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## Evolutionary ecology of the variable breeding system of Chinese penduline tits

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# Chapter 8

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General discussion

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Jia Zheng



## Encountering an amazing avian system

A unique system with the potential to explore the evolution of parental care and mating system was revealed by Persson and Öhrström (1989), who found that in the Eurasian penduline tit (*Remiz pendulinus*), a tug-of-war over parental care occurred, in that either males and females would desert their clutch during the egg-laying stage. Unlike most other passerines where a male and a female form a breeding pair and both partners cooperatively raise the offspring (Cookburn 2006, Remeš et al. 2015, Long et al. 2022), biparental care was never observed within and across populations of this penduline tit species (Pogány et al. 2008). Female-only care and male-only care are the two parental care patterns that exist, and stunningly, 30-40% of clutches failed as a consequence of biparental desertion in Eurasian penduline tits. My studies on a sister species, the Chinese penduline tit (*Remiz consobrinus*), revealed a more complex parental care system. Not only do female-only care and male-only care, and biparental desertion, but also biparental care coexist (chapter 2). Moreover, the two studied populations also exhibit different parental care systems. In one population female-only care prevailed, whereas in another population mainly biparental care was observed (chapter 5).

Penduline tits provide a unique system for exploring two crucial questions: what factors contribute to the diversification of the parental care system between populations of the same species and between species? And why do the variations in parental care evolve less often in other species and genera? To answer these questions, I focus on the Chinese penduline tit system. First, I carried out observational studies to gain a thorough knowledge of the breeding biology and breeding system of the species. This biological information will then give clues and indications for further understanding of the causes of the variations in parental care. Second, the observed different parental care behaviours could imply inconsistent resolutions of sexual conflict either between different care type nests and/or between closely related species. Field experiments are, therefore, important to manipulate brood conditions or parental efforts to reveal the drivers of the different parental care behaviours observed. Finally, theoretical studies can help to better understand how certain ecological factors could mechanistically affect parental care, and why different parenting systems show up in two populations of one species.

In **part I**, I will discuss my research findings from the observational studies on the breeding biology of the Chinese penduline tit and its varied parental care system within and between populations. I explain several potential drivers that may shape the variable parental care system. In **part II**, I will discuss the research findings of the two field experiments: the egg burial experiments reveal a novel function of egg burial behaviour. Differences in breeding between Eurasian and Chinese penduline tits will be compared to illustrate their different evolutionary trajectories of parental care. The parental removal experiment investigates parental care capabilities between parents of uni- and biparental

care nests. I will stress the necessity of not only focusing on feeding frequency while exploring the efficiency of parental care compensation, but also exploring other parental care behaviours. In **part III**, I will discuss the outcomes of my theoretical study: the effects of season length and parental care efficiency on parental care. I propose several manners of how season length could crucially influence parental care in a changing world. In **part IV**, I will raise several projects which may potentially fill some research gaps in researching the evolution of parental care.

## **Part I: Lessons from observational studies**

### **Flexibility of parental care and its potential drivers**

The comparative studies (chapters 2 and 5) have revealed a unique and flexible parental care system in Chinese penduline tits. First, uniparental care, biparental care and biparental desertion coexist in a population. Second, uniparental care is prevalent in the Liaohekou population, whereas biparental care mainly exists in the Xianghai population. Flexible parental care systems were also found in several other species. In plovers (*Charadrius spp.*), biparental care and uniparental care respectively prevail in different populations that have different climate conditions (Vincze et al. 2013), or experience unequal adult sex ratios (Eberhart-Phillips et al. 2018). In rock sparrows (*Petronia petronia*) uniparental care occurs in the Italian and Spanish valleys (Pilastro et al. 2001) but never at high altitude Tibetan plateau (Li et al. 2012), and the proportion of uniparental care nests also varied over years in the Spanish population (Mingozzi et al. 2022). Generally, there are two ways of revealing the drivers of divergent parental care systems in a species. First, collect breeding ecology information across multiple populations and long-term breeding data over years to explore the associations between parental care patterns and ecological and social factors (Eberhart-Phillips et al. 2018; Kubelka et al. 2018). Second, carry out field experiments to manipulate the potential factors that may be related to the divergent parental care (e.g. food addition to the environment to detect the relation between a better resource condition and parental care) .

