The Evolution of Breeding Systems and the Impact of Sexual Conflict and Cooperation in Penduline Tits
(GEBACO WP11)

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Members of the expedition team Penduline Tits in Kazakhstan:

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OBJECTIVES

1. To describe the breeding system of a. White-crowned penduline tits *Remiz coronatus*, and b. Black-headed penduline tits *Remiz macronyx*
2. To investigate to what extent habitat can predict levels of cooperation and conflict in penduline tits.
3. To investigate the impact of conflict and cooperation on the evolution of morphological traits.
4. To investigate the impact of conflict and cooperation on the evolution of behavioural traits.
5. To reconstruct a phylogenetic tree of penduline tits (blood sampling, aimed sample size: 40)

HYPOTHESES & PREDICTIONS

H1. The abundance of food and nest material influences the level of cooperation in breeding.

P1. Black-headed penduline tits, which occur in allegedly food rich reed beds, exhibit higher levels of conflict, including uniparental care and polygamy, than White-crowned penduline tits, which live in the relatively poor foothills of the Tien Shan mountains (biparental care and monogamy).

H2. The level cooperation influences morphology and song via an ongoing process of manipulation and resistance associated with sexual conflict.

P2. The species exhibiting more intense sexual conflict will show a more intense sexual plumage dimorphism and the male will have a more complex song than the species with lower levels of conflict.

H3. The level cooperation in breeding system is reflected in parental behaviour.

P3. The species exhibiting more intense sexual conflict will i. attend the nest less frequently, and ii. attend the nest less synchronously.

Central Asia may be the cradle of the subfamily *Remizinae*. Our phylogenetic tree may reveal this. The ancestral breeding system of the polygamous Eurasian penduline tits *Remiz pendulinus pendulinus*, with habitat characteristics and various morphological traits superimposed on the phylogeny may provide important insight into the evolution of the diverse breeding systems within the relatively confined group of penduline tits.

METHODS

(A)

(B)

Fig. 1. (A) The foothills of the Tien Shan mountain range at Jabagly. The arrow indicates one of the valleys in which the White-crowned penduline tits build their nests, mainly on hawthorn trees (*Crataegus sp.*). Four of these valleys, average distance between them about 2.7km, were included in our research. (B) A typical habitat of Black-headed penduline tits, reed beds along the Topar Lakes, near Topar.

We visited two field sites in Kazakhstan: for the White-crowned penduline tits the foothills of the Tien Shan mountains near Jabagly (42°25'N, 70°29'E) (10 May – 10 June), for Black-headed penduline tits the Topar Lakes, near Topar (45°02'N, 75°01'E) (12 – 26 June) (see fig. 1).

Default protocol field methods for penduline tit research, including monitoring of incubation behaviour, were used (see van Dijk *et al.*, unpublished). Additionally, nest attendance was filmed during the period of egg-laying using the Sony DCR-HC44E digital camcorder, over full daylight periods at a resolution of one frame per 5 seconds (see also van Dijk *et al.*, manuscript for further details on field methodology). Due to the inaccessibility of most nests of the White-crowned penduline tits at Jabagly, the exact phase of egg-laying was not known, but nests were filmed from a stage E of nest building onwards (see van Dijk *et al.*, unpublished), which, at least in Eurasian penduline tits, is when egg-laying takes place. One nest of a Black-headed penduline tit pair (*R. m. ssaposhnikowi*) was monitored for nest attendance at exactly the correct period, at two and three eggs.

Penduline tits are not resident in Kazakhstan, but migrate southwards during winter.

RESULTS

White-crowned penduline tit

(In this report White-crowned penduline tit is the subspecies *R. c. coronatus*)

Habitat

The habitat of the White-crowned penduline tit near Jabagly consisted of, mainly, hawthorn (*Crataegus sp.*) trees with a few willows (*Salix sp.*) and poplars (*Populus sp*.) aligning small streams coming down from the Tien Shan mountains through the foothills (Appendix 1A). The penduline tits build their nests in these trees, and use various, yet typical, materials for their nests - material which appears to be scarcely available. The limited amount of vegetation (beyond the aforementioned trees and some shrubbery, there is not much more than open grassland) results in that food resources are rather poor. Although this requires some measure of quantification (*e.g.* NDVI LandSat images), it seemed to us very much less available than in, for example, our field site in Hungary Fehértó.

