Hidden leks in the Yellow-browed Warbler *Phylloscopus inornatus?* - Investigations from the Khan Khentey reserve (Mongolia)

Prikriti leki pri mušji listnici *Phylloscopus inornatus?* – raziskava iz rezervata Khan Khentey (Mongolija)

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The breeding biology of the Yellow-browed Warbler *Phylloscopus inornatus* is largely unknown. Recently the species was found to breed in clusters and some hypotheses on the function of aggregated breeding sites have been proposed. To obtain new insights, two clusters of Yellow-browed Warblers were observed from May to July 2003 in the Mongolian Khentey. Mist-netting, nest searching, behavioural observations and habitat analysis were conducted. In contrast to the large breeding clusters found in the main area of the species distribution in Siberia, pairs in the Khentey are breeding in single groups of a maximum of 3 nesting pairs. At this southern border of its breeding range the species has problems with immense predation pressure and unequal sex-ratios (approx. 5:1 males to females). As a consequence, four breeding pairs had at least ten nests, which were all predated before young were hatched. Nests are built solely by females and one of the females replaced its nest three times following predation of eggs. There was great fluctuation of territorial males in the clusters, which sometimes contained more than 20 males. Breeding pairs were formed after peaks in the numbers of territorial males. Due to its small breeding groups or clusters, the Khentey has great advantages for understanding and testing the process of cluster formation in this species. Locations of breeding territories were independent of habitat parameters, but centred in the middle of unsuccessfully established territories. Thus, this small dataset strongly supports the hidden lek hypothesis as the main explanation of clustering, saying that males with territories in the centre of a territory-congregation are sexually the most attractive for females. Yellow-browed Warblers could be one of the few and best examples for the correctness of this hypothesis. New data on biometry, breeding biology and behaviour in this species are discussed.

Key words: *Phylloscopus inornatus,* Yellow-browed Warbler, hidden lek, cluster breeding, sex ratio, predation
Ključne besede: *Phylloscopus inornatus,* mušja listnica, skriti lek, rastišče, gnezditev v skupkih, razmerje spolov, predacija

1. Introduction

In central Europe, the Yellow-browed Warbler *Phylloscopus inornatus* is widely known from accidental sightings. In the past there were three subspecies combined under the species *Phylloscopus inornatus*: The Yellow-browed Warbler (formerly known as *Phylloscopus inornatus inornatus*) and the two subspecies of the Hume's / Buff-browed Warbler (formerly known as *Phylloscopus inornatus humei* and *P. i. mandelleii*). Because of morphological, ecological and behavioural criteria the Yellow-browed Warbler and the Hume's / Buff-browed Warbler are now seen as two species, and the second is now called Hume's Warbler *Phylloscopus humei* (Glutz v. Blotzheim & Bauer 1991, Svensson 1992). Breeding sites are relatively rare in the European part of the Ural-mountains, but fairly common east of it. The species is, without large geographic differences, distributed in the taiga-forests of Siberia between the Urals and the Ochotsk-sea (Glutz v. Blotzheim & Bauer 1991).

Recently breeding attempts of Yellow-browed Warblers were reported from the Mongolian Khentey (A. Barkow *unpublished data*, Wichmann 2001, Wichmann & Pokrovskaya 2004), although this is outside the formerly accepted breeding range (Chabry 1989). This area of forest-steppes in northern Mongolia constitutes the southern border of the species' breeding range.

The breeding biology of the Yellow-browed Warbler and the closely related Hume's Warbler is largely unknown (compare Price & Jamdar 1991 for *P. (i.) humeii*). Despite its abundance in some areas, only some parameters of nesting sites and eggs are described in the literature (Witherby *et al.* 1943, Worobjew 1963, Glutz v. Blotzheim & Bauer 1991).

"Cluster breeding" in birds is a quite unusual form of breeding, not found in many species. Breeding pairs are not randomly distributed over a suitable habitat, but clustered in groups. In contrast to colonial breeding, each pair still has its own defended territory. Most species that congregate in clusters for breeding do so for common defence against predators and/or follow an uneven distribution of food. Recent studies showed that the form of the mating system can also lead to cluster breeding (Herremans 1993, Danchin & Wagner 1997, Wagner 1997).

Breeding in clusters for *Phylloscopus inornatus* is briefly discussed in the literature (Bourski & Forstmeier 2000), but its function and frequency are largely unknown or speculative.

2. Study area

Bordering the Russian Federation in the north and the People's Republic of China in the east, south and west, Mongolia is a landlocked country which covers an area of 1.56 million km². It extends 1236 km from north to south and 2405 km from east to west, and is the seventh largest country in Asia.

The Khan Khentey Strictly Protected Area (KKSPA), situated in the northeast of Mongolia, was founded in 1992 (Figure 1). This huge uninhabited area, stretching from the Russian border to the northeast of Ulaanbaatar, lies between 48° and 49°N and from 107° to 110°E. It covers 1.2 million ha and is the fourth largest protected area in Mongolia (Myagmarsuren 2000). Compared with the protected boreal ecosystems in Europe, it is as large as the complete protected forests of Fennoscandia (Von Velsen-Zerweck 2002). Cooperation between Göttingen University and the National University of Mongolia led, in 1998, to the research station "Khonin Nuga" being established by the side of the Eröö river in the western buffer zone of the KKSPA (Figure 1). The study area at Khonin Nuga (49°04'N, 107°24'E) lies at an altitude of 1000 m (+/−50 m) a.s.l. and covers 1.8 km².

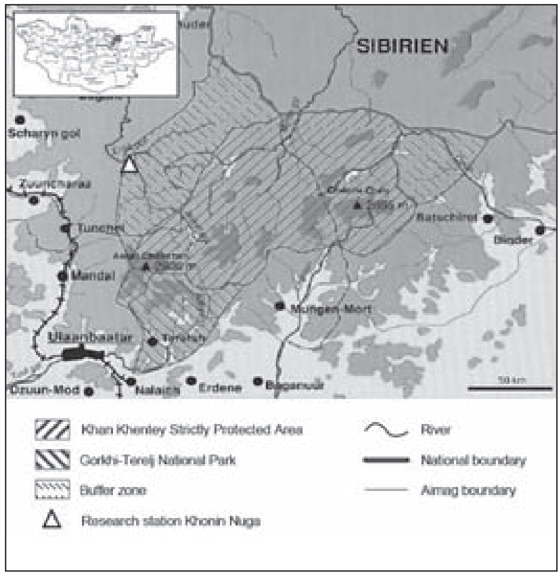

Figure 1: The location of Khan Khentey Strictly Protected Area and the research station Khonin Nuga (after MNE & WWF 1994).

Slika 1: Lokacija rezervata Khan Khentey in raziskovalne postaje Khonin Nuga (povzeto po MNE & WWF 1994).

In Khonin Nuga, Yellow-browed Warblers inhabit *Betula fusca* shrubs, situated between riverine meadow pastures and Asian White Birch *Betula platyphylla* / Siberian Larch *Larix sibirica* forests on hillsides at the base of the northern mountainside. These shrub areas can be divided into a central region of vegetation of relatively homogenous height (approximately 3 metres) with only a few taller trees of Asian White Birch and small numbers of Siberian Larch, that contrasts with the hillside belt of shrubs that includes a lot of umbrella-trees (*Larix sibirica*) and young growth of larch, Siberian Spruce *Picea obovata* and willows (*Salix* sp.).