My study revealed an in-depth knowledge of the breeding biology of Chinese penduline tits, but could not draw a substantial conclusion on what factors influence the divergence of parental care between populations. However, I found several drivers that may shape the parental care system. First, male competition and mating opportunity. in Chapter 5, I found in the Xianghai population, where males suffer from a lower pairing success and spend more time on mate acquisition, had a higher proportion of biparental care than the Liaohekou population. The difficulties for males to pair up with a female reflect a high intensity of competition and a low mating opportunity in that population. Second, the efficiency of uniparental care. I found in Chapter 5 that in the biparental dominated

population, the fledging success of uniparental care nests is lower than in the uniparental dominated population, whereas biparental care nests were not different. The high fitness cost of desertion plus the low re-mating opportunity may jointly impede desertion from being prevalent in the biparental dominated population. These results highlight that parental decision is a flexible behaviour that depends on parents' estimation of the current costs and future benefits from desertion.

The reason that we can only observe offspring desertion in a few avian systems may be that in most bird species, the fitness costs from desertion are much higher than the benefits from remating (Royal et al 2012). This may be triggered by biological traits. For example, the large clutch size in blue tits (*Parus caeruleus*) may prevent parents from ceasing parental care due to the high fitness cost of desertion (Andreasson et al. 2018); Stickleback (Gasterosteidae) broods need abundant oxygen to develop. Male sticklebacks, the caring parent, that are not able to remove embryos to an algae abundant environment have to stay to provide oxygen to the brood by the fanning behaviour (Blouw 1996). In raptors, low food abundance maintains biparental care because higher foraging efforts are demanded in order to feed the offspring adequately (Eldegard and Sonerud 2009; Wieringa et al. 2019). However, in the penduline tits system, in an environment where the parents can alone raise a brood successfully, parents get an opportunity to gain additional reproductive fitness by deserting.

### Seasonal pattern of parental care

Bird species such as Kentish plover (Székely et al. 2000), rock sparrow (Pilastro 2001), and barn owl (*Tyto alba*, Roulin 2002) exhibit various parental care patterns throughout the season in one population. Although nests with different care types were found to show up at different times in a season, the reason for this seasonal pattern lacks investigation. My study also found a seasonal pattern of parental care in Chinese penduline tits where female-only care nests showed up early and biparental care nests showed up late in the season (Chapter 3). Further, I found that the seasonally parental care was associated with a sexually different response to their opportunity of remating: males deserted when there were large numbers of single females in the early season, whereas females did not seem to make care decisions in response to the varied number of single males over the season and they consistently provided care. These sexually divergent reactions to mating opportunities indicate that when confronted with the trade-offs between current and future reproduction, male and female parents make decisions depending on different conditions. Sexually different reactions in breeding behaviours have also been found in other birds. Male but not female European rollers (*Coracias garrulus*) increased the nest visiting rates to protect the nests from predation when a predator was placed beside nests (Expósito-Granados et al. 2016). In barn swallows (*Hirundo rustica*), the effect of spring phenology on the timing of breeding and seasonal fecundity were observed among females

but not among males (Saino et al. 2017). Different sex roles in breeding may lead to the different sensitivities between males and females to environmental cues. Fecundity selection, like the precision of the timing of egg laying, causes more fitness consequences to females; while sexual selection, such as territory establishment and courtship, brings more serious consequences to male fitness (Ball and Ketterson 2007).