The habitat of the White-crowned penduline tits at Topar was rather different, yet with regards to the amount of food and nest material comparable to Jabagly. At Topar their habitat was a small side river of the river Topar, running through the sand dunes. Along this river some reed (*Phragmites australis*) and bulrush (*Typha sp.*). The nests were built in Russian olives (*Eleagnus angustifolius*). Immediately beyond these narrow reed beds semi-desert. The high density of nests of White-crowned penduline tits here was remarkable (see Appendix 1B).

Biometrics and song

(A) (B)

Fig. 2. Male (A) and female (B) White-crowned penduline tit *Remiz coronatus*.

White-crowned penduline tits have a sexually dimorphic plumage, the extent to which has yet to be analysed: Males generally have a wider mask than females which may extend onto the nape, sometimes only leaving a white crown. Males are also more brightly coloured with darker mantle and wing coverts, and whiter crown than females (Fig. 2A). Females may have black on the nape too (Fig. 2B). A characteristics feature of the White-crowned penduline tits plumage compared to Eurasian and Black-headed penduline tit is the complete lack of red-brown feathers on the head and breast.

White-crowned penduline tits are smaller and lighter than Eurasian penduline tits (mean ± SD: 7.36 ± 0.48g versus 9.62 ± 0.87g). Females (7.72 ± 0.52g) seem slightly heavier than males (7.14 ± 0.27g), as usual.

Song seems very similar to Eurasian penduline tits: different syllables are used, but complexity appears not to differ very much from the Eurasian penduline tits. This, however, clearly requires detailed analyses. We were clearly more successful in mistnetting the birds using a playback of White-crowned penduline tit song than with a playback of the song of Eurasian penduline tits.

Parental care

Nests are built by male and female together from stage A onwards, although an unmated male will start on its own. Sometimes the pair seems to work closely together, mostly in earlier stages of nest building, but in general they appear to work pretty much 'independently' of one another (in contrast to the cooperative Cape penduline tits *Anthoscopus minutus*) (Fig. 3).

Of the **18** nests where we observed parental care, **incubation** was **always** carried out by **male and female. However**, at **4** nests the young were **fed** by **only one parent, 2 male-only and 2 female-only**. Additionally, Yevgeni Belousov had observed a feeding female-only in the same season in Aksu-Jabagly National Park.

Clutch size was determined at 4 nests: **6.75** ± 2.63 eggs.
Number of **nestlings** was determined at 6 nests (at various ages): **5.83** ± 2.32 nestlings.

Mate switching has not been observed.
At **3** nests the **clutch** was **abandoned** during incubation.
Predation took place at **1** nest (possibly at 2 nests).

Fig. 3. Male White-crowned penduline tit at its nest.

Summary of collected data

Nests:	**32** (25 at Jabagly, 7 at Topar)
Trapped males:	**22** (19 at Jabagly, 3 at Topar)
Trapped females:	**14** (13 at Jabagly, 1 at Topar)
Sampled nestlings:	31 (all at Jabagly)

All individuals trapped (N = **67**) have been sampled for blood (two of which may not contain enough blood for analysis).
All trapped adults have been photographed for mask size and saturation of back.

Process video:	**7** pairs (all at Jabagly; 5 of which for one day only)
Song recording:	**12** males (all at Jabagly)
Incubation video:	**10** nests (9 at Jabagly, 1 at Topar)

Black-headed penduline tit

(In this report the subspecies *R. m. macronyx* and *R. m. ssaposhnikowi* and any hybrids are lumped under this name, unless otherwise stated)

Habitat

The habitat where we have been searching for Black-headed penduline tits consisted of semi-desert interspersed with small lakes and marshes. The relatively small lakes in these sand dunes apparently contained too little vegetation for penduline tits. It also seemed rather dry containing very little food. Black-headed penduline tits were to be found in more extensive reed beds close to the river Topar (at many places inaccessible) (Fig. 1B). The *ssaposhnikowi* subspecies built its nest in a tree (a Russian olive), although black-headed penduline tits may build their nests in reeds and are thus likely less dependent on trees than, for instance, White-crowned penduline tits. Food resources in these reed beds were plentiful. Nest material too was much more abundant then at Jabagly mainly due to the abundance of reed and bulrush.

