: 1–145. BirdLife International, Cambridge, U.K.
- Cabrera, A. L. & Willink, A. 1973. *Biogeografía de América Latina*. Programa Regional de Desarrollo Científico y Tecnológico (serie de biología monografía no. 13). Organización de Los Estados Americanos, Washington, D.C.
- Canevari, M., Canevari, P., Carrizo, G. R., Harris, G., Mata, J. R. & Straneck, R. J. 1991. *Nueva guía de las aves argentinas*. Fundación Acindar, Buenos Aires.
- CDC 1991. Estudios biológicos en el área del proyecto Mbaracayú, Canindeyú, República del Paraguay: caracterización de las comunidades naturales, la flora y la fauna. Unpublished report, Ministerio de Agricultura y Ganadería/Centro de Datos para la Conservación, Asunción.
- Chesser, R. T. 1994. Migration in South America: an overview of the austral system. *Bird Conservation International* 4: 91–107.
- Collar, N. J., Crosby, M. J. & Stattersfield, A. J. 1994. *Bird to Watch 2: the World List of Threatened Birds*. BirdLife Conservation Series No. 4. BirdLife International, Cambridge, U.K.
- Collar, N. J., Gonzaga, L. P., Krabbe, N., Madroño Nieto, A., Naranjo, L. G., Parker, T. A. & Wege, D. C. 1992. *Threatened Birds of the Americas: the ICBP/IUCN Red Data Book*. International Council for Bird Preservation, Cambridge, U.K.
- Dinerstein, E., Olson, D. M., Graham, D. J., Webster, A. L., Primm, S. A., Bookbinder, M. P. & Ledec, G. 1995. *A Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean*. The World Bank/World Wildlife Fund, Washington, D.C.
- FMB (Fundación Moisés Bertoni) 1992. Plan Operativo: Reserva Natural del Bosque Mbaracayú 1993–1995. Fundación Moisés Bertoni para la Conservación de la Naturaleza. Unpublished report, Asunción, Paraguay.
- FMB (Fundación Moisés Bertoni) 1994. Proyecto trinacional de manejo del Bosque Atlántico Interior. 1a. Etapa: Diagnóstico de los Recursos Socio-Ambientales, Capítulo Paraguay, Vols I and II. Unpublished report, Fundación Moisés Bertoni para la Conservación de la Naturaleza, Asunción, Paraguay.
- Hayes, F. E. 1995. *Status, distribution and biogeography of the birds of Paraguay*. Monographs in Field Ornithology No. 1. American Birding Association, Albany, New York.

- Hayes, F. E., Goodman, S. M. & López, N. E. 1990. North American bird migrants in Paraguay. *Condor* 92: 947-960.
- Hayes, F. E. & Scharf, P. A. 1995. The birds of Parque Nacional Cerro Corá, Paraguay. *Cotinga* 4: 20-24.
- Hayes, F. E., Scharf, P. A. & Ridgely, R. S. 1994. Austral bird migrants in Paraguay. *Condor* 96: 83-97.
- ICBP 1992. *Putting Biodiversity on the Map: priority areas for global conservation*. International Council for Bird Preservation, Cambridge, U.K.
- Keel, S., Gentry, A. & Spinzi, L. 1993. Using vegetation analysis to facilitate the selection of conservation sites in eastern Paraguay. *Conservation Biology* 7: 66-75.
- Laclau, P. 1994. La conservación de los recursos naturales y el hombre en la Selva Paranaense. *Boletín Técnico de la Fundación Vida Silvestre Argentina* No. 20. Fundación Vida Silvestre Argentina/Fondo Mundial para la Naturaleza, Buenos Aires.
- López, N. E. 1992. Observaciones sobre la distribución de psitácidos en el Departamento de Concepción, Paraguay. *Bol. Mus. Nac. Hist. Nat. Parag.* 11: 2-25.
- Lowen, J. C., Bartrina, L., Brooks, T. M., Clay, R. P. & Tobias, J. 1996a. Project Yacutinga '95: bird surveys and conservation priorities in eastern Paraguay. *Cotinga* 5: 14-19.
- Lowen, J. C., Bartrina, L., Clay, R. P. & Tobias, J. A. 1996b. *Biological surveys and conservation priorities in eastern Paraguay*. CSB Conservation Publications, Cambridge, U.K.
- Lowen, J. C., Clay, R. P., Brooks, T. M., Esquivel, E. Z., Bartrina, L., Barnes, R., Butchart, S. H. M. & Etcheverry, N. I. 1995. Bird conservation in the Paraguayan Atlantic Forest. *Cotinga* 4: 58-64.
- Madroño N., A. & Esquivel, E. Z. 1995. Reserva Natural del Bosque de Mbaracayú: su importancia en la conservación de aves amenazadas, cuasi-amenazadas y endémicas del Bosque Atlántico. *Cotinga* 4: 52-57.
- Pearman, M. & Abadie, E. I. (in press) Mesopotamia Grassland and Wetland Survey 1991-1993: conservation of threatened birds and habitat in north-east Argentina. Worldwide Publications, Derby.
- Ridgely, R. S. & Tudor, G. 1989. *The Birds of South America. Vol. 1. The Oscine Passerines*. Oxford Univ. Press.
- Ridgely, R. S. & Tudor, G. 1994. *The Birds of South America. Vol. 2. The Suboscine Passerines*. Oxford Univ. Press.
- Sick, H. 1993. *Birds in Brazil: a natural history*. Princeton Univ. Press.
- Storer, R. W. 1989. Notes on Paraguayan birds. *Occ. Pap. Mus. Zool., Univ. Michigan* 719: 1-21.
- TN 1992. General Reference for the GPS Pathfinder System. Trimble Navigation, Sunnyvale, California.
- Wege, D. C. & Long, A. J. 1995. *Key areas for threatened birds in the Neotropics*. (BirdLife Conservation Series No. 5.) BirdLife International, Cambridge, U.K.

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Re-evaluation of the taxonomic status of *Phylloscopus proregulus kansuensis* Meise