Here, I propose two other reasons for sex-dependent parental care decisions in Chinese penduline tits: (1) The mortality rate of the two sexes may differ during migration and wintering. The prevalence of female-only care in Chinese penduline tits may indicate that females suffer from a higher annual mortality rate than males such that they put all the stakes on reproduction in the current breeding season (from the data we collected from 2019-2021, the adult returning rate is about 1 female: 5 males, Zheng unpublished data). (2) It usually takes half a month for penduline tits to completely build an elaborate nest. Nest initiation forces male penduline tits to spend more time on nest building than females before they get paired up. The limited length of the breeding season, therefore, brings higher time pressures to males in terms of initiating additional broods. Contrastingly, after a breeding round, females can immediately join a single male who has built a nest halfway to produce a second brood. In this way, male deserting and female caring could have been selected as the most efficient strategy over the evolutionary time.

## **Part II. Lessons from experimental studies in the field**

### **Sexually antagonistic coevolution in penduline tits**

Eurasian penduline tits are considered one of the textbook species for the occurrence of intensive sexual conflict over parental care (Persson and Öhrström 1989; Szentirmai et al. 2007). Rigorous competition for the initiation of desertion within pairs underlies their unique breeding system. The high proportion (30-40%) of biparental desertion generated from sexual conflict leads to complete clutch failure. To gain the upper hand in the sexual conflict, during the egg-laying stage, female Eurasian penduline tits bury the eggs under a layer of material to stop males from deserting the nest earlier than themselves (Valera et al. 1997). In Chinese penduline tits, I also reported egg burial behaviour, however, it does not serve to resolve sexual conflict, but fulfils a different and a novel function which has never been revealed in any animals. Chinese penduline tits do not bury eggs to resolve the sexual conflict since males and females bury eggs together, and they both stay in the nests overnight. Instead, our ‘egg protection against wind’ experiment showed that egg burial behaviour could efficiently prevent eggs from rolling out of the wind-swayed nests. A phylogenetic study revealed that Chinese penduline tits are the ancestor species of this genus (Barani-Beiranvand et al. 2017). I propose that since penduline tits live in windy habitats, egg burial may firstly have evolved to impede eggs from rolling out of

the wind-swayed nests, after which it has been used as a resolution of the escalated sexual conflict in the later diverged Eurasian penduline tits.

My study highlights that the same behaviour could flexibly evolve with a subtle difference between species to fulfill different functions, in this case, either only females bury eggs or both sexes bury eggs. Although the Eurasian and Chinese penduline tits share similar breeding traits, their complex parental care systems indicate they may have evolved different resolutions of sexual conflict over parental care. Chinese penduline tits desert the clutch at the onset of incubation instead of during the egg-laying stage like Eurasian penduline tits. This different deserting time directly results in a different reproductive output. The clutch size of male-only care nests is only half the size of the female-only care nests in Eurasian penduline tits (Van Dijk et al. 2012). This clutch size difference further triggers the escalation of sexual conflict, since males get fewer fitness benefits if they stay to care than if females stay. This intensive sexual conflict may consequently lead to only the uniparental care pattern spreading over populations (Pogány et al. 2008). In contrast, the clutch size in female-only and male-only care nests is equal in Chinese penduline tits (Zheng et al. 2021). This may indicate that female Chinese penduline tits did not escalate the sexual conflict by manipulating the clutch size, and thereby maintaining cooperation between males and females during nestling-rearing (biparental care). Therefore, these two species may evolve in divergent directions during the sexually antagonistic coevolution: Eurasian penduline tits evolved toward escalating sexual conflict, whereas Chinese penduline tits evolved toward alleviating the conflict over parental care.

