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BREEDING BIOLOGY OF THE WHITE-BROWED TIT-WARBLER (*LEPTOPOECILE SOPHIAE*) IN ALPINE SHRUBS, SOUTHERN TIBET

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Abstract. We studied the breeding ecology of the White-browed Tit-Warbler (*Leptopoecile sophiae*) in the alpine zone of southern Tibet, elevations 4110–4780 m. The earliest breeder among local passerines, the species initiated egg-laying in early April and ended by late July. We located its domed nests in 13 species of shrubs at an average height of 0.9 m (range 0.2–2.5 m) above the ground. Clutch size averaged 4.7 (range 4–6) eggs, declining through the season. Brood size was 4.3 (range 2–6) at hatching and 3.8 (range 1–5) at fledging. Incubation lasted 20.5 (range 16–23) days, and nestlings fledged at 17.5 (range 14–21) days of age, when they were 4% above the adult weight. Of the nests we observed 66% fledged at least one young. Most pairs were monogamous, and both sexes shared all nesting duties. We noted two females attending a single nest, with a brood of normal size, and egg dumping by an additional female. At the population level, the sex ratio of offspring, determined by sexual differences in plumage of nestlings older than 6 days, did not deviate from equality. Birds breeding late in the season, however, tended to raise more females.

Key words: *alpine habitat*, *cooperative breeding*, *life history*, *nest-site selection*, *offspring sex ratio*, *White-browed Tit-Warbler*, Leptopoecile sophiae.

Biología Reproductiva de *Leptopoecile sophiae* en Arbustos Alpinos del Sur de Tíbet

Resumen. Estudiamos la biología reproductiva de *Leptopoecile sophiae* en la zona alpina del sur de Tíbet, entre los 4110 m y los 4780 m de elevación. Esta especie es la que comienza a criar más temprano entre los paserinos, iniciando la puesta de huevos a principios de abril y terminando a fines de junio. Localizamos sus nidos con forma de cúpula sobre 13 especies de arbustos a una altura promedio de 0.9 m (rango 0.2–2.5 m) por encima del suelo. El tamaño de la puesta promedió 4.7 (rango 4–6) huevos, disminuyendo a lo largo de la estación. El tamaño de la nidada fue 4.3 (rango 2–6) al momento de la eclosión y 3.8 (rango 1–5) al momento de emplumamiento. La incubación duró 20.5 (rango 16–23) días y los pichones dejaron el nidos a 17.5 (rango 14–21) días de edad, cuando se encontraron un 4% por encima del peso del adulto. De los eventos de anidación que observamos, 66% crió por lo menos un pichón hasta el momento de dejar el nido. La mayoría de las parejas fueron monógamas y ambos sexos compartieron las tareas de anidación. Observamos a dos hembras atendiendo un único nido, con una nidada de tamaño normal, y la eyección de huevos por parte de una hembra adicional. A nivel poblacional, la relación de sexos de las crías, determinada por diferencias sexual en el plumaje de los pichones con más de seis días de edad, no se desvió de la igualdad. Sin embargo, las aves que nidificaron al final de la estación tendieron a criar más hembras.

The genus *Leptopoecile* comprises two small (body length ~10 cm) species of alpine habitats, the White-browed Tit-Warbler (*L. sophiae*) and Crested Tit-warbler (*L. elegans*) (Gill and Wright 2006). The former occurs in the Himalayas, Tibetan plateau, and northwestern China, preferring relatively dry alpine shrubland from 2000 up to 5000 m elevation; the latter occurs on the eastern Tibetan plateau, largely in montane coniferous forests above 3000 m elevation (Beaman 1994).

The systematic affiliation of the genus *Leptopoecile* remains uncertain. It has long been attributed to the family Sylviidae (Sibley and Monroe 1990, Zheng 2002), but Alström et al. (2006) placed it within the family Aegithalidae, sister to

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Aegithalos. Largely because of the relative remoteness and inaccessibility of their habitat, little is known so far of the two species' natural history (Beaman 1994). Here we present the first data on the breeding biology of the White-browed Tit-Warbler (*L. s. obscura*), from alpine shrub zones, southern Tibet, at the upper limit of the species' elevational range. The data have value for comparing life history and social systems, clarifying phylogenetic relationships, and assisting the species' conservation.