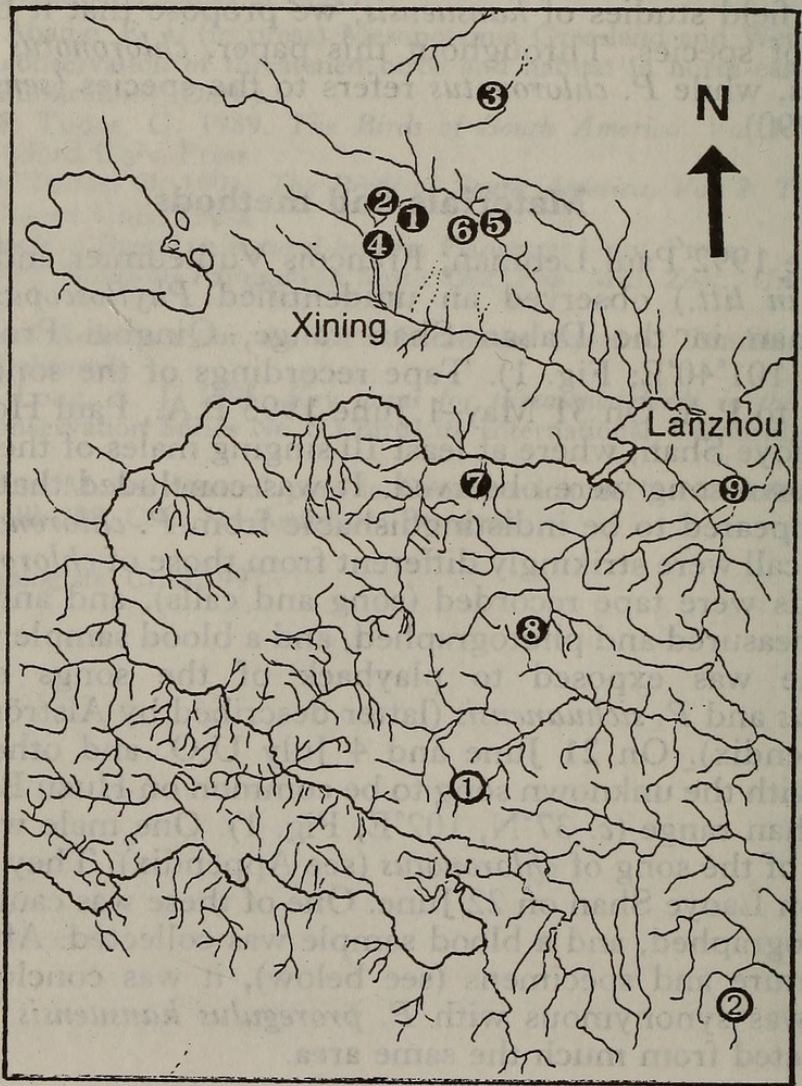
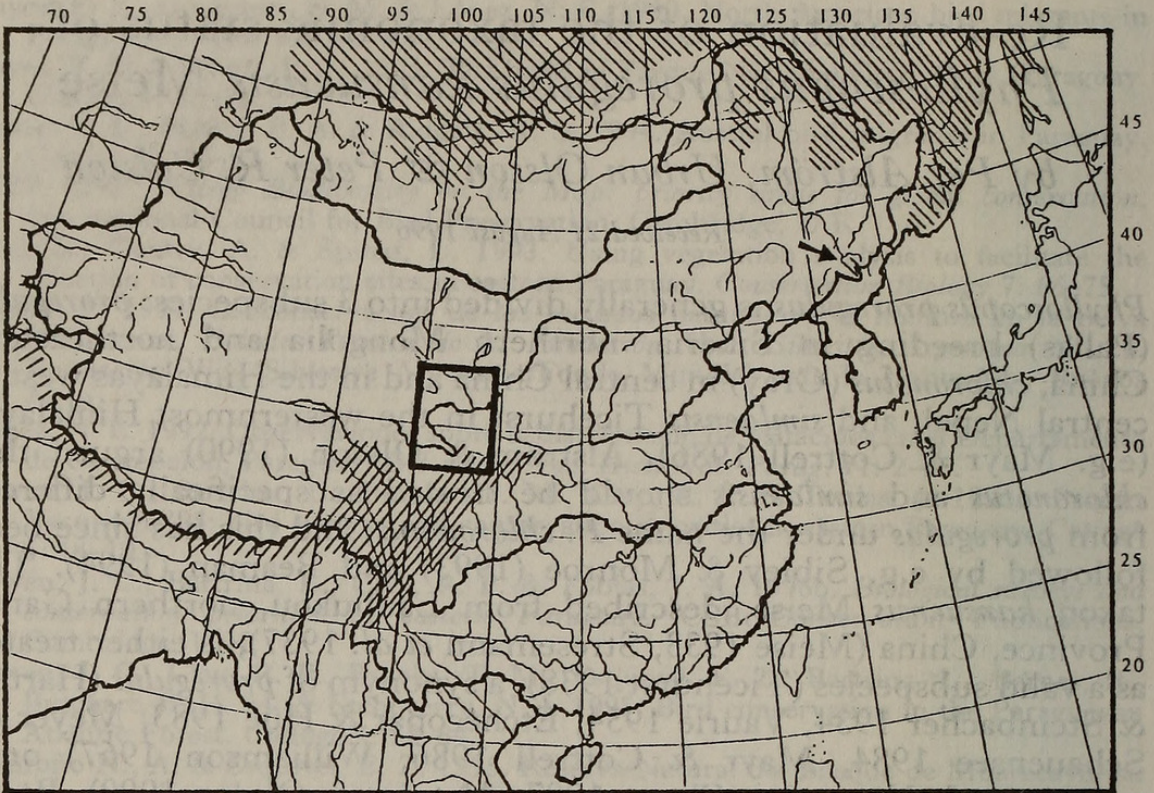
by Per Alström, Urban Olsson & Peter R. Colston

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Phylloscopus proregulus is generally divided into 3 subspecies: *proregulus* (Pallas) breeding in Siberia, northern Mongolia and northeastern China; *chloronotus* (Gray) in central China and in the Himalayas west to central Nepal; and *simlaensis* Ticehurst in the westernmost Himalayas (e.g. Mayr & Cottrell 1986). Alström & Olsson (1990) argued that *chloronotus* and *simlaensis* should be treated as specifically different from *proregulus* under the name *P. chloronotus*, and this has since been followed by e.g. Sibley & Monroe (1993) and Beaman (1994). The taxon *kansuensis* Meise, described from Lauhukou, northern Gansu Province, China (Meise 1933, Stresemann *et al.* 1937), is either treated as a valid subspecies (Ticehurst 1938), a synonym of *proregulus* (Hartert & Steinbacher 1934, Vaurie 1954, Étchécopar & Hüe 1983, Meyer de Schauensee 1984, Mayr & Cottrell 1986, Williamson 1967) or a synonym of *chloronotus* (Cheng 1987, Alström & Olsson 1990). Based on recent field studies of *kansuensis*, we propose that it be elevated to the rank of species. Throughout this paper, *chloronotus* refers to the subspecies, while *P. chloronotus* refers to the species (*sensu* Alström & Olsson 1990).

Materials and methods

On 5 June 1992 Paul Lehman, François Vuilleumier and others (Paul Lehman *in litt.*) observed an unidentified *Phylloscopus* warbler on Laoye Shan in the Daban Shan range, Qinghai Province, China (36°56'N, 101°40'E; Fig. 1). Tape recordings of the song of this bird were sent to P.A. On 31 May–1 June 1993 P.A., Paul Holt and others visited Laoye Shan, where at least 10 singing males of the warbler with the unknown song were observed. It was concluded that morphologically it appeared to be indistinguishable from *P. chloronotus*, but both song and call were strikingly different from those of *chloronotus*. Two of these birds were tape recorded (song and calls), and another one was caught, measured and photographed, and a blood sample was collected. One male was exposed to playback of the songs of *proregulus*, *chloronotus* and *P. sichuanensis* (latter described by Alström *et al.* 1992) (see Appendix). On 21 June and 4 July U.O. and others found the warbler with the unknown song to be common on Huzu Bei Shan in the Daban Shan range (c. 37°N, 102°E; Fig. 1). One male was exposed to playback of the song of *chloronotus* (see Appendix). They also observed 5 males on Laoye Shan on 22 June. One of these was caught, measured and photographed, and a blood sample was collected. After consulting the literature and specimens (see below), it was concluded that this warbler was synonymous with *P. proregulus kansuensis* Meise, which was collected from much the same area.



