



# Breeding biology of the Fan-tailed Gerygone *Gerygone flavolateralis* in relation to parasitism by the Shining Bronze-cuckoo *Chalcites lucidus*

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## Abstract

Apart from a few well-studied examples, there is little information regarding the life history and ecological requirements of brood parasites and their hosts in most cuckoo–host systems, particularly in tropical areas. In New Caledonia, the Fan-tailed Gerygone *Gerygone flavolateralis*, is the exclusive host of the Shining Bronze-cuckoo, *Chalcites lucidus*. Here, the arms race has escalated to the nestling stage, and both host and parasite have polymorphic (difference in skin coloration) nestlings. This is a novel system for the study of brood parasitism, but very little is known about the breeding biology of the Fan-tailed Gerygone and how this may affect the co-evolutionary interactions with the Shining Bronze-cuckoo. We monitored active nests of the Fan-tailed Gerygone during six breeding seasons, using video monitoring and direct observation. Nest attendance periods of host parents were shorter during laying than during incubation, and therefore parasitism was more likely to occur during the laying period. Cuckoo eggs were on average 2 days more developed than host eggs, and thus cuckoo nestlings usually hatched before host nestlings. Fan-tailed Gerygone nestling phenotypes had similar growth and fledging rates and their frequency did not differ between habitats, indicating no apparent trade-off with skin coloration. The precipitation regime affected predation but not the parasitism rate. The current situation in New Caledonia suggests a higher selection pressure on the parasite than on the host. Our study highlights the importance of data on the breeding biology of the host in the context of studies on brood parasitism.

**Keywords** Arms race · Nestling polymorphism · Laying synchrony · Frontline defences · Cuckoo chick ejection

## Zusammenfassung

**Brutbiologie der Fächerschwanzgerygone *Gerygone flavolateralis* unter Berücksichtigung der Parasitierung durch den Bronzekuckuck *Chalcites lucidus***

Abgesehen von wenigen gut untersuchten Beispielen zum koevolutionären Wettrüsten zwischen Brutparasiten und Wirten gibt es, insbesondere in tropischen Gebieten, nur geringe Kenntnisse zur Lebensweise und zu den ökologischen Anforderungen von Kuckucken und deren Wirten. In Neukaledonien ist die Fächerschwanzgerygone, *Gerygone flavolateralis*, der einzige Wirt des Bronzekuckucks, *Chalcites lucidus*. Auf dieser Insel hat sich das Wettrüsten auf die Kükenphase ausgeweitet und sowohl Wirt als auch Parasit haben polymorphe Küken (Unterschiede in der Hautfärbung). Dies eröffnet neue Möglichkeiten für das Studium von Brutparasitismus. Es ist jedoch sehr wenig über die Brutbiologie der Fächerschwanzgerygone und die möglichen koevolutionären Wechselwirkungen mit dem Bronzekuckuck bekannt. Wir haben aktive Nester der Fächerschwanzgerygone über sechs Brutzeiten mit Videokameras und direkten Beobachtungen

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überwacht. Da die Wirte während der Legephase über kürzere Zeiträume am Nest waren als während der Brutphase, ist die Wahrscheinlichkeit höher, dass die Parasitierung während der Legephase stattfindet. Kuckuckseier waren durchschnittlich 2 Tage weiter entwickelt als Wirtseier, so dass Kuckucksküken in der Regel vor den Wirtsküken schlüpfen. Die Phänotypen der Fächerschwanzgerygone waren in verschiedenen Lebensräumen vergleichbar häufig vertreten und zeigten ähnliche Wachstumsraten und Ausflugerfolge. Dies deutet darauf hin, dass die Ausprägung der Hautfarbe keine Auswirkungen zeigt. Niederschlag beeinflusste die Prädationsrate, aber nicht die Parasitierungsrate. Unsere Studie in Neukaledonien weist auf einen höheren Selektionsdruck auf den Parasiten als auf den Wirt hin und unterstreicht die Bedeutung der Kenntnis zur Brutbiologie des Wirtes für Studien zum Brutparasitismus.

## Introduction

The arms race between avian brood parasites and their hosts is a major topic in behavioural ecology, because it offers an insight into co-evolutionary processes in action (Rothstein 1990; Davies 2000). Despite extensive research on the subject, there still is little knowledge on the life history and breeding biology of some cuckoo–host systems, particularly from tropical areas (Payne 2005; Soler 2014). In addition, the study of cuckoo–host interactions has been until recently focused on a few well-known systems in which the arms race is limited to the frontline (before egg laying) or egg stages (Davies 2011; Feeney et al. 2012, 2014), whereas data about cuckoo–host systems in which the arms race escalates to the nestling stage are still rare (Grim 2011). Life history and ecological requirements of both hosts and parasites affect their co-evolutionary interactions (Tewksbury et al. 2006; Feeney et al. 2014; Hackemack et al. 2016), and thus studies on the basic biology of host and brood parasite are fundamental to understanding the ecological mechanisms underlying the arms race.

In Australasia, bronze-cuckoos of the genus *Chalcites* parasitise several small passerine hosts, and their nestlings evict all host eggs or nestlings (Payne 2005). In a few *Chalcites*–host systems, the arms race has escalated to the nestling stage with hosts discriminating the parasite nestlings (Langmore et al. 2003; Sato et al. 2010a; Tokue and Ueda 2010), which in turn selects for mimicry by bronze-cuckoo nestlings (Tokue and Ueda 2010; Langmore et al. 2011). Members of the genus *Gerygone*, which includes 19 small insectivorous species distributed in the Australasian region (Keast and Recher 2001), are often the main hosts of *Chalcites* cuckoos (Payne 2005). Frontline defences (Feeney et al. 2012) are present at least in the Grey Warbler, *Gerygone igata*, which seems to recognise and attack bronze-cuckoos approaching the nest (Briskie 2007), but it is unknown if this occurs in other *Gerygone* species or if frontline defences extend to nest surveillance as in other bronze-cuckoo hosts (Feeney and Langmore 2015). *Gerygone* species do not seem to be able to reject cuckoo eggs (Mulyani 2004; Langmore et al. 2005, 2009; Gloag et al. 2014; Thorogood et al.

