

The co-evolution of bronze-cuckoos (*Chalcites* spp.) and their hosts

テリカッコウ属とその宿主の托卵をめぐる攻防

Doctoral thesis

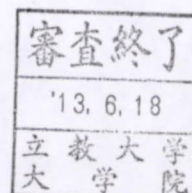
博士論文

2013

立教大学大学院
理学研究科
生命理学専攻

Nozomu J. Sato

佐藤 望



参考論文

1. **Sato NJ**, Tokue K, Noske RA, Mikami OK, Ueda K. 2010. Evicting cuckoo nestlings from the nest: a new anti-parasite behaviour. *Biology Letters*. 6:67 – 69.
2. **Sato NJ**, Mikami OK, Ueda K. 2010. Egg dilution effect hypothesis: a condition under which parasitic nestling ejection behaviour will evolve. *Ornithological Science*. 9:115-121.

Contents

| | |
|---|-----------|
| 参考論文 | 2 |
| Contents | 3 |
| General introduction | 5 |
| Chapter I Evicting cuckoo nestlings from the nest: a new anti-parasitism | |
| behaviour. | 8 |
| Introduction | 8 |
| Methods | 9 |
| Results | 11 |
| Discussion | 12 |
| Chapter II Do hosts of bronze-cuckoos recognize foreign nestlings through | |
| learning? Effects of small clutch size and delays in host chick eviction (idea) | 18 |
| Introduction | 18 |
| How might hosts recognize alien nestlings? | 19 |
| (1) Recognition by discordancy of eggs vs. chicks | 20 |
| (2) Template-based recognition of eggs vs. chicks | 20 |
| Effect of small clutch size in recognition by discordancy | 22 |
| Importance of hatching patterns for the evolution of nestling distinction by | |
| template-based recognition | 23 |
| Possibility of template-based recognition in <i>Gerygone</i> spp. | 24 |
| Conclusion | 25 |
| Chapter III Discrimination by learning against parasite chicks drives the | |
| cuckoo-host co-evolutionary arms race | 28 |
| Introduction | 28 |
| The Model | 30 |
| Discussion | 32 |

| | | |
|-------------------|--|-----------|
| Chapter IV | Egg dilution effect hypothesis: a condition under which parasitic nestling ejection behaviour will evolve | 41 |
| | Intoroduction | 41 |
| | The egg dilution effect hypothesis..... | 43 |
| | Discussion..... | 48 |
| Chapter V | Evolution of nestling ejection in <i>Gerygone</i> spp. driven by the egg dilution effect..... | 57 |
| | Introduction | 57 |
| | Methods | 59 |
| | Results | 60 |
| | Discussion..... | 63 |
| | General discussion | 69 |
| | Acknowledgements | 72 |
| | Reference | 73 |

General introduction

The image of a small bird feeding a huge common cuckoo *Cuculus canorus* young has been attracted scientists and other people for thousands of years. More than 2000 years ago, Aristotle (384–322 BC) wrote about the wonder behaviour of the cuckoo (Peck 1993; Hett 1936). He already knew that female cuckoos lay eggs in nests of small birds, and that the cuckoo nestling evicts all other nest mates from the nest (Davies 2011). The small birds (hereafter “host”) raise the cuckoo nestling even though the nestling kills their offspring (Payne 2005), and grows up to 10 times the size of the adult host (Wyllie 1981). Avian brood parasitism is not uncommon, at least 100 species from 5 families (*Cuculidae*, *Icteridae*, *Indicatoridae*, *Viduidae* and *Anatidae*) parasite their hosts, which represents one percent of all bird species in the world (Davies 2000). Scientists and naturalists, however, principally focus on only one species, the common cuckoo, as model for this co-evolutionary arms race (Rothstein and Robinson 1998; Davies 2000; Payne 2005).

Since parasitism by the common cuckoo reduces the breeding success of its hosts, many hosts have evolved anti-parasite behaviour such as parasite egg rejection,

and the behaviour promotes parasites to evolve counter-adaptations such as laying mimetic eggs. This is a good example of a co-evolutionary arms race (Dawkins & Krebs 1979; Rothstein 1990).

The arms race between the common cuckoo and its hosts occurs in various stages of the hosts' breeding. When a female cuckoo approaches a host nest to lay her egg, many hosts attack the cuckoo (Røskaft et al. 2002; Welbergen & Davies 2009). This behaviour promotes counter-adaptation in female cuckoos: swift and secretive parasitism at times when their hosts are absent from the nest (Chance 1940; Davies & Brooke 1988). Although female cuckoos sometimes lay successfully their eggs in the nest of their hosts, some hosts have developed advanced defense behaviour, such as egg ejection (Bán et al. 2013) or nest desertion (Moskát et al. 2011), and this behaviour promoted that cuckoos evolved laying mimetic eggs (Brooke & Davies 1988).

However, hosts of the common cuckoo have never evolved anti-parasite behaviour against cuckoo nestlings, even though they are not similar to host young and much larger (Davies 2000). This paradox of "lack of nestling rejection in hosts of common cuckoo" (Davies 2000) has been a long-standing question in evolution.

However, recent discoveries of alien nestling recognition and ejection in two Australian warbler species (*Gerygone* spp.) that are hosts of bronze-cuckoos (Chapter I; Tokue & Ueda 2010) provide an opportunity to disentangle the paradox. In the first chapter, I show that large-billed gerygones *G. magnirostris* can eject alien nestling from the nest. In the second chapter, I specifically address the question how the two species of Australian warblers are able to recognize and reject parasitic nestlings. In chapter III, I show that nestling ejection by *Gerygone* species is adaptive even though they recognize parasites by learning. I show in chapter IV that nestling ejection is more adaptive than egg ejection when clutch size is small and double parasitism occurs. In chapter V, I compare behaviour among *Gerygone* species. Their behaviour supports my hypothesis. Finally, I discuss all these aspects in the general discussion.

Chapter I Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour.

Introduction

Since brood-parasitic cuckoos usually reduce their host's reproductive success, hosts exhibit strong defence behaviour against parasitism (Wyllie 1981). The ejection of cuckoo eggs from host nests is one of effective defence mechanism, but it depends on hosts having the ability to discriminate cuckoo egg (Davies 2000). If cuckoo eggs slip through the hosts' detection system, and hatch, hosts accept the cuckoo nestlings and take care of them until when they become independent (Payne 2005).

Why do hosts accept cuckoo nestlings? One hypothesis is that learning to recognize parasitic nestlings is costly (recognition error overweighing benefit) and thus maladaptive for hosts (Lotem 1993). However, two recent studies have shown that two host species; reed warbler *Acrocephalus scirpaceus* and superb Fairy-wren *Malurus cyaneus* have defence mechanisms against parasitism at the nestling stage (Grim *et al.* 2003, Langmore *et al.* 2003). These hosts recognize that their brood has been parasitized by using cues such as the begging call by cuckoo nestling (Langmore *et al.*

2003) or unusually prolonged parental care (Grim *et al.* 2003) and then abandon the nests. It has been suggested that this defense mechanism at the nestling stage should evolve when host defense at the egg stage had been breached by the parasite and is beneficial for hosts because they avoid a future parental investment (Langmore *et al.* 2003). However, the hosts cannot salvage their progeny. Thus, in theory hosts should rescue their progeny by selectively ejecting cuckoo nestlings from their nest before the cuckoo young ejects the hosts' brood, but the behaviour has never been reported until now.

In this chapter, I report this previously unknown behaviour in a host species of an Australian bronze-cuckoo, and discuss whether it represents an anti-parasitic strategy. Using video cameras, I successfully recorded the moment when host birds ejected live cuckoo chicks from their nests.

Methods

The little bronze-cuckoo *Chalcites minutillus* is common in mangroves and rainforests of tropical Australia and Southeast Asia, and specializes in parasitizing warblers of the genus *Gerygone* (Higgins 1999; Noske 2001). The study was conducted

in mangroves in Darwin, Northern Territory, Australia, where I focused on the main Australian host species, the large-billed Gerygone *Gerygone magnirostris* (Brooker & Brooker 1989a). The frequency of parasitism was recorded during 2000-2002. The cuckoos parasitized 41% of the nests of the species (Mulyani 2004), and during 2007-2009, 36% (Tokue unpublished data). Immediately after the cuckoo chick hatches it physically ejects any host eggs and chicks from the nest (Friedmann 1968). The appearance of cuckoo eggs is very different from those of their hosts (Figure 1). In the contrast the cuckoo chicks have blackish skin and white down on the dorsal surface. It is closely resemble to the nestlings of its hosts (Figure 1). Nestling mimicry in the *Vidua* and its host systems is based on being accepted by the foster parents (Payne 2005) and facilitate in parasite young competing for foods (Schuetz 2005, but see also Hauber & Kilner 2007). These conditions cannot explain the nestling similarity of the present system because the cuckoo evicts the host's eggs and young soon after hatching.

I looked for host nests during four years (2006-2009) and recorded the nests and behaviour during the nestling stage at 22 nests (523 hours); 11 parasitized (254 hours) and 11 unparasitized (268 hours) with video cameras (Canon mini-DV FV30 &

FV M 200). The recording period was from the expected hatching date to the day of nestling ejection event or to the fifth day since hatching of parasitic young. The average recording time for each nest was about 7 hours per day.

Results

Of 22 nests I succeeded in capturing live nestling(s) being ejected by an adult host at 5 different host nests (one case was unparasitized nest, four cases were parasitized ones, Table 1). In two cases, only a cuckoo nestling was removed. In other two cases, only a host nestling was evicted. In the fifth case, both cuckoo and host nestlings and a host egg were ejected. In all cases, the host dragged the resisting nestling(s) from the nest, and dropped it under the nest, presumably resulting in its death (Figure 2). Although only two of the adult hosts from the five nests were marked with colour rings, I concluded that the five adults were different individuals judging from their nest position and breeding year. These two marked individuals were known to be the owners of the nests from which they ejected nestlings because they incubated the eggs in those nests.

Any other different types of rejection were not taken on the video in other 17

nests. Host young fledged in 4 out of 10 unparasitized nests. In two nests, outcomes are not known, while the rest of unparasitized nests failed to produce any young. In contrast, cuckoo young fledged from two nests, host young fledged from two nests (cuckoo egg/young disappeared from nest), and from three nests young disappeared before the day that they were expected to fledge.

Discussion

This is the first report of cuckoo hosts physically ejecting cuckoo nestlings from their nests, although nestling rejection (i.e. nest abandonment by hosts containing parasite young) has been reported previously (Langmore *et al.* 2003; Grim *et al.* 2003). I speculate that this ejection behaviour is an anti-parasitism strategy, for the following reasons. First, at least two confirmed nest-owners ejected live nestlings from their nest, suggesting that this behaviour was not infanticide by intruders. Secondly, the similarity between the nestling of the cuckoo and that of its host (Figure 1) suggests that this similarity is a consequence of the host's ability to discriminate odd looking cuckoo nestlings, similar to the outcome seen in cuckoos mimicking hosts' eggs to avoid detection (Brooke & Davies 1988).

Although mangrove gerygone *G. levigaster* save own nestling by ejection behaviour (Tokue & Ueda 2010), this study did not provide sufficient evidence to show that the host adults rescued progeny from host-evicting cuckoo young. Rather some of them killed their own offspring, but this is to be expected since similar recognition errors are known in egg ejecting host species (e.g. Davies & Brooke 1988). Therefore, I need to examine whether the hosts are able to achieve higher fitness by ejecting cuckoo nestlings even with the cost of ejecting their own young.

The evolutionary trajectory of this probable anti-parasitism strategy at the nestling stage may be quite different from that of abandonment of parasitized nests at the same stage. Langmore *et al.* (2003) suggested that defence mechanisms at the nestling stage would evolve only after host defense at the egg stage had been breached by the parasite. Interestingly, the hosts seem to lack any anti-parasitism strategy at the egg stage (cuckoo egg does not mimic host eggs, Figure 1). In fact, I observed only one case of own egg ejection in four years of research and this happened when the egg did not hatch after the full incubation period (Table 1, no. 5).