On 2–3 June 1994 on Emei Shan, Sichuan Province (29°35'N, 103°11'E), P.A. exposed 4 territorial, singing males of *chloronotus* to playback of song of *kansuensis* (see Appendix). On 7–8 June 1994 P.A. found *kansuensis* to be common (c. 45 individuals) in Xinglong Shan, Gansu Province (c. 35°40'N, 103°55'E; Fig. 1). Five of these were exposed to playback of the song of *proregulus* and *chloronotus* and one to *P. sichuanensis* (see Appendix). On 11–22 June 1994 P.A. surveyed the area between Xining, Qinghai Province (36°35'N, 101°55'E; Fig. 1) and Jiuzhaigou, Sichuan Province (c. 33°25'N, 104°05'E; Fig. 1), and from Jiuzhaigou north to Longxi, Gansu Province (34°59'N, 104°46'E; Fig. 1) in order to try to find out whether or not *kansuensis* and *chloronotus* were sympatric. There is very little forest in this area (except in Jiuzhaigou), and most adequate patches of forest along the main road were checked. On 11–14 June 1994 Mengda, Qinghai Province (c. 35°45'N, 102°40'E; Fig. 1) was visited (together with Jesper Hornskov), and *kansuensis* was found to be common (c. 60 individuals; the commonest bird species). Eight of these were exposed to playback of the songs of *proregulus* and *chloronotus* (see Appendix), and 3 males and 1 female were caught and measured. On 15 June 1994 4 *kansuensis* (3 singing males and 1 calling bird, presumably a female) were observed in a small patch of forest at Hezuozhen, Gansu Province (35°00', 102°58'E; Fig. 1), and two of the males were exposed to playback of *proregulus* and *chloronotus* (see Appendix). On 16 June 1994 *chloronotus* was found to be fairly common (≥ 13 singing males and 3 calling birds) in a small forest at Chakou, Gansu Province (c. 34°12'N, 102°25'E; Fig. 1). Three of these were exposed to playback of *kansuensis*. No *kansuensis* were observed at this site. On 17–19 June 1994 Jiuzhaigou was visited, where several *chloronotus* but no *kansuensis* were noted. Between Jiuzhaigou and Longxi no suitable forest was found. On 22 June 1995 P.A. and P.R.C. visited Laoye Shan, where c. 10 *kansuensis* were observed. On 23–25 June 1995 P.A. and P.R.C. surveyed Huzu Bei Shan, where *kansuensis* was common. On one of these a playback test was carried out (see Appendix).

During the playback experiments a speaker with a 20 m long cable was placed in the territory of a singing male. Songs of different taxa were played when the bird was considered to be close enough to the speaker to hear the song clearly. The term "1st approach" is the time when the bird exposed to the playback was first seen to move towards the speaker. "Full response" means that the bird responded by vigorously searching for the source of the sound, while adopting an aggressive posture with slightly raised tail and slightly drooped, quickly flicking wings; usually silent, but sometimes calling, only rarely singing

Figure 1. Distribution of *chloronotus* //// and *proregulus* (only part of range in Siberia shown) \\\\. Detail shows all localities (white figures in black circles) where *kansuensis* has been found: 1, Lauhukou (type locality); 2, Komandse; 3, Hu-dja-dschuang; 4, Laoye Shan; 5, Tschau-tou; 6, Huzu Bei Shan; 7, Mengda; 8, Hezuozhen; 9, Xinglong Shan. Detail also shows localities (figures in open circles) where *chloronotus* has been found in close proximity to *kansuensis*: 1, Chakou; 2, Jiuzhaigou. Based on Stresemann *et al.* (1937) and personal observations.

one or two strophes. The song of *P. proregulus* was tape recorded by P.A. at Changbai Shan, Jilin Province (c. 41°30'N, 128°11'E) in June 1987; the two song types of *P. chloronotus* were tape recorded by P.A. on Emei Shan, Sichuan Province (c. 29°35'N, 103°10'E) in May 1987; the song of *P. sichuanensis* was tape recorded by P.A. in Jiuzhaigou, Sichuan Province in June 1989; and the song of *kansuensis* was tape recorded on Laoye Shan, Qinghai Province in May 1993.

In the Natural History Museum, Tring, U.K., P.A. and P.R.C. examined 1 specimen of *kansuensis* (collected at the type locality; BMNH 1938.5.16.21) and a further 6 on loan from the Zoologisches Museum, Berlin, Germany (collected at or near the type locality; including the holotype), as well as long series of *chloronotus* and *proregulus*. All of the specimens of *kansuensis* and a series of *proregulus* and *chloronotus* were measured by P.A. Wing length was measured with the wing flattened and stretched (maximum chord), and bill length was taken to the skull.