STUDY AREA AND METHODS

We studied the White-browed Tit-Warbler in Xiongse Valley (29° 27′ N, 91° 40′ E), 30 km from the city of Lhasa, Tibet. Annual average temperature at the site is 4.5°C, and annual total precipitation is 566 mm, over 90% of it falling from June to September. Vegetation is characterized by alpine shrubs and meadows. On southern (north-facing) slopes, the *Rosa sericea* and *Berberis hemleyana* community covers elevations between 4000 and 4500 m, and the *Sabina pingii* community dominates from 4500 to 4900 m. On northern slopes, a community characterized by *Spirace alpine* appears at 4000–4200 m, stands of *Rhododendron nivale* mixed with *Salix sclerophylla* between 4200 and 4900 m. Alpine meadows are found between 4900 and 5200 m. The valley contains a stream with its tributaries from both slopes. Along streams, shrub cover is dense and continuous. Tit-warblers are resident in the alpine zones year round, but in winter their numbers decrease greatly (Lu et al. 2007).

Our field work extended over three complete (2000, 2001, and 2005) and two partial (April–July 1999, July–October 2003) breeding seasons. We searched for tit-warbler nests throughout the valley by systematically checking bushes or by following the birds' breeding activities. For each nest found, we described the site's slope aspect (south-facing or north-facing), elevation, distance to the nearest stream, supporting plants and their height, and height of the nest above the ground. We measured each nest's dimensions and recorded its contents (eggs and nestlings). Data on hatching date, hatching success, fledging date, development of young, and sex (by plumage pattern, see below), fledging success, and parental behavior were obtained from systematic nest checks. The prey items transported to nestlings 9 to 12 days old were collected within 1 hr from three nests by a neck-collar method, which did not harm the nestlings when applied properly (Tang 2006). Both male and female tit-warblers have the chestnut crown, white supercilium, and violet-blue rump and uppertail-coverts, but the female's plumage is much duller overall. The best distinction between sexes by plumage lies in the underparts, where the male is violet-blue on the breast, chestnut on the belly, the female pale over the entire underparts. This difference became obvious as nestlings grew, allowing us to recognize their sex. We banded no birds as part of this study, but the dimorphism allowed us to identify the parents' sex as well. Close watch on a nest in which individual birds were kept in sight allowed us to determine the mating system.

For all active nests, we estimated the approximate date of laying of the first egg from the average incubation period or growth curves of young of known age. Because of the remoteness of some nests from our campsite, not all the located nests were inspected regularly, and for different variables our sample size varied. Nest-searching efforts were not spread evenly among the four shrub habitats; rather, we concentrated on the rose–barberry community on southern slopes because it was the birds' principal breeding habitat. This sampling method limited our ability to quantify nesting preference with respect to slope aspect and habitat type. We used only data recorded throughout the breeding season to establish the temporal pattern of nesting. Data from seasons (1999 and 2003) in which the entire nesting period was not studied were used in other analyses if appropriate. For the analysis of nest-site selection, nests found after fledging were included.

We evaluated nesting-plant preferences by means of a selectivity index (Morrison et al. 1992): $E_i = (r_i - p_i)/(r_i + p_i)$, where E_i = selectivity index, r_i = the proportion of actual number of located nests in plant i, and p_i = the mean proportion of plant i in habitat samples of 10 × 10 m. The relative abundance of various shrub species in various habitats in the Xiongse Valley was already known from a general vegetation survey.

Prior to statistical analysis, variables measured as percentages were arcsine-transformed and others were logarithmically transformed to improve normality. If a set of data was distributed normally (according to a one-sample Kolmogorov–Smirnov test), we used parametric programs; if not, we used nonparametric analyses. Significance is two-tailed, and values are given as mean ± SD.

