The expedition was funded by the following sponsors whom we would like to thank: the Loke Wan Tho Memorial Trust, Fauna and Flora Preservation Society, International Council for Bird Preservation, Royal Geographical Society, The Conservation Foundation, Gilchrist Educational Trust, Elmgrant Trust, Percy Sladen Trust, British Ornithologists' Union, British Museum (Natural History), Aldeburgh, Leiston and Saxmundhan Lions Club, Rotary Club of Saxmundham and District and the A. S. Butler Trust.

References:

Collar, N. J. & Stuart, S. N. 1985. *Threatened Birds of Africa and Related Islands*. IUCN/ICBP, Cambridge.

Dee, T. J. 1986. *The Endemic Birds of Madagascar*. ICBP, Cambridge.

Ferguson-Lees, I. J., Franklin, K., Mead, D. & Burton, P. In press. *Birds of Prey: an identification guide to the raptors of the world*. Christopher Helm.

IUCN/UNEP/WWF (ed. M. D. Jenkins) 1987. *Madagascar, an Environmental Profile*. IUCN, Cambridge.

Langrand, O. 1990. *A Guide to the Birds of Madagascar*. Yale University Press.

Sheldon, B. C. & Duckworth, J. W. 1990. Rediscovery of the Madagascar Serpent-eagle *Eutriorchis astur*. *Bull. Brit. Orn., Cl.* 110: 126–130.

Thompson, P. M. & Evans, M. I. In press. The birds of Ambatovaky. *In* P. M. Thompson & M. I. Evans (eds), *A Survey of Ambatovaky Special Reserve, Madagascar*. MERG, London.

Wood, D. S. & Schnell, G. D. 1986. *Revised World Inventory of Avian Skeletal Specimens, 1986*. American Ornithologists' Union and Oklahoma Biological Survey, Norman, Oklahoma.

Addresses: Dr. C. J. Raxworthy, Division of Herpetology, Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A. P. R. Colston, British Museum (Natural History), Tring, Herts HP23 6AP, U.K.

On the taxonomic status of *Phylloscopus affinis* and *Phylloscopus subaffinis*

by Per Alström & Urban Olsson

Received 27 July 1991

Phylloscopus affinis and *P. subaffinis* were originally described as separate species, although there is some confusion surrounding the latter. The former was described by Tickell (1833) under the name *Motacilla Offinis* (lapsus for *affinis*) and the latter by David & Oustalet (1877) under the name *Oreopneuste affinis* (later Ogilvie-Grant (1910) proposed the now valid name *P. subaffinis*). This view was maintained by Ticehurst (1938), Vaurie (1959) and Cheng (1987). However, some recent workers, Williamson (1967) and Watson (1986), have chosen to treat them as conspecific.

Phylloscopus affinis is found from Pakistan and Kashmir eastwards along the Himalayas to Yunnan province, China, and from there northwards to Qinghai province, China. *Phylloscopus subaffinis* breeds in China from Yunnan and Sichuan provinces eastwards to Fujian province. Accordingly, the two species are mostly allopatric, but their distributions

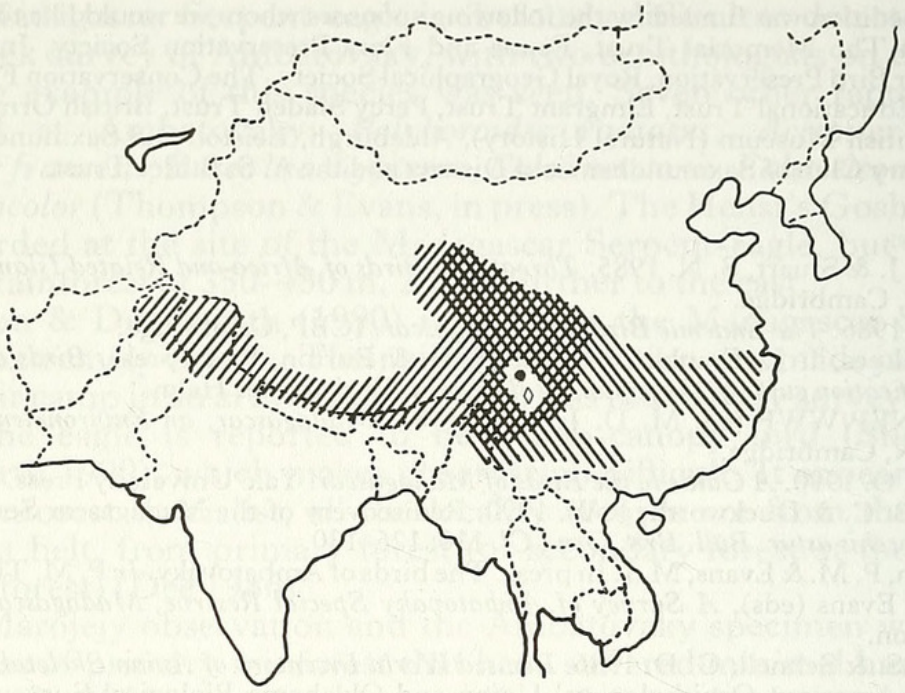


Figure 1. Map illustrating the distribution of *P. affinis* (western shaded area) and *P. subaffinis* (eastern area). The region of known overlap is shown. The locations of Wolong (●) and Emei Shan (◇) are indicated.

overlap in a large area in China, covering parts of Gansu, Sichuan and Yunnan provinces (Fig. 1).

Material and methods

Museum studies

The measurements of a sample of males and females of both species were taken in the American Museum of Natural History, New York, in the British Museum (Natural History), Tring, and in the Institute of Zoology, Academia Sinica, Beijing, China. The sexual classification was made according to the labels. Wing-length (maximum length), tail-length and bill-length (to skull) were measured, the two former with a precision to 0.5 mm, the latter to 0.1 mm.

In addition plumage characters were examined at four museums: British Museum (Natural History), Tring; American Museum of Natural History, New York; Institute of Zoology, Academia Sinica, Beijing, China; and Institute of Zoology, Academia Sinica, Kunming, China.