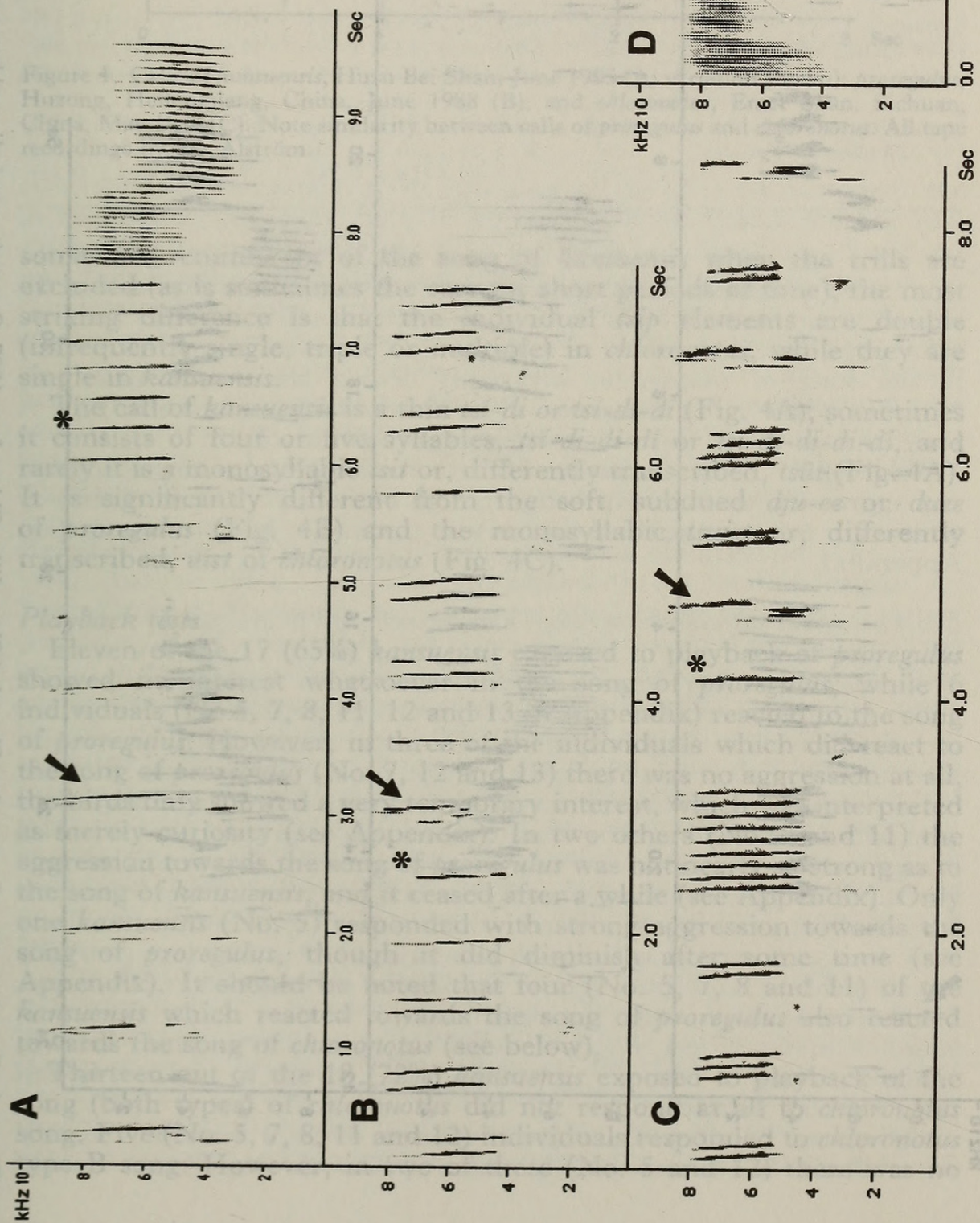
Results

Vocal differences between kansuensis and proregulus/chloronotus

The song of *kansuensis* begins with a series of faltering, thin, high-pitched, slightly harsh *tsrip*, followed by a row of slightly accelerating clear *tsip* notes (often on two different pitches), and ends in a clear c. 1.1–2.2 s long trill (which often changes from high to slightly lower pitch) (Fig. 2A). The trill recalls the song of Wood Warbler *P. sibilatrix* and Emei Leaf Warbler *P. emeiensis* (Alström & Olsson 1995). Sometimes the initial *tsrip* notes are omitted, and sometimes the trill is not given in every strophe (the song then alternates between *tsrip* and *tsip*, the latter often on two pitches, for some time). The song of *kansuensis* is profoundly different from the varied, somewhat Canary *Serinus canaria*-like song of *proregulus* (Fig. 3), although the *tsrip* notes given by *kansuensis* are somewhat similar to those of *proregulus* (one note marked by an arrow in Fig. 2A and 3, respectively).

The song of *kansuensis* is also strikingly different from the two different song types of *chloronotus* (referred to as type A and type B, respectively, by Alström & Olsson 1990; Fig. 2B, 2C and 2D). However, two of the elements in the repertoire of *kansuensis* resemble individual elements in *chloronotus* song. The *tsrip* notes given by *kansuensis* are rather close to *tsrip* notes in *chloronotus* type B song (one marked by an arrow in Fig. 2A, 2B and 2C, respectively), and the *tsip* notes of *kansuensis* are rather similar to individual elements in especially type B song of *chloronotus* (one element marked by an * in Fig. 2A, 2B and 2C, respectively). Accordingly, *chloronotus* type B song is

Figure 2. Songs of *kansuensis* and *chloronotus*. Arrows indicate *tsrip* notes and asterisks *tsip* notes (only one marked in each song). A. Complete song of *kansuensis*, Laoye Shan, Qinghai, China, June 1993. B. Part of song of *chloronotus* type B, Emei Shan, Sichuan, China, May 1987. C. Part of song of *chloronotus*, type B (variation), Emei Shan, Sichuan, China, June 1994. D. Complete song of *chloronotus*, type A, Emei Shan, Sichuan, China, June 1994. All tape recordings by Per Alström.



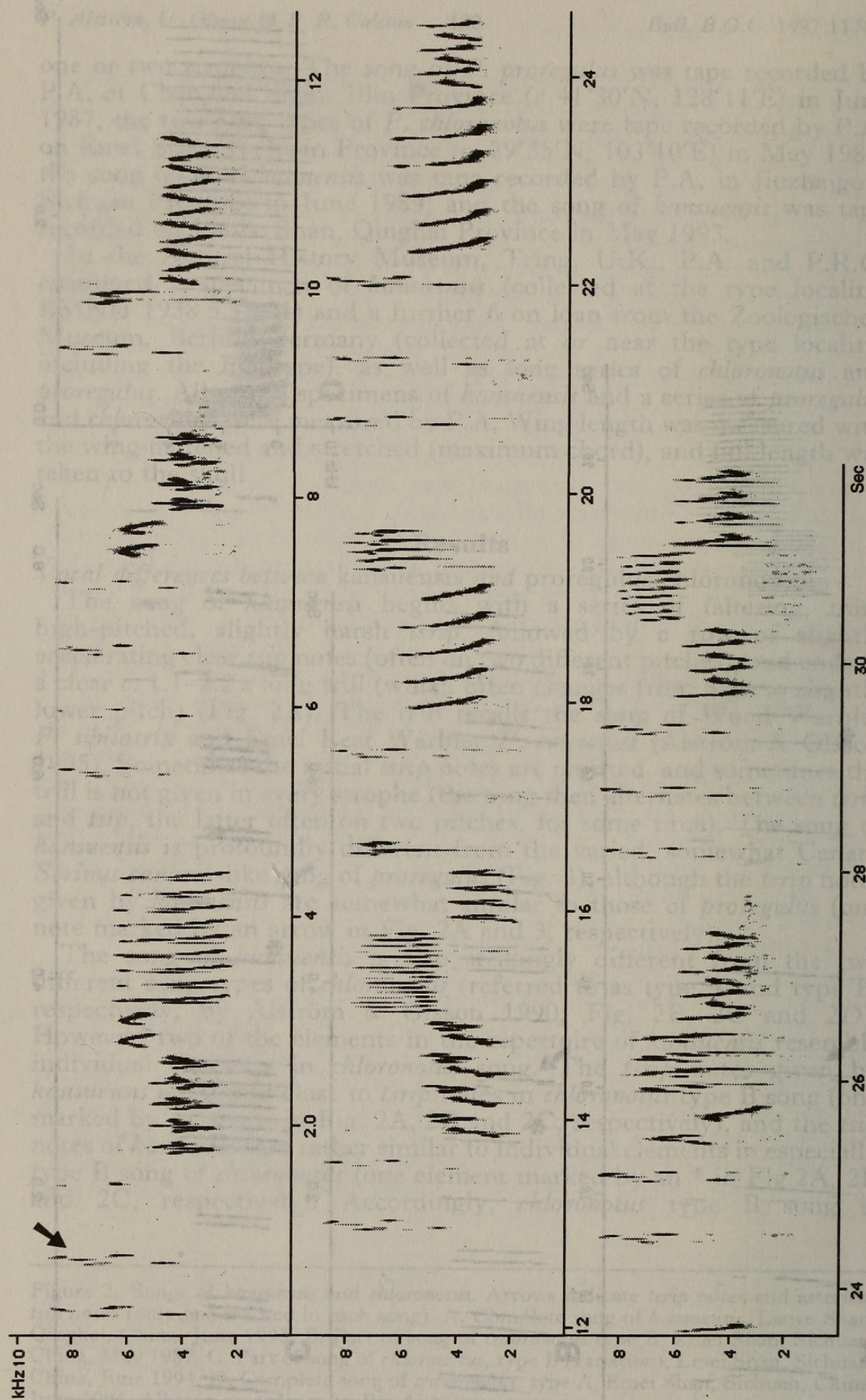


Figure 3. Complete song of *proregulus*, Changbai Shan, Jilin, China, June 1987. One *tsrip* note indicated by an arrow. Tape recorded by Per Alström.

