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Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia

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Abstract

Nestling rejection is a rare type of host defense against brood parasitism compared with egg rejection. Theoretically, host defenses at both egg and nestling stages could be based on similar underlying discrimination mechanisms but, due to the rarity of nestling rejector hosts, few studies have actually tested this hypothesis. We investigated egg and nestling discrimination by the fan-tailed gerygone *Gerygone flavolateralis*, a host that seemingly accepts nonmimetic eggs of its parasite, the shining bronze-cuckoo *Chalcites lucidus*, but ejects mimetic parasite nestlings. We introduced artificial eggs or nestlings and foreign gerygone nestlings in gerygone nests and compared begging calls of parasite and host nestlings. We found that the gerygone ejected artificial eggs only if their size was smaller than the parasite or host eggs. Ejection of artificial nestlings did not depend on whether their color matched that of the brood. The frequency of ejection increased during the course of the breeding season mirroring the increase in ejection frequency of parasite nestlings by the host. Cross-fostered gerygone nestlings were frequently ejected when lacking natal down and when introduced in the nest before hatching of the foster brood, but only occasionally when they did not match the color of the foster brood. Begging calls differed significantly between parasite and host nestlings throughout the nestling period. Our results suggest that the fan-tailed gerygone accepts eggs within the size range of gerygone and cuckoo eggs and that nestling discrimination is based on auditory and visual cues other than skin color. This highlights the importance of using a combined approach to study discrimination mechanisms of hosts.

Key words: begging calls, brood parasitism, co-evolutionary arms race, egg discrimination, nestling discrimination, nestling polymorphism.

Rejection of brood parasite eggs is a common host defense against brood parasitism, whereas seemingly only few hosts reject nestlings of the brood parasite (Davies 2015; Soler 2017). Two main models attempted to explain the evolution of these 2 host defense strategies: "strategy blocking" (Britton et al. 2007) and "rarer enemy" (Grim 2006). Both models are extensions of the "rare enemy effect," which suggests that it is not advantageous to develop a defense against a rare enemy because adaptations are costly (Dawkins 1982). Therefore, high rates of egg rejection make the parasite nestling a rare enemy, which could decrease the selection pressure to evolve host defenses at the nestling stage. However, the 2 models have different predictions. Following the "strategy-blocking" model, a strategy that would be adaptive on its own can be "blocked" by another strategy with lower costs and higher fitness pay-offs (Britton et al.

2007). Thus, mixed strategies of egg and chick rejection should not co-exist in a host population (Britton et al. 2007). In the "rarer enemy" model, any factor preventing parasitism at the nestling stage would also prevent selection for parasite nestling recognition because the host encounters parasite nestlings at a lower frequency than parasite eggs (Grim 2006). This model predicts that nestling discrimination should evolve in hosts that are forced to accept the parasite egg for any reason but also that imperfect egg and nestling discrimination can co-exist in the same host (Grim 2017). The latter scenario seems to be supported by a few hosts that reject (by nest abandonment or ejection) the parasite nestling but usually accept the parasite egg even if it is highly dissimilar from the host eggs (Langmore et al. 2009a; Gloag et al. 2014). However, there is a scarcity of studies testing if and how the 2 strategies can co-exist in the same host and which discrimination cues are employed in one or the other. This might rather be a consequence of a much larger research effort devoted to the laying and incubation stages compared with the nestling stage than of the rarity of nestling rejector hosts (Grim 2007, 2017).

The discrimination of parasite nestlings can involve the use of context-specific cues such as begging calls (Langmore et al. 2003, 2008; Anderson et al. 2010), which are clearly of no help for the discrimination of the parasite egg. The behavior of the parasite nestling could potentially contribute to discrimination; however, the evidence suggests begging calls might act as a super-stimulus to elicit parental feeding but is not necessarily used by the host as a cue for discrimination (e.g., wing shaking; Tanaka et al. 2011). Other cues, for example, odor or body size of the parasite nestling, have not been studied in detail (Grim 2017). On the other hand, visual cues such as color and luminance might potentially be used for the discrimination of both parasite eggs and nestlings. For example, many hosts discriminate the parasite eggs based on markings (Moskát et al. 2008; Spottiswoode and Stevens 2010; Caves et al. 2015) and coloration (Yang et al. 2016; Liang et al. 2017). Similarly, hosts can use natal down and plumage coloration of the parasite nestling as discrimination cues (De Mársico et al. 2012; Noh et al. 2018). Therefore, if a host uses cues that potentially allow discriminating both eggs and nestlings of the parasite, for example, visual cues such as color and luminance, then the 2 rejection strategies might co-exist in a host population, which would support the predictions of the "rarer enemy" model scenario. On the other hand, if a host relies on cues that are only effective at one stage, for example begging calls that could allow discriminating the parasite nestlings but not eggs, then the 2 rejection strategies cannot co-exist in the host population which would support the predictions of the "strategy blocking" model scenario.