However, notably, the above divergent parental care traits (i.e. egg burial, deserting time and clutch size) are all evolutionary consequences, but the causal factors that trigger these divergent patterns remain unknown. Here, I raise several hypotheses to explain the divergence in breeding strategies between the two penduline tit species: (1) Sexual selection may shape sexually antagonistic coevolution differently between the two species. Eye mask size is a sexually selected trait in male Eurasian penduline tits to indicate better individual quality. Males with a larger eye mask have higher mating success (Kingma et al. 2008). However, on average similar eye mask size in male Chinese penduline tits indicated that it does not associate with sexual quality (generally an eye stripe, Zheng et al. 2021). Therefore, I argued that the highly varied morphological traits of eye mask size in Eurasian penduline tits may drive a high intensity of sexual selection (or the other way around), which, in turn, may escalate the intensity of sexual conflict (Kokko and Jennions 2014, Svensson 2019). For example, good-quality males can gain higher fitness from desertion. Because females want to acquire good genes for their offspring, good quality males can exploit the female by forcing them to provide more care after desertion. This may trigger females to resist the male's exploitation by deserting during egg-laying to reduce the clutch size (reproductive fitness) of males, while they can gain an additional



clutch. (2) In the two penduline tit species, different parental care systems may evolve as polymorphic evolutionary outcomes and are not shaped by any external factors. The individual-based model I carried out in Chapter 7 has shown that the same ecological conditions can lead to different distributions of parental care patterns by chance. The two species may follow different evolutionary trajectories to resolve sexual conflict.

### **Food provisioning rate is not enough to estimate parental capabilities**

Parental removal experiments in biparental care species are traditionally used as a method of revealing the extent of sexual conflict between males and females. By analyzing the extent of parental compensations after partner removal, one can detect the amount of feeding each sex withheld during nestling-rearing. For a long time, it has been believed that parents of biparental care species are not capable of raising the whole brood alone and uniparental care only evolves when one parent could efficiently raise the brood by itself (Thomas and Székely 2005, Harrison et al. 2009). Through parental removal experiments, we can test the hypothesis that if parents from biparental care nests really have a lower parenting capability in a natural system with both uniparental care and biparental care.

Chinese penduline tits desert nests during incubation. This provides the full nestling-rearing stage for testing the difference in parenting capabilities between the parents in uni- and bi-parental care nests. My experiments in Chapter 4 revealed that (1) the natural feeding frequency and brooding duration (i.e. time spent in the nests to warm up offspring) do not differ between uniparental and biparental care nests; (2) during the parental removal experiment in biparental care nests, both males and females were able to fully compensate the feeding frequency but they did not compensate for the brooding duration.

Feeding frequency received the most attention in other parental removal studies (Schwagmeyer et al. 2002, Harrison 2009, Cantarero et al. 2019, Goymann 2020). My study indicates that it is important to also look at other parameters that may influence offspring survival. The lower brooding duration during removal experiments in biparental care nests than in natural uniparental care nests indicates that parents in biparental care nests may need to travel longer distances to the foraging sites such that single parents have to shorten the brooding time to provide the more important nutrition provisioning for the nestlings. However, it remains unknown what the consequence of the lower brooding duration is for nestling survival in this species. Most studies investigated the consequence of a shortened incubation duration to hatching success but not during nestling rearing to the fledgling success (Rompré and Robinson 2008, Mougeot et al. 2014). Nevertheless, fledging success of young common terns (*Sterna hirundo*) was positively related to parental attendance during the early nestling rearing period when young were vulnerable and largely relied on the nest conditions provided by parents (Riechert and Becker 2017).

Studies on wood thrushes (*Hylocichla mustelina*) and little penguins (*Eudyptula minor*) have found that a higher nest attendance increased nest success due to the reduction of nest predation (Chiaradia and Knowle 1999; Schmidt and Whelan 2005). Therefore, further studies should (1) compare the temperature difference before and during the removal experiments, because parents did not compensate for the brooding duration during the partner removal. If the temperature decreases due to the lack of brooding, a long-term removal for several days (not for 2 hours as we conducted) is needed to properly investigate its effect on nestling fitness. (2) Long-term removal is also necessary for testing if the predation rate of manipulated uniparental nests is different than that of natural uniparental nests. In these ways, we can further explore if the parental capabilities are different between parents of uni- and biparental care nests.