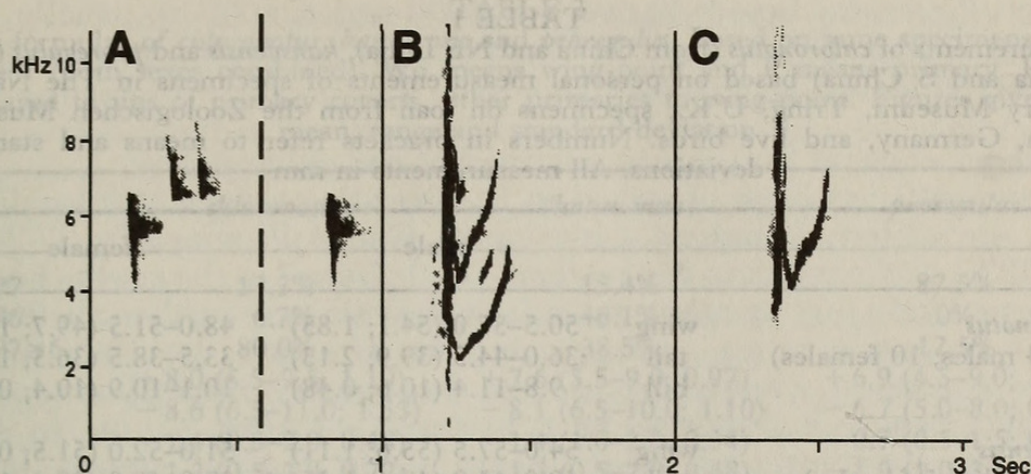


Figure 4. Calls of *kansuensis*, Huzu Bei Shan, June 1995 (A; variation shown); *proregulus*, Huzong, Heilongjiang, China, June 1988 (B); and *chloronotus*, Emei Shan, Sichuan, China, May 1989 (C). Note similarity between calls of *proregulus* and *chloronotus*. All tape recordings by Per Alström.

somewhat reminiscent of the song of *kansuensis* when the trills are excluded (as is sometimes the case for short periods of time); the most striking difference is that the individual *tsip* elements are double (infrequently single, triple or multiple) in *chloronotus*, while they are single in *kansuensis*.

The call of *kansuensis* is a thin *tsí-di* or *tsí-di-di* (Fig. 4A); sometimes it consists of four or five syllables, *tsí-di-di-di* or *tsí-di-di-di-di*, and rarely it is a monosyllabic *tsit* or, differently transcribed, *tsüt* (Fig. 4A). It is significantly different from the soft, subdued *dju-ee* or *duee* of *proregulus* (Fig. 4B) and the monosyllabic *tsuist* or, differently transcribed, *uist* of *chloronotus* (Fig. 4C).

Playback tests

Eleven of the 17 (65%) *kansuensis* exposed to playback of *proregulus* showed no interest whatsoever in the song of *proregulus*, while 6 individuals (No. 5, 7, 8, 11, 12 and 13 in Appendix) reacted to the song of *proregulus*. However, in three of the individuals which did react to the song of *proregulus* (No. 7, 12 and 13) there was no aggression at all, the birds only showed a very temporary interest, which was interpreted as merely curiosity (see Appendix). In two others (No. 8 and 11) the aggression towards the song of *proregulus* was not nearly so strong as to the song of *kansuensis*, and it ceased after a while (see Appendix). Only one *kansuensis* (No. 5) responded with strong aggression towards the song of *proregulus*, though it did diminish after some time (see Appendix). It should be noted that four (No. 5, 7, 8 and 11) of the *kansuensis* which reacted towards the song of *proregulus* also reacted towards the song of *chloronotus* (see below).

Thirteen out of the 18 (72%) *kansuensis* exposed to playback of the song (both types) of *chloronotus* did not respond at all to *chloronotus* song. Five (No. 5, 7, 8, 11 and 12) individuals responded to *chloronotus* type B song. However, in two of these (No. 5 and 12) there was no

TABLE 1

Measurements of *chloronotus* (from China and NE India), *kansuensis* and *proregulus* (from Siberia and S China) based on personal measurements of specimens in The Natural History Museum, Tring, U.K., specimens on loan from the Zoologisches Museum, Berlin, Germany, and live birds. Numbers in brackets refer to means and standard deviations. All measurements in mm

		male	female
<i>chloronotus</i> (n=14 males, 10 females)	wing	50.5–57.0 (54.1; 1.85)	48.0–51.5 (49.7; 1.06)
	tail	36.0–44.5 (39.9; 2.13)	33.5–38.5 (36.5; 1.73)
	bill	9.8–11.4 (10.6; 0.48)	10.1–10.9 (10.4; 0.27)
<i>kansuensis</i> (n=9 males, 5 females)	wing	54.0–57.5 (55.6; 1.11)	51.0–52.0 (51.5; 0.35)
	tail	40.0–44.0 (42.4; 1.45)	37.0–40.0 (38.4; 1.29)
	bill	10.5–11.3 (10.8; 0.24)	10.0–11.1 (10.5; 0.41)
<i>proregulus</i> (n=12 males, 14 females)	wing	49.0–54.5 (51.3; 1.91)	48.0–52.0 (49.8; 1.37)
	tail	34.5–39.5 (36.7; 1.70)	33.0–40.0 (36.2; 1.95)
	bill	9.7–10.7 (10.3; 0.34)	9.7–10.8 (10.3; 0.33)

aggression at all involved, and the reaction was interpreted as merely curiosity. In none of the others was the reaction to the song of *chloronotus* nearly so strong as to the song of *kansuensis*, and the interest in the song of *chloronotus* invariably ceased after some time (see Appendix). Only one *kansuensis* (No. 7) reacted to *chloronotus* type A song, though there was no apparent aggression involved.

None of the 7 *chloronotus* tested with the song of *kansuensis* showed any aggression towards this song, though individual number 3 showed temporary interest the third time it was exposed to *kansuensis* song (see Appendix).

Morphological differences between *kansuensis* and *proregulus*/ *chloronotus*

Kansuensis differs from *proregulus* mainly in being clearly paler yellow on the supercilium (unless very worn, *proregulus* is bright yellow on especially the anterior part of the supercilium, while *kansuensis* shows only a very faint yellowish tinge to the supercilium in front of/above the eye). At least in spring and summer the lower mandible is generally paler in *kansuensis* than in *proregulus*: it is either entirely pale orange or pale orange with a very small dark tip in *kansuensis*, while it has a much more extensive dark tip in *proregulus* (lower mandible frequently appears nearly all dark, although it is sometimes extensively pale orange or even practically all pale orange). Also the legs generally appear paler in *kansuensis* than in *proregulus*, although there is overlap. Furthermore, *kansuensis* has significantly longer wings (Table 1; Mann-Whitney U test, $P_{\text{males}}=0.0002$, $P_{\text{females}}=0.01$) and tail (Table 1; Mann-Whitney U test, $P_{\text{males}}=0.0001$, $P_{\text{females}}=0.04$) and a different wing formula (Table 2).

