

## S17-3 The golden-spectacled warbler (*Seicercus burkii* auct.) — a Sino-Himalayan species swarm

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**Abstract** The Golden-spectacled warbler (*Seicercus burkii* auct.), a widespread “species” in southeastern Asia, consists of a swarm of cryptic species. Recently unmasked independently by a Swedish and a German team, it comprises *S. burkii* s. str. (Himalayas), *S. whistleri* with two subspecies *S. w. whistleri* (Himalayas) and *S. w. nemoralis* (northeast India, north Myanmar), *S. valentini* with two subspecies *S. v. valentini* (central and south China) and *S. v. latouchei* (southeast China), *S. omeiensis* (Sichuan, Myanmar), *S. soror* (central and southeast China), *S. tephrocephalus* (central, south and southeast China, northwest Myanmar, north Vietnam), and *S. affinis* (east Himalayas, central and southeast China, Vietnam). Molecular-genetics confirm a close relationship among those species of the complex with backs colored a glowing green, clearly defined black crown stripes and particular song-syntax characters. In the Chinese mountains up to four species, and in the Himalayas two or possibly three, coexist on a mountain slope in well-defined vertical parapatry. Up to three species also assemble in local sympatry in high population density in Sichuan, China. The species of the *S. burkii* complex live at altitudes ranging from subtropical foothills at 550 m a.s.l. in China to the cold-temperate zone of subalpine coniferous forest in Nepal at 3 800 m (*S. whistleri*) and on the Omei Shan in China at 4 000 m (*S. valentini*).

**Key words** Cryptic species, Species swarm, *Seicercus burkii* complex, Himalayas, China

### 1 Introduction

“Swarms” of closely related species often escape detection because their component members are so extremely similar in their suites of external characters. Therefore, the members of such complexes are often recognized as elements of a single polymorphic species. The case of *Seicercus* is typical of such cryptic complexes in that extreme outward similarity among all members hides internal species limits. Their species-specific morphological characters only appear when seen in the light of acoustic and molecular data, because of which data collection must be extremely careful and precise. Here we report on the *Seicercus burkii* complex in the Himalayas, China and countries close-by. By an array of methods, this complex has been shown to be highly diverse with at least seven biospecies, each of which can be identified by several characters.

### 2 Material and methods

Field studies were carried out in Nepal between 1969 and 2001 (6 trips during the breeding season summing to over 2 years), and in China between 1997 and 2002 (4 trips during the breeding season summing to 20 weeks in three provinces where *Seicercus* is present) (Martens, 1987; Martens and Eck, 1995: 52–64). Skins, song recordings including song specimens, and tissue samples were collected,

with emphasis on combining the documentation of song and tissue sampling with skins.

For molecular-genetic analysis, we sequenced 706 bp of the cytochrome-*b* gene of the mitochondrial genome for 74 samples comprising seven taxa in the complex: *S. burkii* s. str. — 2 specimens, E Nepal; *S. w. whistleri* — 13, west and east Nepal; *S. v. valentini* — 14, Sichuan, Gansu, Shaanxi; *S. omeiensis* — 17, Sichuan, Shaanxi, Cambodia; *S. soror* — 14, Sichuan, Shaanxi, Cambodia; *S. tephrocephalus* — 12, Sichuan, Shaanxi, north Thailand; and *S. affinis intermedius* — 2, Sichuan. Protocols are given in Martens et al. (1999).

In bioacoustical analysis, all recordings were checked, sonographed and measured by means of a Kay Elemetrics Sona-Graph, model 5500.

For external morphological characters we examined some 260 skins from various collections, as well as those taken by us.