Biometrics and song

Black-headed penduline tits have a clearly sexually dimorphic plumage, the extent to which has yet to be analysed:

ssaposhnikowi: Males have a black mask, a chestnut brown crown and nape, and a whitish throat (very much like *Remiz pendulinus caspius*). A deeply coloured dark red-brown mantle and wing coverts, and a lot of red colouration on the breast (Fig. 4A). Females are very much like Eurasian penduline tit males, yet with typical female characteristics: They have a wide mask, but squared rather than conically shaped and interspersed with some grey feathers, in particular at the base of the bill. A grey ring around the eye. A clear red fringe on the head above forehead patch extending to both sides of the crown. Lots of red feathers on the breast. The back is paler than the males (Fig. 4B).

macronyx: Males have a completely black head, a very dark reddish breast and red-brown mantle (Fig. 4C). Females have not been observed in our field (but see Fig. 4D).

Black-headed penduline tits appear to be of similar size and weight as Eurasian penduline tits (mean ± SD: 10.75 ± 0.64g versus 9.62 ± 0.87g). Females (11.20g) seem slightly heavier than males (10.30g), as usual.

Song (and call) is clearly different from Eurasian penduline tits: different syllables are used, at a slightly different frequency, but complexity may not be very different. This, obviously, requires detailed analyses.

(A) 

 (B)

(C) 

 (D)

Fig. 4. (A) Male *R. m. ssaposhnikowi*. (B) Female *R. m. ssaposhnikowi*. (C) Male Black-headed penduline tit, possibly a hybrid *ssaposhnikowi* x *macronyx* since the amount of red-brown on the head and white on the throat patch is markedly less than in a typical *ssaposhnikowi* male (see (A)). (D) Male (top) and female (bottom) Black-headed penduline tit *R. m. neglectus* from Turkmenistan (courtesy photo Y.M. Belousov).

Parental care

The two A-stage nests that we found were built by single males. The other nest, found in stage D, was attended by the pair when we found it. Again, the pair seems to work pretty much independently from each other and cannot be observed at the nest together very often.

At the one nest where we have been able to observe incubation, this was **female-only care**. The male deserted when there were three eggs in the nest: VERY similar to Eurasian penduline tit *Remiz pendulinus pendulinus*. (The eggs were initially covered, and uncovered on the day the male had deserted (Valera *et al.*, 1997)).

Additionally, Black-headed penduline tits in Turkmenistan (*Remiz macronyx neglectus*) appear to exhibit female-only care too. The male has never been observed to take up parental care, nor seems biparental desertion to make up part of the breeding system (Y.M. Belousov, *pers. comm.*). The male in this species is described to desert at 2 eggs (Belousov, 1979).

Clutch size was determined at 1 nest: **6 eggs**
We have not been able to determine the number of nestlings of Black-headed penduline tits.

Summary of collected data

Nests:	**3** (two of which in stage A after which they were abandoned)
Trapped males:	**1** (possibly hybrid *macronyx* X *ssaposhnikowi*)
Trapped females:	**1** (subspecies *ssaposhnikowi*)
Sampled nestlings:	0

All individuals trapped (N = **2**) have been sampled for blood.
All trapped adults have been photographed for mask size and saturation of back.

Process video:	**1** pair (*ssaposhnikowi* pair)
Song recording:	**1** male
Incubation video:	0 nests

In total we have seen:
4 *R. macronyx macronyx* males
4 *R. m. ssaposhnikowi* males
2 *R. m. ssaposhnikowi* females
3 *R. pendulinus*-like females, which likely have been of subspecies *ssaposhnikowi.*

The population of penduline tits at the Topar Lakes thus consists of at least three different (sub)species, including the White-crowned penduline tits *R. c. coronatus*.

CONCLUSIONS

1. Although we have limited data on the Black-headed penduline tits, we can fairly confidentially describe the breeding system of both species: The White-crowned penduline tits exhibits biparental care (NB feeding may be uniparental in some cases), whereas the Black-headed penduline tit seems to exhibit uniparental care (in accordance with observations from Turkmenistan (Y.M. Belousov, *pers. comm.*)), *i.e.* two radically different breeding systems within Kazakhstan. Detailed description (as to the exact share in incubation between male and female, for example) will follow from analyses of videos.
2. Importantly, the predicted relation between breeding habitat and breeding system IS supported: rich habitats were associated to less cooperation and a thus more polygamous breeding system; poor habitats were associated to cooperation resulting in biparental care.
3, 4. From observations in the field we note that both species exhibit sexual dimorphism, although much stronger in the polygamous Black-headed penduline tit. How the plumage dimorphism, song complexity, and behaviour fit the predictions in relation to conflict and cooperation remains to be analysed. We have collected a substantial amount of data to further investigate this.
5. We have collected a sufficient amount of blood samples to be able to reconstruct a phylogenetic tree of penduline tits. DNA samples collected from other populations/species will be included (*i.e. Remiz consobrinus consobrinus, Remiz coronatus stoliczkae, Remiz pendulinus pendulinus, and Anthoscopus minutus*). Ideally, also DNA from Verdin *Auriparus flaviceps* and possibly the Fire-capped tit *Cephalopyrus flammiceps* and Tit-hylia *Pholidornis rushiae* will be included. DNA of the Verdin has been requested from prof Robert Zink, University of Minnesota. Alternatively, Clemens Kuepper, University of Bath, may be able to get DNA from subspecies *A. f. sinaloae*. A number of sequences for *Auriparus flaviceps* are