Field studies

Numerous individuals of both species have been observed, mainly during winter and spring/summer, *P. affinis* in Kashmir, Nepal and Xizang, Qinghai and Sichuan provinces, China, and *P. subaffinis* in Yunnan and Sichuan provinces, China, and northern Thailand. Five live individuals of *P. affinis* and four of *P. subaffinis* have been examined in the hand.

In June 1990 field observations were made and playback experiments carried out at two locations in Sichuan Province, China (Fig. 1). The first area, Wolong National Park (30°50′N, 102°55′E), is a rugged mountain

region, with steep valleys between peaks reaching altitudes of up to 6250 m. Most of the observations were made at an altitude of approximately 3500 m, in the region around and immediately below the tree-limit. Both species occur sympatrically at this location; *Phylloscopus subaffinis* was also found at lower altitude.

The second location is the summit of Emei Shan (29°31′N, 103°20′E). The altitude here is *c.* 3000 m, which is lower than, or just at, the tree-limit. There are patches of spruce *Abies* spp. of varying size, broken up by large open areas covered with dwarf bamboo. Only *P. subaffinis* occurs here.

The recordings of songs and calls were made with a 'Telinga Pro' omnidirectional mono condensor microphone, ranging between 40–18,000 Hz, mounted at the focal point of a 58 cm parabolic reflector, and a Sony WM D6 cassette recorder, operating at standard speed. The same tapeplayer was used in the playback experiments together with a custom-made speaker, 'Telinga'. For each species a tape with a 2-minute segment of fairly continuous song, with the song strophes at natural intervals, was prepared, using recordings by P.A. from May 1987, *Phylloscopus affinis* from Qamdo, Xizang province (30°50′N, 97°20′E), and *P. subaffinis* from Emei Shan. Sonagrams were produced by Richard Ranft, British Library of Wildlife Sounds, London.

There are different ways to set up a playback experiment, depending on what species are involved or what questions one seeks an answer to. Catchpole (1973, 1977, 1978) and Weeden & Falls (1959) describe methods for different purposes. In this study, subjects, locations or time of day could not be chosen randomly. The two species were rather sparse and patchily distributed in the two test areas. Several individuals were exposed to the test situation, but some did not approach when their own species' song was played, or showed so little interest that no proper observations could be made. Only the test situations where a subject clearly reacted to its own species' song are included in this study.

We have chosen to use the method described below, whenever possible. In two of the described test situations (see Appendix 1), the songs were only played once. In the remainder the experiment was repeated.

When a singing male of either species was located, a loudspeaker was placed in a convenient place near the bird. One of us, operating the tape-player, placed himself 15–20 m away from the speaker. The other person was watching from the place with the best view of the speaker and its surroundings. When the bird was in view, the song of the other species was played for 2 minutes, and the bird's actions recorded. This was followed by a brief pause. Next the song of its own species was played for 2 minutes, and again the reaction was recorded. As a double check this whole procedure was in most cases repeated once more, after a short pause.

Two different times were measured: (1) the latency of response, i.e. the time from the start of a played song until the bird first approached the speaker; (2) the total time spent near the speaker. Catchpole (1973, 1977, 1978), who studied *Acrocephalus* warblers in reedbeds, used the time spent within 1 m of the speaker as a reference. This turned out not to be relevant in our study, since the habitat was less uniform. Our two species

also showed a somewhat different behaviour when searching for the presumed intruder (see below), so the word 'near' has a slightly different meaning for each of them.

Results

Biometry

Males of both species have on average longer wings, tail and bill than their respective females (Table 1, Figs 2–4). A statistical comparison between the sexes within each species is shown in Table 2. Because of this sexual dimorphism, it is important to treat each sex separately, when comparing the two species (Table 3).

As *P. affinis* has relatively long wings and short tail, and *P. subaffinis* the other way round, the ratio between wing-length and tail-length seems to be the most useful biometrical value for identifying single specimens of these two species, but even here there is some overlap (Fig. 5). A Mann–Whitney U-test shows highly significant differences for both males, (Z(corrected for ties) = −6.797, $P = 0.0001$; n(*affinis*) = 35, n(*subaffinis*) = 31) and females, (Z(corrected for ties) = −5.349, $P = 0.0001$; n(*affinis*) = 24, n(*subaffinis*) = 25). As would be expected, differences in wing/tail ratio between males and females within each species are slight.

Phylloscopus subaffinis often shows a faint but still rather distinct emargination on the 4th primary (numbered descendently), whereas *P. affinis* shows at the most a trace of emargination on the 4th primary.

In the field, *P. affinis* appears slightly larger and looks more front-heavy, due to longer bill, larger bulk and proportionately shorter tail.

Plumage

The supercilium of *P. affinis* generally looks more prominent and, especially in front of the eye, better defined than in *P. subaffinis*; and it is on average somewhat longer. The colour is a cleaner, clearer yellow than in *P. subaffinis*. In *P. affinis* the supercilium often becomes paler, sometimes almost whitish, towards the rear, whereas in *P. subaffinis* the supercilium is generally more uniformly coloured. *Phylloscopus affinis* frequently shows a faint darker line above the supercilium; *P. subaffinis* rarely shows this. The eye-stripe is usually better defined and contrasts more clearly with the paler and more yellow ear-coverts in *P. affinis*. Normally *P. subaffinis* shows duskier ear-covers and as a result a more indistinct eye-stripe, but the eye-stripe may be quite well defined and similar to that of *P. affinis*. The underparts are more lemon yellow, less buffish, in *P. affinis* than in *P. subaffinis*. However, *P. affinis* often shows a distinct brownish hue to the breast and, particularly, the flanks, but even so the belly is more lemon-yellow than in *P. subaffinis*. The colour of the upperside is very similar in the two species and is of no importance for identification.