Compared to *chloronotus*, there appears to be a tendency for the supercilium to be marginally more yellowish-tinged, the lateral

TABLE 2

Wing formulae of *chloronotus*, *kansuensis* and *proregulus*. Based on same specimens as in Table 1 (both sexes combined). Wp means wing-point and P means primary. P10 is compared to tips of primary coverts, other primaries to wing-point. Figures given are mean, range and standard deviation

	<i>chloronotus</i>	<i>kansuensis</i>	<i>proregulus</i>
wp: P7	13.3%	15.4%	87.5%
wp: P6	6.7%	46.1%	0%
wp: P7=6	80.0%	38.5%	12.5%
P10	+ 8.0 (5.5–9.5; 1.19)	+ 7.6 (5.5–9.0; 0.97)	+ 6.9 (4.5–9.0; 1.39)
P9	– 8.6 (6.5–11.0; 1.53)	– 8.1 (6.5–10.0; 1.10)	– 6.7 (5.0–8.0; 0.83)
P8	– 1.4 (0.5–2.0; 0.48)	– 1.4 (1.0–2.0; 0.34)	– 0.7 (0.5–1.5; 0.32)
P5	– 1.3 (0.5–3.0; 0.72)	– 1.3 (0.5–2.0; 0.48)	– 1.9 (1.0–3.5; 0.64)

crown-stripes marginally paler and greener, and the underside whiter in *kansuensis*, but these differences are so subtle that *kansuensis* and *chloronotus* are essentially identical on plumage. However, the lower mandible is generally clearly paler in *kansuensis* than in *chloronotus* (in the latter it frequently appears nearly all dark, although sometimes pale orange with a very small dark tip). Also the legs generally appear paler in *kansuensis* than in *chloronotus*, although there is overlap. Although *kansuensis* and *chloronotus* are basically very similar on measurements and wing formulae, *kansuensis* has marginally longer wings (Table 1; Mann–Whitney U test, $P_{\text{males}}=0.045$, $P_{\text{females}}=0.006$) and a greater tendency for the 6th primary to be equal to the 7th (Table 2).

Breeding habitat of kansuensis, proregulus and chloronotus

At Laoye Shan (altitude *c.* 2500–2900 m) and Mengda (*c.* 2200–2500 m) *kansuensis* occurs in predominantly deciduous forest (including e.g. birch *Betula* and aspen *Populus*) with some spruce *Picea* mixed in (overall ≤ 10 –*c.* 20%). On Huzu Bei Shan (*c.* 2700–2900 m) it occurs mainly in deciduous forest (predominantly birch) with some spruce and tall junipers *Juniperus* mixed in, much less commonly in predominantly coniferous forest. At Xinglong Shan *kansuensis* occurs mainly in mixed deciduous and spruce forest (the predominant forest type), but also in mainly deciduous as well as mainly spruce forest, at an altitude of *c.* 1700–1800 m. At Hezuozhen *kansuensis* was found in “semi-old” secondary spruce forest with much undergrowth of deciduous bushes at an altitude of *c.* 3200 m (altitude according to locals).

The breeding habitats of *proregulus* and *chloronotus* differ significantly from that favoured by *kansuensis*. *Proregulus* breeds in the taiga, in coniferous forest or mixed forest with a high percentage of conifers (Dement'ev & Gladkov 1954, Flint *et al.* 1984, Rogacheva 1992, pers. obs.). *Chloronotus* breeds chiefly in spruce/fir *Abies* forest or predominantly spruce/fir forest, and only very sparsely in mainly deciduous forest (on mountains, just below the spruce forest belt). In

China *chloronotus* breeds between c. 2000 and c. 4000 m, usually at c. 2600–c. 3100 m (Étchécopar & Hüe 1983, Meyer de Schauensee 1984, Alström *et al.* 1992, pers. obs.).

Breeding ranges of kansuensis, proregulus and chloronotus

Kansuensis has been observed in the breeding season at 9 localities, from the eastern Lenglong Ling, north Gansu Province (c. 37°30'N, 102°30'E) in the north to Hezuozhen, south Gansu in the south (Fig. 1). It seems likely that its range extends at least slightly further northwest, as the mountain range continues in that direction. It is not known where *kansuensis* winters, but due to the severe winter climate in its breeding range, it ought to be considerably further south. In 1993 *kansuensis* apparently left Laoye Shan in mid to late October (Jesper Hornskov *in litt.*).

The breeding range of *proregulus* appears to be disjunct from that of *kansuensis* by at least 1000 km (Fig. 1). Mayr & Cottrell (1986) and Cheng (1987) state that *proregulus* and *chloronotus* intergrade in eastern Qinghai. This surely refers to *kansuensis*. We have found no evidence of *proregulus* breeding in Qinghai.

Chloronotus (including *simlaensis*) breeds from the western Himalayas through central China north to at least Chakou (Fig. 1), at the most 100 km south of Hezuozhen, where *kansuensis* was found. It seems likely that the breeding ranges of *kansuensis* and *chloronotus* actually overlap marginally, although this has not yet been proven.

Discussion

Since *kansuensis* is morphologically more similar to *chloronotus* than to *proregulus*, it may seem surprising that most previous authors (Hartert & Steinbacher 1934, Vaurie 1954, Étchécopar & Hüe 1983, Meyer de Schauensee 1984, Mayr & Cottrell 1986, Williamson 1967) have lumped *kansuensis* with *proregulus* rather than with *chloronotus*. However, Hartert & Steinbacher (*op. cit.*) do not state how many individuals they studied, Vaurie (*op. cit.*) only examined one, and we doubt that any of the others actually examined specimens of *kansuensis*.

The morphological differences between *kansuensis* and *chloronotus* are so slight that, based on these alone, *kansuensis* would be best synonymized with *chloronotus* or considered a very poorly differentiated subspecies of *P. chloronotus*. In contrast, the vocalizations of *kansuensis* are very different from those of *chloronotus*. In fact, the differences in song between *kansuensis* and *chloronotus* are much more pronounced than between different species in some other presumably monophyletic groups of *Phylloscopus* warblers, e.g. *P. occipitalis*–*P. reguloides*–*P. davisoni* (Martens 1980, Alström & Olsson 1993), *P. schwarzi*–*P. armandii* (Martens 1980, Alström & Olsson 1994), and *P. griseolus*–*P. affinis*–*P. subaffinis* (Martens 1980, Alström & Olsson 1992, 1994), and at least as pronounced as between other species of *Phylloscopus*. This alone suggests that the rank of species would be appropriate for *kansuensis*. However, since *chloronotus* has two song types which are nearly as different from each other as from the song of *kansuensis*, the

distinctive song of *kansuensis* might be considered to be just a third, geographically localized, variant of *P. chloronotus* song. This is contradicted by the playback tests which have been carried out, which instead indicate that the songs of *kansuensis* and *chloronotus* would act as prezygotic reproductive isolating mechanisms if there were any sympatry. Especially the playback tests on those *kansuensis* (No. 16 and 17) and *chloronotus* (No. 5, 6 and 7) which were found in close proximity to each other (separated by at the most 100 km), combined with the apparent lack of intergradation between these two taxa (as indicated by the lack of individuals with intermediate vocalizations¹), strongly suggest that *kansuensis* and *chloronotus* should be considered separate species. It is curious that 5 of the *kansuensis* tested showed some interest (though there was no or relatively little aggression involved) in the type B song of *chloronotus*, while only one individual reacted with curiosity to *chloronotus* type A song. Since *chloronotus* reacts equally strongly to both of its two song types (Alström & Olsson 1990 and Appendix), the reason why *kansuensis* showed more interest in the type B song than in the type A song does not seem to be a case of the former song type being more important in territory defence than the latter. It seems possible that *kansuensis* considers the type B song to be more reminiscent of its own song than the type A song. In general, response from one taxon to playback of song of another taxon is of little taxonomic relevance. Response to playback of heterospecific closely related sympatric taxa has been noted in several cases, presumably because of interspecific territorialism (e.g. Emlen *et al.* 1975, Catchpole 1978, Catchpole & Leisler 1986, Prescott 1987, Elfström 1990, Baker 1991). Response to playback of allopatric taxa is equally uninformative in this context, and may simply be a result of similarities between the songs of the taxa involved (cf. Ratcliffe & Grant 1985); the song's function as a reproductive isolating barrier is unlikely to be fully developed if the taxa are geographically separated. The fact that *kansuensis* and *chloronotus* exist so close to each other without any signs of intergradation indicates that they have evolved independently of each other for a substantial period of time. Significant interbreeding would presumably have merged the two forms. The differences in breeding habitat are further evidence of speciation (Richman & Price 1992).