In 2003, I found two areas with a large number of clumped territories (clusters) of Yellow-browed Warblers (see Figure 2) in Khonin Nuga. One of these clusters ("Patch 1") was also colonized the year before (A. Barkow *unpublished data*), the other ("Patch 2") was new. Patch 1 (~2.7 ha) lies in the south-western part of the area in the smooth transition zone between *Betula fusca* shrubs and the hillside forest (see Figure

Figure 2: The location of patch 1 (photo at the top), situated north of hillside forests, and patch 2 (photo at the bottom) in the centre of the valley (photo: P.H.W. Biedermann).

Slika 2: Lokacija območja 1 (zgoraj), severno od gozdov na pobočju in območja 2 (spodaj) na sredi doline (foto: P.H.W. Biedermann).

2). Patch 2 (~0.9 ha) lies in the centre of the *Betula fusca* shrub, bordered by rows of larch and birch aged about 30 years (see Figure 2). Nearly the whole study area was burnt down 30 years ago, which explains the high density of shrubs instead of forest.

In central Siberia, Yellow-browed Warblers prefer younger regrown vegetation in burnt habitats (Glutz v. Blotzheim & Bauer 1991, Forstmeier *et al.* 2001).

3. Methods

In 2003 the whole study area (1.8 km^2) was covered by two censuses a day, between 10 May and 15 May to look for Yellow-browed Warblers; then, until 3 Jul, the area was surveyed once a day.

When the first individuals arrived on 12 May, I started to catch birds full-time with mist nets until 21 May. After that mist netting was continued for only half a day until 7 Jun. Catching in the morning between 8.00 and 11.00 h was particularly efficient. More birds were caught when the weather was bad (around 80% of ringed birds when the cloud density was more than 50%). All birds were marked by colour rings, for recognition later in the field and released next to the net where they were caught.

Yellow-browed Warblers cannot be sexed by plumage. Most birds were thus sexed by wing-length (males: ≥ 66 mm; females: ≤ 64 mm) (for techniques and more information see Svenson 1992), the remainder by their behaviour in the field. In addition to wing-length, the length of the 8th primary (1st primary next to 1st secondary) and body-weight were measured.

Additionally, I surveyed the area (in particular both patches mentioned above) for ringed and non-ringed individuals. Each Yellow-browed Warbler was documented, including its location and behaviour (particularly territorial, feeding, mating and nesting behaviour). Nesting territories were estimated by mapping singing posts and territorial behaviour. A male was considered to "own" a tree if it was observed singing in it. Two males were never recorded singing in the same tree, except at territory borders. From this observation it was possible to distinguish between two types of territories. The first was the centre of the territory where all the singing posts, territorial behaviour and nests were recorded – this area was defended against other males. The second territory was the whole area in which males were not observed every day (especially when there were a lot of territorial males around) and where they usually did not sing. Each time non-ringed birds were observed, I replaced the nets on the following day in an attempt to catch them.

When females started to build nests I tried to locate the nest sites. Each nest was checked every morning around 7.00 h for eggs. During the period of nest-building it is surprisingly easy to locate females. At this time of season shrubs are foliating and females often contact the male with calls after leaving the nest (for similar observations on *P. (i.) humeii* see Price & Jamdar 1991).

Behaviour patterns, like territorial behaviour between males, nest-building behaviour of females, anti-predator and mating behaviour were observed (see Results).

At the end of the breeding season all nest sites were analysed for material used, direction of nest entrance and habitat.

At the end of June, when only two pairs were left in the area, an attempt was made to obtain footprints of terrestrial nest predators with a sand-filled hole on a path near one nest. Around another nest, six small-mammal traps were placed at a distance of 5 metres. Habitat parameters of "long-time territories" were compared with those of the area bordering the patch. At randomly chosen points (3 x 3 m) the mean height and diameter of *Betula fusca* shrubs and the number of wood-trunks were measured. "Long-time territories" are defined as areas where birds stayed more than two days (N = 8). The numbers of small / large Asian White Birches, Siberian Larches and other trees in plots of 50 x 50 m within and outside territories with nests were recorded.

4. Results

4.1. Catching phenology

During 18 catching days I ringed 29 individuals (24 males, 5 females), with one to nine mist nets (9143.75 net-hours x m^2 or 0.00317 caught birds / net-hour x m^2). The first territorial males arrived in the study area on 15 May. The first female was caught on 18 May. Ringing was most successful during the first three days of the study when more than one third of the total catch were ringed (10 males, 1 female). After that only three birds could be caught until the 1 Jun, when again ten males and one female were ringed (Figure 3).

The sex ratio of those caught by mist-netting was 24 males to 3 females. The two other females were caught in front of their nests. Most individually ringed specimens were not seen again after the first capture (17 males, 2 females). All mated individuals remained in the study area for more than ten days (Figure 4).

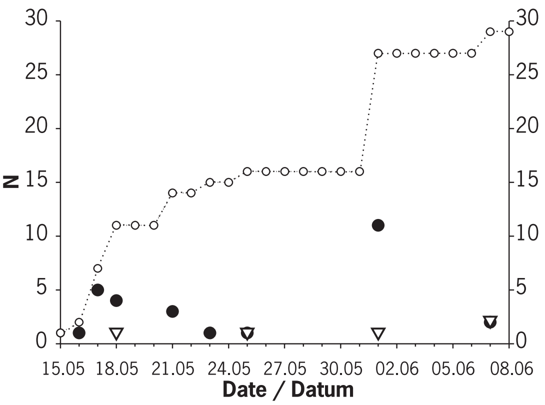

Figure 3: Numbers of Yellow-browed Warblers *Phylloscopus inornatus* caught during the survey. Open circles and dotted line denotes cumulative total ringed, filled circles number ringed each day and triangles females ringed each day.

Slika 3: Število mušjih listnic *Phylloscopus inornatus* ujetih med raziskavo. Odprti krožci in pikčasta črta pomenijo skupno število obročkanih ptic, polni krožci število obročkanih ptic po dnevih, trikotniki pa število obročkanih samic po dnevih.

4.2. Biometrics

The biometry of captured birds was very similar to the sparse data already published. Five females, with wing length 52 – 55 mm (mean 53.4 mm, SD 1.0) and weight 5.5 – 6.5 g (5.9 g, SD 0.4), and 24 males, with wing length 55 – 60 mm (mean 57.5 mm, SD 1.2); weight 5.5 – 7.0 g (mean 6.4 g, SD 0.4). Glutz v. Blotzheim & Bauer (1991) give a mean wing length of 54.0 mm and a mean weight of 6.0 g for females (N = 47), and a mean wing length of 57.0 mm and a mean weight of 6.0 g for males (N = 75) (data from Hopei / NE China for April / May and August / October).