2017), but can discriminate and eject the parasite nestling from the nest (Sato et al. 2010a, 2015; Tokue and Ueda 2010). This host defence strategy has been reported for the Large-billed Gerygone, *G. magnirostris* (Sato et al. 2010a), and the Mangrove Gerygone, *G. laevigaster* (Tokue and Ueda 2010), from Australia, which are parasitised by the Little Bronze-cuckoo, *Chalcites minutillus*, and in the Fan-tailed Gerygone, *G. flavolateralis* (Sato et al. 2015; Attisano et al. 2018), which is parasitised by the local subspecies of the Shining Bronze-cuckoo, *Chalcites lucidus layardi*, in New Caledonia. Besides these examples, no other *Gerygone* hosts of bronze-cuckoos have been reported to discriminate and eject parasite nestlings. Other hosts of brood parasites can discriminate the parasite nestling (Langmore et al. 2003) or fledgling (Grim 2007), but they do so only after the loss of their entire clutch or brood. *Gerygone* hosts, in contrast, discriminate the parasite nestling before it can evict host eggs or nestlings (Sato et al. 2010a, 2015; Tokue and Ueda 2010; Attisano et al. 2018) and thus save their clutch or brood except for the egg ejected by the parasite before laying. Life history and parasitism dynamics of the Shining Bronze-cuckoo and its *Gerygone* hosts have been extensively studied in Australia (Brooker et al. 1988; Brooker and Brooker 1989; Noske 2001) and New Zealand (Gill 1982a, b, 1983a, b; Anderson et al. 2013; Briskie 2003, 2007). However, very little information is available for the Fan-tailed Gerygone from New Caledonia (Barré et al. 2013).

The Fan-tailed Gerygone from New Caledonia has two different nestling colour phenotypes, dark grey (dark hereafter) and pinkish-grey (bright hereafter), which can occur in monomorphic and polymorphic broods (Sato et al. 2015; Attisano et al. 2018). Although variation within the same brood could potentially lead to recognition errors (Stokke et al. 2002; Moskát et al. 2008), Fan-tailed Gerygone parents recognise and eject the parasite nestling within 24 h from hatching (Sato et al. 2015; Attisano et al. 2018). Grey Warblers from New Zealand also have polymorphic nestlings (Gill 1983b), but this species is neither an egg (Thorogood et al. 2017) nor nestling ejector (J. Briskie, personal communication). The two nestling morphs of the Fan-tailed Gerygone differ in

melanic pigmentation and are easily distinguished from each other by visual inspection. Melanic pigmentation in birds is known to influence physiological mechanisms such as immune response to pathogens (Gangoso et al. 2015), anti-oxidative stress response (Almasi et al. 2012), thermoregulation (Clusella-Trullas et al. 2008) and protection against UV radiation (Roulin 2014) and it can ultimately influence behaviour in adulthood (Ducrest et al. 2008; Dreiss et al. 2012). It is unknown if and how the melanism of Fan-tailed Gerygone nestlings affects their growth rate and survival via developmental, physiological or environmental effects.

The aim of this study was to describe the life history of the Fan-tailed Gerygone and the factors influencing its breeding success. We were also interested in collecting observations of natural and experimental behaviour to find evidence of other forms of anti-parasite defence, besides the ejection of parasite nestlings. Our specific goals were to (1) assess which environmental factors affect the breeding success of the Fan-tailed Gerygone, (2) investigate the behaviour of Fan-tailed Gerygone parents around the nest and estimate the timing of parasitism, and (3) estimate growth rate and fledging success of the two host nestling phenotypes.

## Methods

We conducted fieldwork on the main island (Grande Terre) of New Caledonia over six breeding seasons (2011/12–2017/18) during the months of September–January. Our field sites were located in the Parc des Grandes Fougères (PGF; 21°38.664'S, 165°46.160'E), 4 km southwest from PGF (Farino; 21°39.822'S, 165°45.950'E) and 40 km west of PGF (Deva; 21°35'58.89" S, 165°23'55.61" E). Field sites included tropical rainforest (PGF), savannah with small patches of dry forests and relatively open grassland habitats (Farino), and dry forest and savannah (Deva). In PGF, the mean annual rainfall was about 1500 mm and mean annual temperature 20 °C, whereas Farino was about 5–10% drier and warmer. Average annual rainfall in Deva was about 1000 mm and temperature 23 °C (data by Direction des Affaires Vétérinaires, Alimentaires et Rurales, DAVAR and Météo France). The 2013/14, 2015/16 and 2017/18 breeding seasons were dry (cumulative rainfall in PGF from September to December between 215 and 267 mm), whereas the other three seasons were wet (396–490 mm). We assigned all nests in the PGF area to rainforest habitat and all nests in the Farino and Deva area to savannah habitat.

## Nest monitoring

We searched for active gerygone nests by following adults flying to their nests. Fan-tailed Gerygone nests were usually located either near the ground or in the tree canopy, but for practical reasons we only monitored nests at heights lower than 3 m. We checked all nests containing eggs at least twice a week and increased the frequency to daily visits towards the estimated hatching date. We checked the developmental stage of the eggs by candling (Brinsea Ovoscope) and estimated their incubation stage based on known developmental stages for passerine eggs (Lokemoen and Koford 1984). After hatching, we checked the nest daily until the chicks fledged or the nest was depredated. We recorded GPS location, height and dimensions of the nest (width, length, entrance diameter, hood length and bottom tail length), clutch size, brood size, chick colour morph and breeding success of both host and parasite, as well as predation events. We weighed the eggs and took digital photos to measure egg dimensions and volume with an egg measurement plug-in (Troszianko 2014) in ImageJ (Schneider et al. 2012).

Because of the high predation rate, during the seasons 2012/13–2015/16, we enclosed some active nests with a chicken-wire cage (mesh size ca. 4 cm) placed at about 0.5 m around the nest. We always installed cages in the late incubation or early hatching period to avoid disturbance to host parents during the laying period and to avoid inadvertently reducing the natural parasitism rate. The cages allowed host parents to pass through and reach the nest, but kept it out of reach of the main avian predators. Territories of the breeding pairs usually extended about 50–60 m around the nest (authors' unpublished data). At every visit, we approached the nest carefully to locate the breeding pair, and noted whether they were engaged in territorial disputes with other individuals or mobbing possible predators.

## Video recording

In the 2011/12 and 2012/13 breeding seasons, we used a continuously recording video camera system placed 1–2 m from the nest entrance to monitor nest visits by parents, applying the method described in detail in Gula et al. (2010). We placed the video cameras after detecting the first laid egg until fledging or nest failure. We watched the video footage at 20× speed and assigned the behaviour of adult gerygones according to three categories: (1) inside nest (adult incubating or brooding), (2) on nest edge (perching on the nest entrance rim, feeding the nestlings or removing faecal sacs, with no other adult inside the nest) or (3) outside nest (no adult within 1 m of the nest). To minimise bias, only one observer (F.T.) scored the video footage. We reduced video playback to 1.5× speed each time we observed a change in the behavioural category and noted the start time of the

behaviour with an accuracy of 2 s. We defined the length of each behavioural bout as the time interval between the start of a behaviour and the start of the consecutive behaviour, leading to a continuous sequence of daily behavioural categories. To analyse daily activity patterns, we calculated the time of occurrence of a behaviour as the mid-time between the start and end times of the behaviour and assigned it to full hours (e.g. the time of a behaviour that started at 09:45 and ended at 10:05 was counted as 09:55 and thus classified as occurring between 09:00 and 10:00). None of the video-monitored nests was abandoned by the parents.