These factors suggest that the host may have by passed the egg rejection, and

went straight to the evolution of nestling ejection. The lack of egg rejection, and the evolution of nestling ejection, may be due to a coincidence, or constraints such as small bill size (Rohwer & Spaw 1988), physical structure of the nest, e.g. domed nest (Langmore *et al.* 2009b; Brooker *et al.* 1990). Future research on this apparently unique system may give us new insights into the co-evolution of avian brood parasitism.

Table 1. Details and outcomes of nests from which nestlings were ejected.

| No. | Nest contents when 1 st nestling was ejected | | | | Which was ejected | | Outcome |
|-----|---|---------|-------|---------|-------------------|-----|-------------------------------|
| | C egg | C young | H egg | H young | C | H | |
| 1 | - | 1 | 2 | - | 1 | 0 | depredated |
| 2* | - | 1 | - | - | 1 | - | depredated |
| 3 | - | - | - | 3 | - | 1 | two host young fledged |
| 4* | 2 | - | - | 1 | 0 | 1 | one cuckoo fledged |
| 5 | - | 1 | 2 | - | 1 | 2** | failure, entire brood ejected |

C = cuckoo, H = host

*both adults at the nest were colour-banded for individual recognition.

**one young and one host egg ejected.

(a)



(b)

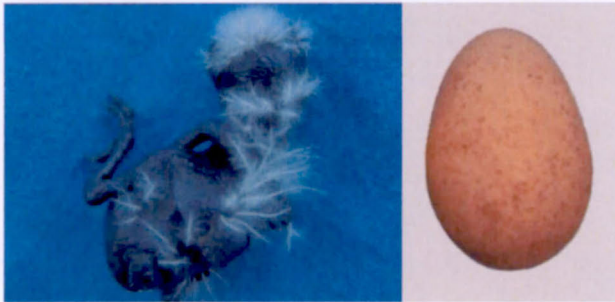


Figure 1. An Australian brood parasite and its host, (a) little bronze-cuckoo nestling (left) and egg (right); (b) large-billed gerygone nestling (left) and egg (right).



Figure 2. Nestling ejection behaviour. The nestling of little bronze-cuckoo *Chalcites minutillus* was ejected from the nest by the nest owner; large-billed gerygone *Gerygone magnirostris* that has colour band.

Chapter II Do hosts of bronze-cuckoos recognize foreign nestlings through learning? Effects of small clutch size and delays in host chick eviction (idea)

Introduction

As avian brood parasites reduce the breeding success of their hosts, many hosts have evolved anti-parasite behaviours such as parasite egg rejection, and these behaviours promote parasites to evolve adaptations such as mimetic eggs (Winfrey 1999). These interactions are a good example of a co-evolutionary arms race (Kilner 2013). For rejection of foreign eggs by hosts, there are two main possible cognitive mechanisms of egg discrimination: recognition by discordance and template-based recognition (Moskát et al. 2010). Although both mechanisms are valuable for egg recognition, they do not seem to be suitable for nestling recognition by hosts of the Common Cuckoo *Cuculus canorus*, because the cuckoo nestling evicts all eggs from the nest before they hatch (Wyllie 1981). Therefore hosts cannot recognize parasites by discordancy. It is also risky for these hosts to learn a template for recognition, because it is possible that hosts treat the cuckoo nestling as the template for their own progeny if

they are parasitized in their first breeding attempt (Lotem et al. 1992; Lotem 1993). However, two *Gerygone* species do eject foreign nestlings even though the cuckoo nestlings mimic the host nestlings (Chapter I; Tokue & Ueda 2010). This raises the question of how hosts distinguish own nestlings from cuckoo nestlings. In the chapter, I argue that hosts reject cuckoo nestlings by using template-based recognition because the small clutch size in *Gerygone* hosts makes it difficult to recognize by discordancy and because host and parasite chicks coexist in the nest.

How might hosts recognize alien nestlings?

The lack of nestling recognition by many hosts of avian brood parasites has been a long-standing mystery. However, recent discoveries of nestling recognition in some hosts (Chapter I; Langmore et al. 2003; Shizuka and Lyon 2010; Tokue and Ueda 2010) provide an opportunity to begin disentangling the cognitive mechanisms involved in such anti-parasitism behaviours. Here, I discuss why two species of Australian warblers, *Gerygone magnirostris* and *G. levigaster*, are able to recognize and reject parasitic nestlings.

Many hosts of avian brood parasites have evolved anti-parasitism behaviour

such as foreign egg rejection (Davies 2011). Two main cognitive mechanisms of egg discrimination have previously been proposed: recognition by discordancy and template-based recognition (Rothstein 1974; Lahti & Lahti 2002; Moskát et al. 2010).

These two mechanisms do not seem to be mutually exclusive and it has been shown that some hosts use both mechanisms (Moskát et al. 2010).

(1) Recognition by discordancy of eggs vs. chicks

In recognition by discordancy, hosts reject the minority egg type in a clutch (Moskát et al. 2010). In this case, hosts can recognize an alien egg if own eggs are representing the majority of eggs in the nest. During the chick stage, in contrast, chicks of some brood parasites, such as those of the Common Cuckoo *Cuculus canorus*, evict all other eggs in the nest before they hatch (Willie 1981), thus making it impossible for hosts to reject parasite chicks by discordancy.

(2) Template-based recognition of eggs vs. chicks

In template-based recognition, hosts compare the characteristics of eggs with a template that is inherited and/or learned. For example, Great Reed-warblers *Acrocephalus arundinaceus* use an imprinting-like mechanism to recognize their own eggs during the first breeding attempt (Lotem et al. 1992). Template-based recognition

that relies on learning in this way is limited however by the host's opportunity to use its own chicks as templates for recognition. If the parasite nestling evicts all host eggs, naïve hosts that are parasitized at the first breeding would only learn to recognize the cuckoo nestling and reject their own chicks for the rest of their lives (Lotem 1993).

Both discordancy and template-based recognition mechanisms are therefore influenced by the behaviour of cuckoo nestling, and makes hosts difficult to recognize foreign nestlings. However, recent discoveries suggest that at least two Australian warbler species *Gerygone* spp., hosts of the little bronze-cuckoo *Chalcites minutillus*, reject parasite nestlings (Chapter I; Tokue & Ueda 2010). Host parents of both species eject parasite nestling even though host and parasite nestlings coexist in the nest (Tokue & Ueda 2010), presumably by discriminating between them despite parasite nestlings visually mimicking host nestlings (Langmore et al. 2011). This requires an explanation for how the hosts distinguish their own nestlings from cuckoo chicks. In this chapter, I suggest that the hosts reject cuckoo nestlings by using template-based recognition and that small clutch size of the hosts plays an important role in the evolution of nestling discrimination.

Effect of small clutch size in recognition by discordancy

Recognition by discordancy can only lead to parasite egg/nestling rejection if host offspring represent the majority in the clutch, unless hosts have a prior knowledge about the appearance of their eggs (Lahti & Lahti 2002). Given that female brood parasites remove a host egg while they lay their egg (e.g. many species of cuckoos including *Chalcites*), discordancy requires that the clutch size of hosts is at least three. In the two *Gerygone* species, however, the clutch size consists mostly of two or three eggs (Yom-Tov 1987; Noske 2001; Tokue 2011). This suggests that these two host species would not always be able to use discordancy as a reliable cue for egg/nestling rejection. Moreover, females of *Chalcites* cuckoos occasionally lay egg in already parasitized nests by another female (multiple parasitism) (Brooker & Brooker 1989), which increases the chances that the host offspring would become the minority in the clutch if the clutch size is small (see Moskát et al. 2010). Therefore, as long as such a life history trait is invariable, the small clutch size of hosts will sometimes prevent the recognition of parasite eggs and nestlings by discordancy, which should affect the evolution of their defense strategy against cuckoo parasitism.

Importance of hatching patterns for the evolution of nestling distinction by template-based recognition

In template-based recognition, the host uses learned and/or innate information regarding its own eggs to discriminate against alien eggs. Lotem (1993) hypothesized that template-based recognition using a learning mechanism has risk for hosts that reject alien nestlings (also see discussion above). A key component of this hypothesis is the hatching pattern. Due to special adaptations such as a short incubation period, *Cuculus* eggs can typically hatch earlier than those of hosts and the cuckoo nestling evicts host eggs before they hatch (Davies 2000). Therefore, these hosts do not have the opportunity to learn to recognize their own chicks when they are parasitized. In contrast, eggs of American Coots *Fulica americana*, typically hatch ahead of conspecific brood parasite eggs, thus these hosts are able to imprint correctly on their own chicks and reject parasitic eggs (Shizuka & Lyon 2010). In light of these patterns, it is worth examining the relative timing of egg-laying and incubation periods of the hosts of *Chalcites* bronze-cuckoos. The little bronze-cuckoos and shining bronze-cuckoos (*C. lucidus*) sometimes lay their eggs during the incubation period of hosts (Gill 1983;

Tokue 2011). In addition, the incubation period of the little bronze-cuckoo (ca. 16 ± 1 days) is equal to that of their host, the mangrove Gerygone, *G. levigaster* (Tokue 2011). As a result, the host nestlings sometimes hatch before the cuckoo chick is able to evict them (Gill 1998; Tokue 2011). I hypothesize that, despite the efforts by the cuckoo chick to eliminate its nest mates, the relative hatching pattern and the delay in eviction could provide host parents the opportunity to learn recognizing their own chicks. Even if the host imprints on both the cuckoo and their own chicks, the cost of misimprinting would be significantly reduced, it would be no worse than that of a host that accepts all chicks (Lotem 1993; Shizuka & Lyon 2010).

Possibility of template-based recognition in *Gerygone* spp.

The two gerygones mostly lay only 2-3 eggs in one breeding attempt, which makes it difficult to recognize their own eggs and nestlings by discordancy. They can eject alien chicks that do not represent the minority in the nest (Chapter I; Tokue & Ueda 2010). Therefore, they might recognize alien chicks by template-based recognition. In this case, the hosts could have evolved ejection behaviour against alien eggs and nestlings. Why the hosts would eject only nestlings? I proposed one possible

answer in the chapter IV of this thesis: the chick ejection strategy is more adaptive than egg ejection when hosts have small clutch size and their nests are often several times parasitized by cuckoos (egg dilution effect hypothesis). This is because a cuckoo egg in a host nest reduces the risk of a remaining host egg being replaced by another cuckoo female that parasitizes the same nest subsequently, thus hosts can achieve greater success when they accept cuckoo eggs and only eject cuckoo chicks. The egg dilution effect should increase with smaller clutch size (Chapter IV) and under the conditions that cuckoos selectively remove the rival cuckoo eggs to prevent their own chick from being evicted by the rival cuckoo chick. Nevertheless, there are only few previous studies reporting removal of a cuckoo egg by another cuckoo (Davies & Brooke 1988; Brooker et al. 1990; also see Langmore et al. 2009), so this requires further investigation.

Conclusion

The clutch size of hosts is not only important for the “egg dilution effect” but also for the mechanism of recognition of alien offspring. Small clutch size of 1-2 makes recognition by discordancy impossible. In contrast, small clutch size does not affect

against template-based recognition as long as the template is correctly acquired. Therefore, hosts with small clutch size such as the two *Gerygone* species may use template-based recognition for the rejection of alien nestlings. Nevertheless, since the hosts have to learn recognizing their own offspring, or to evolve an innate template, template-based recognition may have an evolutionary disadvantage over recognition by discordancy, which does not require learning or another prerequisite mechanism. If so, it would make anti-parasitic defense strategies difficult to evolve per se. In fact, many hosts of *Chalcites* cuckoos, which usually lay a clutches of 2-4 eggs in Australia (Langmore et al. 2005), have not evolved any rejection behaviour (Davies 2000). Also temporal coexistence of both nestlings of cuckoo and its host can affect the recognition mechanisms (Lotem 1993). When the cuckoo nestlings expel host eggs before they hatch, hosts lose the reference required for a template-based recognition mechanism of nestlings, particularly if parasitism occurs during the first breeding attempt (Lotem 1993). This risk of misrecognition, however, is much lower for hosts those nestlings coexist with parasite nestlings in the same nests (Lotem 1993). Therefore, I argue that these factors, namely small clutch size of the hosts and coexistence of parasite and host

nestlings may have promoted the evolution of nestling ejection behaviour through template-based recognition.