Males that remained in the study area for more than one day (N = 7) were slightly smaller (mean wing length = 57.1 mm, SD 1.77) in contrast to those that were not sighted again (57.6 mm, SD 1.0, N = 17). No significant correlation was observed between wing length and body weight of the two groups (t-test: wing length (t) = 0.92, P > 0.05; Mann-Whitney Rank Sum test: T(weight) = 92; P > 0.05) (Figure 5). The three mated males had the largest wing length (mean = 58.3 mm) but the smallest body mass (mean = 6.2 g compared to 6.4 g); the sample size was too small to test for statistical significance. It appeared that larger and heavier males arrived earlier in the year (see Figure 5), but the correlation was weak (Spearman rank order correlation: P (wing length) = 0.10; P (weight) = 0.58). The sample size of measured females was too small to do statistical tests.

4.3. Bird counts

The first two singing males were recorded on 15 May (patch 1). This date is about one week later than the year before (A. Barkow *unpublished data*), probably due to bad weather with snow at higher altitudes. Patch 2 was first settled on 22 May. After that four to five flocks (with 8 to 22 males) were observed that migrated through the area (see Figure 6), as well as many territorial males which established short-term territories for one to ten days in the two small patches (2.7 + 0.9 ha). The number of singing males fluctuated greatly. The greatest numbers recorded were 7.4 (patch 1) and 13.3 (patch 2) territorial males per hectare (Figure 6). Most of the males were observed in patch 1 (max. 20 males; in contrast to max. 12 males in patch 2).

The high density of territorial males did not result in high breeding densities, because of the almost complete absence of females. Although a lot of the

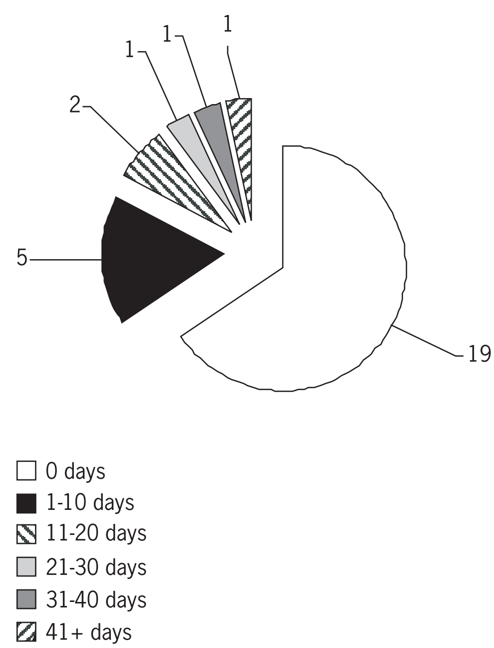

Figure 4: Number (proportion) of birds and how long they stayed in the study area. Most birds left the area soon after ringing.

Slika 4: Število (delež) ptic glede na dolžino postanka na območju raziskave. Večina ptic je območje zapustila kmalu po obročkanju.

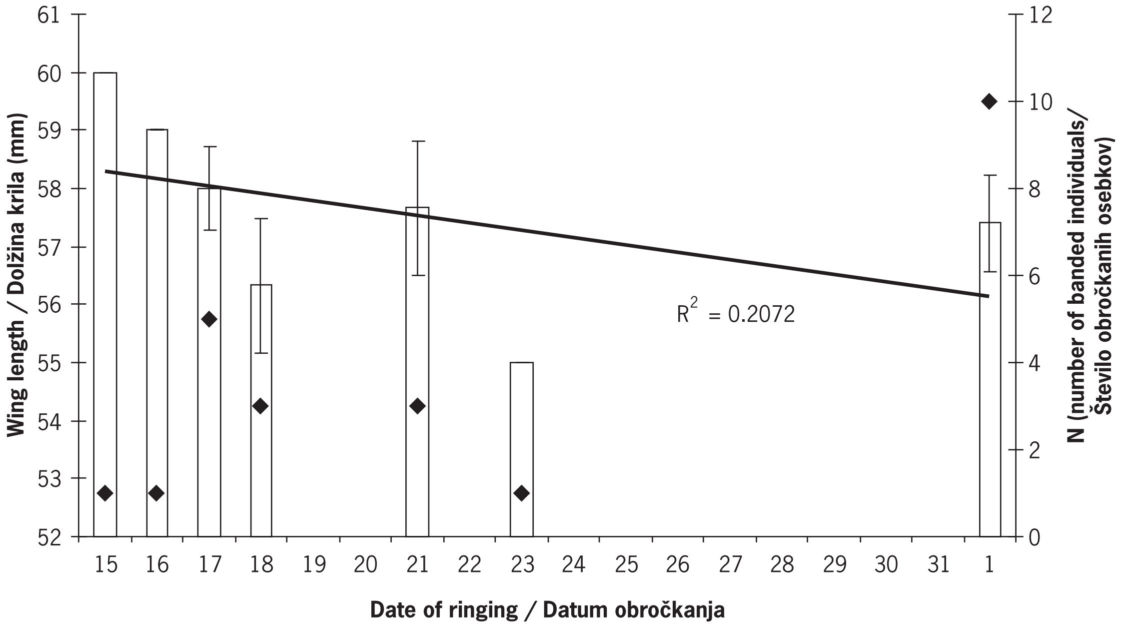

Figure 5: The dependence of wing length of ringed males on ringing date (15 May 2003 to 1 Jun 2003). R^2 is the variance of the regression line (= square of residuals). Diamonds (♦) represent N for the particular day. Individuals at the beginning of the season were not significantly larger than individuals at the end of the season.

Slika 5: Odvisnost dolžine kril od datuma obročkanja (15.5.2003 – 1.6.2003). R^2 pomeni varianco regresijske premice. Diamanti (♦) predstavljajo število osebkov. Osebki na začetku sezone niso bili signifikantno večji od osebkov ob koncu sezone gnezdenja.

males were ringed (see above) there were never more than three ringed males in the study area. On days with large numbers of singing males I usually caught new females. The last flock of males left the area on 20 Jun. The last bird was observed on 4 Jul.

4.4. Breeding biology

By recording colour-ringed males it was possible to see which individuals established "real" (long-time) territories. 7 males (5 in Patch 1 and 2 in Patch 2 – 29.2% of all males) stayed for longer than one day in the area. Other males, which obviously did not mate, left the area within 10 days of being first sighted. 3 males mated (2 in patch 1, 1 in patch 2).

Only one of the three ringed females was seen again after ringing. It was mated with one of the males in Patch 1. Two additional females were ringed in front of their nests, by non standard mist-netting.

In total there were 4 breeding pairs (3 in Patch 1, 1 in Patch 2) in the area – one of the males was bigyn with 2 females. The 4 pairs observed during the study built at least 9 or 10 nests, which were all predated during the egg laying period.

The first nest-building female was seen on 23 May (Figure 7). The last nest was left, probably after predation of eggs, on 4 Jul (by the same female). During that time four females laid a total of 15 – 16 eggs in at least 10 different nests (1st female: 4 nests, 2nd: 1, 3rd: 3, 4th: 2). Most nests were predated after the first egg was laid (N = 6), one nest with two, one with three and one with four eggs. After predation, nests were abandoned and the females started to built new nests one to ten days later (only once did a female lay an egg in an already predated nest).