RESULTS

NEST-SITE CHOICE

Tit-warblers nested at elevations ranging from 4110 to 4780 m. More nests (54% of 225) were located between 4300 and 4500 m than below 4300 m (32%) and above 4500 m (14%; $\chi_2^2 = 28.55$, $P < 0.001$). Forty-three percent of nests were less and 57% were more than 100 m from a stream. Shrub cover around nests was <50% (34% ± 10) at 118 of 225 sites, >50% (71% ± 17) at the remaining 107.

Nests were found in 13 species of shrubs (11 and 4 species on southern and northern slopes, respectively). On southern slopes, *Berberis hemleyana* was strongly preferred (67% of 210, selective index = +0.24). Although *Rosa sericea* supported 19% and *Caragana bicolor* 9% of tit-warbler nests, they were less favorable relative to their occurrence (selective index = −0.35 and −0.10, respectively). On northern slopes, 40% of 15 nests were located in *Caragana jubata*, 33% in *Rhododendron nivale*. However, the former was selected more often (selective index = +0.78) and the latter less often (selective index = −0.39) than expected from their abundance. All species combined, the average height of plants supporting nests was 1.7 m (± 0.3, range 0.8–2.7, n = 225). Nest height above the ground varied from 0.2 to 2.5 m (0.9 ± 0.4), with 60% <1 m.

NESTING PHENOLOGY

Egg-laying dates ranged from early April to late July, with a peak in mid-April or early May (Fig. 1). The tit-warblers began to breed earlier in 2000 (median laying date 27 April) than in 2001 (12 May) and 2005 (14 May). Clutches were initiated later with increased elevation (partial correlation coefficient, controlled for year, $r = 0.20$, $n = 88$, $P = 0.06$).

NEST, EGG, AND CLUTCH SIZE

Tit-warblers built a domed nest with an entrance (diameter = 3.1 ± 0.3 cm, range 2.5–3.6, n = 14) near the top (Fig. 2). The nest's external walls were invariably built of moss, grass stems, hairy seeds, and animal hair (domestic yak, sheep, or Woolly Hare, *Lepus oiostolus*). The inside was lined with the feathers of two galliform birds, the Tibetan Eared Pheasant (*Crossoptilon harmani*) and Tibetan Partridge (*Perdix hodgsoniae*), along with animal hair. Mean measurements of 21 nests were as follows: external

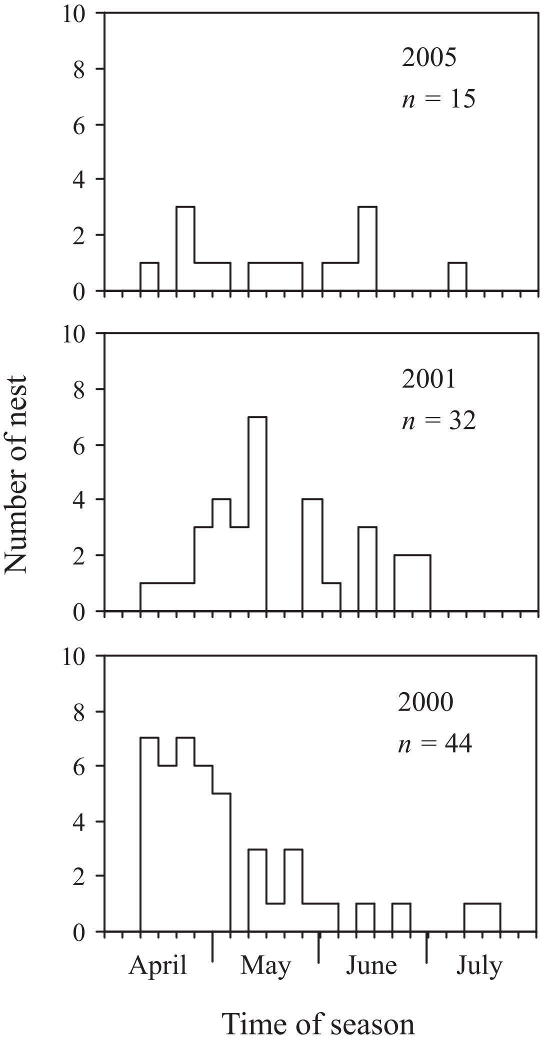

FIGURE 1. Temporal distribution of the date of laying of the first egg by White-browed Tit-Warblers nesting in alpine habitat in the Xiongse Valley, near Lhasa, Tibet. The time of clutch initiation is arranged in 5-day periods.