The overall similarity between *kansuensis*, *P. chloronotus* and *P. proregulus* suggests that they share a common ancestor and thus form a monophyletic group. On plumage, wing-formula, size and song *kansuensis* shows a greater similarity to *chloronotus* than to *proregulus*.

¹We assume that the offspring from any mixed pairs of *kansuensis* and *chloronotus* would have aberrant songs compared to their parent taxa. This assumption is supported by reports of aberrant songs in suspected hybrids between *Phylloscopus bonelli* × *P. sibilatrix* (Bremond 1972, Fouarge 1972) and *P. trochilus* × *P. collybita* (Da Prato & Da Prato 1986). However, since song appears to be to a great extent learned in "song-birds" in general (see review in Catchpole & Slater 1995), it is possible that the song of hybrids would be very similar to or indistinguishable from the species which is more numerous in the area where it was born.

This, together with the distributional pattern, suggests that *kansuensis* and *chloronotus* diverged more recently, and thus are more closely related to each other than to *proregulus*. In analogy with the proposed treatment of *kansuensis* and *chloronotus* as separate species, *kansuensis* and *proregulus* must also be treated as specifically different. The playback tests support this treatment. However, three *kansuensis* (No. 5, 8 and 11) reacted with some aggression toward the song of *proregulus*, and in one of these (No. 5) the response was almost as strong as to the song of *kansuensis*. It should be noted that these three birds also responded to *chloronotus* type B song. As discussed above, it is important to keep in mind that only absence of response to playback may have some taxonomic relevance. The differences in breeding habitat between *kansuensis* and *proregulus* further support the view that they are better treated as separate species.

It is clear that *kansuensis* is not conspecific with *P. sichuanensis*. These two were found in sympatry at Laoye Shan, Xinglong Shan, Mengda, Hezuozhen and Chakou, and morphologically and vocally they are significantly different (Alström *et al.* 1992). Also, the two *kansuensis* (No. 1 and 3) which were exposed to playback of the song of *P. sichuanensis* did not respond at all to it. Moreover, where both taxa occurred together, there was a difference in average habitat preference, *sichuanensis* favouring less-tall secondary growth at lower altitude than *kansuensis*.

P. proregulus (*sensu lato*) has been variously named Pallas's Warbler, Pallas's Leaf Warbler, Pallas's Willow Warbler, Lemon-rumped Warbler and Pale-rumped Warbler. We support Beaman (1994) in using the name Pallas's Leaf Warbler for *P. proregulus* (*sensu stricto*), Lemon-rumped Warbler for *P. chloronotus* (*sensu* Alström & Olsson 1990), and suggest the name Gansu Leaf Warbler for *P. kansuensis*. There are two reasons why we prefer the name Gansu Leaf Warbler rather than "Qinghai Leaf Warbler" (which might be thought a more suitable name, since nearly all of the records of *kansuensis* are from Qinghai Province and only a few from Gansu Province): firstly, the name Gansu Leaf Warbler is a translation of the scientific name (Gansu is the modern spelling of Kansu), and, secondly, the name Qinghai would surely be mis-pronounced by most people (correct pronunciation "Chinghigh").

Summary

Phylloscopus proregulus kansuensis Meise has variously been treated as a distinct subspecies, a synonym of *P. chloronotus* (*proregulus*) *chloronotus* or a synonym of *P. (p.) proregulus* (most authors). It is morphologically only very slightly different from *chloronotus*, though more clearly separable from *proregulus* (especially by its much paler yellow supercilium). Both song and calls are strikingly different from those of both *chloronotus* and *proregulus* (most different from latter). Unlike *chloronotus* and *proregulus* it breeds mainly in deciduous or mixed forest. In the breeding season it is parapatric with *chloronotus* (without any known geographical overlap), while it appears to be widely allopatric with *proregulus*. Playback tests indicate that the songs would act as prezygotic reproductive isolation mechanisms if there were any sympatry. We suggest that *kansuensis* be treated as a distinct species and that the English name be Gansu Leaf Warbler.

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References:

- Alström, P. & Olsson, U. 1990. Taxonomy of the *Phylloscopus proregulus* complex. *Bull. Brit. Orn. Cl.* 110: 38–43.
- Alström, P. & Olsson, U. 1992. On the taxonomic status of *Phylloscopus affinis* and *Phylloscopus subaffinis*. *Bull. Brit. Orn. Cl.* 112: 111–125.
- Alström, P. & Olsson, U. & Colston, P. R. 1992. A new species of *Phylloscopus* warbler from central China. *Ibis* 134: 329–334.
- Alström, P. & Olsson, U. 1993. Blyth's Leaf Warbler *Phylloscopus reguloides* found breeding in Thailand. *Forktail* 9: 150–152.
- Alström, P. & Olsson, U. 1994. Identification of Tickell's and Buff-throated Warblers. *Dutch Birding* 16: 89–94.
- Alström, P. & Olsson, U. 1995. A new species of *Phylloscopus* warbler from Sichuan Province, China. *Ibis* 137: 459–468.
- Baker, M. C. 1991. Response of male Indigo and Lazuli buntings and their hybrids to song playback in allopatric and sympatric populations. *Behaviour* 119: 225–242.
- Beaman, M. 1994. *Paelearctic Birds. A Checklist of the Birds of Europe, North Africa and Asia north of the foothills of the Himalayas*. Stonyhurst.
- Bremond, J. C. 1972. Recherche sur les paramètres acoustiques assurant la reconnaissance spécifique dans les chants de *Phylloscopus sibilatrix*, *Phylloscopus bonelli* et d'un hybride. *Gerfaut* 62: 313–323.
- Catchpole, C. K. 1978. Interspecific territorialism and competition in *Acrocephalus* warblers as revealed by playback experiments in areas of sympatry and allopatry. *Anim. Behav.* 26: 1072–1080.
- Catchpole, C. K. & Leisler, B. 1986. Interspecific territorialism in reed warblers: a local effect revealed by playback experiments. *Anim. Behav.* 34: 299–300.
- Catchpole, C. K. & Slater, P. J. B. 1995. *Bird Song: biological themes and variation*. Cambridge Univ. Press.
- Cheng, T.-h. 1987. *A Synopsis of the Avifauna of China*. Science Press, Beijing. Paul Parey, Berlin.
- Da Prato, S. R. D. & Da Prato, E. S. 1986. Appearance and song of possible Chiffchaff × Willow Warbler hybrid. *Brit. Birds* 79: 341–342.
- Dement'ev, G. P. & Gladkov, N. A. (eds). 1954. *Ptitsy Sovetskogo Soyuza*. Vol. 6. Moscow.
- Elfström, S. T. 1990. Individual and species-specific song patterns of Rock and Meadow Pipits: physical characteristics and experiments. *Bioacoustics* 2: 277–301.
- Emlen, S. T., Rising, J. D. & Thompson, W. L. 1975. A behavioural and morphological study of sympatry of indigo and lazuli buntings in the great plains. *Wilson Bull.* 87: 145–179.
- Étchécopar, R. D. & Hüe, F. 1983. *Les Oiseaux de Chine, de Mongolie et de Corée: Passereaux*. Papeete, Tahiti.
- Flint, V. E., Boehme, R. L., Kostin, Y. V. & Kuznetsov, A. A. 1984. *A Field Guide to Birds of the USSR*. Princeton Univ. Press.
- Fourage, J. 1972. Observation d'un Pouillot considéré comme hybride du Pouillot de Bonelli et du Pouillot siffleur (*Phylloscopus bonelli* × *Ph. sibilatrix*). *Gerfaut* 62: 280–284.
- Hartert, E. & Steinbacher, F. 1934. *Die Vögel der Paläarktischen Fauna*, suppl. vol.
- Martens, J. 1980. Lautäußerungen, verwandtschaftliche Beziehungen und Verbreitungsgeschichte asiatischer Laubsänger (*Phylloscopus*). Berlin.
- Mayr, E. & Cottrell, G. S. (eds) 1986. *Checklist of Birds of the World*. Vol. 11. Museum of Comparative Zoology, Harvard.