Nest building took females a minimum of 3 – 7 days, before laying the first egg. Eggs were laid on consecutive days. During the day, laying females were never seen at the nest or in its vicinity.

One of the females probably never laid eggs – it was the second female of a male – and abandoned the completed nest (and the area) after five days of building.

4.5. Nest analysis

Nine nests were collected after the birds left the area and analyzed for dimensions, nesting materials,

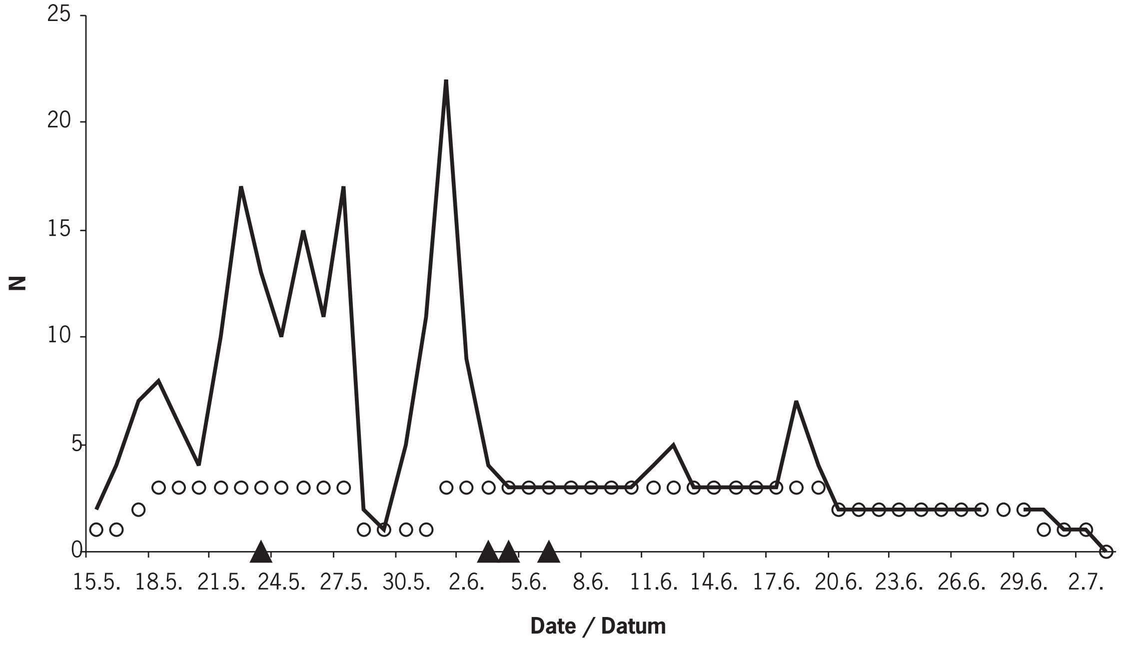

Figure 6: Total number of singing males on both patches over the breeding season in 2003. Open circles (○) represent total number of known (ringed) singing males. Full triangles (▲) mark the appearance of new matings.

Slika 6: Skupno število pojočih samcev na obeh raziskovalnih območjih v gnezdilni sezoni v letu 2003. Prazni krožci (○) predstavljajo skupno število znanih (obročkanih) pojočih samcev. Polni trikotniki (▲) označujejo novo parjenje.

location and habitat. The nests were built by four different females, four of them by one female.

All nests were built in small holes in the ground. They were globular shaped with the entrance on one side. Like in other *Phylloscopus* species only the female builds.

The nests comprised an outer and an inner nest, differing in the nesting materials used. In Khonin Nuga, Yellow-browed Warblers built the outer nest with 7 different materials (see Figure 8), which were collected mainly in the immediate vicinity of the nest. Field surveys showed that all nest materials could be found within 20 metres of the nest sites (90% up to 10 m). The following were found in descending order: long dry grass (>15 cm), moss, short dry grass (< 5 cm), old leaves, dry horsetail *Equisetum* sp., bark (*Salix* sp.) and rotten wood (*Betula platyphylla*).

The inner nests contained only three components: needles (*Larix sibirica*), animal hairs (horse, wild pig, deer etc.) and short dry grass (<15 cm). With the exception of animal hairs all materials of inner nests were found up to 10 m from nests.

Nests were solely built by females. There was a tendency to mate with males that owned territories in the centre of a patch, i.e. in the centre of the other males' territories. Mating and nest building always followed days with peak numbers of territorial males (see also Figure 6).

During nest building the female called frequently – in 8 out of 14 approaches to the nest site with new nest material (mean of 3.9 calls). In 2 out of 15 departures (13.3%) she called again (mean of 1.5 calls). Thus, to locate new nests one should look out for calling birds, usually females, in occupied territories.

All nine nests were found among *Betula fusca* shrubs (1.8 – 2 m height) in the transition zone between dense and more open shrubs, with an average distance of one to three metres between bushes. Half the nests were built in holes at the roots or under old branches directly at the base of *Betula fusca* bushes (one at the base of a Sibiran Larch) or not more than half a metre away. The other half were built in tussocks. In both cases only the entrance could be seen, the rest being covered by branches and mainly old grass (Figure 9). This camouflage was not constructed by the bird; the nest was simply built under it. Normally nests were directly on the ground. Two were 10 cm and 20 cm above the ground (in these cases the nesting site was very wet). Nests were always covered by overhanging branches. In most cases there was a landmark, like

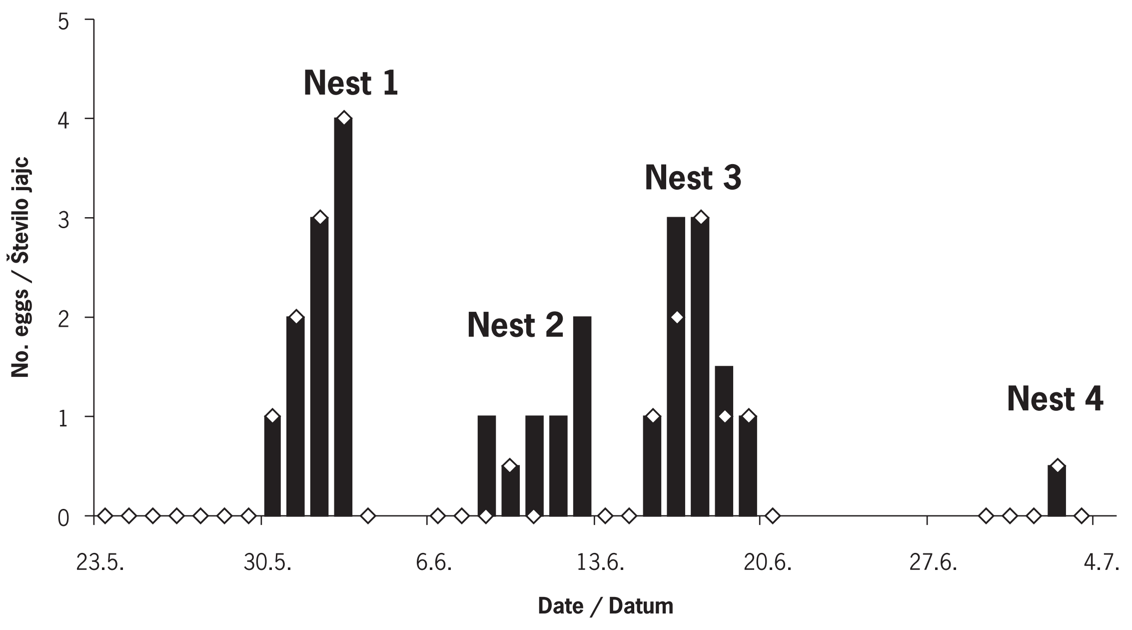

Figure 7: The black columns indicate the number of eggs in the whole study area (patches 1 and 2) over the breeding season in 2003. The open diamonds indicate the number of eggs of pair 1. Nests 2 and 4, that were abandoned before the first egg was laid, were assumed to contain 0.5 eggs (probability of 50% that one egg was laid).