diameter (the widest part of the nest wall) 11.1 cm (± 1.5, range 8.9–15.5), depth (from the entrance rim to the bottom of the inner cup) 9.3 cm (± 1.1, 7.1–11.2), height (from the top to the bottom of outside the dome) 13.9 cm (± 1.7, 9.2–16.2), dry weight 35.9 g (± 5.9, 28.0–52.0).

Eggs were whitish with reddish-brown spots on the ends. Fresh egg mass averaged 1.14 ± 0.07 g (range 1.0–1.2, $n = 11$), dimensions 15.6 (± 0.5, 14.7–17.0) × 11.6 mm (± 0.3, 10.4–12.0, $n = 44$).

With one exception, clutch size varied from four to six eggs (4.69 ± 0.49, $n = 102$), with four-egg nests accounting for 32% and five-egg nests for 67%. The exception was a single nest containing nine eggs. Clutch size did not change significantly from year to year ($F_{2, 86} = 1.22$, $P = 0.30$) but decreased strongly as the season progressed (partial correlation coefficient, controlled for elevation and year, $r = -0.38$, $n = 66$, $P = 0.001$) and decreased slightly with increased elevation ($r = 0.22$, $P = 0.08$, controlled for egg-laying date and year).

PARENTAL BEHAVIOR

Both sexes constructed the nest over about 2 weeks ($n = 4$ pairs) with a similar effort by each (females made 47% and males 53% of 187 material-carrying trips, 637 min observations of 3 nests). Nest building took place throughout the day but more frequently in the morning (20 trips hr^{-1} for both sexes, 139 records during 466 min) than in the afternoon (12 trips hr^{-1}, 48 records during 241 min).

The average interval between completion of the nest and laying of the first egg was 6.6 days (± 4.1, range 2–20, $n = 19$ nests). The interval was longer for early (April–May) clutches (7.2 ± 4.4 days, $n = 15$) than for late (June–July) clutches (4.5 ± 1.7 days, $n = 4$). One egg per day was laid in the morning ($n = 34$ eggs in 18 nests monitored daily). Incubation began with the last egg ($n = 14$ nests) and lasted 20.5 ± 2.8 days (range 16–23, $n = 10$). Of 58 daytime visits to 21 nests with eggs 50% revealed the female incubating, 43% the male incubating, and 7% no bird in the nest.

Of 22 visits to 10 nests with chicks, 9 revealed the female brooding, 13 the male. Females performed 44% and males 56% of 160 provisioning trips (1329 min observation of 11 nests). The average interval between successive provisioning trips of both sexes was 9.9 ± 9.6 min ($n = 114$). We also noted a case in which two females and one male collectively reared a five-nestling brood. The nestlings' diet consisted mainly of Lepidoptera (63% of 16 food items collected from the young of 3 nests), the remainder of Orthoptera (19%) and Diptera (19%). Nestling period (the time between hatching and fledging of the nestlings in a clutch) lasted 17.5 ± 2.0 days (range 14–21, $n = 11$).

Throughout the breeding season, tit-warblers did not regularly defend their nests. In only two cases during nest building were males seen attacking conspecific males near the nest. We noted almost no birds around nest sites during the nest-ready interval or egg-laying period (>200 visits to >50 nests).