- Meise, W. 1933. Neue Formen aus Kansu. *Orn. Monatsberichte* 41: 82.
- Meyer de Schauensee, R. 1984. *The Birds of China*. Washington, D.C.
- Prescott, D. R. C. 1987. Territorial responses to song playback in allopatric and sympatric populations of alder (*Empidonax alnorum*) and willow (*E. trailii*) flycatchers. *Wilson Bull.* 99: 611–619.
- Ratcliffe, L. M. & Grant, P. R. 1985. Species recognition in Darwin's Finches (*Geospiza*, Gould). III. Male responses to playback of different song types, dialects and heterospecific songs. *Anim. Behav.* 33: 290–307.
- Richman, A. D. & Price, T. 1992. Evolution of ecological differences in the Old World leaf warblers. *Nature* 355: 817–821.
- Rogacheva, H. 1992. *The Birds of Central Siberia*. Husum.
- Sibley, C. G. & Monroe, B. L. 1993. *A Supplement to Distribution and Taxonomy of Birds of the World*. Yale Univ. Press.
- Stresemann, E., Meise, W. & Schönwetter, M. 1937. Aves Beickianae. Beiträge zur Ornithologie von Nordwest-Kansu nach den Forschungen von Walter Beick (†) in den Jahren 1926–1933. *J. Orn.* 85: 529–530.
- Ticehurst, C. B. 1938. *A Systematic Review of the Genus Phylloscopus*. British Museum, London.
- Vaurie, C. 1954. Systematic notes on Palearctic birds. No. 9. Sylviinae: the genus *Phylloscopus*. *Amer. Mus. Nov.* 1685.
- Williamson, K. 1967. *Identification for Ringers. The Genus Phylloscopus*. B.T.O., Tring.

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Appendix

Playback experiment data

kansuensis

Individual No. 1, Laoye Shan 31 May 1993

- *proregulus* (2 min). No response. ● *sichuanensis* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). Full response. ● *proregulus* (2 min). No response. ● *sichuanensis* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). Full response.

Individual No. 2, Huzu Bei Shan 21 June 1993

- *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). Full response.

Individual No. 3, Xinglong Shan 8 June 1994

- *proregulus* (2 min). No response. ● *sichuanensis* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 5 s followed by full response rest of time. ● *chloronotus* type B (4 min). No response. ● *chloronotus* type A (4 min). No response. ● *proregulus* (4 min). No response. ● *kansuensis* (2 min). 1st approach at 8 s followed by full response rest of time. ● *sichuanensis* (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 9 s followed by full response rest of time. ● *proregulus* (2 min). No response. ● *kansuensis* (2 min). 1st approach at 4 s followed by full response rest of time.

Individual No. 4, Xinglong Shan 8 June 1994

- *proregulus* (2 min). No response. ● *kansuensis* (2 min). 1st approach at 8 s followed by full response rest of time. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 5 s followed by full response rest of time. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach 18 s followed by full response rest of time. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 110 s followed by full response rest of time.

Individual No. 5, Xinglong Shan 8 June 1994

● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 7 s followed by full response rest of time. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 3 s followed by full response rest of time. ● *chloronotus* type A (2 min). Came close to speaker twice (at 18 s and 42 s), but showed no aggression. ● *kansuensis* (2 min). 1st approach at 4 s followed by full response rest of time. ● *proregulus* (2 min). 1st approach at 4 s followed by full response rest of time. ● *proregulus* (after the speaker had been moved c. 20 m; 4 min). 1st approach 3 s. Less strong response than before, on and off during rest of time. ● *chloronotus* type A (2 min). No response.

Individual No. 6, Xinglong Shan 8 June 1994

● *chloronotus* type B (2 min). No response. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 6 s followed by full response rest of time. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 5 s followed by full response rest of time. ● *chloronotus* type B (2 min). No response.

Individual No. 7, Xinglong Shan 8 June 1995

● *proregulus* (4 min). Came to c. 3 m from speaker at 25 s, but moved away at c. 35 s. Showed no aggression. No further response. ● *chloronotus* type A (4 min). 1st approach at 6 s. Appeared curious, not aggressive. At 36 s c. 3 m from speaker. Moved away after that. ● *chloronotus* type B (4 min). 1st approach at 18 s. At 50 s c. 3 m from speaker. Remained close to speaker rest of time; appeared slightly annoyed. ● *kansuensis* (2 min). 1st approach at 8 s followed by full response rest of time. Much more agitated than when *proregulus* and the two types of *chloronotus* were played. ● *proregulus* (2 min). No response. ● *chloronotus* type B (2 min). 1st approach at 9 s, but no further response. ● *kansuensis* (2 min). 1st approach at 7 s followed by full response rest of time.

Individual No. 8, Mengda 12 June 1994

● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 10 s followed by full response rest of time. ● *chloronotus* type B (4 min). 1st approach at 5 s followed by full response until c. 25 s, thereafter gradually turning uninterested, and after c. 1 min no response at all. ● *proregulus* (4 min). 1st approach at 28 s followed by full response for c. 1 min, then gradually less interested. ● *chloronotus* type A (4 min). No response. ● *chloronotus* type B (4 min). No response. ● *kansuensis* (2 min). 1st approach at 7 s followed by full response rest of time.

Individual No. 9, Mengda 12 June 1994

● *kansuensis* (a few s). Immediately full response. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 18 s followed by full response rest of time. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *kansuensis* (2 min). 1st approach at 4 s followed by full response rest of time. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 27 s followed by relatively weak response rest of time.

Individual No. 10, Mengda 12 June 1994

● *kansuensis* (a few s). Immediately full response. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). 1st approach at 14 s followed by full response rest of time. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (2 min). No response. ● *kansuensis* (2 min). Relatively weak response.

Individual No. 11, Mengda 12 June 1994

● *kansuensis* (c. 30 s). Immediately full response. ● *proregulus* (2 min). No response. ● *chloronotus* type A (2 min). No response. ● *chloronotus* type B (4 min). 1st approach at 24 s. Some response; approached speaker, flicked wings now and then. At c. 2 min 10 s it moved away. Response interpreted as mainly curiosity. ● *kansuensis* (2 min). 1st approach at 6 s followed by full response rest of time. Much stronger response than to *chloronotus*. ● *proregulus* (4 min). 1st approach at c. 20 s. Some response; approached speaker, flicked wings now and then until c. 2 min, when it moved away. Response interpreted as mainly curiosity. ● *chloronotus* type A (4 min). No response. ● *chloronotus* type B (4 min). 1st



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