### Part III. Lessons from theoretical studies

#### Applying individual-based models to study the evolution of parental care

Parental care is a complicated behaviour and the mechanisms underlying its evolutionary diversification are not well understood (Royle et al. 2012, O'Connell 2020). Social interaction and seasonality (Chapter 3), different resolutions of sexual conflict between sister species (Chapter 4), and parental capability (Chapter 6) are all associated with the formation of the variable parental care (Chapters 2 and 5). However, it is rather difficult to figure out how and to what extent these factors interact to determine the evolutionary outcome of parental care.

To better understand how season length and uniparental care efficiency (the fledging success achieved by a single parent in relation to that achieved by biparental care) affect parental care in a system like penduline tits, I constructed an individual-based model in Chapter 7. I found that first, two alternative parental care patterns can evolve under the same ecological conditions, which may explain why different populations of the same species can differ in parental care. Second, In line with intuitive expectation and empirical findings, biparental care evolves when uniparental care efficiency is low while uniparental care evolves otherwise. Interestingly, in the latter case, both male-only care and female-only care can evolve, despite the fact that males and females differ a lot in prezygotic parental investment (males spend more time on nest-building). Third, season length has an intricate effect on the evolution of parental care. I found a periodic pattern that reflects how many breeding attempts fit into a breeding season. The pattern is intricate because males of penduline tits invest more time into prezygotic care than females – accordingly, the number of breeding attempts fitting into a season may be different for males than for females.

Although the model was tailored to penduline tits, I think that season length may be an important determinant of parental care in other species as well. At least three mechanisms may be responsible for this. (1) Parental care will be affected based on the time pressure for the breeding parents before a season change. Let's take season extension as an example. If a season is only enough for early arrived individuals to have a second nest, an extended season may release the time pressure so that more breeders can gain a second brood. This may lead to more biparental care for the first broods; if a season length is enough for most of the individuals to finish a second brood, the extended season may increase the chance for the early arrived individuals to have a third breeding attempt. This may lead to a higher rate of offspring desertion for the first two broods. (2) A change of season length may not only adjust the time budget of breeding for parents, but it may also change the efficiency of parental care. Longer season length may be induced by climate change, which can lead to shifts in the resource peak (Hidalgo et al. 2019, Barras et al. 2021) and/or changes in nestling development conditions in nests (Zuckerberg et al. 2018, Van de Ven et al. 2020). These effects of climate change together with a changed season length may bring more complex effects to species with different tolerances to ecological threats or with different parental care capabilities. (3) Sex different roles and energy allocations may be important in the reaction to a change of season length. In our penduline tits system, males and females may undergo different selective pressure, since males need to spend more time building nests and females spend more energy producing eggs.

Individual-based models provide a chance of understanding the mechanism of parental care by simulating the breeding process of birds. Animals' breeding events can be programmed depending on their behavioural traits (i.e. nest building, egg-laying, nestling feeding). Ecological and social factors become parameters which can be adjusted, so you can look into their effects on the evolution of parental care over varied ecological scenarios. In this way, not only associations but also causations can be investigated. Moreover, individual variation caused by stochasticity during the simulated evolutionary time reflects realistic natural evolutionary circumstances. This stochasticity may interfere with the evolutionary outcomes, which leads to different predictions than analytical models. Lastly, by means of individual-based simulations, we can tailor models by coding to animals' qualitative biological traits and generalize the evolutionary outcomes more sophisticatedly.

## Part IV. Further research perspectives

In this thesis, I have revealed the variable parental care system of Chinese penduline tits and tried to explore the reasons for its variation. After conducting observational, experimental and theoretical studies during my PhD, I realise that first, it is not sufficient to understand the parental care variations only on one unique species/clade. Similar breeding traits in different species may interact with parental care in different ways; second, although theoretical studies have discussed different perspectives of the evolution of parental care, some aspects are still neglected; third, most of the theoretical studies consider sexual conflict as the most crucial influence on parental efforts, however, the fitness benefits from parental cooperation may be underestimated. Therefore, I will propose several projects for further exploration of the diversity of breeding systems from different perspectives.