Bare parts

In *P. affinis* there is little or no dark at the tip of the lower mandible, whereas in *P. subaffinis* the tip is extensively dark. In long series of

TABLE 1

Mean values and standard deviations for three biometrical traits measured. The wing/tail ratio is the most useful value for classification

	Wing-length			Tail-length			Bill-length			Wing/tail ratio		
	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.
P. affinis												
♂	35	59.3	2.20	35	44.4	2.92	33	12.5	0.62	35	1.34	0.060
♀	24	55.2	2.27	24	41.5	2.68	24	12.4	0.46	24	1.33	0.068
P. subaffinis												
♂	31	53.7	2.34	31	45.6	2.77	31	12.1	0.57	31	1.18	0.042
♀	25	51.2	1.64	25	43.8	1.74	24	12.0	0.52	25	1.17	0.048

TABLE 2

Males are on average larger than females in the three biometrical traits measured. In both species a nonparametric ranking test (Mann–Whitney U-test) shows significant differences in both wing-lengths and tail-length between males and females. The difference in bill-length is, however, slight and not significant

	n		Z	
	♂	♀	(corrected for ties)	*P*
P. affinis				
wing	35	24	−5.108	0.0001
tail	35	24	−3.413	0.0006
bill	33	24	−0.713	0.4759
P. subaffinis				
wing	31	25	−3.929	0.0001
tail	31	25	−2.557	0.0106
bill	31	24	−0.902	0.3668

TABLE 3

For both species the difference in wing length is highly significant, when each sex is compared separately (Mann–Whitney U-test). The difference in tail length, is significant only between females. While the tail is on average longer in *subaffinis*, *affinis* shows an on average significantly longer wing. This produces a visible difference in morphological structure between the two species

	n		Z	
	affinis	*subaffinis*	(corrected for ties)	*P*
♂ wing	35	31	−6.298	0.0001
tail	35	31	−1.501	0.1334
bill	33	31	−2.607	0.0091
♀ wing	24	25	−5.238	0.0001
tail	24	25	−3.351	0.0008
bill	24	24	−2.375	0.0175

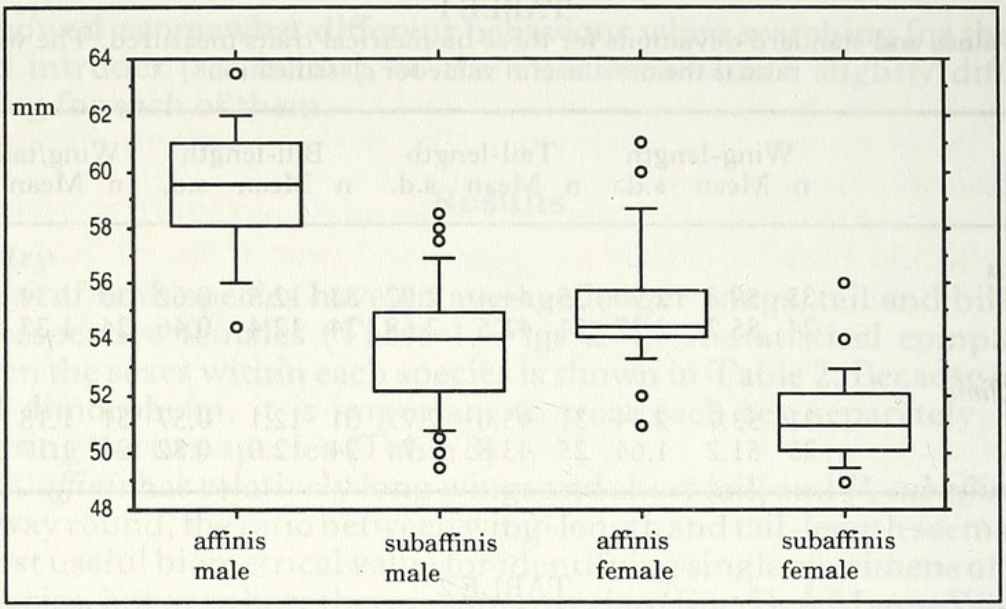


Figure 2. Box plots comparing wing-lengths between *P. affinis* and *P. subaffinis*. Males are shown to have significantly longer wings than their respective females. The necessity for sexing a sample is clearly shown if one compares male *subaffinis* with female *affinis*: in an unsexed sample there would appear to be a massive overlap. However, comparing each sex separately, *affinis* is clearly a longer-winged bird.

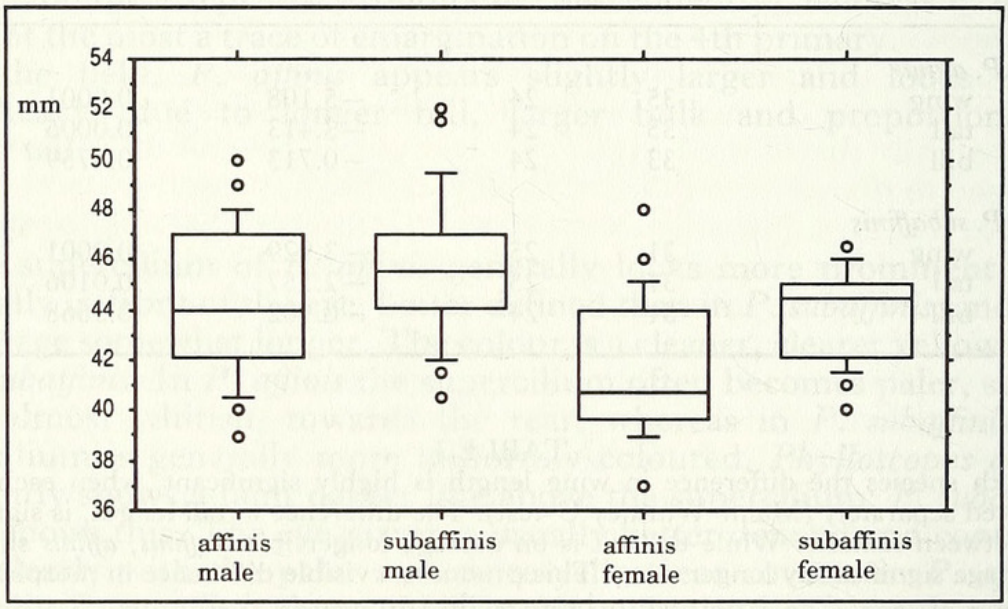


Figure 3. Box plots comparing tail-lengths between *P. affinis* and *P. subaffinis*. There is a great deal of overlap between the values. Although the differences are not significant between males, females of *subaffinis* have longer tails than female *affinis*.

specimens a slight overlap is apparent. The legs are on average somewhat paler in *P. affinis*, but can be identical in the two species.