### Adult measurements

We captured adult gerygones using mist nets placed 1–2 m from the nest entrance before laying. Each bird was banded with coloured plastic leg rings to allow visual identification. We collected biometrics (body mass, tarsus length, wing chord, bill length, bill depth, bill width) and 10–30  $\mu$ l of blood to determine sex and parentage (Gazda et al. 2015; Bojarska et al. 2018).

Fan-tailed Gerygone parents always ejected the Shining Bronze-cuckoo chick within 24 h from hatching (Sato et al. 2015), which made it difficult to collect biometrics of the cuckoo nestlings in a consistent manner. Therefore, we collected the cuckoo egg from nine parasitised nests, and replaced it with a dummy dark olive-brown egg resembling the size and appearance of a Shining Bronze-cuckoo egg. The collected cuckoo eggs were then artificially incubated (Brinsea Mini Advance) at 37.2 °C. We also monitored the incubation length of five cuckoo eggs naturally incubated by their host parents to correct for a possible incubator effect on the development of the cuckoo eggs. We estimated the age of cuckoo eggs by candling (Brinsea OvaScope) and checked the development of artificially incubated eggs every 2 days until hatching. As cuckoo females can pre-incubate eggs internally (Birkhead et al. 2011), we estimated the duration of this internal incubation boost as the difference in incubation advancement of the Shining Bronze-cuckoo egg compared to Fan-tailed Gerygone eggs from the same nest. After hatching, we placed the cuckoo chicks in the gerygone nests from which they originated and removed the dummy cuckoo eggs. If the original nest was depredated, we placed the cuckoo chick in a different nest at the same developmental stage.

### Host nestling measurements

In the 2014/15 and 2015/16 field seasons, we followed the growth of gerygone nestlings of either morph by measuring tarsus and mass across multiple days (range 5–15 days) during the period from hatching until fledging. We modelled growth curves for tarsus and mass of each gerygone

nestling with a logistic function, as typically used in studies of growth of passerine nestlings (Starck and Ricklefs 1998), fitted using the *gnls* function of the package *nlme* (Pinheiro et al. 2016) in R 3.2.1 (R Core Team). We used asymptote, inflection point and growth rate of the sigmoid growth curves obtained as fixed effects in a generalized nonlinear mixed models with the function *nlme* of the package *nlme*. We ran two generalized nonlinear mixed models, using mass and tarsus as response variables, and using nestling and nest identity as random effects to account for individual variation and for nest effect (shared genetic background, parental effects) on nestling growth rates (Sofaer et al. 2013).

### Adult mobbing behaviour

In the 2015/16 field season, we chose four pairs in which both adults were fitted with colour-coded leg bands and tested their behavioural response against a stuffed adult cuckoo presented at the nest. We placed the stuffed cuckoo at a distance of 2 m from the nest entrance while the host parents were away from the nest. We presented it for 3 min, beginning the moment parents returned to the nest and video-recorded their behaviour with a camera (Sony CX455 Handycam) operated from a hide at about 5 m from the nest.

All means are provided with 95% confidence intervals.

## Results

### Nest location and territorial defence

During the six breeding seasons, we found 305 nests: 188 nests were active (containing at least one egg or nestling) and we were able to follow the breeding outcome of 142 nests. The monitored nests were at heights between 0.3 and 2.3 m ( $n = 68$ ,  $79 \pm 3$  cm) and were mainly built at the thin end of twigs in shrubs/young trees ( $n = 43$ ) or attached to ferns ( $n = 18$ ). Nests were on average  $117 \pm 15$  mm high ( $n = 45$ ) and  $60 \pm 5$  mm wide ( $n = 45$ ), with an average entrance diameter of  $28 \pm 3$  mm ( $n = 42$ ), entrance hood length of  $32 \pm 10$  mm ( $n = 39$ ) and with a bottom tail  $105 \pm 46$  mm long ( $n = 38$ ). The presence of the protective cage did not affect clutch size (cage vs. no cage,  $2.3 \pm 0.07$  vs.  $2.3 \pm 0.07$ ), brood size ( $1.8 \pm 0.09$  vs.  $2.0 \pm 0.11$ ) or fledging success ( $1.5 \pm 0.14$  vs.  $1.6 \pm 0.15$ ), but decreased the predation rate (Table 1). In two instances, parents abandoned a caged nest due to human disturbance not directly linked to the presence of the cage. Numbers (percentage) of Fan-tailed Gerygone nests with known outcome ( $n = 142$ ) in relation to nest protection (no cage vs cage), habitat (forest vs savannah) and rainfall (dry vs wet breeding seasons).

Breeding pairs often engaged in fights with conspecific, especially in proximity of their nest location. Males

**Table 1** Numbers (percentage) of Fan-tailed Gerygone, *Gerygone flavolateralis*, nests with known outcome ( $n = 142$ ) in relation to nest protection (no cage vs. cage), habitat (forest vs. savannah) and rainfall (dry vs. wet breeding seasons)

Category	<i>n</i>	Successful for host			Unsuccessful for host		
		Non-parasitised	Parasitised	Parasitism			
				Parasitised then other failure	Predation		Other failure
					Parasitised then predated	Predated	
No cage	94	16 (17%)	1 (1%)	5 (5%)	7 (7%)	48 (51%)	17 (18%)
Cage	48	20 (42%)	3 (6%)	2 (4%)	2 (6%)	9 (18%)	12 (24%)
Forest	71	18 (25%)	2 (3%)	6 (8%)	4 (6%)	23 (32%)	18 (25%)
Savannah	71	18 (25%)	2 (3%)	1 (1%)	5 (7%)	34 (48%)	11 (15%)
Dry	79	17 (21%)	3 (4%)	2 (2%)	7 (9%)	42 (53%)	8 (10%)
Wet	63	19 (30%)	1 (1%)	6 (9%)	2 (3%)	15 (24%)	20 (32%)

Successful nests had at least one fledgling. Other failures include egg hatching failure, nest abandonment by host parents and nest damage due to heavy rainfall

(identified via colour bands and genetic sexing) engaged in territorial displays such as singing in proximity of their territory borders and chasing away conspecific intruders, whereas females emitted alarm calls directed at the intruder but never engaged in fights. We captured 101 adult Fan-tailed Gerygone of which 59 were captured at 44 active nests. Males were larger than females in body mass, tarsus length and wing chord, whereas bill length, width and depth did not differ between the sexes (Table 2). We found no difference in body mass, tarsus length and wing chord across sites, whereas the bills of adults in Deva were shorter and thicker than those of adults from PGF and Farino (Table 2).