(1) *Comparative analysis: relationship between nest characteristics, offspring development modes and parental care systems.* Parental care efforts largely depend on the demands of offspring during development. For avian species, the nest is an important breeding item that can provide thermal regulation and protection against predation. In nature, generally 5 types of nests can be observed: ground nests, platform nests, cup nests, cavity nests and woven nests. Different nest types may provide different contributions to alleviate the efforts of parents. For example, ground nests provide the least protection and thermal regulations for the chicks, and woven nests provide good thermal regulation and protection but require parents to provide large amounts of effort during nest-building. Besides, nest characteristics are also related to the development mode of offspring. Precocial birds build simple ground nests so that the offspring can easily move out of the nest and feed themselves. Altricial birds create more sheltered nests because the nestlings are vulnerable to extreme temperatures and predation. However, we still do not know the evolutionary order and interactions of offspring development mode, nest characteristics and parental care systems. Through comparative analyses, we can detect the phylogenetic relationships of species, development mode and nest characteristics. It may be a promising methodology to reveal the evolutionary procedures of the three components.

(2) *Evolution of the timing of desertion.* In most species with uniparental care, offspring desertion occurs several days before the fledging of nestling. Either the male or the female presumably abandons the brood once they consider the partner can finish offspring care alone. In some precocial species, one parent leaves a few days after the chicks hatch. Penduline tits, however, express two unique time points of desertion namely either at the onset of incubation or during the egg-laying stage. The varied deserting time could be caused by differences in biological traits between species. For example, the demands of continuous incubation may need ground-nesting parents to incubate in turns, thus

parents are unlikely to desert the clutch before chick-hatching. Individual-based models that are constructed to simulate animals with different breeding traits (e.g. nest traits, development mode, etc) are also vital for exploring the mechanism of the variation of deserting time.

(3) *Effects of climate change on the evolution of parental care.* Climate change has a global influence on the length and quality of the breeding season. For migratory species, it is crucial to quickly adapt to the ecological consequences brought by climate change. Empirical studies have found that populations of different species showed varied demographic dynamics: some species suffer from dramatic population decline but some others quickly adjust with regard to ecological cues and adapted sustainably at the population level. Migratory birds may be able to predict the season quality based on some environmental cues. However, it is still unknown to what extent birds are able to predict the changes and how much the predictability could affect the breeding behaviour. Through modelling biological traits of species from different avian clades, we can simulate how the individual ability of predicting environmental changes can influence the evolution of parental care, how various influences are over avian clades with different breeding traits, and explore its effects on population adaptations.

(4) *Parental alternation gives a fitness bonus.* Sexual conflict is a core concept when studying the evolution of parental care. The classic theoretical studies argued that due to sexual conflict, parents evolve to withhold their parental efforts to some extent, and the effort paid by each parent when paired would be lower than their individual optimal effort (Lessells and McNamara 2012, McNamara and Leimar 2020). This theory has been supported by some studies through manipulative experiments in different species (Wiebe 2010, Iserbyt et al. 2015). However, in the last few years, studies found that in some species, males and females feed offspring in alternation and gain a higher brood success from this (Bebbington and Hatchwell 2016, Lejeune et al. 2019). Johnstone et al. (2014) used a theoretical model to reveal that parents can reach a rhythm of turn-taking, that promotes parents to feed at a higher frequency than the individual optimal effort because increasing the visiting rate of one parent leads to a concomitant increase in the other parent. Males and females need to cooperate to start reproduction. The contrasting parental care behaviour norms that evolved in nature and were discussed in theoretical studies indicate that further models should reconsider the optimal efforts from parents in combination with the promoting effects of cooperation, and not only focus on the consequence of sexual conflict.