Slika 7: Črni stolpci označujejo število jajc na celotnem območju raziskovanja (1 in 2) prek sezone v letu 2003. Prazni diamanti označujejo število jajc para 1. Pri gnezdih 2 in 4 je privzeta vrednost 0,5 (verjetnost izleženega jajca 50%).

a tree or a higher bush, very close to the nest, that was used by males as singing post. Most nests (70%) were found close to the border of males' territories, and replacements were surprisingly close to former, predated nests, with a minimum distance of 13 m. This corresponds to the relatively small size of male territories. The nesting sites of two females which were mated with the same male (bigyn), were 50 m apart. There was a slight preference for directing nest entrances to the north (Figure 10), although this appears to be more location than climate dependent.

4.6. Territory size, habitat and territorial behaviour:

Figure 2 shows the dimensions of the two patches that were settled by territorial males. Four of all the males recorded stayed in the area for more than ten days and only in these cases was it possible to identify territory size. During periods when there were no other (i.e. "short-term") territorial males in the area (see Figure 6), territories measured, on average, 4700 m² (SD 641.2 m²; max. 5650 m²; min. 4250 m²; N = 4). On days with many other males present, resident males concentrated their defended areas to an average size of 1687.5 m² (SD 566.2 m²; max. 2500 m²; min. 1200 m²; N = 4). In this case the territory of an unmated male appeared nearly twice as big as the territories of the three mated males. Due to the facts of rough terrain and unclear territory-borders at some places it was difficult to measure the sizes exactly. Thus, an error of +/- 100 m² is possible.

No differences in vegetation characteristics could be observed between patches and their surrounding habitat in the study area (Table 1). Comparisons were characterized by t-tests for the height of shrubs (P = 0.92; N = 20), diameter of shrubs (P = 0.6; N = 20), number of small birches or larches (P = 0.11, P = 0.79; N = 8), number of tall birches or larches (P = 0.52, P = 0.27; N = 8), total number of trees (P = 0.47; N = 8) and Mann – Whitney Rank Sum test for number of wood-trunks (P = 0.96; N = 20).

Males appeared to defend territories only in the morning until noon. Singing was unusual in the afternoon, especially at the beginning of the season, during this time the birds probably deserted the area, probably to the surrounding forests. This could be confirmed by observations of non-ringed individuals in the nearby forests during the afternoon.

4.7. Some behavioural observations

New birds arrived in the area during the night. In the morning males occupied territories for short periods (see Figure 4 & 6). Only males that stayed longer than 2 days used singing posts on tops of trees or in high shrubs; the others usually sang while moving, but with decreased intensity. These males, which were obviously migrating through the area, appeared to be attracted by other singing males and stimulated to sing themselves. The fact that they were moving all the time made it very hard to localize and observe them.

During the mating period, the singing activity of mated males decreased. Singing fluctuated during the day – if one male started to sing many others were stimulated to do the same. There were thus times apparently without any territorial birds, and 5 minutes later the opposite.

Wing flicking was a common behaviour of males, and wing drooping in concert with the song was seen mainly against other males at territory borders (in a different sense, sometimes also to the mate). There the two (sometimes three) rivals sat face to face at distances of 2 – 3 m, singing and threatening each other. They then became very excited, frequently flew a few metres, and started again with the same behaviour. Real fights were never observed, but long chases and conflicts at territory-borders were common.

An often heard call was a high "tsuiist", used as a contact call between sexes and, as a slightly different function, as a warning call. In the latter case calls were repeated at intervals of 1 s for sometimes more than 30 min. Males warned especially persistently against cuckoos (*Cuculus canorus, C. horsfieldii*) and sometimes also attacked them. In this case the birds called additionally with a "schääh-schääh-schääh-schääh" that sounded very similar to the "mobbing-calls" of tits. They continued mobbing until the cuckoo left the area.

Although cuckoos were very common in the area and warning behaviour could be observed nearly every day, I never observed other Yellow-browed Warblers from the same patch joining the attacking pair.

Immediately after the arrival of females, pairs were formed and females started to build nests. During nest building, females were commonly seen visiting bare patches on the ground, investigating suitable hollows, and picking up items of potential nesting materials. Males often joined their females and sometimes might engage in chasing males. Copulation was very secretive and could never be recorded with certainty.

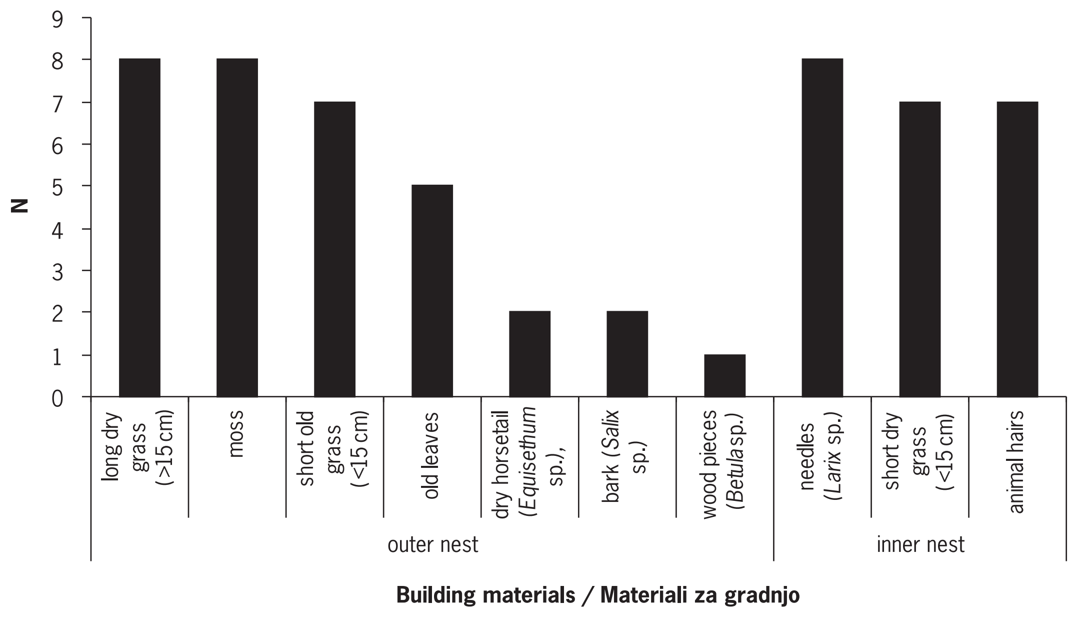

Figure 8: Building materials found in 9 nests of Yellow-browed Warbler *Phylloscopus inornatus*. The height of the bars represents the number of nests in which the specific material was found.