Vocalizations

The song of *P. affinis* is a short, quick series of soft notes, almost invariably preceded by a call note: *chep-chi-chi-chi-chi-chi*. The speed

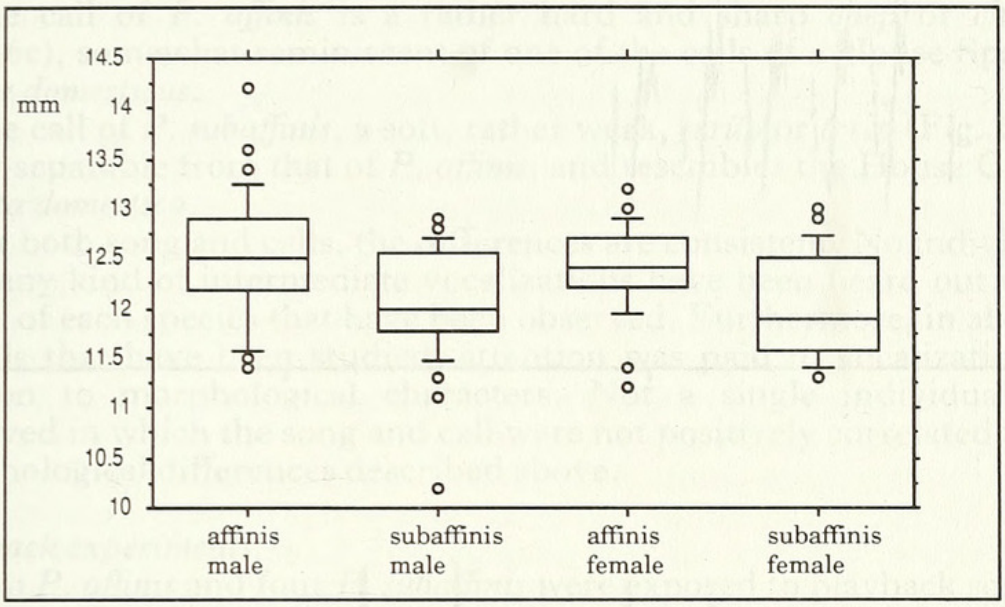


Figure 4. Box plots comparing bill-lengths between *P. affinis* and *P. subaffinis*. There appears to be no difference between the sexes. The apparent difference between the two species is significant only between males, when the sexes are compared separately.

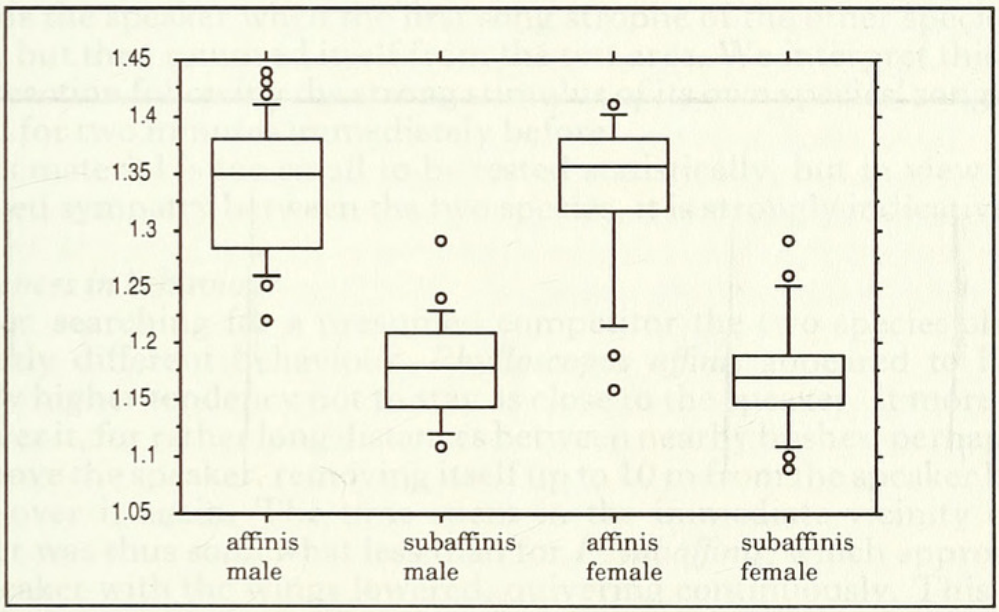
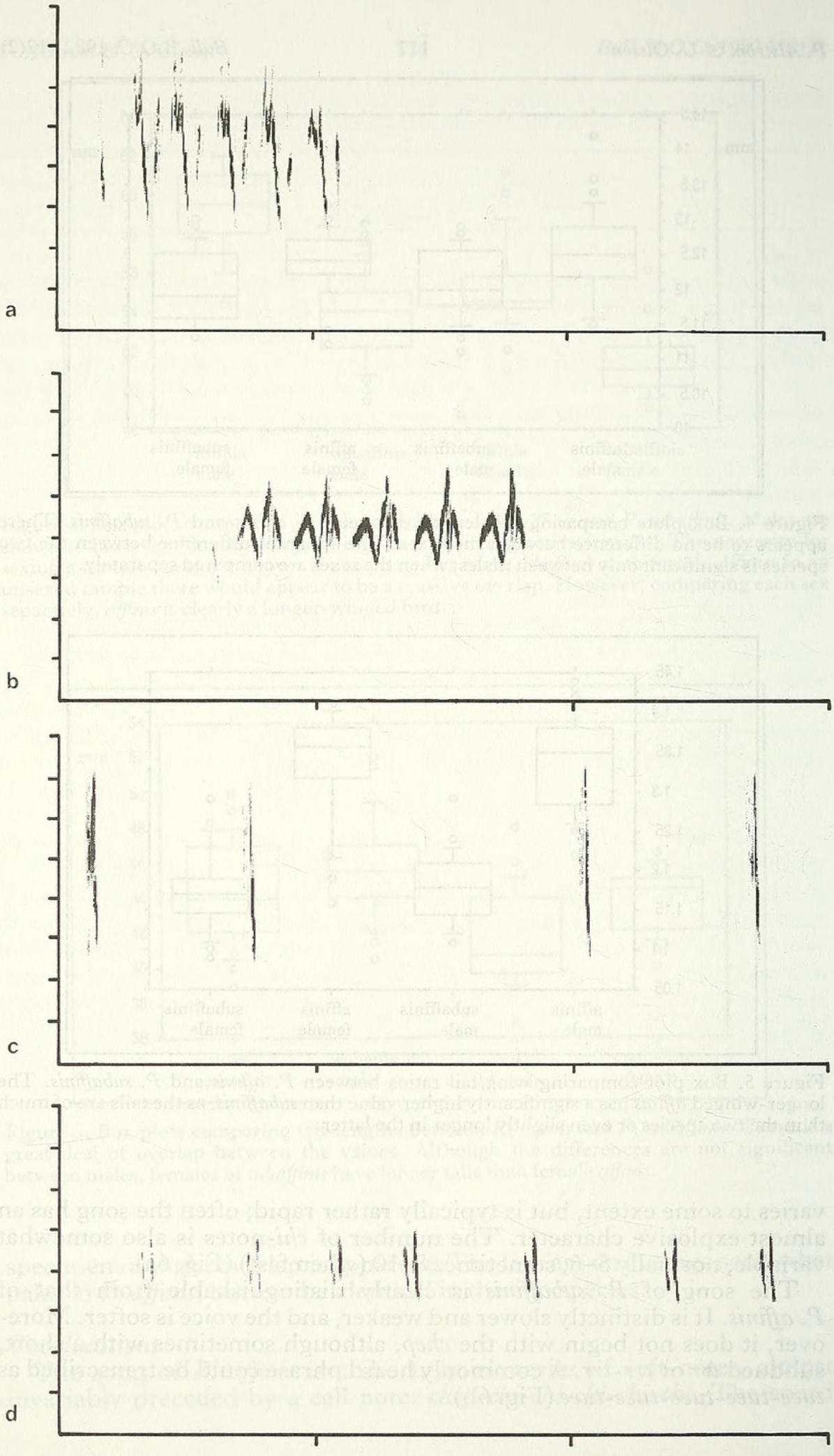