NESTLING GROWTH

At hatching nestlings were naked. Their eyes opened fully on day 7, by which their sex was recognizable by plumage (male: reddish-brown in the crown and abdomen; female: gray in these parts). Young fledged when they weighed 7.3 ± 0.5 g (range 7.3–8.0, $n = 6$), about 104% of the adult weight. We estimated the growth-rate constant of the logistic model for body mass as 0.41 and asymptotic mass as 7.6 g. There was a marginally significant difference between the body weights of male and female offspring in a brood, with the former being 0.1 g heavier than the latter (paired-sample t-test, $t = 2.01$, df = 22, $P = 0.057$).

SEX RATIO WITHIN BROODS

The brood sex ratio (the proportion of male nestlings in a brood) averaged 0.51 ± 0.21, (range 0–0.80, $n = 25$) for complete broods (the number of nestlings older than 6 days in the brood was the same as the initial clutch size), 0.55 ± 0.30 (0–1.00, $n = 25$) for partial broods (at least one nestling died before fledging), and 0.54 ± 0.26 (0–1.00, $n = 57$) for total broods sampled at fledging (including those found during the nestling period). None of these ratios deviates significantly from equality (paired-samples t-test, all $P > 0.25$). Complete broods did not differ significantly in sex ratio from partial broods (independent-samples t-test, $t = 0.59$, df = 47, $P = 0.56$). After removal of the broods whose initial clutches contained unfertilized eggs, the similarity remained ($t = 1.26$, df = 42, $P = 0.22$). Thus nestling mortality was sex-independent.

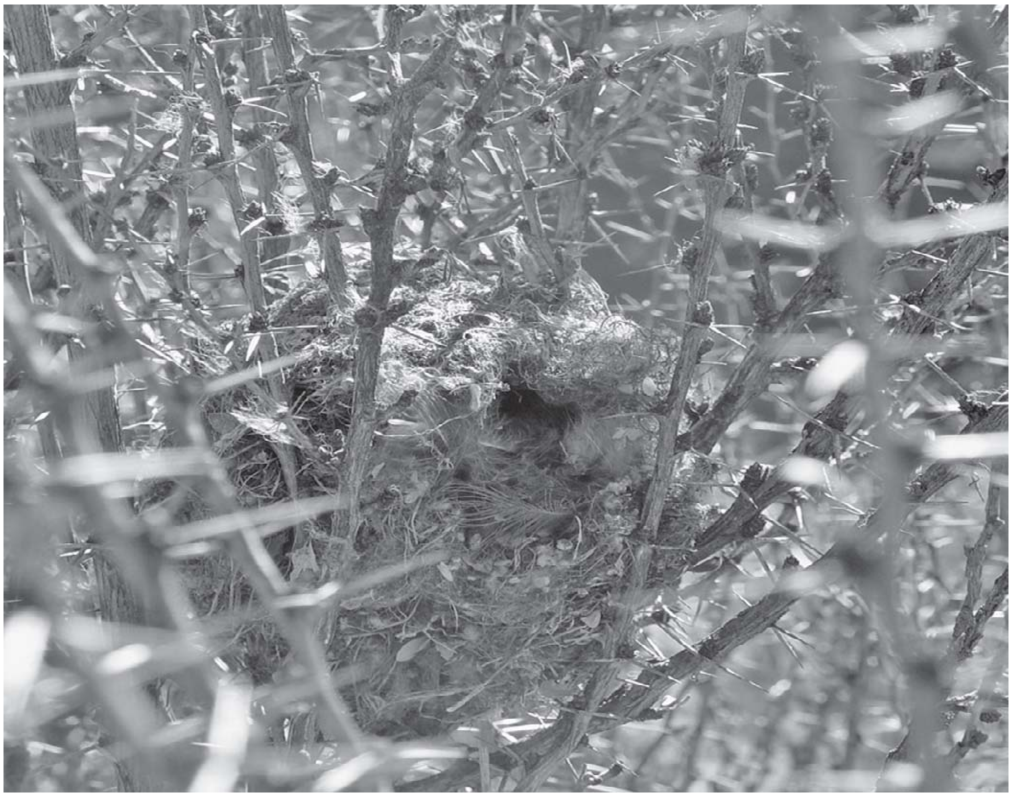

FIGURE 2. A nest of the White-browed Tit-Warbler.