In this study, we investigate egg and nestling discrimination in the fan-tailed gerygone *Gerygone flavolateralis*, which is the exclusive host of the shining bronze-cuckoo *Chalcites lucidus* in New Caledonia. The gerygone ejects newly hatched cuckoo nestlings from the nest (Sato et al. 2015; Attisano et al. 2018), but seemingly always accepts the cuckoo egg. The shining bronze-cuckoo egg has a dark olive-brown color and is larger in size than the gerygone egg. Thus, the cuckoo egg might either escape host discrimination if it was cryptic in a dark dome-shaped nest (Langmore et al. 2009a) or evade ejection if the host was unable to grasp the parasite egg in its bill (Moksnes et al. 1991; Rasmussen et al. 2010). The physical limitations of a host to grasp and eject the parasite egg have been assessed using 2 indices of host bill size: the tomial ratio (Rothstein 1975), which is the ratio of the bill length of the host and the width of the parasite egg, and the grasp-index (Rohwer and Spaw 1988),

which is the product of bill length and bill width. Both indices have been used to compare ejection rates in hosts of the brown-headed cowbird *Molothrus ater* (Rasmussen et al. 2010) and common cuckoo *Cuculus canorus* (Moksnes et al. 1991); however, a similar comparative analysis for hosts of bronze-cuckoos within the Australasian region is still lacking.

The New Caledonian cuckoo-gerygone system also includes nestling polymorphism (Sato et al. 2015) as the nestlings of both the host and the parasite have 2 skin color morphs, pinkish-gray (bright) and dark-gray (dark). The 2 host nestling morphs can co-exist in mixed broods and the cuckoo morphs mimic several visual features of the host morphs such as presence of natal down and coloration of gape flanges and skin (Attisano et al. 2018). Polymorphism in egg appearance is known to occur in several parasite–host systems (Gibbs et al. 2000; Yang et al. 2020); however, nestling polymorphism is a much rarer occurrence in birds (Kilner 2006) and the New Caledonian system is, to our knowledge, the only example of nestling polymorphism in both the host and parasite. This system thus offers the unique possibility of investigating egg and nestling ejection strategies in the same host by comparing cues that are potentially shared between strategies (e.g., visual cues such as color and luminance) and cues that are specific to only one stage (e.g., egg size or nestling begging calls).

We conducted a series of experiments using artificial eggs or nestlings and cross-fostered host nestlings to test specific cues involved in the discrimination of eggs and nestlings (Table 1). We used artificial eggs varying in their appearance and size to test if fan-tailed gerygones discriminate eggs based on visual cues and if ejection is constrained by the egg size. Similarly, we used artificial nestlings mimicking the 2 nestling morphs to test if nestling ejection is based on visual cues such as skin color. We additionally cross-fostered fan-tailed gerygone nestlings to test the relative importance of skin coloration (same or different than the foster brood), timing (before or after the foster brood), and natal down (present or absent) in the ejection response of the host. Finally, we compared begging calls of parasite and host nestlings to assess if fan-tailed gerygones might use auditory cues for nestling discrimination. We hypothesized that: (1) fan-tailed gerygones are able to discriminate artificial eggs based on their appearance but do not eject large eggs, thus the cuckoo egg is not cryptic in the gerygone nest but evades ejection because of its size; (2) fan-tailed gerygones discriminate foreign nestlings based on their skin color and natal down, thus they should more often eject artificial nestlings and foreign cross-fostered nestlings if these do not match the appearance of the brood; (3) fan-tailed gerygones additionally use auditory cues to discriminate parasite nestlings from their own chicks.

Materials and Methods

Fieldwork and model species

We conducted fieldwork at 3 sites on the main island (Grande Terre) of New Caledonia during 8 breeding seasons (September–January) in 2011/12–2015/16 and 2017/18–2019/20: Parc des Grandes Fougères (PGF, 21°37′ S, 165°45′ E), Farino (21°39′ S, 165°46′ E) and Domaine de Deva (Deva, 21°35′ S, 165°22′ E). The field sites include areas of tropical rainforest, thicket, and savannah. The fan-tailed gerygone is a small insectivorous bird (adult mass 6.0–6.2 g, length 10 cm) and breeds from September to January with a peak in October/November (Attisano et al. 2019). We searched for active nests in known territories and by following adults flying to their nests. The dome-shaped nests can be located at various

Table 1 Cues for ejection of foreign eggs and nestlings tested in each experiment (indicated by the symbol "X")