Chapter III Discrimination by learning against parasite chicks drives the cuckoo-host co-evolutionary arms race

Introduction

In the previous chapter, I suggested that discrimination for nestling ejection by two *Gerygone* spp. uses template-based recognition even though this mechanism is not adaptive for hosts of common cuckoo *Cuculus canorus* (Lotem 1993). In this chapter, I provide theoretical reconciliation to this controversy by evaluating the conditions in which cuckoo chick rejection through learning is more adaptive than chick acceptance.

One mystery in nature is why cuckoo hosts indifferently raise alien-looking parasite chicks despite their fine discrimination against parasite eggs (Davies 2000). Lotem (1993) provided a theoretical solution to this question by postulating that monopolization of host nests by common cuckoo *Cuculus canorus* chicks deprives host parents of the opportunity to learn which is their own offspring, thereby preventing the evolution of host discrimination ability. However, recent discoveries contradict this theory: host parents of some bronze-cuckoos (*Chalcites* spp.) actually discriminate

against parasite chicks though the parasites eventually monopolize host nests (see chapter I), and even further, parasite chicks evolved visual mimicry as resistance (Langmore et al. 2011). Here, I propose a theoretical reconciliation to this controversy by showing how the hosts' ability to learn to recognize nestlings can be adaptive.

In the case of the common cuckoo, parasite chicks evict host eggs from the nest before they hatch (Davies 2000; Lotem 1993; Figure 1A). Under this condition, naïve parents that are parasitized during their first breeding attempt would encounter only a cuckoo chick, thereby imprint on the parasite and kill all future progeny of their own as alien. This deficit critically damages the advantage of a chick rejecter, thus its fitness can never surpass even that of an acceptor who indiscriminately accepts cuckoo parasitism (Lotem 1993). However, if eviction by parasite chicks occurs well after host chicks hatch, this will give naïve hosts time to imprint on their own offspring. Such a delayed host chick eviction typically occurs in *Chalcites* cuckoo-host systems, resulting in temporal coexistence of host and parasite chicks generally lasting several days (Tokue 2011; Gill 1998; Figure 1B). I included this aspect into the model (i.e., *I*) to consider whether a naïve parasitized host correctly imprints on its own offspring, hence

acquiring a tolerable template by which hosts would not mistake their own chicks as alien (Figure 1C).

The Model

The model subtracts the fitness of two respective confronting strategies, acceptor and egg rejecter, from that of chick rejecter to determine its fitness advantages over the opponents. I assumed that both egg and chick rejecters learn the characteristics either of the eggs or chicks in the nest during their first breeding attempt in life (i.e., imprinting), and reject or accept parasites based on this template in the all subsequent breeding attempts (Lotem et al. 1992). Acceptors never learn, hence always raise cuckoo chicks when parasitized in any stage of life (Lotem 1993). Rejecters during the first breeding respond to parasitism in the same way as the acceptor because they have no prior template to detect parasitism.

I defined the fitness of rejecters as w_{ij} , consisting of the sum of reproductive successes gained in all possible situations times the probabilities of being parasitized (Table 1). Symbols i and j denote the number of parasitism events a host nest suffers in the first breeding attempt in life (i) during which the hosts acquired the template, and

those in later life (j) when they actually exert their template to deal with parasitism.

Occurrence probability of parasitism events is represented by the product of probabilities p and m as follows: $1 - p$ for 0 (no parasitism), $p(1 - m)$ for 1 (singular parasitism), and pm for 2 (multiple parasitism), as I do not assume more than two cuckoo females parasitizing the same host nest. I assume that p is constant for all years.

The fitness of acceptor is thus defined as $(1 - p)C$ times the number of breeding attempts through life ($C =$ clutch size of host).

Due to the lack of templates in naïve rejecters, the difference in fitness between a chick rejecter and an acceptor is the fitness benefit gained during breeding attempts in later years. The formula for the predicted advantage of chick rejecter over acceptor reduces to

$$m\left(\frac{1}{C} - 1\right) + lC - 1 > 0, \quad [1]$$

given that l is 1 (i.e., chick rejecter surely learn own nestling), and the C , clutch size of host is greater than 2. The left side of this inequation yields the surfaces in figure 2A & 3. Graphs were drawn using R (R Core Team 2013) with the *wireframe* function of the *lattice* package (Sarkar D 2008).

Apart from l , the difference between chick and egg rejecters is represented by the benefit of the chick rejecter, described as b_m (chick rejecter of w_{02} – egg rejecter of w_{02}) in figure 1C (see Table 1; Chapter IV): b_m depends on whether the subsequently parasitizing cuckoo female removes a rival cuckoo egg or a host egg in replacement of its own. The resulting pay-offs are as follows: removing a host egg results in host's pay-off $C - 1$ at probability $\left(\frac{1}{C}\right)$; replacing a cuckoo egg results in host's pay-off $C - 2$ at probability $\left(\frac{C-1}{C}\right)$, as 1 cuckoo egg out of C eggs had been in the nest. The assumed intolerance of egg rejecters toward parasite eggs is consistent with empirical evidence (Lawes & Marthews 2003), which eventually reduces the fitness benefit of hosts by the number of parasitism events their nest suffers (Chapter IV). The inequation for the difference in fitness reduces to

$$\frac{m}{C} + C(l-1) > 0 \quad [2]$$

under the same condition as [1], described graphically as well in figure 2B & 4.

Discussion

The predicted advantages of chick rejecters differ depending on the opponent strategies (Figure 2); compared to acceptors, chick rejecters are favored as chick rejecter

hosts gain greater fitness benefits when at least half of naïve host parents in a population could achieve imprinting own nestling, i.e., $l = 0.5$ and $m = 0$ (Figure 2A, 3). In contrast, to outstrip egg rejecters, perfect learning ($l = 1$) is not sufficient for chick rejecters because egg rejecters always correctly imprint on their own eggs (Lotem 1993), and both rejecters thus gain equal benefits (when $m = 0$ in Figure 2B). Therefore, chick rejecters need additional benefits to be favored. I introduced m (frequency of multiple parasitism) to the model, representing how likely a single host nest is parasitized by multiple cuckoo females (Figure 1C; Chapter IV). Under multiple parasitism, chick rejecters that accept cuckoo eggs laid in replacement of their own, give subsequently parasitizing cuckoo females the possibility to remove the rival cuckoo egg. Therefore, chick rejecters can have one more surviving offspring than egg rejecters (b_m in Figure 1C) that reject every parasite egg (Požgazova 2011). This benefit decreases marginally with increasing clutch size, C (Chapter IV). Acceptance of cuckoo eggs, small clutch sizes and multiple parasitism are indeed common in host-parasite systems of bronze-cuckoos (Davies 2000).

The model predicts that chick rejection per se is difficult to evolve as it

depends not only on stationary coexistence of host and parasite chicks but also on additional benefits. This is consistent with the rarity of chick rejection in cuckoo-host systems, hitherto found only in some bronze-cuckoos (Chapter I, IV; Langmore et al 2008; Davies 2011 ;Colombelli-Négrel 2012). If multiple parasitism has actually an effect on the evolution of observed chick rejection (Požgazová et al 2011), this implies that hosts even need to exploit the competition among parasites. Moreover, bronze-cuckoo chicks mimic not only the appearance of host chicks (Langmore et al. 2011), but even their vocalization to secure host care (Shizuka & Lyon 2010). It is unclear whether host parents' learning is the major evolutionary drive of these mimics (but see Jetz et al 2008); however, it is probable because innate responses can easily lead to misidentification of nestlings where traits serving as cues for host parents could be phenotypically variable (Lotem 1993; Jetz et al 2008; Langmore 2011).

The model also provides insights into how most parasitic cuckoos and their hosts have fought fierce battles to disguise and to detect the identity of parasite chicks in their co-evolutionary arms races. The original clutch size of hosts might play a major role here, as larger clutch size gives advantage to chick rejecters when confronting

acceptors, while it disfavors chick rejecters against egg rejecters (Figure 2), which previous models failed to detect (Brooker & Brooker 1996; Lawes & Marthews 2003).

In the light of the prevalence of egg mimicry by brood parasites (Davies 2000; Colombelli-Négrel et al. 2010), these predictions indicate that egg rejecters would outcompete chick rejecters in most cases, which would be the case in *Cuculus* hosts as they have relatively larger clutches. Thus in *Cuculus* cuckoos, females strive to help their non-mimetic chicks evict all host eggs before they hatch (e.g., finely tuned timing of egg-laying) (Davies 2000; Colombelli-Négrel et al. 2010) to avoid coexistence with host chicks. By contrast, controlling the timing of hatching seems difficult for *Chalcites* cuckoos because of the relatively small clutch sizes of hosts (Chapter V), which provide cuckoo females a small margin to lay their eggs at a proper timing. This should favor mimetic parasite chicks among already hatched host brood mates to avoid discrimination (Figure 1B).

Table 1. Fitness w_{ij} of both types of rejecters as experienced breeders

| i | j | Egg rejecter | Chick rejecter |
|-----|-----|------------------------------------|---|
| 2 | 2 | $pm \cdot pm$ | $pm \cdot pm l$ |
| 2 | 1 | $pm \cdot p(1-m)$ | $pm \cdot p(1-m) l$ |
| 2 | 0 | $pm \cdot (1-p)\mathbf{C}$ | $pm l \cdot (1-p)\mathbf{C}$ |
| 1 | 2 | $p(1-m) \cdot pm$ | $p(1-m) \cdot pm l$ |
| 1 | 1 | $p(1-m) \cdot p(1-m)$ | $p(1-m) \cdot p(1-m) l$ |
| 1 | 0 | $p(1-m) \cdot (1-p)\mathbf{C}$ | $p(1-m) l \cdot (1-p)\mathbf{C}$ |
| 0 | 2 | $(1-p) \cdot pm(\mathbf{C}-2)$ | $(1-p) \cdot pm \left\{ (\mathbf{C}-1) \left(\frac{1}{C} \right) + (\mathbf{C}-2) \left(\frac{C-1}{C} \right) \right\} \dagger$ |
| 0 | 1 | $(1-p) \cdot p(1-m)(\mathbf{C}-1)$ | $(1-p) \cdot p(1-m)(\mathbf{C}-1)$ |
| 0 | 0 | $(1-p) \cdot (1-p)\mathbf{C}$ | $(1-p) \cdot (1-p)\mathbf{C}$ |

Fitness pay-offs in boldface, which lack in situations where hosts accept parasitism

hence gain no benefit. Probabilities related to parasitism in i and j are separated by

interpuncts (\cdot). $\dagger b_m$ (see Figure 1C) represents the benefit gained here for a chick

rejecter compared to an egg rejecter.