Often pairs remained together and used the same nesting area over multiple breeding seasons. We followed the breeding attempts of 11 pairs over multiple seasons (4 pairs over 2 seasons, 6 pairs over 3 seasons, 1 pair over 4 seasons). In each case, the new nest was within 50 m (mean = 32 m, SD = 18 m,  $n = 11$ ) from the nest site used in the previous season. We found no evidence of successful multiple breeding attempts in the same season in our field sites, but 7 pairs laid a replacement clutch after the first one was lost due to predation, and in each case they built a new nest near the location of the previous nest (mean = 28 m, SD = 5 m,  $n = 7$ ).

### Breeding activity, clutch size and brood size

We found the earliest gerygone nest with nestlings (about 11 days old) on 28 September (estimated laying date of the last egg 27–29 August), and the latest nest with eggs on 11 January. Therefore, the breeding season of gerygones ranged from end of August to February with a peak in November: 1 (1%) active nest found in September, 52 (27%) in October, 104 (56%) in November, 29 (15%) in December, and 2 (1%) nests in January. The clutch/brood size ranged from 1 to 3 eggs/chicks (148 clutches: 1 egg: 28%, 2 eggs: 55%, 3 eggs: 17%; 107 broods: 1 chick: 36%, 2 chicks: 49%, 3 chicks: 15%). The average clutch size (host plus parasite eggs) was not different between parasitised and non-parasitised nests (Table 3). Female cuckoos replaced one host egg with one of their own and, as a consequence, the average host brood size in parasitised nests was lower compared to non-parasitised nests (Table 3). During six breeding seasons, we found multiple parasitism in only one nest which contained two cuckoo eggs and two host eggs. The nest was depredated before hatching.

Habitat and season affected neither clutch size (forest vs. savannah:  $2.1 \pm 0.2$  vs.  $2 \pm 0.1$ , dry vs. wet season:  $1.9 \pm 0.1$

**Table 2** Biometrics (mean  $\pm$  95% CI) of adult Fan-tailed Gerygone by sex and site ( $n$  in parentheses)

	Males	Females	PGF	Farino	Deva
Body mass (g)	6.2 $\pm$ 0.1 (56)	6.0 $\pm$ 0.1 (40)	6.1 $\pm$ 0.2 (25)	6.2 $\pm$ 0.1 (48)	6.0 $\pm$ 0.1 (23)
Tarsus length (mm)	18.9 $\pm$ 0.2 (55)	18.4 $\pm$ 0.3 (39)	18.7 $\pm$ 0.3 (25)	18.6 $\pm$ 0.2 (47)	18.9 $\pm$ 0.5 (22)
Wing chord (mm)	53.1 $\pm$ 0.5 (49)	50.7 $\pm$ 0.5 (36)	52.2 $\pm$ 0.8 (18)	52.5 $\pm$ 0.6 (42)	51.4 $\pm$ 1 (25)
Bill length (mm)	12.7 $\pm$ 0.2 (52)	12.7 $\pm$ 0.2 (39)	12.9 $\pm$ 0.3 (21)	12.9 $\pm$ 0.2 (46)	12.0 $\pm$ 0.3 (24)
Bill width (mm)	3.7 $\pm$ 0.1 (51)	3.6 $\pm$ 0.1 (36)	3.5 $\pm$ 0.2 (19)	3.6 $\pm$ 0.1 (44)	3.9 $\pm$ 0.1 (24)
Bill depth (mm)	2.7 $\pm$ 0.1 (50)	2.7 $\pm$ 0.1 (36)	2.7 $\pm$ 0.1 (19)	2.7 $\pm$ 0.1 (43)	2.9 $\pm$ 0.1 (24)

**Table 3** Egg measurements, duration of breeding periods, clutch and brood sizes, and hatching/fledgling success (values in parentheses for parasitised nests) of Fan-tailed Gerygone and Shining Bronze-cuckoo in New Caledonia

Stage	Parameter	Fan-tailed Gerygone		Shining Bronze-cuckoo	
		<i>n</i>	Mean ± CI	<i>n</i>	Mean ± CI
Egg	Egg mass (g)	15	1.2 ± 0.0	3	1.9 ± 0.3
	Egg length (mm)	16	17.3 ± 0.3	7	19.7 ± 0.9
	Egg width (mm)	16	12.5 ± 0.1	7	13.4 ± 0.3
	Egg volume (µl)	16	1363 ± 41	7	1815 ± 110
	Clutch size <sup>a</sup>	123 (30)	2.1 ± 0.1 (1.2 ± 0.3)	(30)	(1.0 ± 0.1)
	Laying interval (days)	12	3 ± 0.5		
	Internal incubation (days)			5	2 ± 0.2
	Incubation phase (days)	29	18 ± 1	14	16 ± 1
Nesting	Nestling phase (days)	14	14 ± 1		unknown
	Hatching success <sup>b</sup>	246 (35)	45% (40%)	(31)	(48%)
	Brood size <sup>c</sup>	97 (11)	1.9 ± 0.1 (1.3 ± 0.3)	(15)	(1.0 ± 0.0)
	Proportion of nests with hatchlings <sup>d</sup>	123 (30)	50% (37%)	(30)	(50%)
Fledging	Number of fledglings per successful nest <sup>e</sup>	35 (3)	1.6 ± 0.2 (1.3 ± 0.6)	(3)	(0)
	Proportion of nests with fledglings <sup>f</sup>	97 (11)	36% (27%)	(15)	(0%)
	Fledging success <sup>g</sup>	179 (14)	31% (29%)	(15)	(0%)

<sup>a</sup>Number of eggs per nest of all nests with known number of eggs

<sup>b</sup>Percentage of eggs that hatched of all eggs monitored to the hatchling stage

<sup>c</sup>Number of hatchlings per nest of all nests with known number of hatchlings (excluding nests with no hatchling)

<sup>d</sup>Of all nests monitored from egg to hatchling stage

<sup>e</sup>Of all nests with known number of fledglings (excluding nests with no fledgling)

<sup>f</sup>Of all nests monitored from hatchling to fledgling stage

<sup>g</sup>Proportion of hatchlings that fledged of all hatchlings monitored to the fledgling stage