Slika 8: Gradbeni materiali pri devetih gnezdih mušje listnice *Phylloscopus inornatus*. Višina stolpca pomeni število gnezd v katerih je bil najden določen material.

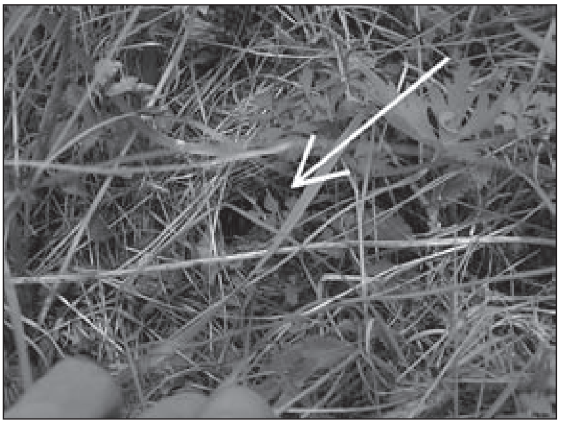

Figure 9: Example of a nest of Yellow-browed Warbler *Phylloscopus inornatus*. The white arrow marks the entrance. This nest was predated with four eggs. All the nests looked like "mouse-holes" in the ground. They were left undamaged after predation (photo: P.H.W. Biedermann).

Slika 9: Gnezdo mušje listnice *Phylloscopus inornatus*. Bela puščica označuje vhod. Gnezdo je imelo štiri jajca in je bilo izropano. Vsa gnezda so videti kot "mišje luknje" v tleh. Po predaciji niso bila poškodovana (foto: P.H.W. Biedermann).

4.8. Predation

At least eight of the nests found were predated during the study period (see also "breeding biology"). Predation of eggs always occurred at night (between 21.00 and 7.00 h).

I was not able to catch any potential predator with small-mammal traps or to find any footprints with sand-filled holes. Predators never left signs in or around the nests. Eggs were removed complete; shells were never found. Nests were completely undamaged, and even the entrance hole size was unchanged.

The most probable predators in the area were a stray dog from the research camp and Siberian Chipmunks *Tamias sibiricus*. The former would be likely to damage or destroy nests totally.

Siberian Chipmunks were sometimes seen in the forests on the slopes of the valley. Although I never observed them in the study area, they are the most likely animals to steal eggs without leaving any damage.

Cuckoos (*Cuculus canorus, C. horsifieldii*) are very common in the area, but Yellow-browed Warblers evolved a persistent mobbing behaviour (see also 4.7. Some behavioural observations). Cuckoos are unlikely nest predators in this case, because I never found any cuckoo-eggs in the nests and predation occurred only during the night.

The importance of predators like crows, weasels, foxes and especially snakes is probably underestimated, because they have never been observed. Small mammals like voles, mice or shrews were completely absent from the area, because of very cold winters without snow-cover (Sheftel *pers. comm.*).

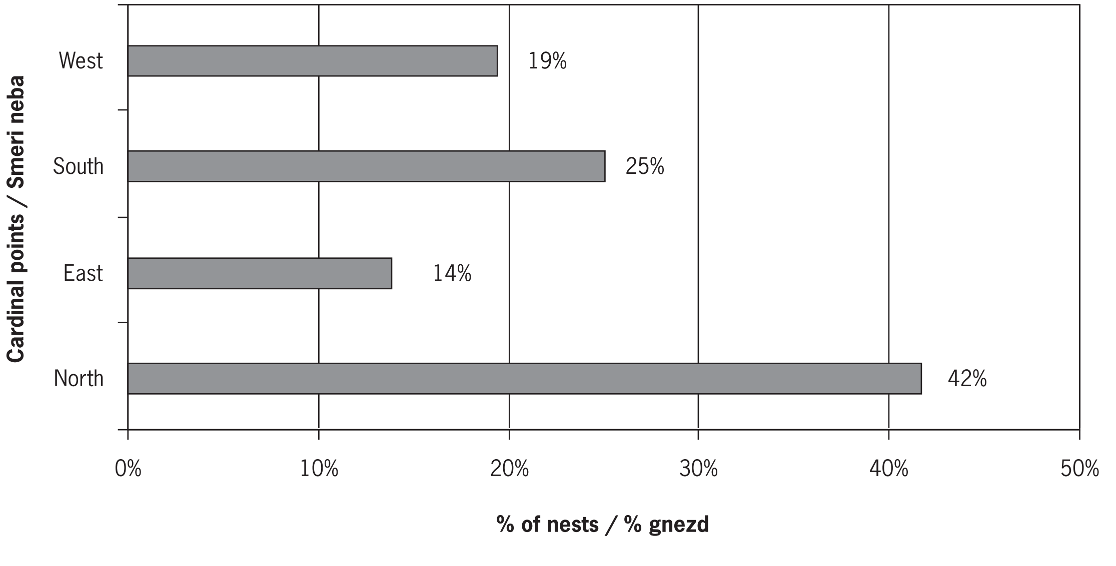

Figure 10: Proportion of nests whose entrances were directed to the four cardinal points

Slika 10: Delež gnezd glede na smer vhodov

Table 1: Habitat comparison between randomly chosen points (plots) within and outside the patches: *Betula fusca* shrubs are compared for shrub height and diameter and tree structure is compared for different species (*Betula fusca* and *Larix sibirica*) and their height. No significant differences were found.

Table 1: Primerjava habitata med naključno izbranimi točkami na in izven popisnega območja: grmovje *Betula fusca* glede na višino in premer ter struktura dreves (*Betula fusca* in *Larix sibirica*) glede na višino in število. Razlike niso statistično značilne.

				N					
		Height/ Višina* (cm)	Diameter/ Premer* (cm)	Wood-trunks/ Debel*	Birch/ Breza <10 m**	Birch/ Breza >10 m**	Larch/ Macesen <10 m**	Larch/ Macesen >10 m**	All trees/ Vseh dreves**
Outside patches/ Zunaj površin	Mean	200.0	84.0	1.3	3.0	10.6	25.2	5.8	44.6
	SD	44.9	46.0	0.5	2.2	5.6	27.1	3.3	30.5
	N	10	10	10	5	5	5	5	5
Inside patches/ Znotraj površin	Mean	202.5	97.5	1.7	6.0	13.7	30.0	9.3	59.0
	SD	57.0	62.0	1.2	2.0	7.0	11.3	5.1	8.9
	N	8	8	8	3	3	3	3	3
P (t-test)		0.92	0.60	0.96***	0.11	0.52	0.79	0.27	0.47

* at randomly chosen points with a size of / naključne točke 3 x 3 m (9 m²)
** at randomly chosen plots with a size of / naključne točke 50 x 50 m (2500 m²)
*** Mann-Whitney test

5. Discussion

Compared with the main breeding grounds in Siberia, *P. inornatus* breeds near Khonin Nuga in very low densities (Bourski & Forstmeier 2000, Sheftel *pers. comm.*). Reasons for this may be the immense predation pressure (also A. Barkow *unpublished data*), unequal sex ratios (approx. 5:1 for males) and probably not ideal habitat. The sex ratio could be partly overestimated, because females are more inconspicuous and move less, making them harder to catch with mist-nets (but see Wagner 1997 and Herremans 1993 with similar sex ratios for *P. sibilatrix*). Although males tried to attract females, most of them were unsuccessful and left the area after one or two days.