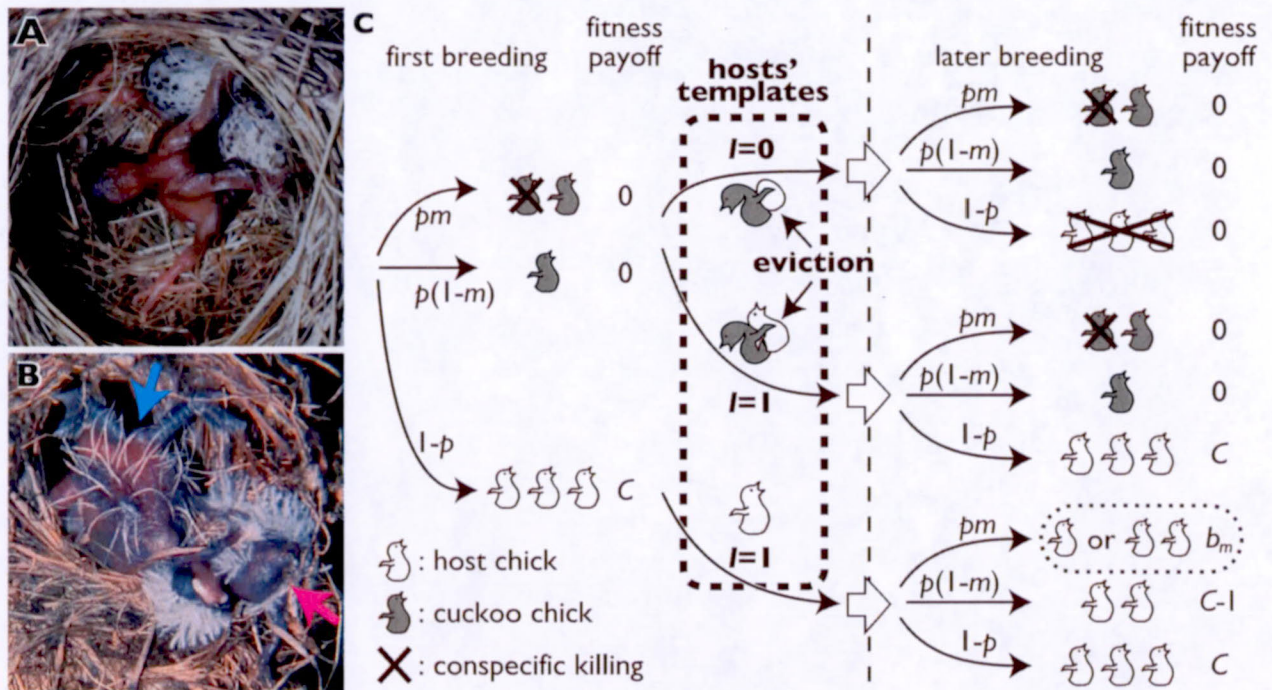


Figure 1. A *Cuculus* cuckoo chick evicting a host egg (A, © H. Uchida) and a mimetic *Chalcites* cuckoo chick (cyan arrow) evicting a host chick (magenta arrow) (B, © Y. Létocart). Schematic representation of how eviction by cuckoo chicks affects the success of chick rejecters achieved through the acquired templates (C, see the main text for details). Conspecific killing denotes situations in which a cuckoo chick is evicted from a multiply parasitized nest by another cuckoo chick, and in which host chicks are killed by their parents as a consequence of misimprinting.

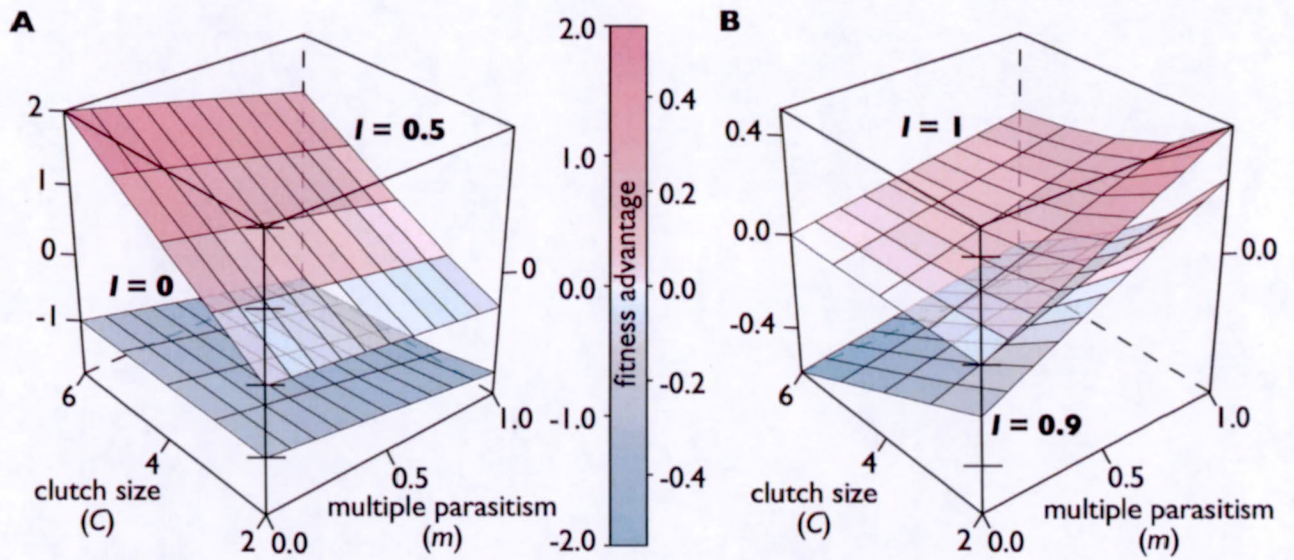
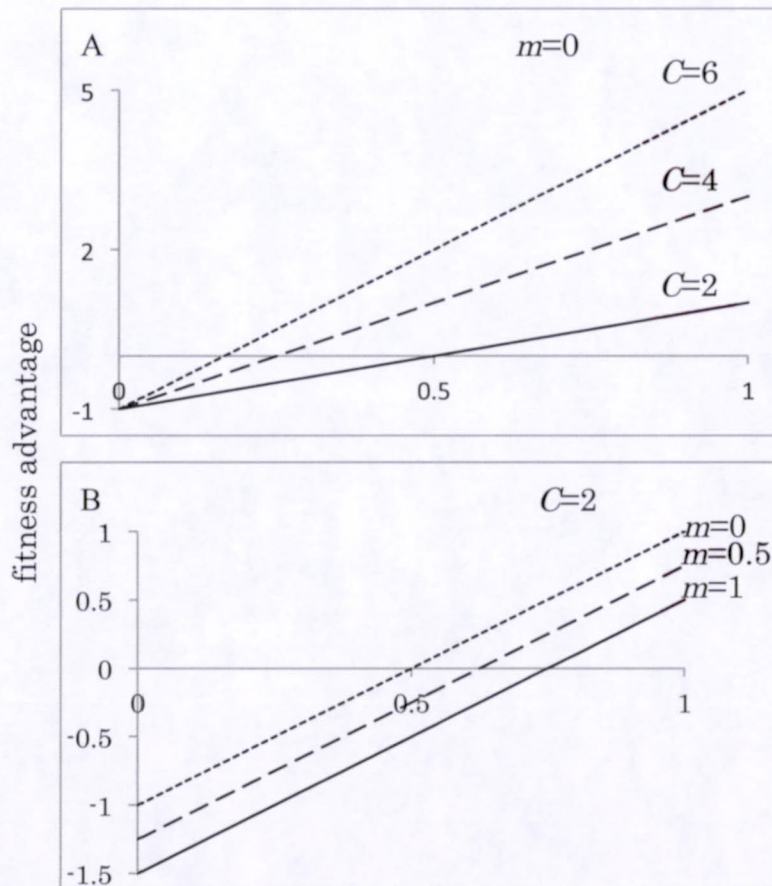
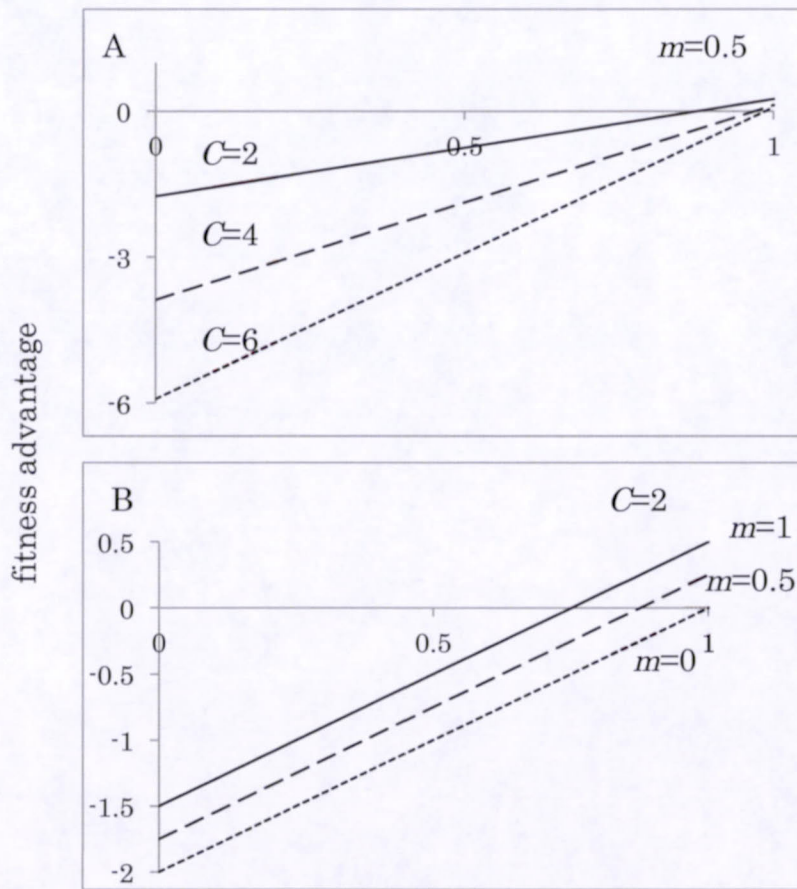


Figure 2. Predicted fitness advantages of chick rejecter over acceptor (A) and over egg rejecter (B) in relation to host's original clutch size, C , and probability of being multiply parasitized, m . Levels of I were altered to illustrate transitional states. Gradation of while colours represents the advantageousness of chick rejecter (magenta) and of respective opponent strategies (cyan; increasing negatively), antagonizing each other around 0 where advantages of both sides are in equilibrium (whitish zones) as scaled in the centred bar.



probability of naïve host correctly imprints on its own offspring, l

Figure 3. Predicted fitness advantages of a chick rejecter over an acceptor in relation to the host's original clutch size (C), probability of a naïve host that correctly imprints on its own offspring (l), and probability of being multiply parasitized (m). Chart **A** shows that the fitness advantage of a chick rejecter increases with increasing C and increasing l when m is 0. Chart **B** shows that the fitness advantage of a chick rejecter increases with decreasing m and increasing l when C is 2.



probability of naïve host correctly imprints on its own offspring, l

Figure 4. Predicted fitness advantages of a chick rejecter over an egg rejecter in relation to the host's original clutch size (C), probability of a naïve host that correctly imprints on its own offspring (l), and probability of being multiply parasitized (m). Chart **A** shows that the fitness advantage of a chick rejecter increases with decreasing C and increasing l when m is 0.5. Chart **B** shows that the fitness advantage of a chick rejecter increase with increasing m and increasing l when C is 2.

Chapter IV Egg dilution effect hypothesis: a condition under which parasitic nestling ejection behaviour will evolve

Introduction

Avian brood parasitism drives a co-evolutionary arms race between brood parasites and their hosts (Davies 2000). For example, many hosts have evolved an ability to recognize and reject unlike foreign eggs. On the contrary parasites have evolved better egg mimicry to counter host defences. However, once a foreign egg escapes the detection system by the host, it is accepted, the host rear the parasite nestlings until it has fledged despite the fact that the parasitic nestling often looks very unlike the host nestling (Wyllie 1981). Why does the host accept alien nestlings? One possibility is that learning to recognize parasitic nestlings is costly, with the risk of misimprinting outweighing the benefit of recognition, and thus the evolution of nestling-ejection behaviour is maladaptive for hosts (Lotem 1993).

However, I have reported that the large-billed gerygone *Gerygone magnirostris*, one of the major hosts of the little bronze-cuckoo *Chalcites minutillus*, in northern Australia, physically ejects cuckoo young from the nest (Chapter I). Given that

the little bronze-cuckoo nestlings closely resemble the large-billed gerygone nestlings, the host's ability to eject foreign nestlings seems to have selected for the bronze-cuckoos which morphologically resemble the host in order to avoid detection (Chapter I). However, the host seems to never reject foreign eggs even though the little bronze-cuckoo's eggs appear very different from their own (Mulyani 2004; Sato et al. 2010b; see also Brooker & Brooker 1998).

This behaviour raises two important questions: why has parasitic nestling ejection evolved only in some gerygone species (Tokue & Ueda 2010; Chapter I, V), and why have the large-billed gerygone evolved this strategy without having first evolved egg rejection behaviour often observed in other hosts, even though egg rejection seems to be a superior strategy given that success results in no risk of the host's own eggs being ejected by the little bronze-cuckoo young?

These puzzles may be explained by the following four previously proposed hypotheses. First, the evolutionary lag hypothesis (Winfrey 1999) states that cuckoo eggs are accepted because the hosts have had insufficient time for the selection of the necessary genetic variants for the ability to reject foreign eggs. Second, the bill-size

constraint hypothesis (Rohwer & Spaw 1988) argues that small bill-sizes of hosts make the evolution of egg ejection behaviour physically impossible. Third, the mafia hypothesis (Soler et al. 1995; Briskie 2007) proposes that parasitic birds enforce acceptance by destroying eggs or nestlings of hosts that eject a parasitic egg. Finally, the cryptic egg hypothesis (Langmore et al. 2009b; Brooker et al. 1990) states that cuckoo eggs have evolved to be cryptic inside the dark interiors of the enclosed host nests, and therefore they are not rejected because they are difficult to detect.