available from GenBank (COI, cytb, RAG1, and mtDNA). The Fire-capped tit and Tit-hylia seem rather elusive. Hopefully some museum specimens, for instance, may be a solution.

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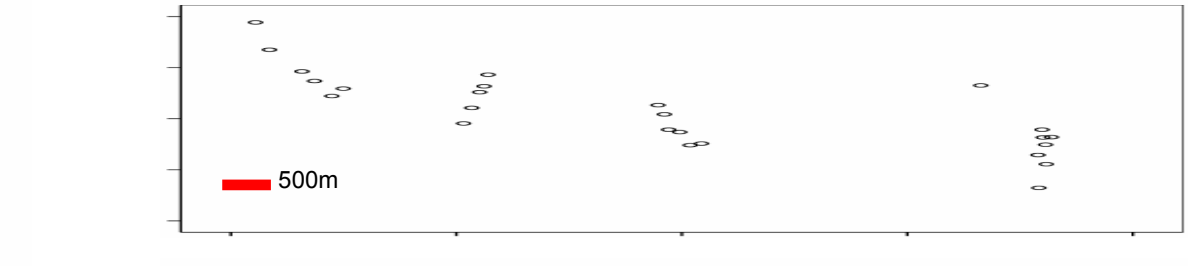
Jabagly

APPENDIX 1

(A)