It is obvious that most birds migrated further north, because the number of nesting pairs per cluster is quite small compared with those in Siberia (Forstmeier *pers. comm.*). Birds that remain appear to be smaller, their size decreasing with later arrival dates (both non-significant).

Another hypothesis is that most migrating birds have difficulty in getting to Khonin Nuga, because of the huge Mongolian steppes and deserts to the south. Small passerines are probably not able to fly across this barrier (Mühlenberg & Wichmann *pers. comm.*). This would be supported by the late arrival of the birds in the area, compared with their main breeding grounds, although further north, they arrive in central Siberia only some days later – 17 to 26 May for males, 24 May to 2 Jun for females (Sheftel *pers. comm.*, Bourski & Forstmeier 2000).

The pressure of egg predators appears to be immense, destroying all clutches of Yellow-browed Warblers in the study area in 2003. In similar habitats in Siberia, Siberian Chipmunks are important predators of bird nests and *Phylloscopus fuscatus* shows an adaptive plasticity in nest-site selection in response to changing predation risk (Forstmeier *et al.* 2004). In years with high chipmunk abundance, nests are built significantly higher above the ground and nest bushes are more isolated from other bushes than in years with low densities. Yellow-browed Warblers show no obvious plasticity in nest-sites in response to egg predation, but usually replace predated nests immediately. It is remarkable that nests are replaced up to four times and built within a few (>3) days. Most *Phylloscopus* species appear to replace their nests once after predation, but building time is usually longer (5 – 16 days depending on the species) (Glutz v. Blotzheim & Bauer 1991). In the most closely related *P. humeii*, predation does not usually appear to lead to the laying of second clutches (Price & Jamdar 1991) and nest-building takes 4 – 8 days (Glutz v. Blotzheim & Bauer 1991), or 5 – 16 days (Price & Jamdar 1991). More than one replacement is known only for *Phylloscopus sibilatrix*, which builds its nests within 2 – 4 days (Glutz v. Blotzheim & Bauer 1991).

Yellow-browed Warblers lay slightly smaller eggs (mean 13.7 mm x 10.8 mm, N = 26) (Witherby *et al.* 1943, Worobjew 1963, Glutz v. Blotzheim & Bauer 1991) than *Phylloscopus proregulus* (mean 14.5 x 10.9 mm, N = 60) and *P. humeii* (mean 14.3 x 11.3 mm, N = 60), although their body size is slightly larger. Thus, Yellow-browed Warblers invest more in the quantity of eggs, probably adapted to the need for a higher replacement rate. An additional adaptation to predators is probably the egg-laying in the early morning and absence from the nest during the daytime, as also observed in *P. humeii* (Price & Jamdar 1991).

Dates of first arriving birds, first nest-building and egg-laying in the study area are similar to those recorded for other *Phylloscopus* species (Glutz v. Blotzheim & Bauer 1991) at comparable latitudes.

Nest measurements (see Table 2) were very similar to those for the closely related *P. (i.) humeii* (Price & Jamdar 1991) and its subspecies *P. (i.) mandelleii* (Glutz v. Blotzheim & Bauer 1991). Total weights of nests were, with an average of 7.89 g, very different from the 9.6 to 27.8 g for *Ph. (i.) humeii*. This might be explained by the common replacement of nests and / or the different nesting materials used in different habitats.

Indeed Price & Jamdar (1991) found some different materials for *P. (i.) humeii*. As in the present results, he found mainly grass. 72% of his nests contained birch-bark, and 79% some moss (N = 33). In some nests he found pine needles and animal-hairs. Koshvar (in Glutz v. Blotzheim & Bauer 1991) additionally found feathers in inner nests, which I and Price & Jamdar (1991) could not find.

It is still not clear whether the species is able to raise successful broods in the study area. Individuals are possibly capable of estimating rodent densities (these are likely to be the main predators) from their scent-marks (Viitala *et al.* 1995) and therefore avoid the area. However, Sheftel (*unpublished data*) observed very low densities of mice, shrews and voles in the study area in 2003.

The relatively small number of territorial males per cluster and relatively low breeding densities in the present study area compared to Siberia (around 30 breeding pairs in Bourski & Forstmeier 2000) make for big advantages for studying the social system of Yellow-

Table 2: Nest parameters of Yellow-browed Warbler *Phylloscopus inornatus* compared with those for closely related species. Due to the globular shape of the outer nest there are 2 diameters.

Tabela 2: Parametri gnezda mušje listnice *Phylloscopus inornatus* v primerjavi s sorodnimi vrstami. Zaradi ovalne oblike ima zunanje gnezdo dva premera.

	Outer nest / Zunanje gnezdo					Inner nest / Notranje gnezdo			Total weight/ Skupna teža(g)
	Diam. 1 (mm)	Diam. 2 (mm)	Width of cup/ Širina skodelice (mm)	Entrances/ Vhod (mm)	Height/ Višina (mm)	Diam. (mm)	Height (mm)	Weight/ Teža (g)	
Mean	105	123.75	61.25	26	55	62.5	30	1	7.89
SD	7.82	11.11	2.17	2.12	6.55	2.5	5	0	3.86
Min.	95	110	60	23	45	60	25	1	4
Max.	120	150	65	28	65	65	35	1	16
N	9	8	4	4	7	4	2	1	9
Min.*	83	95	43	25	85	43			9.6
Max.*	140	217	70	50	155	70			27.9
N*	18	18	18	18	17	18			15
Mean**		115			101				17.1
SD**		13			11				4.0
Min.**									12
Max.**									25.5
N**		33			33				38
Mean***	100	105		30		55-60			

*Kovshar *et al.* 1974
**Price *et al.* 1991 for *P. (i.) humeii*,
***Beick 1937 for *P. (i.) mandeleii*

browed Warblers. The process of cluster formation is slower and its mechanisms are easier to observe.

Territories are aggregated, similarly to other *Phylloscopus* species (Price & Jamdar 1991, Glutz v. Blotzheim & Bauer 1991). The size of the defended territory is smaller than that recorded for *P. trochilus* (2000 – 7000 m² in Lawn 1982, Tiainen 1983) and *P. bonelli* (2000 – 6000 m² in Prenn 1932), but appears to be larger than for *P. trochiloides* (200 – 800 m² Blagosklonow 1991). Fluctuations of territory size in Yellow-browed Warblers appear to be similar to those recorded for *P. sibilatrix*: Mildenberger (1940) talks of "…varies in size during the breeding period…", and Fourage (1968) adds "… with a nesting-territory that has a size of 1200 – 1900 m²…".