Here I propose a novel, but not mutually exclusive hypothesis termed the egg dilution effect (EDE) hypothesis that well explains the benefit of accepting parasitic eggs and the evolution of rejecting parasitic nestlings in host. The details of the EDE hypothesis are presented, followed by an evaluation of the different hypotheses to determine which is more suitable to explain the observed phenomena in the large-billed gerygone.

The egg dilution effect hypothesis

In the EDE hypothesis, cuckoo eggs act as insurance of host egg survival through a dilution effect that serves to protect against parasitism by multiple female

cuckoos. This hypothesis requires two conditions to be met which are found in certain host species including the large-billed gerygone: multiple parasitism of the same nest during a single breeding season, and the removal of one egg from host nests by the parasitizing species (Davies 2000).

To examine this hypothesis, I assume two strategies. In strategy A, a host ejects cuckoo eggs but not cuckoo nestlings, while in strategy B, a host ejects cuckoo nestlings but not the eggs. I also assume that 1) nests are parasitized twice and only after the host clutch is completed, 2) hosts, using strategy A, regularly eject the first cuckoo egg before the second cuckoo lays her egg, 3) hosts eject cuckoo eggs and nestlings without mistakes, 4) eggs and nestlings do not die other than by ejection of the host and cuckoo and 5) hosts adopted strategy B, eject cuckoo nestlings before killing of host brood.

When the first female cuckoo lays an egg in the nest of a host using strategy A, the clutch size (C) of the host reduces to $C-1$ because a cuckoo removes one host egg from the nest. Subsequently, the host ejects the cuckoo egg, and $C-1$ host eggs still remain in the nest. After a second female cuckoo lays in the same nest, the number of

host eggs becomes $C-2$. The $C-2$ eggs then hatch and fledge which represents the pay-off of strategy A. In contrast, the pay-off of strategy B is more complex. After the first cuckoo lays an egg into the nest, the nest has $C-1$ host eggs and one cuckoo egg. When another female cuckoo parasitizes the nest, she removes one egg from the clutch at random, with the probability of a host egg being removed is $(C-1)/C$ and that of a cuckoo egg being removed is $1/C$. If both host and cuckoo eggs are remained in the nest after the second parasitism hatch, the cuckoo young hatched is ejected by the host and then host young successfully fledge. The expected pay-off of strategy B is represented by $C-2+1/C$, which is always greater than the pay-off of strategy A by $1/C$. Figure 1 illustrates this argument for clutch size $C=3$.

The relative pay-off of strategy B compared to A (strategy B/ strategy A) increases as the host clutch size decreases (Table 1). For example, when the clutch size is six, the relative pay-off is nearly one, however, when the clutch size decreases to two, the theoretical relative pay-off increases to infinity. Of particular note, when the clutch size is equal to the number of parasitism events, the pay-off of strategy A is zero. The advantage of strategy B is also greater with increasing numbers of parasitism events

(Figure 2A).

In the EDE hypothesis, I assume that a female cuckoo removes an egg randomly at one parasitizing event. However, if the cuckoo selectively removes rival cuckoos' eggs to save their own chick from being evicted by the rival cuckoo chick, strategy B becomes more beneficial as the probability of the first-laid cuckoo egg being removed by the second cuckoo is greater than $1/C$. Indeed, females of the Common cuckoo tend to remove cuckoo eggs more frequently than host eggs (Davies and Brooke 1988). In addition, Brooker et al. (1990) proposed that the horsfield's bronze-cuckoo *Chalcites basalis* evolved egg mimicry to avoid being ejected by competing female cuckoos (but see Langmore et al. 2009a). It is worth noting that the egg dilution effect also operates in an identical manner against predators that do not destroy all host eggs during a single predation event.

Under the conditions described above, the EDE hypothesis demonstrates that strategy B always wins against strategy A. However, this outcome becomes more complicated when I consider one risk which threatens strategy B, namely, when a parasitic nestling ejects the hosts' brood before the host ejects the parasitic young.

Clearly, strategy B is superior only when cuckoo nestlings are ejected before the occurrence of such an event. Another factor affecting the outcome of strategy B is that for simplicity, I assumed that hosts eject parasitic eggs and young without mistakes. The success of this strategy varies if I consider the error rate of discrimination, for example, when the error rate in discriminating parasite eggs is equal to that of discriminating parasite young, the relative pay-off (strategy B/ strategy A) is identical to those shown in table 1 and figure 2A. If the error rate in discriminating parasite eggs is larger than that for parasite young, the advantage of strategy B is greater. In contrast, when the error rate is higher for the discrimination of parasite young, the superior strategy depends on the difference between the benefit of the dilution effect and the risk of ejecting one's own young. However, even if the host cannot distinguish between its own and parasite young and regardless of the error rate for the discrimination of parasite eggs, when the clutch size is equal to the number of parasitism events strategy B will always be superior to strategy A (Figure 2A). Under conditions of small clutch sizes and multiple parasitism, strategy B is more likely to evolve.

Based on our observations and published findings, the large-billed gerygone

appears subject to these conditions. The predominant clutch sizes of large-billed gerygones are two (36.8%) and three (54.2%) (2.65 ± 0.66 SD, N=190) (Mulyani 2004), while the parasitism rate of large-billed gerygone nests is high (41%, N=155) (Mulyani 2004), and 13.5% of parasitized nests (N=148) contain more than one cuckoo egg (Brooker & Brooker 1989). Brooker & Brooker (1989) also described that the incidence of multiple parasite eggs per the large-billed gerygone nest seems to be particularly high compared to other *Chalcites* species. With the assumption that parasitism rates correlate with the frequency of multiple parasitism, when compared with other hosts of host-evicting brood parasites, the large-billed gerygone has a unique combination of small clutch size and high parasitism rates (Figure 2B).

Discussion

The previously proposed hypotheses seem insufficient to explain the observed nestling ejection behaviour in the absence of egg rejection in the large-billed gerygone. The evolutionary lag hypothesis is implausible, as it appears sufficient evolutionary time for the occurrence and selection of the necessary mutation(s) for nestling ejection behaviour has passed. The bill-size constraint hypothesis also seems to be inadequate

given that hosts who suffer from this constraint have evolved other anti-parasitic strategies, such as abandoning parasitized nests at the egg stage (Davies 2000) and burying cuckoo eggs in the bottom of nests (Sealy 1995). Although the mafia hypothesis cannot be refuted, our research team did not observe the little bronze-cuckoos revisiting parasitized the large-billed gerygone nests in more than ten large-billed gerygone nests that were monitored for a long period. Although the cryptic egg hypothesis proposes a reasonable explanation, it cannot explain why nestling ejection has been observed in only some gerygone species.

The EDE hypothesis can explain this behaviour as follows: nestling ejection is likely to evolve in those hosts with small clutch sizes and high parasitism rates as the relative fitness of this strategy versus egg ejection is higher. The required conditions of the EDE hypothesis are consistent with the ecology of large-billed gerygone (Figure 2A, B). Still, EDE and cryptic egg hypotheses are not mutually exclusive. For example, cryptic eggs which more difficult for the host and probably rival cuckoo to distinguish their own eggs from parasite eggs, increases the benefit of accepting parasitic eggs with EDE. Although I cannot dismiss the possibility that nestling ejection exists in other

species but has yet to be detected, in such cases, the EDE represents an additional effect for increasing the host benefit of accepting parasitic eggs and assisting in the evolution of rejecting parasitic nestlings.

Table 1. Expected and relative pay-offs of strategies A and B for hosts who are parasitized twice.

| strategy | clutch size | | | | | |
|------------------------|-------------|------|------|------|------|------|
| | 2 | 3 | 4 | 5 | 6 | 7 |
| A | 0 | 1 | 2 | 3 | 4 | 5 |
| B | 0.5 | 1.33 | 2.25 | 3.2 | 4.17 | 5.14 |
| relative pay-off (B/A) | ∞ | 1.33 | 1.13 | 1.07 | 1.04 | 1.03 |

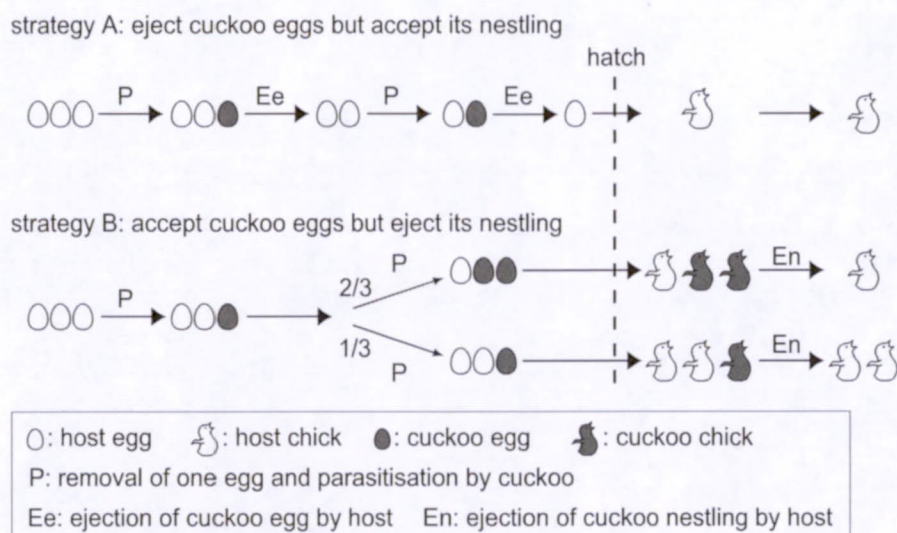


Figure 1. Egg dilution effect hypothesis

A female cuckoo usually removes one egg from the host nest. Host A, an egg ejector, constantly loses one of its own eggs with every parasitism event, while host B, an egg acceptor, has a lower probability of loss. The relative pay-off of host B compared to host A increases with multiple parasitism, and with decreasing clutch sizes of the host (e.g., when clutch size is two, typical of the studied hosts, host B is expected to raise an average of 0.5 chicks while host A would fail to raise any offspring). Host B additionally benefits if cuckoos selectively remove rival cuckoo eggs to prevent their own chick from being evicted by the conspecific chick.

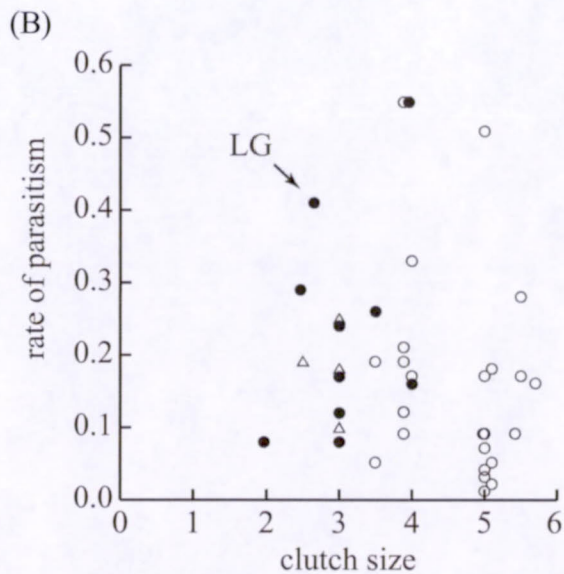
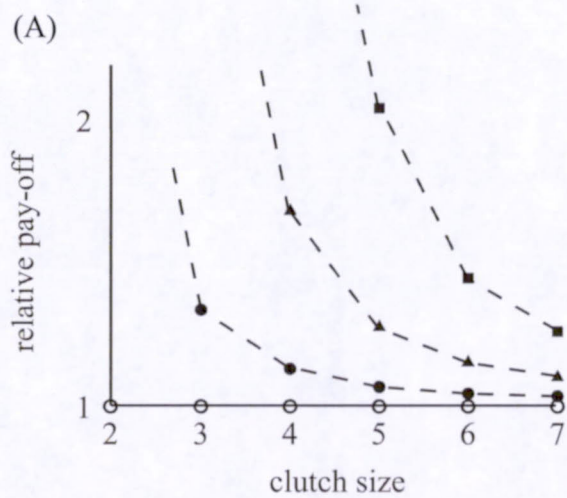


Figure 2. (A) Relative pay-off of strategy B to A (B/A). Open circles, closed circles, triangles, and squares represent nests parasitized from one to four times, respectively. (B) Comparison of clutch sizes and rates of parasitism among host species whose brood is destroyed by parasite hatchlings. Closed circles, open circles, and open triangles represent hosts of *Chalcites*, *Cuculus*, and *Chrysococcyx* species, respectively. The details of this analysis are included in the Appendix 1.