Figure 5. Box plot comparing wing/tail ratios between *P. affinis* and *P. subaffinis*. The longer-winged *affinis* has a significantly higher value than *subaffinis*, as the tails are of much th in the two species or even slightly longer in the latter.

varies to some extent, but is typically rather rapid; often the song has an almost explosive character. The number of *chi*-notes is also somewhat variable, normally 5–6, sometimes 8–10 (when fast) (Fig. 6a).

The song of *P. subaffinis* is clearly distinguishable from that of *P. affinis*. It is distinctly slower and weaker, and the voice is softer. Moreover, it does not begin with the *chep*, although sometimes with a short, subdued *trr* or *trr-trr*. A commonly heard phrase could be transcribed as *tuee-tuee-tuee-tuee-tuee* (Fig. 6b).


a
b
c
d

The call of *P. affinis* is a rather hard and sharp *chep* or *ch(r)ep* (Fig. 6c), somewhat reminiscent of one of the calls of a House Sparrow *Passer domesticus*.

The call of *P. subaffinis*, a soft, rather weak, *trrüp* or *trrip* (Fig. 6d), is easily separable from that of *P. affinis*, and resembles the House Cricket *Acheta domestica*.

For both song and calls, the differences are consistent. No individuals with any kind of intermediate vocalizations have been heard out of the 100+ of each species that have been observed. Furthermore, in all individuals that have been studied, attention was paid to vocalizations in relation to morphological characters. Not a single individual was observed in which the song and call were not positively correlated to the morphological differences described above.

Playback experiments

Two *P. affinis* and four *P. subaffinis* were exposed to playback song; of these, one *P. affinis* and three *P. subaffinis* were exposed to the complete test situation, with both songs repeated, and the remaining one of each species to the shorter version (see Appendix 1). With one exception, none of the individuals tested showed any interest in the other species' song. The exception was *P. affinis* individual no. 2 Wolong 900622, which dived towards the speaker when the first song strophe of the other species was heard, but then removed itself from the test area. We interpret this as an over-reaction following the strong stimulus of its own species' song being played for two minutes immediately before.

This material is too small to be tested statistically, but in view of the observed sympatry between the two species, it is strongly indicative.

Differences in behaviour

When searching for a presumed competitor the two species showed distinctly different behaviour. *Phylloscopus affinis* appeared to have a slightly higher tendency not to stay as close to the speaker. It more often flew over it, for rather long distances between nearby bushes, perhaps 1 or 2 m above the speaker, removing itself up to 10 m from the speaker before flying over it again. The time spent in the immediate vicinity of the speaker was thus somewhat less than for *P. subaffinis*, which approached the speaker with the wings lowered, quivering continuously. This latter behaviour was not seen in *P. affinis*. The birds then stayed mainly within 3 m of the speaker.

Figure 6. Sonagrams illustrating the differences in vocalizations between *P. affinis* and *P. subaffinis*. Made by Richard Ranft, British Library of Wildlife Sounds. Band width 369 Hz. Horizontal scale gives time in seconds, vertical scale gives kHz 0–8.

a *P. affinis* typical song. Recording by Per Alström, Qamdo, Tibet, early May 1987 (BLOWS no. 26125).

b *P. subaffinis* typical song. Recording by Per Alström, Emei Shan, Sichuan Province, China, mid-May 1987 (BLOWS no. 26127).

c *P. affinis* typical call. Recording by Per Alström, Qamdo, Tibet, early May 1987 (BLOWS no. 26126).

d *P. subaffinis* typical call. Recording by Per Alström, Wolong, Sichuan Province, China, May 1989 (BLOWS no. 26128).

Discussion

Habitat

Phylloscopus affinis usually breeds in open bushy areas at the upper tree-limit and in alpine scrub. It has been reported to breed between 3000 and 4880 m above sea-level (Schäfer 1938, Inskipp & Inskipp 1985, Meyer de Schauensee 1984). Ali & Ripley (1983) state that it breeds above 2700 m in Nepal.