### 3 Results

#### 3.1 Morphology

The *S. burkii* complex comprises medium-sized leaf warblers, all of which are remarkably uniform in coloration and patterning: greenish back, glowing yellow underside

with fine differences in tone, and head with a green or gray median crown stripe and two blackish lateral crown stripes of definition varying between species (color plates and photos in Martens et al., 1999, 2000, 2003; Alström and Olsson, 1999). The eyes are surrounded by yellow feathers that form a delicate ring which varies in width between species. In all species, the inner vanes of the outer tail feathers T6 and T5 always bear white markings, larger in *S. whistleri* and present on T4 in all species except *S. soror*. Relative dimensions, such as length of wing and tail, and their proportions, also differ significantly among members, wing/tip index and tail/wing index providing particular insights into feather proportions and relative length of tail and wing (Martens et al., 1999, 2003).

### 3.2 Bioacoustics

Songs within the *burkii* complex, in most cases easily recognized by the human ear, have a simple syntactic structure; each male employs many conspicuously different verse types but all follow species-specific patterns. The species fall into two groups on verse structure: *S. whistleri*, *S. valentini* and *S. soror* in one, and *S. burkii* s. str., *S. omeiensis*, *S. tephrocephalus* and *S. affinis intermedius* in the other. In the verses of the first group, a temporally offset introductory element with descending frequency is followed by a group of two (rarely three) elements. This element group is repeated once or rarely twice, which completes the verse. Within this group, *S. whistleri* and *S. valentini* are especially similar in their songs, which are also noteworthy for the small frequency bandwidth of the verses ( $\xi = 2.4$  kHz in both species,  $n = 12$  and  $n = 30$ , respectively). Slight differences between *whistleri* and *valentini* songs show up in the slightly lower frequency of the latter. *S. soror* stands apart in its much broader frequency band ( $\xi = 4.4$  kHz;  $n = 25$ ).

Verse syntax is more irregular in the second group. A common feature is a trilled ending to many verses. This applies to 80% of verses in *S. affinis intermedius*, 51% in *S. tephrocephalus*, 48% in *S. omeiensis* and 39% in *S. burkii* s. str. The songs of *S. omeiensis*, *S. tephrocephalus* and *S. burkii* also have a broad bandwidth ( $\xi = 4.0$ – $4.7$  kHz), but that of *S. affinis intermedius* is very narrow ( $\xi = 2.3$  kHz). In both sonagram and auditory impression, the songs of *S. omeiensis* and *S. tephrocephalus* resemble one another closely. That of *S. tephrocephalus* always begins with one or two broadband modulated introductory elements (for sonagrams, see Alström and Olsson, 1999, 2000; Martens et al., 1999, 2000, 2003).

All seven species give quite different and clearly distinguishable calls (Martens et al., 1999; Alström and Olsson, 1999). These may be brief, steeply rising (*S. burkii* s. str.) or softer, descending (*S. valentini*) individual calls, or groups of two sharp calls each descending in frequency (*S. tephrocephalus*, *S. omeiensis*, *S. whistleri*). Complicated “calling songs” are produced by *S. soror* and *S. affinis intermedius*, and in the latter species each individual has a call repertoire.

### 3.3 Molecular genetics

The deep incision in the cladogram (cf. Martens et al., 1999) separates two species groups: (i) one with *S. affinis intermedius*, *S. burkii* and *S. tephrocephalus*, and (ii) the other with *S. whistleri*, *S. valentini*, *S. omeiensis* and *S. soror*. The species in the first group are colored a glowing green on their upper surfaces, and their crown stripes stand out clearly in black. Their distribution is predominantly southern, either in subtropical regions or limited to lower altitudes in the Himalayas (*burkii* s. str.).

The species of the second group are dull green on the upper surface, and their dark lateral crown stripes tend to be ill-defined and faded, often with a scattering of lighter gray or greenish feathers. They are centered in the northern parts of central China and the Himalayas, at relatively high altitudes in the mountains where *S. whistleri* and *S. valentini* always occupy the uppermost belt in species altitudinal sequences, up to temperate coniferous forests. The genetic distance values between individual species range from 5% to 9% (uncorrected; Martens et al., 1999) and are highest between species of the two main clades; the lowest values lie within each of the two species groups.