Appendix 1. Frequency of parasitism and clutch size of hosts

| Parasite | Host | Parasitism rate | Clutch size | Source | |
|---------------|--|---|-------------|--------|-----------------------------------|
| Common Cuckoo | <i>Cuculus</i> <i>canorus</i> | | | | |
| | Tree Pipit | <i>Anthus</i> <i>trivialis</i> | 0.07 | 5 | Wyllie 1981, Handbook* vol. 13 |
| | Meadow Pipit | <i>Anthus</i> <i>pratensis</i> | 0.09 | 5.42 | Wyllie 1981, Langmore et al. 2005 |
| | Pied Wagtail | <i>Motacilla alba</i> | 0.03 | 5 | Wyllie 1981, Handbook* vol. 9 |
| | | | 0.09 | 5 | |
| | Dunnock | <i>Prunella</i> <i>modularis</i> | 0.02 | 5.1 | Wyllie 1981, Langmore et al. 2005 |
| | | | 0.02 | 5.1 | |
| | | | 0.18 | 5.1 | |
| | | | 0.05 | 5.1 | |
| | Reed Warbler | <i>Acrocephalus</i> <i>scirpaceus</i> | 0.19 | 3.89 | Wyllie 1981, Langmore et al. 2005 |
| | | | 0.55 | 3.89 | |
| | | | 0.09 | 3.89 | |
| | | | 0.21 | 3.89 | |
| | | | 0.12 | 3.89 | |
| | Great Reed Warbler | <i>Acrocephalus</i> <i>arundinaceus</i> | 0.51 | 5 | Wyllie 1981, Handbook* vol.11 |
| | Sedge Warbler | <i>Acrocephalus</i> <i>schoenobaenus</i> | 0.09 | 4.98 | Wyllie 1981, Langmore et al. 2005 |
| | Robin | <i>Erithacus</i> <i>rubecula</i> | 0.01 | 5 | Wyllie 1981, Langmore et al. 2005 |
| | | | 0.04 | 5 | |
| | | | 0.17 | 5 | |
| Little Cuckoo | <i>Cuculus</i> <i>poliocephalus</i> | Bush warbler <i>Cettia diphone</i> | 0.33 | 4 | Higuchi 1998, Handbook* vol. 11 |

| | | | | | | |
|---------------|-----------------------------|----------------------------------|---------------------------------|------|------|---|
| | | Wren | <i>Troglodytes troglodytes</i> | 0.16 | 5.7 | Higuchi 1998, Langmore <i>et al.</i> 2005 |
| | | Ijima's willow warbler | <i>Phylloscopus ijimae</i> | 0.19 | 3.5 | Higuchi 1998, Handbook* vol. 11 |
| | | Meadow bunting | <i>Emberiza cioides</i> | 0.17 | 4 | Higuchi 1998, Walters 1980 |
| | | Bull-headed shrike | <i>Lanius bucephalus</i> | 0.17 | 5.5 | Higuchi 1998, Handbook* vol. 13 |
| | | Middendorf's grasshopper warbler | <i>Locustella ochotensis</i> | 0.28 | 5.5 | Higuchi 1998, Handbook* vol. 11 |
| | | Japanese White-eye | <i>Zosterops japonica</i> | 0.05 | 3.5 | Higuchi 1998, Handbook* vol. 13 |
| Didric Cuckoo | <i>Chrysococcyx caprius</i> | Masked Weaver | <i>Ploceus velatus</i> | 0.1 | 3 | Wyllie 1981, Walters 1980 |
| | | | | 0.18 | 3 | |
| | | red bishop | <i>Euplectes orix</i> | 0.1 | 3 | Wyllie 1981, Walters 1980 |
| | | | | 0.25 | 3 | |
| | | Lesser Masked Weaver | <i>Ploceus intermedius</i> | 0.19 | 2.5 | Davies 2000, Walter 1980 |
| | Chrysococcyx | Pririt Puhh-back Flycatcher | <i>Batis pririt</i> | 0.08 | 2 | Wyllie 1981, Handbook* vol. 11 |
| Klaas Cuckoo | cyx klaas | Yellow-bellied Bush Warbler | <i>Eremomela icteropygialis</i> | 0.29 | 2.5 | Wyllie 1981, Handbook* vol. 11 |
| Little | <i>Chalcites</i> | Large-billed | <i>Gerygone</i> | 0.41 | 2.65 | Mulyani 2004 |
| Bronze-Cuckoo | <i>Minutillus</i> | Gerygone | <i>magnirostris</i> | | | |
| Horsfield's | <i>Chalcites</i> | Splendid Fairy-wren | <i>Malurus splendens</i> | 0.17 | 3 | Brooker1989 |
| Bronze-Cuckoo | <i>basalis</i> | | | 0.24 | 3 | Brooker1989 |
| | | Western Thornbill | <i>Acanthiza inornata</i> | 0.12 | 3 | Brooker1989 |
| | | superb fairy-wren | <i>Malurus</i> | 0.16 | 4 | Langmore 2007 |

| | | | | | | |
|---------------|------------------|-------------------|--------------------|------|-----|-------------|
| Shining | <i>Chalcites</i> | Yellow-rumped | <i>Acanthiza</i> | 0.26 | 3.5 | Brooker1989 |
| Bronze-Cuckoo | <i>lucidus</i> | Thornbill | <i>chrysorrhoa</i> | | | |
| | | Western Thornbill | <i>Acanthiza</i> | 0.08 | 3 | Brooker1989 |
| | | | <i>inornata</i> | | | |
| | | | <i>Gerygone</i> | | | |
| | | Gray Warbler | <i>igata</i> | 0.55 | 4 | Gill 1998 |

Chapter V Evolution of nestling ejection in *Gerygone* spp. driven by the egg dilution effect

Introduction

The common cuckoo *Cuculus canorus* is one of the model species for research of avian brood parasitism (Willie 1981; Davies 2011; Kilner 2013). Although numerous host species of the common cuckoo have evolved various anti-parasite strategies like rejection of the cuckoo egg from the nest, cuckoos sometimes elude these defences. If the cuckoo egg hatches, the hosts will always raise the alien nestling even though the cuckoo nestling evicts all other nest mates (Davies 2000). The question why hosts raise huge alien nestlings, is still unsolved even though previous theoretical studies attempted to solve it (Lotem 1993; Grim 2006; see chapter IV).

Recently, ejection of parasite nestlings has been observed in two Australian warbler species *Gerygone* spp., which are hosts of the little bronze-cuckoo *Chalcites minutillus* (formerly *Chrysococcyx minutillus*) (Tokue & Ueda 2010; Chapter I). These new discoveries provide a chance to solve the puzzle of the evolution of nestling ejection. Both species eject parasite nestlings but not alien eggs (Chapter I; Tokue & Ueda 2010). I suggested in chapter IV that the two *Gerygone* species accept parasite

eggs to save their own offspring (egg dilution effect hypothesis). The nests of these hosts are sometimes parasitized by more than one bronze-cuckoo females (Brooker & Brooker 1989a; Tokue 2011). As bronze-cuckoos usually remove one egg from the host nest when they lay their own egg (Brooker & Brooker 1989b), the second bronze-cuckoo might replace the parasite egg instead of a host egg. In this case, hosts can save their own offspring from the parasitism of the first bronze-cuckoo (egg dilution effect). The effect increases with decreasing hosts' clutch size because the probability for each single egg to be replaced is $1/\text{clutch size}$. Additionally, the worth value of one egg in a small clutch is higher than that in a large clutch. Besides, under the assumption that bronze-cuckoos can distinguish between host and cuckoo eggs, there is always a gain for the host in accepting a parasite egg, because the second bronze-cuckoo will replace the first cuckoo egg (Davies & Brooke 1988; Brooker et al. 1990; see also chapter IV). The hypothesis therefore suggests that multiple parasitism and small clutch size of hosts promote the evolution of parasite nestling ejection and parasite egg acceptance by the host.

Here, I test the egg dilution effect hypothesis comparing four *Gerygone*

species which are different in clutch size, frequency of parasitism, and frequency of multiple parasitism in three regions of Oceania. All species are parasitized by *Chalcites* spp. The large-billed gerygone *Gerygone magnirostris* and the mangrove gerygone *G. levigaster* eject parasite nestlings (Chapter I; Tokue & Ueda 2010), while the grey gerygone *G. igata* has never been observed to eject nestlings (Gill 1983; 1998). Possible ejection behaviour of the fan-tailed gerygone *G. flavolateralis* was unknown, which is why I studied this species in New Caledonia. I found that this species also ejects parasite nestlings.

Methods

I conducted fieldwork in the Parc provincial des Grandes Fougères (PGF, 300–860 m above sea level, 21° 37' S, 165° 46' E) on the mainland of New Caledonia from 2011 to 2013 during the breeding seasons of the fan-tailed gerygone (September-January) (del Hoyo et al. 2003). PGF is a 45-km² reserve and its vegetation consists mainly of medium-altitude rainforest, including secondary forest with scrub, savanna, and pine plantations.

I searched for nests of the fan-tailed gerygone within the PGF and

subsequently monitored their fate. Whenever I found an egg of the shining bronze-cuckoo *Chalcites lucidus* in a nest, I continuously filmed the nest throughout the incubation and nestling periods using infrared video cameras and digital recorders (see Gula et al. 2010). A total of 7 nests were monitored over 2,100 hours.

Statistical analyses were performed using R version 2.15.3 (The R Foundation for Statistical Computing). I compared clutch size, frequency of parasitism and frequency of multiple parasitism in the four *Gerygone* species (Table 1). To compare clutch size in the four species, I used a generalized linear model (GLM) with a Poisson distribution and log link. I used a generalized linear model (GLM) with a binomial distribution and logit link to compare frequency of parasitism and of multiple parasitism.

Results

I found 33 active nests in 2011 and 2012, of those 11 nests (33.3%) were parasitized by the shining bronze-cuckoo. In one nest, a cuckoo replaced another cuckoo egg (frequency of multiple parasitism = 9%). The mean clutch size of the fan-tailed gerygone was 2.0 (SE=0.7, n=13) in unparasitized nests. In parasitized nests,

I recorded four occasions in which the cuckoo offspring was ejected by an adult fan-tailed gerygone by video cameras (Table 1). In other nests, cuckoo nestlings died either because of predation or desertion by the hosts.

The first case of nestling ejection was observed on the 10th of November 2011. The host's nest had one cuckoo egg and one host egg from the 24th of October to 9th of November. The ejection event occurred in the early morning (05:57). One of the host parents (of unknown sex) come back to the nest and looked into the nest for about 20 seconds, and then ejected the cuckoo nestling from the nest. After the event, one of the host parents (probably female) incubated the own egg for a few more days. As the own egg did not hatch within the normal incubation length, the nest was abandoned.

The other three cases of ejection occurred in 2012. In the second case, the nest contained one cuckoo egg and one host egg on the 14th of November, thereafter in the next nest check on the 19th of November, only a host nestling remained. Although the ejection event was not clearly visible on the video footage, the host probably ejected the alien offspring at 18:10 on the 17th of November. The host nestling might have fledged afterwards. The third event occurred at 15:37 on the 28th of November by the

host (of unknown sex) on the same day that the cuckoo chick hatched. The nest contained one cuckoo egg and two host eggs from the 12th to the 27th of November. After the eviction, the host abandoned the nest that still contained the two own eggs. The fourth event probably occurred on the 11th of November. The nest had only one cuckoo egg when I found it on the 7th of November. The egg disappeared before the 13th of November. Although the video footage is not clear, the ejection might have occurred at 18:09 on the 11th of November. The host deserted the nest after the event. Since no predator visited the nest during monitoring from the 10-13th of November, it is likely that the host ejected the alien offspring. Although the hosts of the four nests were not marked with rings, I assume that the four ejecting adults were different individuals based on the location of nests and timing of breeding.