A stepwise multiple regression analysis with sex ratio as the dependent variable and brood size, laying date, and nesting elevation as the independent variables revealed laying date to be the only significant predictor of the model in each brood category, with more females in late broods (complete brood, $F_{1,23} = 4.97$, $P = 0.036$, partial correlation coefficient $r = 0.42$; partial brood, $F_{1,23} = 10.51$, $P = 0.004$, $r = 0.56$; total broods, $F_{1, 55} = 23.80$, $P < 0.001$, $r = 0.45$; Fig. 3).

REPRODUCTIVE SUCCESS

A total of 403 eggs (88 nests) produced 307 hatchlings (76%, 75 nests), giving a brood size of 4.27 ± 0.72 (range 2–6). Hatching failure of the remaining 96 eggs was due to nest desertion (41 eggs in 8 nests, including the 9-egg clutch), egg disappearance (24 eggs in 5 nests), infertility, detected by breaking the shell (19 eggs in 18 nests), or embryo death (12 eggs in 3 nests). Of the 307 hatchlings of known fate, 258 (84%) fledged successfully, giving a brood size of 3.79 ± 1.06 (range 1–5, $n = 68$ nests). Failure during the nestling period resulted from complete (24 nestlings in 6 nests) or partial brood loss (16 nestlings in 11 nests). The proportion of nesting attempts from which at least one nestling fledged was 66% (71 of 108 attempts). If the complete depredation clutches (disappearance of entire contents) is attributed to predators, the rate of nest predation is 34% (13 of 38 failed nests). Neither year, date, elevation, nor clutch size contributed to variation in reproductive success (logistic regression, $\chi_4^2 = 2.14$, $n = 62$ nests, $P = 0.71$), despite a success rate decreasing from 2000 (72%, 33 of 46) through 2001 (67%, 20 of 30) to 2005 (50%, 8 of 16).

DISCUSSION

In the alpine zone we studied White-browed Tit-Warblers began to breed in early April, about one month earlier than did other local passerines (Lu 2004, 2005, 2006, 2008). How, in early spring, do the birds overcome the cold and dearth of food, the two major factors determining birds' breeding schedules (Lack 1968, Brown et al. 1999)? First, the domed nests tit-warblers construct are well-insulated because they consist of compact soft materials and five times as heavy as the adult body mass. The thermal properties may protect the incubating parents and their offspring against the cold (Hansell and Deeming 2002). Second, field observations showed that moths (Lepidoptera), the birds' principal prey, emerged earlier in spring than did other arthropod taxa in the alpine zone, and adult tit-warblers spent most of their time at cliffs to search for the insects.

Relative to several lowland species of Aegithalidae, the alpine tit-warblers lay small clutches (Table 1), following the pattern of many families of birds (Badyaev 1997, Badyaev and Ghalambor 2001, Lu 2005). This pattern is less pronounced, however, when comparison is made with some species of Sylviidae. The tit-warblers spend more time incubating eggs and caring for young than do the Aegithalidae and Sylviidae listed in Table 1, consistent with the frequently reported pattern (Badyaev 1997, Badyaev and Ghalambor 2001). Low temperature and poor food availability in the alpine zone, which impose high energetic costs on the parents and their offspring, should be reflected in the life history of the tit-warblers. Limited oxygen availability at high elevations could be an additional factor slowing the conversion of