Phylloscopus subaffinis breeds in scrub and at forest edge at high elevation, although normally lower than *P. affinis*. According to Etchécopar & Hüe (1978) it breeds between 3000 and 4000 m. Meyer de Schauensee, on the other hand, gives 915–3660 m, which is more in accordance with our own observations (*c.* 1900–3500 m).

The two species are mostly allopatric, but their distributions overlap in a large area in China, mainly along the edge of the Tibetan plateau. In the study area in Wolong, an area of sympatry, we found no differences in habitat preferences where they occurred together. *Phylloscopus subaffinis*, however, was distributed between altitudes of approximately 1900 and 3500 m, whereas *Phylloscopus affinis* was not seen below 3400 m during the breeding season.

Morphology

Williamson (1967) and Watson, in Mayr & Cottrell (1986), treat *P. subaffinis* as a subspecies of *P. affinis* because they claim to have seen specimens showing intermediate colouration on the upper- and underparts. They interpret this as morphological intergradation due to hybridization. Williamson lists specimens intermediate in this respect, taken mainly outside the breeding season in central China, Manipur and upper Burma. P.A. has examined 15 of the 17 specimens Williamson specifically refers to (see Appendix 2). These are all clearly either *P. affinis* or *P. subaffinis* and none appears to be intermediate (see Appendix 2). However, eight of these specimens were originally mislabelled. Eleven specimens from Gyi-Dzin-Shan are said to be "brown above, as in *subaffinis*, but while seven are characteristically deep buff beneath, four have some yellow admixture and in this respect recall *affinis*". P.A. has managed to find 10 of these specimens. Seven of them are clearly *subaffinis*, while the other three are *affinis*, which accounts for the difference in colour of underparts noted by Williamson (1967). Williamson further refers to three specimens from the Likiang and Talifu valleys, which are "brown enough above for *subaffinis*, but only two are deep buff beneath, one being much yellower". Two of these are indeed *subaffinis*, whereas one is clearly *affinis*, explaining the difference in underparts colour. A male from Kansu province 11 May and a female from Mekong valley, Yunnan province, 27 August are said to be "like *subaffinis* below but too greenish above". To P.A. these two specimens look like *affinis* in the colouration of the underparts, as well as in all other respects.

P. subaffinis arcanus was described by Ripley (1950), based on three specimens from Nepal in the non-breeding season. This form was recognized by Vaurie (1954), who wrote that "*arcanus* is a separable form, but its validity and status require further study". Williamson (1967) thought that the description of *arcanus* suggested an intergrade between *affinis* and

subaffinis. Watson (1986), who examined the type of *arcanus*, agreed with Williamson that *arcanus* is intermediate and used this as an argument for treating *affinis* and *subaffinis* as conspecific. However, it appears that *arcanus* is in fact synonymous with *Cettia f. flavolivacea* (Alström, in prep.).

Since no single morphological feature appears to be diagnostic for distinguishing between the two species, one must consider a combination of morphological characters, such as colouration of underparts and supercilium, face pattern, bill pattern and structure. Taking all these characters into account, all individuals examined by us have fallen into two distinct groups. Indeterminable specimens are probably extremely rare, if they exist at all. As a rule, morphological differences between closely related species of *Phylloscopi* are slight, and the differences between *P. affinis* and *P. subaffinis* are not less than between, for example, Willow Warbler *P. trochilus* and Chiffchaff *P. collybita* (with the exception of the wing formula). To conclude, we cannot find any evidence of hybridization between *P. affinis* and *P. subaffinis*. On the contrary, the morphological data support the view that the two forms are stable, even in the area of sympatry.

Playback experiments

In our opinion vocal characteristics are as a rule more important in the genus *Phylloscopus* than are morphological features, in determining whether or not two forms belong to the same species. The consistent differences in vocalizations between the two species in this study are in themselves a strong indication against conspecificity and we regard it as highly unlikely that two morphologically different forms occurring sympatrically would show such consistent vocal differences if they were conspecific. The question is, of course, where the birds themselves draw the line.

In assessing the taxonomic status between two debated forms, we consider playback experiments to be one of the most powerful tools. An individual defending a territory can be expected to locate and attack all intruding singing competitors. In a large number of passerines, song constitutes the primary signal mechanism in species-recognition, when announcing a territory. Visual signals usually come in at a later stage, when an intruder is already present and located. In assuming the hypothesis that a male of species A would respond to the song of any other male of the same species entering its territory, one can test if the song of another individual is considered to belong to a competitor. As has been shown by others, interspecific competition may cause individuals of various species to respond to the song of members of other species or even families (e.g. Catchpole 1986, Reed 1982). Falls & Szijj (1959) found that two closely related species of meadow-larks *Sturnella* responded to each other's song, but only when they occupied adjacent territories. A similar study by Goldman (1973) of the reactions by Field Sparrows *Spizella pusilla* to the song of the Chipping Sparrow *S. passerina* revealed that the only individual that responded was one in a territory bordered by several Chipping Sparrow territories. Thus a positive response is in itself of little or no taxonomic value.

An individual that does not respond to a certain song, however, is likely not to consider the other singer a competitor. However, there may be various reasons for this not being valid evidence in taxonomy. (1) If the territory-defending individual is at a stage in the breeding cycle where competition is less detrimental to its own breeding success, it may not respond to a song that would have evoked such a response at a different stage in the breeding cycle. At some stages and, of course, outside the breeding season, most individuals will not be bothered by other individuals singing in the vicinity. (2) The singing individual may not yet have established a firm territory. The played-back song may then be interpreted as coming from the 'proper' territory holder and the singer might retreat without a fight. (3) If the song that is played was recorded near the territory of the tested bird, the territory-holding individual may recognize the song and react less persistently than to a song from a strange individual that it does not recognize (Weeden & Falls 1959). (4) In a single test of one individual, the location of the speaker in the territory may be important. The bird might defend peripheral parts of the territory less vigorously (Ickes & Ficken 1970). (5) Visual signals may be more important in announcing territory ownership. (6) Certain visual signals may be needed in combination with the song, in order to evoke the proper response.

