Breeding systems in penduline tits: 
Sexual selection, sexual conflict and 
parental cooperation

Outline of PhD thesis

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I  INTRODUCTION

Sexual reproduction has long been considered a mutually cooperative behaviour between a male and a female to produce offspring. The roles of the sexes, however, differ from the very beginning of reproduction (gamete production), and this often leads to different evolutionary interests of males and females over various aspects of reproduction (sexual conflict, Parker, 1979).

Males and females are both under sexual selection to increase their reproductive success (Darwin, 1871; Andersson, 1994). Sexual selection is a complex process, because selection on a certain trait does not necessarily have to positively affect the reproductive success in both sexes. Sexual selection, therefore, may involve two processes: by classical sexual selection those traits evolve which result in increasing reproductive success of males and females, whereas in the process of sexual conflict the traits under selection often have antagonistic effects on male and female reproductive success (Arnqvist and Rowe, 2005).

Separating these two processes proved to be difficult, indeed, they are not mutually exclusive (see Cordero and Eberhard, 2003; Arnqvist and Rowe 2005), as both of these processes may produce consistent results. A possible way to separate them is to focus on the selection forces resulting in female preference (Chapman et al., 2003).

On the one hand, numerous theoretical and empirical studies investigated and found evidence for classical sexual selection acting *via* male contests and female choice. On the other hand, we know much less about the process of sexual conflict and only recently started to understand its importance in the evolution of morphological and behavioural traits, and its role in speciation and breeding system evolution (Arnqvist and Rowe, 2002; Chapman et al., 2003; Arnqvist et al., 2000; van Dijk and Székely, 2008).
Sexual conflict may arise in different stages of reproduction, for instance over the number of mates (or matings), or over the amount of provided care for the offspring (pre- and post-zygotic sexual conflict, separately, Royle et al., 2002). Accumulating evidence suggests that environmental constraints, sexual selection (including sexual conflict and classical sexual selection), and breeding system evolution are in a complex, multi-way interaction.

II  THESIS OBJECTIVES AND METHODS

In this PhD thesis I investigated two processes of sexual selection, and their effects on morphology, behaviour and breeding system evolution. I used a combination of field and laboratory experiments to test predictions of sexual selection and sexual conflict theories in penduline tits (Remizinae). The avairy experiments were carried out in Göd Biological Station of Eötvös University (22 km from Budapest), whereas fieldwork was carried out in South Hungary (Eurasian penduline tit) and South Africa (Cape penduline tit).

Penduline tits are small passerine birds with extremely variable breeding systems and habitats, and this makes the subfamily an ideal group to investigate the interactions between breeding environment, sexual selection and reproductive system. I chose two species with contrasting breeding strategies: the Eurasian penduline tit Remiz pendulinus with intense sexual conflict, uniparental care and biparental desertion (Szentirmai et al., 2007; Persson and Öhrström, 1989), and the Cape penduline tit Anthoscopus minutus with extensive cooperation, biparental care and facultative cooperative breeding (Dean, 2005).
1. The evolution of sexual signals via classical sexual selection and sexual conflict

The first part of my thesis has two aims. First, in aviary and field experiments I investigated which male traits are involved in sexual selection in Eurasian penduline tits. Based on previous field studies, I tested female preference for male mask size and nest size, and whether male mask size signals in male contests. Besides, in a field experiment I tested the role of repertoire size in signalling male contesting abilities.

Second, in a field investigation I tested whether the cost of desertion is related to male mask size for females thus classical sexual selection or sexual conflict is more likely shaping the evolution of male mask size in Eurasian penduline tits.

2. Sex differences and post-zygotic sexual conflict in Eurasian penduline tits

Studies of different Eurasian penduline tit populations across Europe exhibit similar within-population variance in parental care so that uniparental care is more frequently provided by females than by males (Franz, 1991; Persson and Öhrström, 1989; Szentirmai, 2005). My aim was to investigate potential reasons leading to the observed care patterns. First, by field observations of incubating and brood-feeding male and female parents and comparing the survival of their broods I tested whether female Eurasian penduline tits are better parents thus selected for providing more frequently care than males (parental quality hypothesis, Erckmann, 1983). Second, I tested the flexibility of parental care decisions between subsequent nests of males and females to investigate how within-population variance in parental care builds up in Eurasian penduline tits.
3. Implications of sexual conflict and cooperation on male-female coevolution

Eurasian and Cape penduline tits are close relatives that appear to represent the two endpoints of the sexual conflict – cooperation axis. By directly comparing their morphology, behaviour and breeding systems using the same methodology in Hungary and South Africa, respectively, in the last part of my thesis I investigated the evolutionary footprints of sexual conflict and cooperation.

III RESULTS AND CONCLUSIONS

I investigated three male traits, and showed experimentally that two of them are involved in sexual selection in Eurasian penduline tits. In line with a field study (Kingma et al., 2008), my results from an aviary choice test showed that male mask size is preferred by female Eurasian penduline tits. The dominance test on the same trait, however, suggested that mask size has no dual function (cf. Berglund et al., 1996) as it is not involved in male contests. Field observations revealed that from the female’s side, mating with males having large mask is a costly behaviour, since males with large mask more frequently deserted their nest than males with small mask. Male mask size therefore appears to evolve via sexual conflict in Eurasian penduline tits.

Contrasting to previous field observations (Hoi et al., 1994; Grubbauer and Hoi, 1996), I found no female preference for nest size. I discuss various plausible explanations to this discrepancy, including context-dependent female preference.

The field experiment investigating the role of male song revealed that song is involved in the intra-sexual signalling of male Eurasian penduline tits, because resident males advertise honestly their competitive ability with their repertoire size.
Comparison of male-female parental behaviour and offspring survival of male-cared and female-cared broods suggest that there is no sexual difference in parental abilities in Eurasian penduline tits. The reason for the observed female-biased parental care therefore remains unresolved. To advance this issue I suggest possible directions for future studies including the comparison of the relative costs and benefits of offspring desertion in males and females (Andersson and Iwasa, 1996).

Male and female Eurasian penduline tits differ in their flexibility in regard to desertion behaviour. Male desertion was influenced by environmental changes because males deserted the brood early in the breeding season, and tended to care late in the season, whereas female desertion was consistent between subsequent nests by some females caring and some deserting. Therefore, within-population variance in parental care builds up differently for males and females. Mechanistic (e.g. differences in neuroendocrin system) as well as possible evolutionary processes maintaining the coexistence of different strategies are discussed.

I found consistent results with predictions of the sexual conflict theory by comparing the morphology, behaviour and breeding system of Eurasian and Cape penduline tits. Eurasian penduline tits exhibited strong sexual dimorphism in morphology, and its song was more complex than that of the Cape penduline tit. In nest attendance, Cape penduline tits were more cooperative. Future studies are needed to investigate the validity of these results beyond these two species.

In conclusion, my results strongly suggest that sexual conflict is a powerful evolutionary force that acts parallel and in interaction with the classical model of sexual selection in the evolution of secondary sexual signals, behaviour and breeding systems.
IV REFERENCES


V PUBLICATIONS

Published papers included in the thesis


Manuscripts in revision and to be submitted

Pogány Á, Menyhárt O, DeVoogd TJ, Székely T. Acoustic signalling in Eurasian penduline tits Remiz pendulinus: The effects of intruder song on behaviour of resident males and females. Manuscript (Chapter V)


Conference presentations related to the thesis


do not explain female-biased care. 12th International Behavioral Ecology Congress, Ithaca, USA.