When comparing the four gerygone species (Table 2), the clutch size of the grey gerygone, which is the only species that does not evict parasite nestlings, is significantly larger than those of the other three gerygone species ($p < 0.0001$; Figure 1). In contrast, the frequency of parasitism ($p < 0.01$) and the frequency of multiple parasitism ($p < 0.05$) in the grey gerygone is significantly lower than those of the other

three gerygone species (Figure 2).

Discussion

The egg dilution effect hypothesis (Chapter IV) predicts that clutch size of a nestling ejector is lower than that of a non-ejector. As predicted, clutch size of the grey gerygone, which is non-ejector, was larger than those of other three nestling ejectors (*Gerygone* spp.) (Figure 1). However, the hypothesis cannot explain why the grey gerygone has not evolved any rejection behaviour such as egg ejection. One possibility might be that there is low parasitism pressure on the grey gerygone. Although the grey gerygone breeds twice in the breeding season, shining bronze-cuckoos arrive later at the host breeding area and lay their eggs only during the second breeding peak of the gerygone. Therefore, grey gerygones can breed without parasitism during their first breeding peak (Gill 1998), which might prevent an adaptation to the parasite. In contrast, the other gerygone species are parasitized throughout the breeding season because bronze-cuckoos do not migrate in those regions. As a result, frequency of parasitism on the grey gerygone is lower than that of the others (Figure 2). Second, the hypothesis needs multiple parasitism (Chapter IV). As the hypothesis predicts, ejector species are

multiply parasitized, whereas the grey gerygone is never subsequently parasitized (Figure 2).

In conclusion, I showed in this chapter that clutch size and multiple parasitism influence the evolution of nestling ejection and I suggest that the egg dilution effect promotes the evolution of nestling ejection.

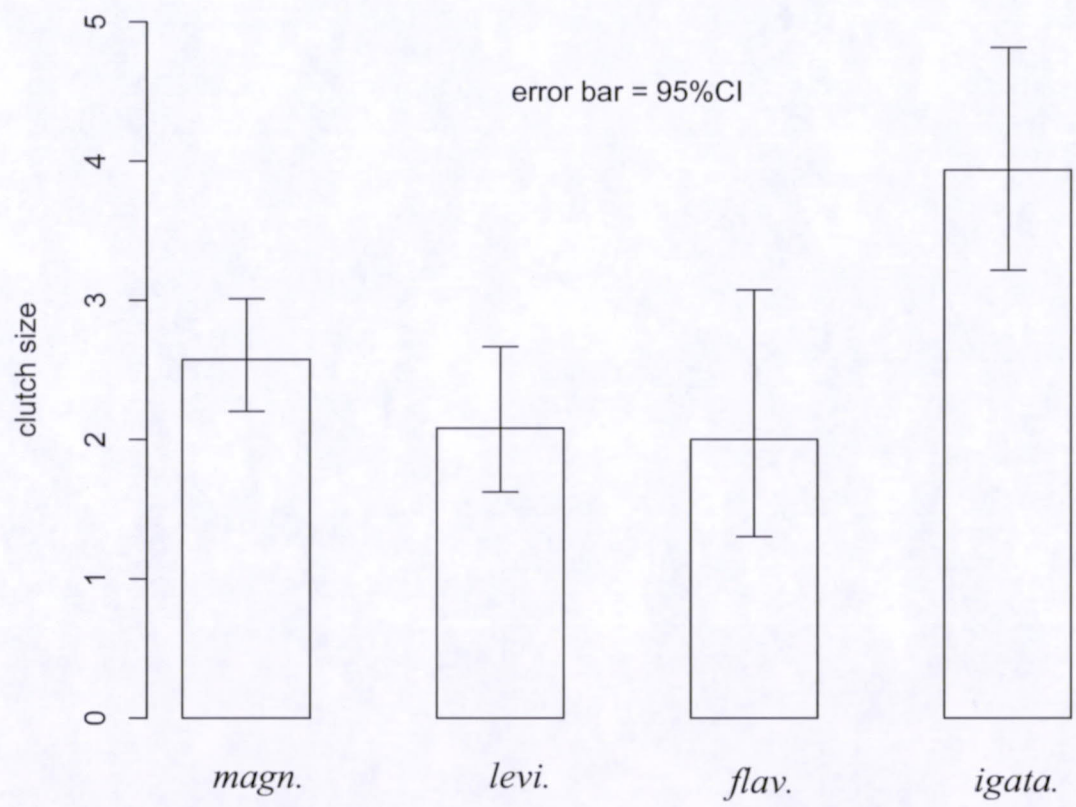


Figure 1. Comparison of mean (with 95% confidence intervals) clutch size in four *Gerygone* species.

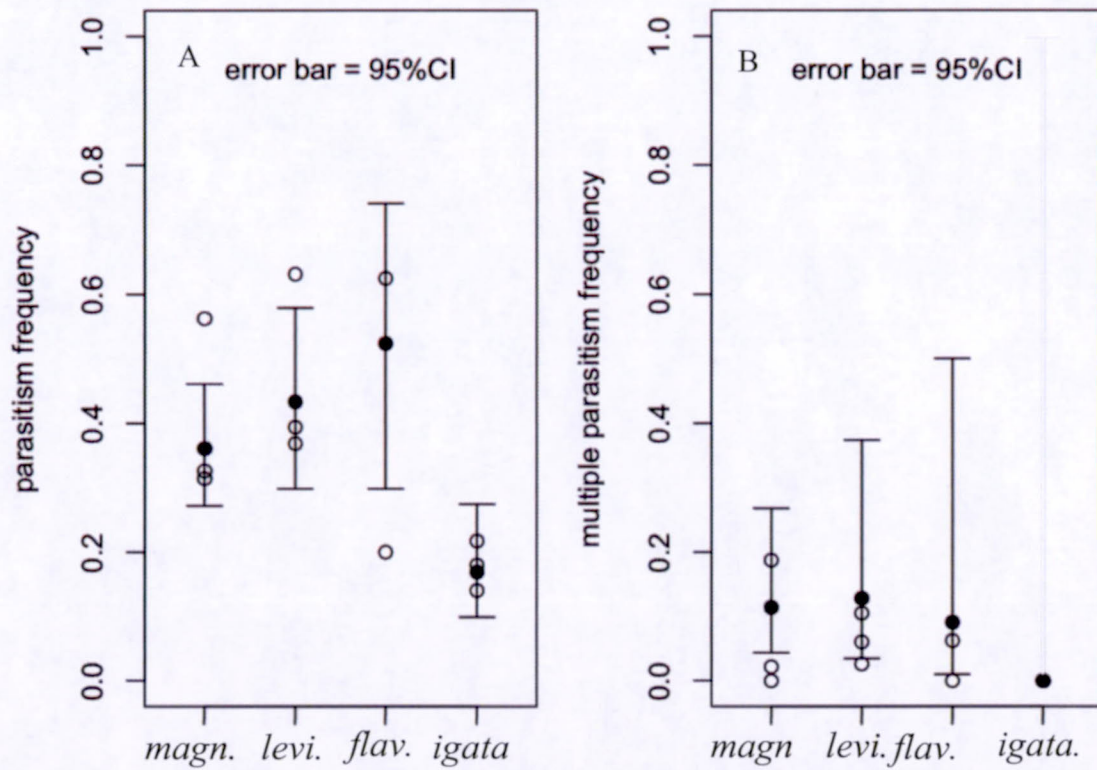


Figure 2. Comparison of frequency of parasitism (A) and frequency of multiple parasitism (B) in four gerygone species. The open dots represent single studies and the black dots averages (with 95% confidence intervals).

Table 1. Outcomes of breeding attempts by the fan-tailed gerygone during which cuckoo nestlings were ejected.

| No. | Nest contents when 1 st nestling was ejected | | | | Which was ejected | | Outcome |
|-----|---|---------|---------|---------|-------------------|---|-------------------------|
| | C egg | C young | H egg | H young | C | H | |
| 1 | 0 | 1 | 1 | 0 | 1 | 0 | Host egg did not hatch |
| 2 | 0 or 1* | 0 or 1* | 0 or 1* | 0 or 1* | 1 | 0 | One host young fledged |
| 3 | 0 | 1 | 2 | 0 | 1 | 0 | Host abandoned the nest |
| 4 | 0 or 1* | 0 or 1 | 0 | 0 | 1 | 0 | Nest was empty |

C = cuckoo, H = host

*It is not clear whether a chick hatched

Table 2. Clutch size, frequency of parasitism, and frequency of multiple parasitism in four gerygone species

| | <i>G. magnirostris</i> | <i>G. levigaster</i> | <i>G. flavolateralis</i> | <i>G. igata</i> |
|----------------------------------|------------------------|----------------------|--------------------------|-----------------|
| Clutch size (SD) | 2.6 (0.73) | 2.1 (0.72) | 2.0 (0.68) | 3.9 (0.3) |
| Sample size | 61 | 50 | 13 | 60 |
| Frequency of parasitism | 0.36 | 0.43 | 0.45 | 0.28 |
| Frequency of multiple parasitism | 0.11 | 0.12 | 0.09 | 0 |
| Reference | Tokue 2011 | Tokue 2011 | This study | Gill 1983; 1998 |

General discussion

In chapter I of this thesis, I described bronze-cuckoo nestling ejection behaviour by the host. This behaviour was thought to be maladaptive for a long time because hosts of the common cuckoo never reject any nestling (Davies 2000). However, the evolution of ejection behaviour does not seem impossible because at least three *Gerygone* species have evolved the behaviour in Australia and New Caledonia (Chapter I; Tokue & Ueda 2010; Chapter V). Therefore, this behaviour should be adaptive for hosts of bronze-cuckoos, although it seems to be maladaptive for hosts of the common cuckoo. I challenged this former belief in chapter II, III and IV.

First, I attempted in chapter II to figure out how hosts discriminate nestlings. A host of the common cuckoo uses its memory to discriminate and eject odd eggs (Lotem et al. 1992). In a similar way, hosts that can discriminate nestlings seem to use their memory because the alien nestling is not always the minority in the nest. In this case, hosts are not able to recognize the parasite by discordance. Therefore, hosts have to learn recognizing their offspring or need an innate memory. Lotem (1993) showed that nestling ejection behaviour would be too costly if hosts of the common cuckoo

imprinted on eggs and chicks in their first breeding attempt as their offspring. Therefore, hosts should not evolve nestling ejection.

In chapter III, I challenged to this theory to show how hosts can reduce the cost of chick discrimination. The key factor for the cost is the evicting behaviour of the cuckoo chick. The common cuckoo chick usually evicts all host eggs before they hatch. In contrast, some bronze-cuckoo chicks sometimes evict host nestling because the chick does not hatch earlier than host chicks (Tokue 2011). This difference is important for hosts, because the timing of eviction seems to reduce the cost of nestling ejection. I demonstrated this reduction of cost using a mathematical model in chapter III. It is unclear why cuckoo chicks sometimes hatch after host nestlings. There are several possibilities. One is that hosts have evolved a shorter incubation length as an anti-parasitism strategy. A second possibility is that cuckoos could not set to lay own egg before host's incubation period because the host nests is domed and then the cuckoos can not know the timing. To find out which possibility is most likely, it would be necessary to collect data of incubations lengths from related species.

In chapter IV, I showed a mathematical model that small clutch size of hosts

and high frequency of multiple parasitism by bronze-cuckoos promote nestling ejection.

These aspects are not in the focus of studies on avian brood parasitism because these factors seemed not to be associated with anti-parasitism behaviour of hosts (Langmore et al. 2005). It is also possible that still other factors affect anti-parasitism strategy and parasite strategy.

In the last chapter, I tested the egg dilution effect hypothesis in comparing four gerygone species. I showed that clutch size of the grey gerygone, which has not evolved nestling ejection behaviour, is larger, whereas the frequency of multiple parasitism is lower than those of other gerygone species that eject parasite nestlings. These results support the egg dilution effect hypothesis.