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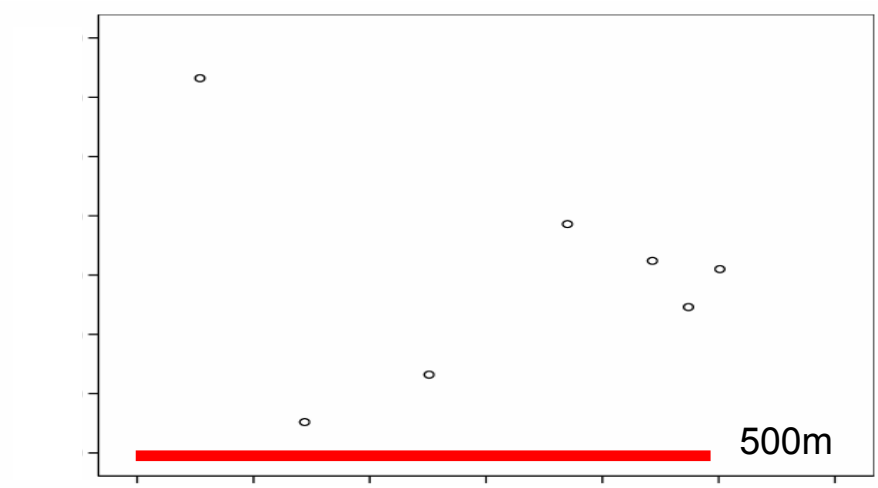
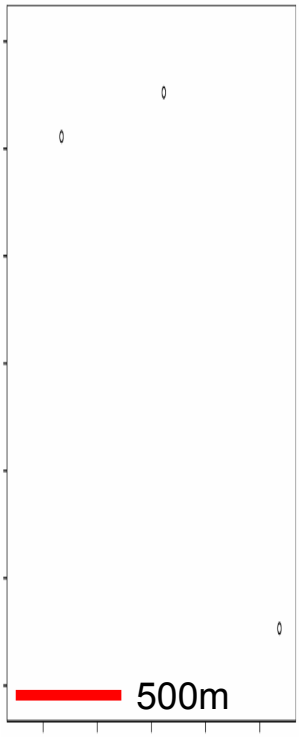
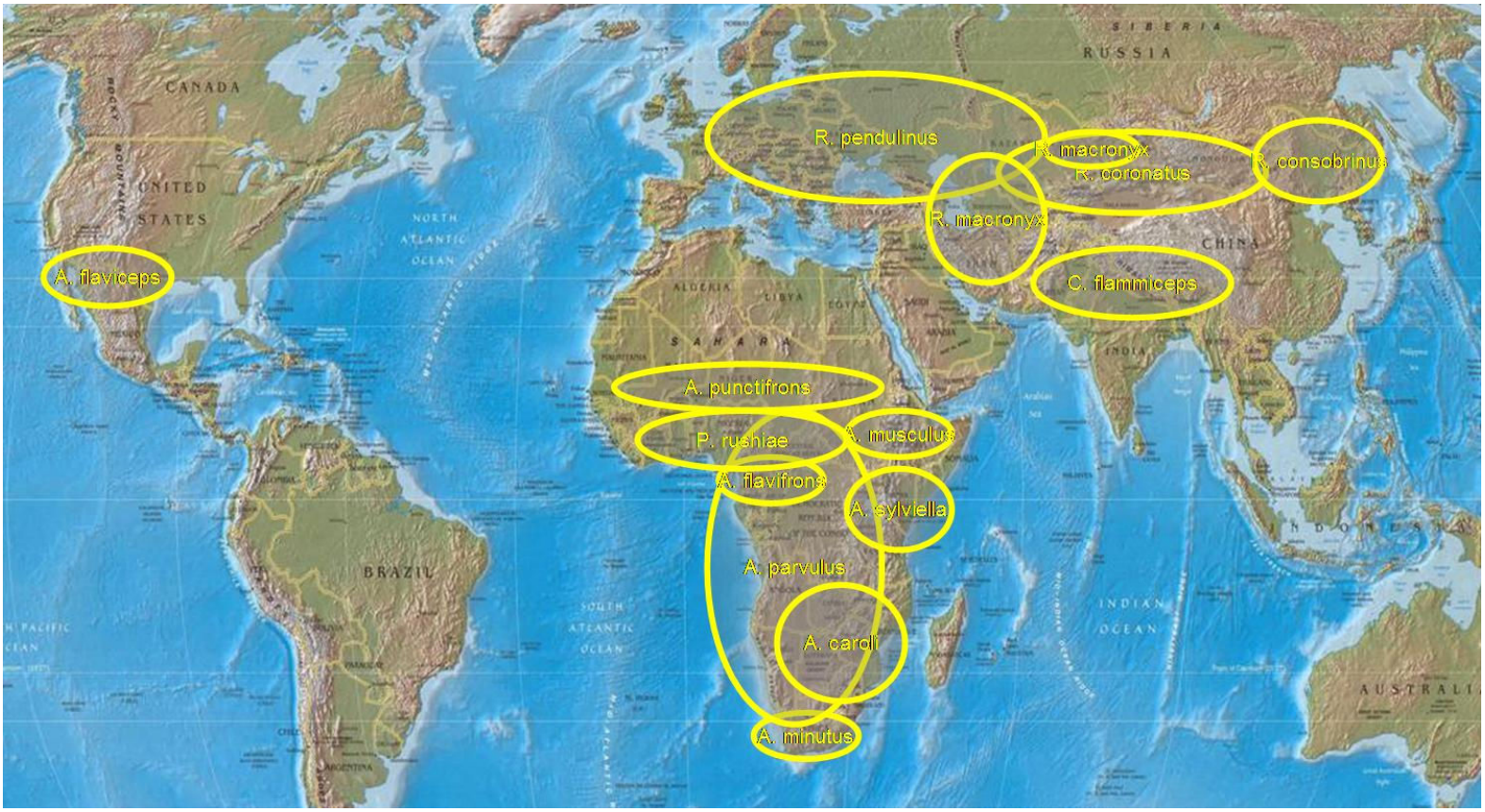


(C)



Maps indicating distribution and density of nests of (A) White-crowned penduline tit at Jabagly, (B) White-crowned penduline tit at Topar lakes, and (C) Black-headed penduline tit at Topar Lakes.

APPENDIX 2



Distribution of all 14 penduline tit species of the world (NB *Anthoscopus sylviella* is not mentioned in Harrap & Quinn 1996; *Remiz macronyx* is not given the species status by Sibley & Monroe 1993). Noteworthy are *Auriparus flaviceps, Cephalopyrus flammiceps,* and *Pholidornis rushiae* given their 'odd' distribution and slightly different (nest building) behaviour.