To avoid the above-mentioned pitfalls the individuals tested were always exposed to their own species' song. The vigorous response displayed by the birds tested shows that they were in fact alert for intruders. Judging from the absence of response to the song of the opposite species, they do not seem to consider each other competitors. On at least two occasions both species have been attracted to the speaker at the same time. Each male reacted to its own species' song, and was able to see the other male. Despite this, no signs were observed of aggressive behaviour between them. All these facts, in combination, strongly indicate that *P. affinis* and *P. subaffinis* should be treated as separate species.

Summary

The taxonomic status of the two closely related species, *Phylloscopus affinis* and *P. subaffinis*, has been studied. These species have variously been treated as conspecific and as separate species. Studies of museum material show that, of the three morphological traits measured, there is a significant difference between the two species in wing-length, *affinis* having the longer wing. The tail-length is on average longer in *subaffinis*, which in combination with the wing-length produces an even more marked difference in proportions. No single plumage or bare-part feature is diagnostic, but the vast majority of specimens can be correctly classified into one of the two species by a combination of characters. There are consistent differences in both song and calls between the two species. No individuals with songs or calls in conflict with morphological features have been observed. In Wolong, an area of sympatry, the two species occur side by side, apparently without paying much attention to each other. Playback experiments indicate that the two species do not regard each other as competitors. All the individuals tested searched vigorously for the source of their own species' song, but in no case reacted significantly to the other species' song. During the search for the source of the song, they also behaved differently. *Phylloscopus subaffinis* moved about in the vegetation fairly close to the speaker, drooping and quivering its wings, while *P. affinis* was never seen to lower or quiver its wings. The two species have somewhat different habitat preferences, overlapping mainly in the region near the tree-limit. *Phylloscopus subaffinis* has its distribution mainly below the tree-limit, and *P. affinis* mainly at the highest forested levels and in the alpine zone above.

Acknowledgements

We are most grateful to professors Cheng Tso-hsin and Tan Yao-kuang at the Institute of Zoology, Academia Sinica, Beijing, who provided invaluable assistance. The sonagrams were prepared by Richard Ranft at the British Library of Wildlife Sounds. Peter R. Colston at the British Museum (Natural History), Tring, examined specimens and helped in locating references. Philip Angle of the U.S. National Museum of Natural History, Washington, kindly made specimens available. We are also grateful to the staff of the American Museum of Natural History, New York, and Mary Le Croy in particular, for their kind assistance. Raimo Neergaard and Matti Åhlund provided valuable assistance in the preparation of this manuscript. Ben King and Per Sundberg made many valuable suggestions for improvements.

References

Ali, S. & Ripley, S. D. 1983. *Handbook of the Birds of India and Pakistan.* Compact edn. Oxford Univ. Press.

Catchpole, C. K. 1973. The functions of advertising song in the Sedge Warbler (*Acrocephalus schoenobaenus*) and the Reed Warbler (*A. scirpaceus*). *Behaviour* 46: 300–320.

Catchpole, C. K. 1977. Aggressive responses of male Sedge Warblers (*Acrocephalus schoenobaenus*) to playback of species song and sympatric species song before and after pairing. *Anim. Behav.* 25: 489–496.

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. 1986. Interspecific territorialism in Reed Warblers: a local effect revealed by playback experiments. *Anim. Behav.* 34: 299–300.

Cheng, Tso-Hsin 1987. *A Synopsis of the Avifauna of China.* Science Press, Beijing & Paul Parey, Hamburg and Berlin.

David, A. & Oustalet, E. 1877. *Oiseaux de Chine.* Libraire de l'Académie de Médecine, Paris.

Etchécopar, R. D. & Hüe, F. 1983. *Les Oiseaux de Chine: Passereaux.* Editions Boubée, Paris.

Falls, J. B. & Szijj, L. J. 1959. Reactions of Eastern and Western Meadowlarks in Ontario to each other's vocalizations. *Anat. Rec.* 134: 560.

Goldman, P. 1973. Song recognition by Field Sparrows. *Auk* 90: 106–113.

Ickes, R. A. & Ficken, M. S. 1970. An investigation of territorial behavior in the American Redstart utilising recorded songs. *Wilson Bull.* 82: 167–176.

Inskipp, C. & Inskipp, T. 1985. *A Guide to the Birds of Nepal.* Christopher Helm, London.

Mayr, E. & Cottrell, G. W. (eds) 1986. *Check-list of Birds of the World.* Vol. 11. Museum of Comparative Zoology, Harvard.

Meyer de Schauensee, R. 1984. *The Birds of China.* Smithsonian Institution Press, Washington.

Ogilvie-Grant, W. R. 1900. *Bull. Brit. Orn. Cl.* 10: 37.

Reed, T. M. 1982. Interspecific territoriality in the Chaffinch and Great Tit on islands and the mainland of Scotland: playback and removal experiments. *Anim. Behav.* 30: 171–181.

Ripley, S. D. 1950. New birds from Nepal and the Indian region. *Proc. Biol. Soc. Washington* 63: 101–108.

Schäfer, E. 1938. Ornithologische Ergebnisse zweier Forschungsreisen nach Tibet. *J. Orn.* 86, Sonderheft.

Ticehurst, C. B. 1938. A Systematic Review of the Genus *Phylloscopus.* Trustees of the British Museum, London.

Tickell, S. R. 1833. List of Birds, collected in the Jungles of Borabhúm and Dholbhúm. *J. As. Soc. Bengal* 2: 569–583.

Vaurie, C. 1954. Systematic notes on palearctic birds. No. 9. Sylviinae: the genus *Phylloscopus. Am. Mus. Novit.* no. 1685.

Vaurie, C. 1959. *The Birds of the Palearctic Fauna: Passeriformes.* H. F. & G. Witherby, London.

Weeden, J. S. & Falls, J. B. 1959. Differential responses of male Ovenbirds to recorded songs of neighboring and more distant individuals. *Auk* 76: 343–351.

Williamson, K. 1967. Identification for ringers 2, The genus Phylloscopus. BTO Field Guide no. 8 (revised edition).