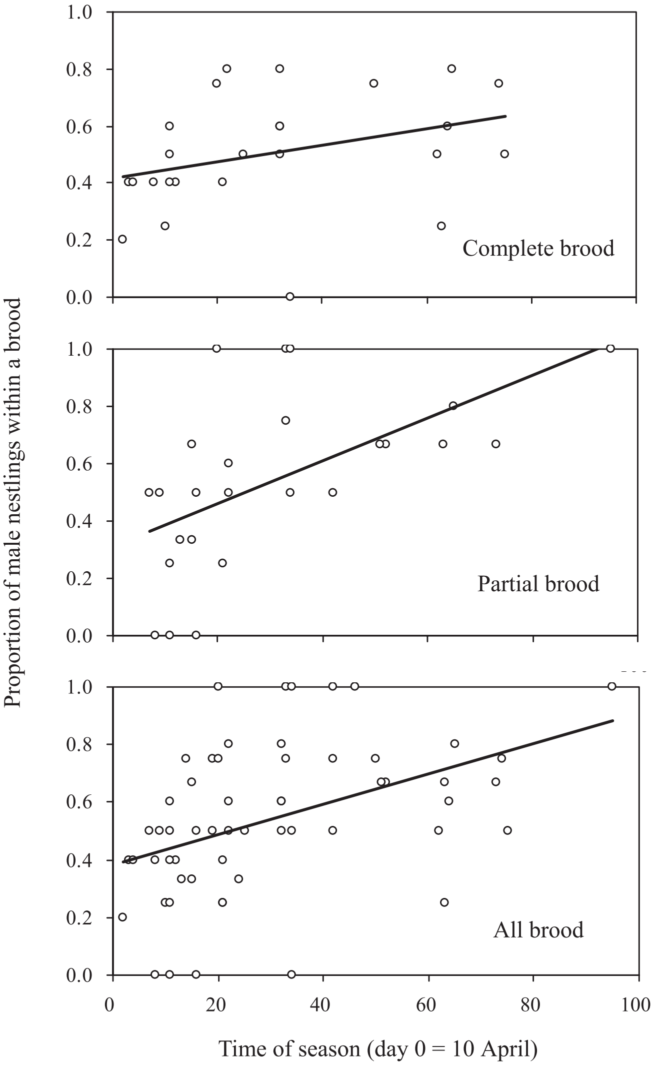

FIGURE 3. Sex ratio of complete, partial, and total broods in relation to laying date of White-browed Tit-Warblers nesting in alpine habitat near Lhasa, Tibet.

food into reproductive output in adults and slowing the development of young (review in Dillon et al. 2006).

The observation of more than one female attending a single nest with a brood normal size suggests that this species may be a cooperative breeder with females as helpers. The nine eggs, double the normal clutch size, in a single nest, are more likely to have resulted from a helper dumping and less likely to have resulted from intraspecific nest parasitism, as seven- and eight-egg clutches were never found. This observation further suggests the species to be a joint nester. This probability is supported by the male tit-warblers' making a large contribution to incubation and young care, the feature shared by all joint-female species (Vehrencamp and Quinn 2004). Nevertheless, helping in the tit-warbler is apparently rare because, although no birds were marked, we observed only one case of two adults of the same sex visiting a nest simultaneously in spite of substantial effort (nest construction, 637 min observations of 3 nests; egg laying, 180 min of 18 nests; feeding young, 1329 min of 11 nests; post-fledging, 40 min of 5 families). In contrast, helpers at the nest are frequent in *Aegithalos* (Long-tailed Tit, *A. caudatus*, 50%, Russell and Hatchwell 2001; Black-throated Tit, *A. concinnus*, 50%, Guo et al. 2006), as well as in the Seychelles Warbler (*Acrocephalus sechellensis*, 27%, Komdeur 1994). Egg dumping by helpers in the tit-warbler, if any, was only 1% (1 of 102 nests), compared with 10–16% in several passerines in which helpers at the nest are frequent (Vehrencamp and Quinn 2004).

Because joint nesting has been seen among both the Aegithalidae (Sharp et al. 2005, Guo et al. 2006) and Sylviidae (Richardson et al. 2001), the behavior cannot contribute to clarifying the systematic placement of the tit-warblers (Alström et al. 2006). This social system is more frequent in the former (2/8) than the latter (1/221), however, if the Timaliidae are excluded from the Sylviidae (Zheng 2002). Two facts further suggest a closer relationship of the tit-warbler with the Aegithalidae: (1) Clutch size decreases as elevation increases in the Aegithalidae but not in the Sylviidae (Table 1). (2) Nest structure may reflect evolutionary origin (Nguembock et al. 2007). A domed nest is typical of all species of Aegithalidae so far studied (Fang and Ding 1997, Guo et al. 2006). Although this nest type is also found among some species of Sylviidae, the walls of their nests are lined mostly with grass stems (e.g., *Phylloscopus*, Bi 2004; *Cettia*, Wang 2002), in contrast to the variety of soft materials used by both the tit-warblers and the long-tailed tits of the genus *Aegithalos*.