### 3.4 Distribution

The *S. burkii* complex, as currently understood, ranges along the entire Himalayan chain, from an area to the west of northern Pakistan as far as southeast Tibet, then from the forested regions on the eastern flank of the Tibetan plateau northwards to south Gansu (Lianhua Shan, *S. v. valentini*), and along the southern and northern flanks of the Qinling Mountains (*S. v. valentini*, *S. omeiensis*, *S. soror*, *S. tephrocephalus*) to Guandong and the Wuyi Shan in Fujian (*S. valentini latouchei*, *S. tephrocephalus*, *S. affinis intermedius*). In the south, its distribution is bounded by Mt. Victoria in Myanmar in the west (*S. omeiensis*, *S. tephrocephalus*, *S. whistleri nemoralis*) and by the northern and perhaps parts of southern Vietnam in the east. It is likely that the complex is widespread throughout central and southern China in forested mountains above ca. 500–600 m a.s.l., occasionally in dense populations and even in secondary growth (Cheng 1987, 2000). The ranges of individual species are much more poorly documented. *S. burkii* s. str. and *S. whistleri* are almost exclusively Himalayan, *S. affinis* is Himalayan and Chinese, *S. omeiensis* Chinese and Burmese, *S. soror* and *S. valentini* only Chinese, and *S. tephrocephalus* is widespread within China, Myanmar and northern Vietnam.

### 3.5 Ecology

All members of the complex are forest birds. They inhabit open and secondary stands as well as closed primary forests. The forest communities occupied, however, differ much between individual species, and range from tropical forests (*S. tephrocephalus*) to temperate coniferous forests up to 3 800 m in the Himalayas (*S. whistleri*). There are exceptions where up to four species may live in sympatry, but usually local species are separated in altitu-

dinal zones of often differing vegetation in mostly narrow bands of up to 650 m in China (*S. omeiensis*) and 1 500 m in Nepal (*S. whistleri*); most zones are considerably narrower and often sharply delimited. Such parapatric zoning has been documented most accurately in the Omei Shan (Alström and Olsson, 1999; Martens et al., 1999).

This altitudinal “layering” of species may appear different on different mountain complexes, but the sequence of species is always maintained, from (sub)tropical ones to those of cool-temperate affinity. In the case of China, the species sequence from the foot of the mountains into the tops of peaks seems to be as follows: *S. tephrocephalus*, *S. soror*, *S. affinis*, *S. omeiensis*, *S. valentini*. Where altitudinal range is limiting, either *S. tephrocephalus* or *S. soror* lives at the foot of the mountain, not both. Closer to the peak lies *S. omeiensis*, and above that a belt of *S. valentini* that regularly extends to the upper limits of habitat. In the Himalayas, *S. burkii* s. str. occupies the lower belt, and *S. whistleri* the upper.

Early data indicated that ecological exclusion between the species was incomplete, but could not distinguish whether observed overlap was due to occasional vagrants of out-of-zone species (e.g., occasional *burkii* in the zone of *whistleri* in Nepal, *soror* in the range of *valentini* and *affinis* in the range of *soror* on the Omei Shan), or whether local syntopy was frequent, even routine. We have since been able to document, with tape recordings, skins and tissue samples, that three species in the Qincheng Shan live sympatrically together in high density at 1 200 m a.s.l.: *S. soror*, *S. tephrocephalus* and *S. omeiensis*.

## 4 Discussion

The *Seicercus burkii* complex is a species swarm that was discovered from analyses using modern methods (Alström and Olsson, 1999; Martens et al., 1999). Earlier reviews (Bangs, 1929; Stresemann, 1940) failed to sort out the complexity of the group due to lack of basic field data. Most intriguing is the lack of morphological variation among the species. Because of this, previous revisers saw the complex as a continuous morphological “series”, were not in a position to take account of other characters, and so overlooked species boundaries. The individual species are distinguished by a delicate mosaic of characters involving coloration, head and tail patterning, length of wings and tail and feather proportions.