In Khonin Nuga, the large number of short-term territorial males with very small (if any "real") territories attracts females, with the result that the central male(s) gets mated. These central males appear to be the first in the area and to establish their territories before the arrival of other males. The number of singing males strongly attracts more males and females. New matings were observed after peaks of territorial male numbers. This appears to be like a lek-system, where a number of males try to attract females (Danchin & Wagner 1997) and compete for them. However, to the observer, it is a somewhat different phenomenon – territorial males are aggregated but distributed over some hectares – the lek is not obvious but hidden ("hidden lek").

Bourski & Forstmeier (2000) set up four hypotheses for clustering in *P. inornatus* and tested the first two in their Siberian study: (1) Birds react to locally superabundant insects. They found no increase in prey abundance inside the cluster and rejected this hypothesis. (2) Birds are attracted by another species' vigilance or nest defence behaviour, as shown by Slagsvold (1980) for *Turdus pilaris* colonies. They also rejected this one. (3) Clustering enhances communal defence against predators through increased vigilance (Rogacheva 1992). (4) Clustering males profit by attracting females more effectively, as supposed for the Wood Warbler by Herremans (1993).

Regarding the third hypothesis, I could never observe communal mobbing behaviour. Defence against potential predators always involved the breeding pair alone. Birds from neighbouring territories were only interested when predators entered their territory. Although birds with central territories (this should be males with the highest status, because females mated only with them) could have the advantage of being warned in advance when predators are invading the area.

The most likely explanation for clustering in this species is the fourth hypothesis, which can be viewed as the hidden lek hypothesis (Wagner 1997). A large number of males attracts females to a certain spot (lek), where they compete for them. Males that are able to get central positions in the lek are of high quality and most likely to reproduce with visiting females.

My analysis shows that habitat quality and choice of nesting habitat are not related to the quality of the male. In view of the scarcity of females and patchy (but sufficient) distribution of preferred habitat, aggregation of territories might be of direct advantage to the males, by improving their chances of mating. The formation of units with a "supersexy" function might constitute an important part of the reproduction strategy, in which the attraction of relatively rare females is the major task. In my study I found that one of these central males attracted two females to his territory (bigyn). Attracting two females to one territory is also known for *P. (i.) humeii* (Price & Jamdar 1991), *P. trochilus* (Lawn 1982, Tiainen 1982) and *P. collybita* (Schönfeld 1978). Furthermore, promiscuity (extra pair copulations) is being discovered in more and more passerine bird species that were formerly assumed to be monogamous (Herremans 1993, Foerster *et al.* 2003, Westneat & Sherman 1997). One fact that supports this idea is that females tended to build their nest close to territory borders, in the vicinity of extra pair males.

Males that claim territories far away from other, high quality males, may be less able to attract a mate, forcing them to readjust their territorial claims and breed near other males, and might copulate with their mates. Additionally, even males that risk losing paternity (unmated males) might cluster to attempt extra pair copulations with receptive females (see hidden lek hypothesis by Wagner 1997).

However, this explanation requires reasons why pairs do not leave the lek after mating. It might be the very productive habitat (which provide sufficient food for all birds), but only for a short time of the year (which leads to a form of time pressure on the birds). It is also important to discuss why birds leave the area in the afternoon, especially early in the breeding season. This might be caused by limited food resources at this time of the year (see similar diurnal altitudinal migrations for *P. (i.) humeii* in Price & Jamdar 1991).

Additionally, males might be expected to retaliate against unfaithful mates by withholding parental care or by evicting the female from the territory. Wagner (1997) considers that the male biased sex ratio, which I also observed in Yellow-browed Warblers, may give females leverage over their mates. It would force solitary males to nest near more preferred males to find mates, resulting in the observed pattern of clumping.

I have no obvious explanation for the rather variable location of territory clusters in different years (A. Barkow *unpublished data*, Forstmeier *pers. comm.*, Wichmann 2001), but the hidden lek hypothesis predicts variable clumped distributions in a habitat that is below saturation (for more information see Wagner 1997).

Leks are established more randomly, simply by meetings of males in a fitting habitat, which start to sing and attract more males. Other possible explanations are different predation pressure or avoidance of other *Phylloscopus* species (as in Bourski & Forstmeier (2000) and Forstmeier *et al.* (2001). The only other *Phylloscopus* species in my study area – *P. borealis* and *P. fuscatus* occurred in very low densities and I would reject this explanation in this case.

Some bird species form genetically related groups of individuals that cooperate to their mutual evolutionary advantage (Sherman 1999). This cannot be excluded in Yellow-browed Warblers without genetic analysis.

Future studies should focus more on the genetic relationship, age and paternity of the individuals that form the clusters. Yellow-browed Warblers could be one of the best examples of the hidden lek hypothesis (Wagner 1997).

6. Povzetek

Gnezditvena biologija mušje listnice *Phylloscopus inornatus* je v glavnem slabo poznana. V zadnjem času so raziskovalci prišli do spoznanja, da gnezdi v skupkih (rastiščih, lekih) in pojavilo se je kar nekaj hipotez, ki skušajo pojasniti takšen način gnezditve. Dva takšna skupka je opazoval avtor od maja do julija leta 2003 v rezervatu Khan Khentey, v severni Mongoliji, z namenom dodatno raziskati takšen način gnezditve.

Pri delu je uporabljal lovljenje z mrežami, iskanje gnezd, opazovanje obnašanja in habitatno analizo. V tem rezervatu so gnezditveni skupki relativno majhni glede na gnezdišča v Sibiriji in obsegajo le največ 3 pare. Tukaj, na jugu gnezditvenega areala, je vrsta izpostavljena velikim pritiskom predacije, obenem pa je razmerje med spoloma neenako (ca. 5:1 samci proti samicam). štirje gnezdeči pari so tako imeli najmanj deset gnezd, ki so bila vsa oplenjena, še preden so se zvalili mladički. Gnezda gradijo samo samice in ena od samic je kar trikrat znova zgradila gnezdo po predaciji. V skupkih pojočih samcev se bila velika številčna nihanja, včasih so vsebovali več kot dvajset osebkov. Gnezdeči pari so se formirali po števičnih viških pojočih samcev. Ker so skupki na tem področju majhni, nudijo veliko možnosti za raziskavo mehanizmov formacije skupkov. Lokacije gnezditvenih območij so bile neodvisne od habitanih parametrov, bila pa so na sredi med neuspešno vzpostavljenimi teritoriji. Ta primer je močen dokaz za hipotezo skritih lekov, kot glavno razlago za tvorbo skupkov; ta hipoteza pa predvideva, da so samci na sredi skupkov spolno najbolj privlačni za samice. Mušja listnica bi lahko bila eden od redkih primerov za točnost te hipoteze. Predstavljeni so tudi podatki o biometriji, gnezditveni biologiji in obnašanju te vrste.

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