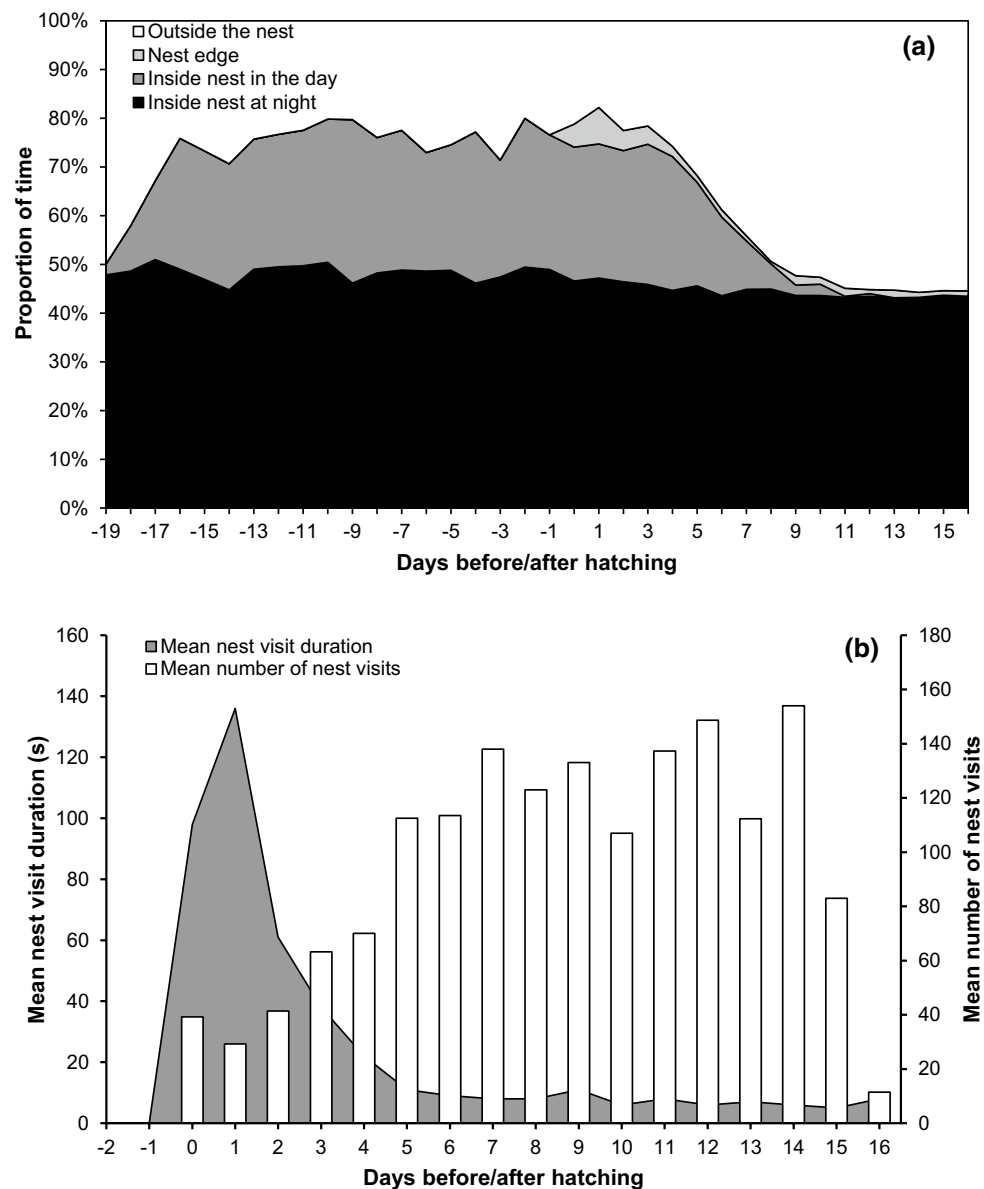
vs.  $2.2 \pm 0.2$ ) nor brood size (forest vs. savannah:  $1.8 \pm 0.2$  vs.  $1.8 \pm 0.2$ , dry vs. wet season:  $1.7 \pm 0.2$  vs.  $1.9 \pm 0.2$ ). We determined the nestling morph composition at hatching in 88 broods: 66 were bright, 14 dark and 8 polymorphic. Neither habitat ( $\chi^2 = 0.662$ ,  $df = 2$ ,  $p = 0.718$ ) nor season ( $\chi^2 = 1.162$ ,  $df = 2$ ,  $p = 0.559$ ) influenced the frequency of the three brood types. All cuckoo nestlings were bright.

### Activity patterns at the nest

Over the course of two breeding seasons, we recorded a total of 2232 video hours during 109 days (64 days during the egg laying/incubation period and 45 days during the nestling period) at six Fan-tailed Gerygone nests, of which two were parasitised by Shining Bronze-cuckoos. On average, each nest was video monitored for  $17.5 \pm 6.5$  days. Fan-tailed Gerygones started incubating around the time they laid the second egg. Only females incubated and they spent on average 46% of the day (range 11.01–11.38 h) inside the nest over the entire nesting period, including the egg laying period (Fig. 1a). During the egg laying period (–19 to –17 days before hatching), females incubated 9% of daylight hours (range 0.32–4.88 h). After completing the clutch (–16 days before hatching) until the chicks were

5 days old, females spent 27% of the daylight time (range 6.43–6.77 h) incubating or brooding (Fig. 1a). The time both parents spent outside the nest was on average longer and concentrated in particular hours of the day during the laying period (–19 to –17 days before hatching; Fig. 2a), whereas it was shorter and more evenly distributed during the day in the period from the beginning of incubation until hatching (–16 to 0 days before hatching; Fig. 2a). We observed the hatching order in 8 non-parasitised clutches: half hatched synchronously and half asynchronously (1 day apart). In two clutches of three eggs, the third egg hatched 1–2 days after the first two eggs. From day 5 after hatching onwards, brooding time sharply decreased until 12 days after hatching when females no longer spent time inside the nest during the day (Fig. 1a). Both parents provided food for the chicks, and, from the day of hatching (day 0) until the day of fledging (16 days after hatching), they visited the nest on average  $95 \pm 23$  times per day (Fig. 1b). Both host parents vocalised at each nest visit to elicit a begging response from their nestlings. From hatching (day 0) until fledging (day 15 after hatching), the average length of time parents spent around the nest was evenly spread across the daytime hours (Fig. 2b).