Careful calibration of these characters was all the more necessary because as many as four species in the complex may live in vertically adjacent zones on a mountain slope, and up to three species can occur side by side in one area. Only in rare cases can species can be determined from allopatric breeding grounds. Vocalizations helped significantly in separating the “morphological continuum” into species units. Yet this approach, too, was not without its snags, because several widely disjunct populations were found to have convergently similar songs and calls even though relatively well separated morphologically (*S. burkii* s. str./*S.*

*omeiensis*; *S. whistleri*/*S. valentini*). Even within narrowly circumscribed habitats, we found different species with voices that were very difficult to distinguish by sonagram as well as listener (*S. omeiensis*/*S. tephrocephalus*). To function as pre-mating isolating mechanisms, vocalization differences would have been expected to be especially distinctive here, to prevent interspecific mating; and, indeed, we did not find any signs of hybridization.

Molecular-genetic characters provided the ultimate confirmation that *S. burkii* auct. was a complex of at least seven well-differentiated species. The molecular phylogeny also showed that great similarity in song did not necessarily imply close kinship of the singers, as was found for *S. burkii* s. str. and *S. omeiensis*. Each of the clearly distinguishable “molecular species” was distinctly structured genetically within itself, as evidenced by up to nine haplotypes of the *cyt-b* gene. The high distance values indicate that the species are not very young. Following the 2% differentiation per million years rule (Zink and Klicka, 2000), the species range from 2.5 to 4.5 million years old, taking their origin back to the late Pliocene.

Little is still known about the distributional ranges of the individual species. In addition to one widely distributed subtropical species (*S. tephrocephalus*), there are several narrowly localized endemics, such as *S. omeiensis* with two disjunct populations in Sichuan and Myanmar and, at the subspecies level, *S. valentini latouchei* in Fujian Province. Even less is understood about how these distributional patterns have been formed. How did niche partitioning and altitudinal zonation develop in the parapatric taxa? We can only conclude from the rich structure of the *cyt b* haplotypes within individual species that none of the species passed through a strict population “bottleneck”, perhaps during the Pleistocene ice ages, which would have sifted out haplotypes in refugia. Speciation in the *Seicercus burkii* complex thus provides new and impressive evidence that in the transitional zone between China and the Himalayas, where the Palearctic and Indomalayan fauna mingle, evolutionary processes may have long remained little or even undisturbed.

The following species and subspecies are now distinguished in the *S. burkii* complex (Alström and Olsson, 1999, 2000; Martens et al., 1999, 2000, 2003), as follows:

### Group 1:

*Seicercus affinis*, with two subspecies: *S. a. affinis* (Hodgson, 1854) and *S. a. intermedius* (La Touche, 1898);

*Seicercus burkii* (Burton, 1836);

*Seicercus tephrocephalus* (Anderson, 1871) = *S. tephrocephalus* “group 4” sensu Alström and Olsson, 1999, syn. *Cryptolopha burkii distincta* La Touche, 1922 = *S. distinctus* sensu Martens et al., 1999.

### Group 2:

*Seicercus whistleri*, with two subspecies: *S. w. whistleri* Ticehurst, 1925 and *S. w. nemoralis* Koelz, 1954;

*Seicercus valentini*, with two subspecies: *S. v. valentini* (Hartert, 1907) and *S. v. latouchei* Bangs, 1929;

*Seicercus omeiensis* Martens, Eck, Päckert and Sun, 1999 = *S. tephrocephalus* "group 6" sensu Alström and Olsson, 1999;

*Seicercus soror* Alström and Olsson, 1999 = "*S. latouchei*" sensu Martens et al., 1999, nec *latouchei* Bangs, 1929.

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