In conclusion, I showed in this study that evolutionary process of ejection behaviour in cuckoo hosts. In addition, this study suggests that the arms race of the common cuckoo and its hosts is not representative for other cuckoos. Therefore, it is important to attempt cross-species comparison in the future to clarify the co-evolutional arms race.

Acknowledgements

Many people have helped for my doctoral thesis. My studies of bronze-cuckoo and their hosts have been done together with Osamu Mikami, Richard Noske, Keita Tanaka and Kihoko Tokue. It is a pleasure to thank them, and the Japan Society of the Promotion of Science grant no. 18405009, 2325500, 30625059 and 24-4578, and Rikkyo University Special Fund for Research, for funding the study.

I thank Henri Bloc, Jim Briskie, Miles Burford, Kazuhiro Eguchi, Steph Hodges, Masaoki Kamioki, Yoann Kawa, Noriyoshi Kawasaki, Sayaka Mori, Toru Nakahara, Mao Nakamura, Tomoki Okida, Yuji Okahisa, Leslie Poulson, Kieran Tibble, Mailee Stanbury, Tatsuya Sanno, Keletaona Seelino, Chihiro Ueda, Noriyuki Yamaguchi, and Daisuke Yamashita for help in data collection. I also thank Craig Barnett, Mélanie Françoise, Shumpei Kitamura, Mark Hauber, Ros Gloag, Daizaburo Shizuka, Toshitaka Suzuki, David Wheatcroft for valuable comments in my study. Finally a special thank to Ueda laboratory in Rikkyo University, the Parc des Grandes Fougères and the field station of Canterbury University for help my study. I dedicate this thesis to my parents, Kazuko and Kiyoshi.

References

- Aristote. 1936. Aristotle. Minor Works... With an English Translation by WS Hett. Mass., Harvard University Press.
- Bán, M., C. Moskát, Z. Barta, and M. E. Hauber. 2013. Simultaneous viewing of own and parasitic eggs is not required for egg rejection by a cuckoo host. *Behavioral Ecology*.
- Briskie, J. V. 2007. Direct observations of Shining Cuckoos (*Chrysococcyx lucidus*) parasitising and depredating Grey Warbler (*Gerygone igata*) nests. *Notornis* **54**:15.
- Brooke, M. d. L. and N. Davies. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335**:630-632.
- Brooker, L., M. Brooker, and A. Brooker. 1990. An alternative population/genetics model for the evolution of egg mimesis and egg crypsis in cuckoos. *Journal of Theoretical Biology* **146**:123-143.
- Brooker, L. and B. Michael. 1998. Why do splendid fairy-wrens always accept cuckoo eggs? *Behavioral Ecology* **9**:420-424.
- Brooker, M. and L. Brooker. 1996. Acceptance by the splendid fairy-wren of parasitism by Horsfield's bronze-cuckoo: further evidence for evolutionary equilibrium in brood parasitism. *Behavioral Ecology* **7**:395-407.
- Brooker, M. G. and L. Brooker. 1989a. The comparative breeding behaviour of two sympatric cuckoos, Horsfield's Bronze-Cuckoo *Chrysococcyx basalts* and the Shining Bronze-Cuckoo *C. lucidus*, in Western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. *Ibis*

131:528-547.

- Brooker, M. G. and L. Brooker. 1989b. Cuckoohosts in Australia. RZSNSW.
- Brooker, M. G., L. Brooker, and I. Rowley. 1988. Egg deposition by the bronze-cuckoos *Chrysococcyx basalis* and *Ch. lucidus*. *Emu* **88**:107-109.
- Chance, E. P. 1940. The truth about the Cuckoo. Country life, Limited.
- Colombelli-Négrel, D., M. E. Hauber, J. Robertson, F. J. Sulloway, H. Hoi, M. Griggio, and S. Kleindorfer. 2012. Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Current Biology*.
- Davies, N. 2011. Cuckoo adaptations: trickery and tuning. *Journal of Zoology* **284**:1-14.
- Davies, N. and M. d. L. Brooke. 1988. Cuckoos versus reed warblers: adaptations and counteradaptations. *Animal Behaviour* **36**:262-284.
- Davies, N. B. 2010. Cuckoos, cowbirds and other cheats. Poyser.
- Dawkins, R. and J. R. Krebs. 1979. Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **205**:489-511.
- Del Hoyo, J., A. Elliot, and J. Sargatal. 1992. Handbook of the Birds of the World. Barcelona: Lynx Editions.
- Friedmann, H. 1968. The evolutionary history of the avian genus *Chrysococcyx*.
- Gill, B. 1998. Behavior and ecology of the shining cuckoo, *Chrysococcyx lucidus*. OXFORD ORNITHOLOGY SERIES **9**:143-151.
- Gill, B. J. 1983. Brood-parasitism by the Shining Cuckoo *Chrysococcyx lucidus* at Kaikoura, New Zealand. *Ibis* **125**:40-55.
- Grim, T. 2006. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evolutionary Ecology Research* **8**:785-802.

- Grim, T., O. Kleven, and O. Mikulica. 2003. Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism? *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**:S73-S75.
- Gula, R., J. Theuerkauf, S. Rouys, and A. Legault. 2010. An audio/video surveillance system for wildlife. *European Journal of Wildlife Research* **56**:803-807.
- Hauber, M. E. and R. M. Kilner. 2007. Coevolution, communication, and host chick mimicry in parasitic finches: who mimics whom? *Behavioral Ecology and Sociobiology* **61**:497-503.
- Higgins, P. J. 1999. *Handbook of Australian, New Zealand & Antarctic Birds. Vol. 4, Parrots to Dollarbird.* Oxford University Press Melbourne.
- Higuchi, H. 1998. Host use and egg color of Japanese cuckoos. *OXFORD ORNITHOLOGY SERIES* **9**:80-93.
- Lahti, D. C. and A. R. Lahti. 2002. How precise is egg discrimination in weaverbirds? *Animal Behaviour* **63**:1135-1142.
- Langmore, N. and R. Kilner. 2007. Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalis*. *Animal Behaviour* **74**:995-1004.
- Langmore, N. and R. Kilner. 2009. Why do Horsfield's bronze-cuckoo *Chalcites basalis* eggs mimic those of their hosts? *Behavioral Ecology and Sociobiology* **63**:1127-1131.
- Langmore, N. and R. Kilner. 2010. The coevolutionary arms race between Horsfield's Bronze-Cuckoos and Superb Fairy-wrens. *Emu* **110**:32-38.
- Langmore, N., R. Kilner, S. Butchart, G. Maurer, N. Davies, A. Cockburn, N. Macgregor, A. Peters, M. Magrath, and D. Dowling. 2005. The evolution of egg

- rejection by cuckoo hosts in Australia and Europe. *Behavioral Ecology* **16**:686-692.
- Langmore, N., M. Stevens, G. Maurer, and R. Kilner. 2009a. Are dark cuckoo eggs cryptic in host nests? *Animal Behaviour* **78**:461-468.
- Langmore, N. E., A. Cockburn, A. F. Russell, and R. M. Kilner. 2009b. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology* **20**:978-984.
- Langmore, N. E., S. Hunt, and R. M. Kilner. 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**:157-160.
- Langmore, N. E., G. Maurer, G. J. Adcock, and R. M. Kilner. 2008. Socially acquired host-specific mimicry and the evolution of host race in horsefield's bronze-cuckoo *chalcites basalis*. *Evolution* **62**:1689-1699.
- Langmore, N. E., M. Stevens, G. Maurer, R. Heinsohn, M. L. Hall, A. Peters, and R. M. Kilner. 2011. Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society B: Biological Sciences* **278**:2455-2463.
- Lawes, M. J. and T. R. Marthews. 2003. When will rejection of parasite nestlings by hosts of nonevicting avian brood parasites be favored? A misimprinting-equilibrium model. *Behavioral Ecology* **14**:757-770.
- Lotem, A. 1993. Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature* **362**:743-745.
- Lotem, A., H. Nakamura, and A. Zahavi. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behavioral Ecology* **3**:128-132.
- Moskát, C., M. Bán, T. Székely, J. Komdeur, R. W. Lucassen, L. A. van Boheemen, and M. E. Hauber. 2010. Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood

- parasites. *The Journal of Experimental Biology* **213**:1976-1983.
- Moskát, C., E. C. Rosendaal, M. Boers, A. Zölei, M. Bán, and J. Komdeur. 2011. Post-ejection nest-desertion of common cuckoo hosts: a second defense mechanism or avoiding reduced reproductive success? *Behavioral Ecology and Sociobiology* **65**:1045-1053.
- Mulyani YA (2004) Reproductive ecology of tropical mangrove-dwelling warblers: the roles of nest predation, brood parasitism and food limitation. PhD thesis, Charles Darwin University.
- Noske, R. A. 2001. The breeding biology of the mangrove gerygone, *Gerygone laevigaster*, in the Darwin region, with notes on brood parasitism by the little bronze-cuckoo, *Chrysococcyx minutillus*. *Emu* **101**:129-135.
- Payne, R. B. and L. L. Payne. 1998. Nestling eviction and vocal begging behaviors in the Australian glossy cuckoos *Chrysococcyx basalis* and *C. lucidus*. *Oxford ornithology series* **9**:152-172.
- Payne, R. B. and M. D. Sorensen. 2005. *The cuckoos*. OUP Oxford.
- Peck, A. L. 1993. *Historia animalium*. Loeb Classical Library.
- Požgayová, M., P. Procházka, L. Polačiková, and M. Honza. 2011. Closer clutch inspection—quicker egg ejection: timing of host responses toward parasitic eggs. *Behavioral Ecology* **22**:46-51.
- Rohwer, S. and C. D. Spaw. 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evolutionary Ecology* **2**:27-36.
- Røskaft, E., A. Moksnes, B. G. Stokke, V. Bicić, and C. Moskát. 2002. Aggression to dummy cuckoos by potential European cuckoo hosts. *Behaviour*:613-628.

- Rothstein, S. I. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. *The Auk* **91**:796-807.
- Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics* **21**:481-508.
- Rothstein, S. I. and S. K. Robinson. 1998. *Parasitic birds and their hosts: studies in coevolution*. Oxford University Press on Demand.
- Sato, N. J., O. K. Mikami, and K. Ueda. 2010a. The egg dilution effect hypothesis: a condition under which parasitic nestling ejection behaviour will evolve. *Ornithological Science* **9**:115-121.
- Sato, N. J., K. Tokue, R. A. Noske, O. K. Mikami, and K. Ueda. 2010b. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biology Letters* **6**:67-69.
- Schuetz, J. G. 2005. Reduced growth but not survival of chicks with altered gape patterns: implications for the evolution of nestling similarity in a parasitic finch. *Animal Behaviour* **70**:839-848.
- Shizuka, D. and B. E. Lyon. 2009. Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature* **463**:223-226.
- Soler, M., J. Soler, J. Martinez, and A. Moller. 1995. Magpie host manipulation by great spotted cuckoos: evidence for an avian mafia? *Evolution*:770-775.
- Stoddard, M. C. and R. M. Kilner. 2013. The past, present and future of 'cuckoos versus reed warblers'. *Animal Behaviour*.
- Tanaka, K. D. and K. Ueda. 2005. Horsfield's hawk-cuckoo nestlings simulate multiple gapes for begging. *Science* **308**:653-653.
- Tokue, K. 2011. Cuckoo versus hosts with unique defence strategy at nestling stage:

- Evolutionary arms-race in the tropic. PhD thesis, Tokyo: Rikkyo University.
- Tokue, K. and K. UEDA. 2010. Mangrove Gerygones *Gerygone laevigaster* eject Little Bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* **152**:835-839.
- Welbergen, J. A. and N. B. Davies. 2009. Strategic variation in mobbing as a front line of defense against brood parasitism. *Current Biology* **19**:235-240.
- Winfrey, R. 1999. Cuckoos, cowbirds and the persistence of brood parasitism. *Trends in ecology & evolution* **14**:338-343.
- Wyllie, I. 1981. *The cuckoo*. BT Batsford.
- Yom-Tov, Y. 1987. The reproductive rates of Australian passerines. *Wildlife Research* **14**:319-330.