**Fig. 1 a** Proportion of time the Fan-tailed Gerygones spent in the nest (only females), outside the nest and on the nest edge during an entire day (both parents). The decrease in time spent in the nest at night is caused by the progressive increase in day length during the breeding season. **b** Mean duration (grey area) and number (vertical bars) of nest visits by Fan-tailed Gerygones in relation to the day of hatching (day 0)



### Nestling growth and fledging success

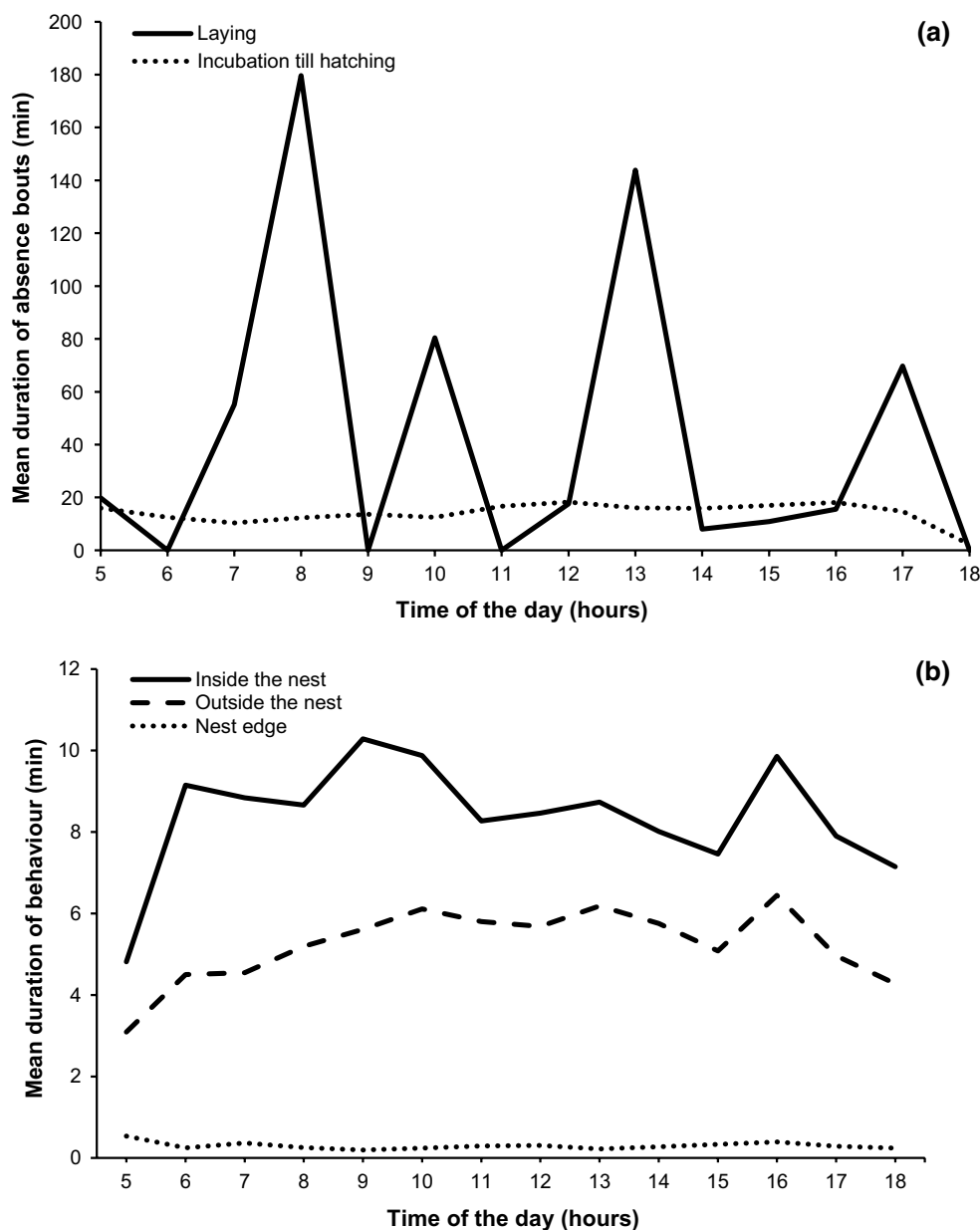
Growth rates of body mass and tarsus were not affected by the skin colour of host nestlings (NLME; mass growth rate:  $p = 0.877$ ; tarsus growth rate:  $p = 0.959$ , Fig. 3a) or habitat (NLME; mass growth rate:  $p = 0.217$ , Fig. 3b). The mean number of host fledglings was not different in parasitised and non-parasitised nests (Table 3). Only 36% of all nests produced at least one fledgling and only 31% of all hatchlings reached the fledgling stage (Table 3). Parasitism affected neither the proportion of nests with fledglings ( $\chi^2 = 0.06$ ,  $df = 1$ ,  $p = 0.805$ , Table 3) nor the

fledging success ( $\chi^2 = 0.001$ ,  $df = 1$ ,  $p = 0.968$ , Table 3). The number of fledglings did not differ between habitat (forest vs. savannah:  $1.5 \pm 0.2$  vs.  $1.6 \pm 0.4$ ) or season (dry vs. wet:  $1.4 \pm 0.2$  vs.  $1.7 \pm 0.4$ ).

### Parasitism and predation

During the entire study, 30 (16%) of 188 active nests were parasitised. There was no difference in frequency of parasitism between caged and not caged nests ( $\chi^2 = 0.84$ ,  $df = 1$ ,  $p = 0.359$ ), forest and savannah ( $\chi^2 = 3.513$ ,  $df = 1$ ,  $p = 0.06$ ) or dry and wet seasons ( $\chi^2 = 0.022$ ,  $df = 1$ ,