Addresses: Per Alström, Kungsgatan 3, 462 33 Vänersborg, Sweden; Urban Olsson, University of Göteborg, Dept. of Zoology, Section of Morphology and Systematics, Box 25059, 400 31 Göteborg, Sweden.

APPENDIX 1

Playback experiment data

Phylloscopus affinis
Individual no. 1 Wolong 900620

- 2 minutes song *P. subaffinis*. Was seen in the vicinity, when *P. subaffinis* individual no. 1 was tested (see below). Showed no reaction to the song of *P. subaffinis*.
- 2 minutes song *P. affinis*. Approached after a short while and continued to fly back and forth over the speaker as *P. subaffinis* moved away. Neither individual paid any attention to the other.

Individual no. 2 Wolong 900622

- 3 minutes song *P. affinis*. First approach after *c.* 60 seconds immediately diving towards the speaker. (1 minute was added to this test on the assumption that the delayed first approach was because the bird had been too distant at the beginning of the playback). Flew back and forth over the speaker for the remainder of the test. Both song and calls were given occasionally. Did not vibrate wings.
- 2 minutes song *P. subaffinis*. Dived towards the speaker when the first song strophe was heard after a short pause, then moved away.
- 2 minutes song *P. affinis*. First approach after 3 seconds, immediately diving towards the speaker. Then flew back and forth in the vicinity of the speaker.

Phylloscopus subaffinis
Individual no. 1 Wolong 900620

- 2 minutes song *P. subaffinis*. Approached after a short while and stayed close to the speaker. Held head and wings lowered and vibrated the wings. Both songs and calls were given occasionally.
- 2 minutes song *P. affinis*. Moved gradually away from the speaker. At the same time *P. affinis* approached. Neither individual paid any attention to the other. See *P. affinis* individual no. 1.

Individual no. 2 Emei Shan 900628

- 2 minutes song *P. affinis*. No reaction; continued singing in the vicinity.
- 2 minutes song *P. subaffinis*. First approach after 20 seconds. Flew back and forth near the speaker. Held head and wings lowered and vibrated the wings.
- 2 minutes song *P. affinis*. No reaction. Moved away somewhat from the speaker. Sang in the vicinity.
- 2 minutes song *P. subaffinis*. First approach 6 seconds. Flew back and forth near the speaker. Held head and wings lowered and vibrated the wings.

Individual no. 3 Emei Shan 900628

- 2 minutes song *P. affinis*. No reaction.
- 2 minutes song *P. subaffinis*. First approach after 10 seconds. Flew back and forth between bushes near the speaker. Held head and wings lowered and vibrated the wings.
- 2 minutes song *P. affinis*. Moved away from the speaker; then began singing in the vicinity.
- 2 minutes song *P. subaffinis*. First approach after 5 seconds. Flew back and forth between bushes near the speaker. Held head and wings lowered and vibrated the wings.

APPENDIX 1 *Continued*

Playback experiment data

Individual no. 4 Emei Shan 900629

- 2 minutes song *P. affinis*. No reaction.
- 2 minutes song *P. subaffinis*. First approach after 10 seconds. Flew back and forth between bushes near the speaker apparently searching for it. Held head and wings lowered and vibrated the wings.
- 2 minutes song *P. affinis*. No reaction. Started singing and moving about normally.
- 2 minutes song *P. subaffinis*. First approach after 5 seconds. Flew back and forth over the speaker between nearby bushes. Vibrated the wings.

APPENDIX 2

Specimens in the British Museum (Natural History) specifically referred to by Williamson (1967) as intermediate between *P. affinis* and *P. subaffinis*.

W = wing-length (maximum length); T = tail-length; W/T = wing/tail ratio; B = bill to skull (mm).

BM 1903.8.8.504 *P. subaffinis* (no species name on label). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 49.5, T 42.0, W/T 1.18, B 11.5.

BM 1903.8.8.508. *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 56.5, T 48.5, W/T 1.17, B 11.6.

BM 1903.8.8.509 *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 54.5, T 44.5, W/T 1.23, B 11.2.

BM 1903.8.8.510. *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 55.0, T 48.0, W/T 1.15, B 11.9.

BM 1903.8.8.511. *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 50.0, T 44.5, W/T 1.12, B 11.4.

BM 1903.8.8.512. *P. affinis* (correctly labelled). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 59.5, T 46.0, W/T 1.29, B 12.1.

BM 1903.8.8.513. *P. affinis* (correctly labelled). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 55.5, T 39.5, W/T 1.41, B 12.5.

BM 1903.8.8.514. *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March, 1902. Collected by G. Rippon. W 55.5, T 46.0, W/T 1.21, B 12.5.

BM 1903.8.8.515. *P. subaffinis* (incorrectly labelled *P. affinis*). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 56.0, T 49.5, W/T 1.13, B 11.6.

BM 1903.8.8.516. *P. affinis* (correctly labelled). Gyi-Dzin-Shan, Yunnan province, China, March 1902. Collected by G. Rippon. W 53.5, T 39.0, W/T 1.37, B 12.4.

BM 1906.12.17.355. *P. subaffinis* (incorrectly labelled *P. affinis*). Lijiang & Talifu Valleys, Yunnan province, China, 14 April 1906. W 54.5, T 46.5, W/T 1.17, B 12.0.

BM 1906.12.17.356. *P. affinis* (correctly labelled). Lijiang & Talifu Valleys, Yunnan province, China, 14 April 1906. W 60.0, T 44.0, W/T 1.36, B 13.5.

BM 1906.12.17.357. *P. subaffinis* (incorrectly labelled *P. affinis*). Lijiang & Talifu Valleys, Yunnan province, China, 14 April 1906. W 53.5, T 43.5, W/T 1.23, B 11.9.

BM 1949. Whi. 1. 12290. *P. affinis* (correctly labelled). Male, Kansu province, China, 11 May. W 56.0, T 42.0, W/T 1.33, B 11.5.

BM 1922.12.7.298. *P. affinis* (correctly labelled). Female, Mekong valley, NW Yunnan province, China, 27 August. W 55.5, T 42.5, W/T 1.31, B 12.3.