TABLE 1. A comparison of breeding parameters of White-browed Tit-Warblers breeding in high-elevation Tibet with those of several species of Aegithalidae and Sylviidae breeding in lowland China.

Species	Latitude (° N)	Elevation (m)	Clutch size	Incubation period (days)	Nestling period (days)	Male parental investment	Source[a]
Leptopoecile sophiae	29	4400	4.7	19.9	16.9	all duties	1
Aegithalos caudatus	32	500	7.0	14.0	15.0	all duties	2
Aegithalos concinnus	31	275	5.9	14.5	14.0	all duties	3
Cettia diphone	32	100	4.5	15.0	14.5	feeding young	4
Locustella fasciolata	44	200	6.0	13.0	?	feeding young	5
Acrocephalus bistrigiceps	43	500	5.0	13.5	11.5	feeding young	6
Phylloscopus affinis	29	4400	4.0	13.3	15.7	feeding young	7
Phylloscopus humei	35	2800	3.9	?	13.8	feeding young	8
Phylloscopus inornatus	37	2800	4.5	11.0	11.0	feeding young	9
Megalurus pryeri	47	138	5.4	11.9	10.1	no duty	10

[a] 1, This study; 2, Fang and Ding (1997); 3, Guo et al. (2006); 4, Wang (2002); 5, Jin et al. (2006); 6, Yang (1990); 7, Lu (2008); 8, Bi (2004); 9, Liu and Chen (1988); 10, Li and Wang (2006).

Nest predation (34%) constituted a much smaller fraction of the nest failures of the tit-warblers than is typical (80% on average) of most lowland birds (Ricklefs 1989). This difference could be related to the low diversity and density of predators on bird nests in the alpine habitat (Lu 2005). Also, the cryptic coloration of tit-warbler nests may reduce their detectability by predators, although many pairs nested in a time when the foliage of the shrub supporting the nest had not fully developed.

At the population level, the sex ratio of complete tit-warbler broods (equal to primary sex ratio) did not deviate from 1:1, in accord with Fisher's (1930) equilibrium theory of sex allocation. However, the production of females in individual broods increased as the season progressed, and the bias was not due to differential mortality after hatching. A similar pattern has been reported in other birds (Husby et al. 2006). Modern sex-ratio theory suggests that despite the chromosomal sex determination, birds should be able to allocate their investment adaptively toward males or females according to the fitness return of each sex (Trivers and Willard 1973). Parents in good condition should overproduce the sex with a higher variance in reproductive success and with a greater cost to produce. In cooperatively breeding species, females tend to have a higher variance in reproductive success (Hauber and Lacey 2005). Therefore, our finding that females are more likely to be the helping sex supports the hypothesis of early-cohort advantage, i.e., that early breeders, which often are in good condition, should produce more females (Wright et al. 1995). Nevertheless, adaptive implications of the sex-ratio-adjustment strategy adopted by the tit-warblers, in which male nestlings are slightly larger than female nestlings, especially its possible link with the species' cooperative breeding system, remain to be further explored.

The number of tit-warbler nests located in this study area obviously declined since 2005. We only found three active and nine old nests in 2007 despite the search efforts similar to those of previous years (usually over 40 for both active and old nests). The tit-warblers nested low in the bushes, the majority (85%) of which were lower than 2 m and had suffered from cutting by local people for firewood. In contrast, on the northeastern Tibetan plateau Crested Tit-warblers often place their nests >5 m from the ground in conifers (X. Lu pers. obs.). Thus disturbance of nesting vegetation is unlikely to be the cause of population decline. Other ecological conditions, unpredictable in the alpine zone, may be responsible for the sharp decline.

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