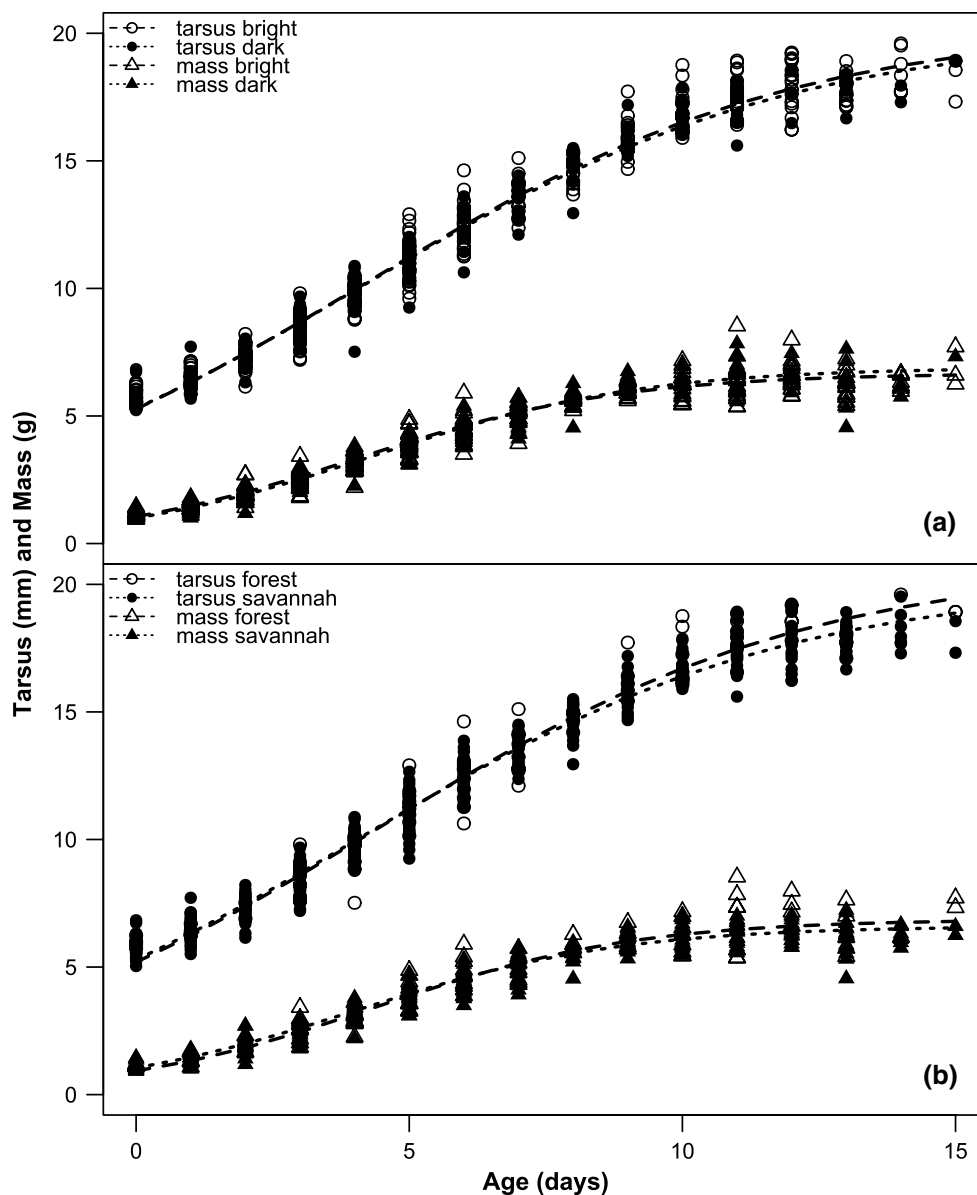
**Fig. 2 a** Mean daily duration of parental absence from the nest during egg laying (19–17 days before hatching) and from incubation until hatching (16–0 days before hatching). **b** Mean daily duration of time spent inside the nest, outside the nest and on the nest edge during the period from hatching (day 0) until fledging (day 15 after hatching)



$p = 0.882$ ). We did not directly observe or video record egg laying by a Shining Bronze-cuckoo but we recorded one cuckoo arriving at the entrance of a gerygone nest containing a young host nestling and two host eggs. The cuckoo landed on the nest around 11:30 as soon as one of the gerygone parents left after feeding the nestling. One of the host parents (which we assumed to be the male) immediately attacked the cuckoo. The cuckoo did not enter the nest but perched on the entrance rim of the nest for about 7 s, despite being attacked by the gerygone clamped on its back. We found the nestling to be missing during the nest inspection the day after the event, and only became aware of the cuckoo visit after watching the recorded footage.

Cuckoo laying occurred from 3 days before to 4 days after the last gerygone egg was laid. In four cases, the nest contained a single cuckoo egg incubated by the host mother. Of 31 cuckoo eggs that we found, 15 hatched, 3 were sterile, 10 predated and 3 abandoned (it is unclear if abandonment was caused by parasitism or human disturbance). We were able to establish the hatching order in seven parasitised nests: in five nests the cuckoo hatched 1–2 days before the first gerygone, in one nest it hatched on the same day as the gerygone nestlings, and in one nest it hatched 1 day after the first gerygone nestling. According to this hatching pattern, most of the cuckoo eggs were laid before incubation by the host began. Cuckoo eggs were on average 2 days more developed than gerygone eggs (Table 3), thus cuckoo females





**Fig. 3** Logistic growth curves of Fan-tailed Gerygone nestlings in relation to skin colour (a) and habitat (b)

pre-incubated their eggs before laying. There was no difference in incubation length between cuckoo eggs artificially incubated ( $16 \pm 2$  days,  $n=9$ ) and cuckoo eggs incubated by their host parents ( $16 \pm 2$  days,  $n=5$ ). Host parents ejected all cuckoo nestlings from the nest within 24 h from hatching in seven bright, three dark, one polymorphic and four broods of undetermined composition. Although we never observed a cuckoo nestling being accepted by their host in our monitored nests, we observed cuckoo fledglings being fed by their presumed host parents in four instances: two in Deva and two in a site about 100 km southwest of PGF.

Of the four pairs experimentally tested for mobbing response, three responded to the cuckoo presentation, and in each case the male promptly attacked the stuffed

cuckoo by clinging on its rump and pecking at its head, whereas the female emitted alarm calls directed at the stuffed cuckoo but never attacked it. Even though we regularly observed potential avian nest predators around nests, they were never mobbed by gerygone pairs. Predation rates were higher in dry compared to wet years ( $\chi^2 = 15.92$ ,  $df = 1$ ,  $p < 0.001$ ), not different between habitats ( $\chi^2 = 3.425$ ,  $df = 1$ ,  $p = 0.06$ ) and lower when protective cages were placed around the nests ( $\chi^2 = 14.78$ ,  $df = 1$ ,  $p < 0.001$ ; Table 1).

## Discussion

A female Shining Bronze-cuckoo has more opportunities to successfully parasitise a host nest during the laying period of the Fan-tailed Gerygone because host parents left their nest unattended for longer intervals during this period, especially in the early morning and afternoon. This should decrease the chances of being detected at the nest by host parents and increase the chances for the cuckoo to lay its egg early, allowing the cuckoo nestling to hatch first and monopolise the host nest. In New Zealand, Shining Bronze-cuckoo nestlings at the age of 3–5 days evict the younger host nestlings (Gill 1983a) and a cuckoo nestling hatching later than the host nestlings may not have the ability to compete with them (Briskie 2007). It is likely that Shining Bronze-cuckoo nestlings in New Caledonia evict host nestlings at a comparable age (see photos in Sato et al. 2015). Thus, cuckoo laying has to occur no later than 2–4 days after the first host egg, leaving a relatively short time window for the parasitism to occur. As we found in this study, Shining Bronze-cuckoo cuckoo eggs usually have a 2-day incubation advance compared to host eggs, which favours an earlier hatching of the cuckoo nestling. Parasitism during the incubation period is unlikely to occur because Fan-tailed Gerygone females spend more time inside the nest, and both parents spend less time away from the nest, in periods evenly distributed across the day. Most of the cuckoo eggs that we found were laid during the host-laying period based on the age estimation by candling and the hatching pattern. In the four observed cases in which the host female incubated only one cuckoo egg but no host eggs, it was not possible to determine whether the female cuckoo replaced one egg (host or cuckoo) in the nest with its own or whether she laid into a previously empty host nest. The first option seems more plausible because Shining Bronze-cuckoo females from New Zealand and Australia replace one egg (host or cuckoo) with their own (Briskie 2007; Gloag et al. 2014). The same situation seems to occur in New Caledonia, because we found no difference in average clutch size between parasitised and non-parasitised clutches. To our knowledge, our observation of a single Shining Bronze-cuckoo egg incubated by the host has not been reported in any other gerygone hosts. This might be a relatively frequent occurrence in New Caledonia as clutches of Fan-tailed Gerygone are on average smaller than other gerygone species (Gill 1983b; Gloag et al. 2014), and clutches of one egg are common (Sato et al. 2015; this study). Thus, Shining Bronze-cuckoos in New Caledonia may parasitise clutches of one but still remove the single host egg.

Fan-tailed Gerygones seem unable to discriminate a cuckoo egg in the nest, like gerygones from Australia (Mulyani 2004; Langmore et al. 2005; Gloag et al. 2014) and

New Zealand (Thorogood et al. 2017). Several authors have suggested that dark bronze-cuckoo eggs may be cryptic in dark nests and thus escape visual detection by the host (Harrison 1968; Marchant 1972; Brooker et al. 1990; Mulyani 2004; Langmore et al. 2009). This may be true when the cuckoo egg is laid amidst multiple host eggs, but it seems unlikely with a single cuckoo egg in the nest. It looks more likely that in these cases the single cuckoo egg escaped discrimination not because it was cryptic but rather because it offered tactile stimuli to an already incubating female (Marchetti 2000). This is supported by the observation that Fan-tailed Gerygone females abandon their nest if all the eggs or nestlings are removed (e.g. by predation), but rarely do so when at least one egg or nestling is present (authors' unpublished data). Sato et al. (2010b) suggested that small host clutches may be advantageous when multiple parasitism is common and when female cuckoos replace other cuckoo eggs rather than host eggs. Both these conditions occur in bronze-cuckoos (Briskie 2007; Gloag et al. 2014). Although we might have underestimated the occurrence of multiple parasitism, it seems to be rare in our study sites compared to other studies (Mulyani 2004; Gloag et al. 2014). However, the small clutch size of the Fan-tailed Gerygone may still be advantageous because it decreases the laying period and thus reduces the time window during which parasitism by the Shining Bronze-cuckoo may occur (but see Medina et al. 2017).

Shining Bronze-cuckoos from New Zealand take up to 18 s to lay an egg inside the host nest (Brooker et al. 1988; Briskie 2007). Although we did not directly observe a cuckoo laying, we assume that Shining Bronze-cuckoos in New Caledonia behave similarly to their New Zealand conspecifics and therefore laying may occur even during the short absence periods of the host parents. However, Fan-tailed Gerygone parents vigorously defend their nest from approaching cuckoos, similar to the Grey Gerygone of New Zealand (Briskie 2007). Female cuckoos must closely monitor host activity around the nest to ascertain whether or not eggs have been laid and seize the opportunity of laying an egg as soon as the nest is left unattended (Yang et al. 2010). The immediate cuckoo visit after host parents left that we recorded suggests close monitoring of the host nests, even though we might have captured on video an attempt to kill the host chicks rather than an attempt of parasitism. Shining Bronze-cuckoos in New Zealand are known to kill host nestlings (Briskie 2007). Such a behaviour may lead to the re-nesting of the host, which allows the cuckoo to parasitise these hosts during their following breeding attempt (Hauber 2014).

The timing of cuckoo laying might also be an important factor to avoid host detection. Our results suggest that Shining Bronze-cuckoo females have higher chances to lay their eggs in the early morning and early afternoon during the

host-laying period because both host parents are away from the nest for longer periods. However, we were unable to determine the exact time of laying for the cuckoo eggs that we found. In New Zealand, Briskie (2007) did not identify any particular time of the day for cuckoo egg laying. In Australia, Brooker et al. (1988) reported that *Chalcites* cuckoos lay in the morning, but they only conducted early morning observations. These studies and our observations indicate that female cuckoos may not have any laying time preference.

In all parasitised nests that reached the hatchling stage, the cuckoo chicks were always ejected by the host parents within 24 h from hatching before they could evict any host eggs or nestlings (Attisano et al. 2018). Fan-tailed Gerygone parents spend relatively long periods on the nest edge during the first 2 days after hatching, presumably inspecting the nest, regardless of the nest being parasitised or not. Thus, the early hatching period may be the sensitive time window during which Fan-tailed Gerygone parents may accept or reject the parasite nestling. The long visits during this period may allow host parents to inspect their brood and assess the identity of nestlings. In our study, the parasite breeding success was too low to be detected with 30 parasitised nests (thus under 3%). Although parasitism decreased the mean brood size of the host, it did not affect the overall fledging success in our study. Nestling mortality rates were high and usually not all nestlings survived to fledging in non-parasitised nests. Due to the effective host defence of the Fan-tailed Gerygone, the effect of parasitism in this system was therefore not additive to the natural nestling mortality and did not negatively affect the fledgling success.

The main nest predators of Fan-tailed Gerygone are native birds (authors' unpublished data). Predation rates tended to be higher in savannah habitat and dry years whereas the parasitism rate was relatively stable across habitats and seasons. This is likely due to differences in searching strategies between cuckoos and predatory birds. A predatory bird may opportunistically locate and prey upon a nest in the foliage, whereas a cuckoo female must observe the activity of host parents and acquire information about the stage of their breeding attempt to parasitise the nest during the brief moments when it is left unattended. In dry years, a sparser vegetation cover might render nests more visible and increase the chances of predation, whereas it should not have the same effect on the abilities of the cuckoo to monitor the nest.

The two host nestling morphs had similar growth rates and fledging success and occurred in similar frequencies across habitats, showing no apparent trade-offs related to skin coloration. Our findings support the hypothesis that nestling polymorphism in gerygones has likely evolved as a counter adaptation to cuckoo mimicry. The proportion of bright to dark host nestlings was roughly 3:1, and we

only found bright cuckoo nestlings (Attisano et al. 2018). In other areas where dark cuckoo morphs are present (Sato et al. 2015), we would expect that the proportion of dark host chicks is higher. This would fit with a negative frequency-dependent selection scenario in which the frequencies of cuckoo and host nestling phenotypes fluctuate based on their relative fitness value (Thorogood and Davies 2012). Nestling colour itself may not be the main cue used by Fan-tailed Gerygone host parents to discriminate cuckoo nestlings (Attisano et al. 2018), but it may be maintained because there are no apparent trade-offs related to skin coloration. Therefore, the arms race in New Caledonia seems to point to stronger selection pressure on the parasite for improved nestling mimicry (Attisano et al. 2018), whereas predation should be a more important selection pressure than parasitism on the host.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest. The Province Sud of New Caledonia issued all permits (3045-2011, 2437-2012, 2532-2013, 2801-2014, 2476-2015, 2372-2017) for handling and collection of the nestlings. The 1st Warsaw Local Ethics Committee for Animal Experimentation approved all experimental procedures.

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