	Color	Luminance	Color-match of the brood	Size	Natal down	Timing of introduction
Artificial eggs Exp. 1	X			X		
Artificial eggs Exp. 2		X		X		
Artificial nestlings			X			
Cross-fostered nestlings			X		X	X

heights (range 0.4–20 m), but for practical reasons, we restricted our study to nests lower than 3 m. We found a total of 344 active nests (containing at least one host or parasite egg/nestling), out of which 68 were parasitized and 74 (72 non-parasitized and 2 parasitized) survived to fledging. Upon finding an active nest, we determined the age either of the eggs by candling (Lokemoen and Koford 1996) or of the nestlings based on their development stage. This allowed us to estimate the nest age considering a 2-day laying interval between eggs, 18 days of incubation, and 14 days of brooding (Attisano et al. 2019). Despite extensive video recording (>16,000 h during laying and incubation), we never observed gerygones removing foreign material (leaves, twigs, berries, or similar) from the nest and never directly recorded the presence of such material in the nest, because the dome-shaped structure reduces the chances of foreign material falling inside the nest. We also never observed gerygones removing unhatched eggs, although they remove eggshell soon after hatching of the chicks (gerygone or cuckoo). We observed 4 cases in which a nestling (6–9 days old) died of natural causes, 2 in a single-chick brood, and 2 in a 2-chick brood, but the parents removed none of the carcasses. Three of these nests were soon abandoned by the parents (2 single-chick broods and one 2-chick brood), whereas at one nest (with a 2-chick brood) the parents raised the surviving nestling until fledging without removing the dead chick.

The size of an average fan-tailed gerygone egg is 18.4×13.3 mm (range: length 15.6–21.0 mm, width 12.0–14.6 mm) with a mass of 1.3 ± 0.02 g (mean $\pm$ 95% confidence interval [CI], $n = 122$), whereas an average shining bronze-cuckoo egg is 22.5×14.8 mm (range: length 18.9–23.8 mm, width 13.0–15.8 mm) with a mass of 1.9 ± 0.04 g ($n = 22$). There is no egg mimicry as the cuckoo egg is covered with a dark-brown pigment and is clearly distinct from the whitish-gray egg with brown speckles of its gerygone host (Figure 1A). We never observed ejection of own or cuckoo eggs by the fan-tailed gerygone, neither directly on camera nor indirectly via a reduction in clutch size during the incubation period. We also have no reason to believe that fan-tailed gerygones reject cuckoo eggs as they rarely abandoned their nest (6% of 344 active nests) and the presence of a cuckoo egg in the nest did not increase the frequency of nest abandonment ($\chi^2 = 1.299$, $df = 1$, $P = 0.254$). The cuckoo always removes one host egg before laying its own and multiple parasitisms of the same nest are rare (1 out of 68 parasitized nests). As part of other concurrent field observations, we temporarily swapped real gerygone or cuckoo eggs with a model egg mimicking their respective size and coloration in >40 occasions. We placed the real eggs in incubators for a period of 1–7 days and returned the hatchlings to their nests. We never observed the fan-tailed gerygone ejecting artificial eggs or abandoning the nest.

Hatchlings of the host and parasite have similar size, but cuckoo hatchlings are slightly heavier (1.4 g, range 1.2–1.8, $n = 3$) than fan-tailed gerygone chicks (1.1 g, range: 0.9–1.5; $n = 46$). Out of 222 host chicks, 75% were bright and 25% dark, and out of 130 host broods, 69% contained only bright chicks, 23% only dark chicks

and 8% were mixed. The dark morph of the parasite was rare as out of 26 parasite chicks all but 1 was bright. The bright parasite morph mimics visual features of both host morphs (Attisano et al. 2018), nevertheless gerygones ejected 88% (29 of 33) of newly hatched cuckoo chicks within few hours from hatching, regardless if the cuckoo chicks did ($n = 11$) or did not match ($n = 4$) the host brood color. All the accepted cuckoo chicks (4 of 33) evicted the still unhatched host eggs.

Artificial eggs and nestlings

We conducted 2 egg ejection experiments to test if fan-tailed gerygones used color, luminance, or size as cues for the discrimination and ejection of foreign eggs (Table 1). We made artificial eggs using modeling clay (Fimo Air, Staedler), which hardened after being exposed to air but still remained soft enough to record imprints of bill marks on the surface, allowing us to record if the host attempted to peck or grasp the artificial egg without being able to remove it from the nest. We prepared all artificial eggs at least 1 week before their use in the experiments and left them to dry in a ventilated location to allow any residual smell left by human manipulation or paint to dissipate. We controlled for the mass of the artificial eggs by inserting fishing beads in the clay to reach the average mass of a gerygone egg (1.3 g).

For Experiment 1, we used 3 types of artificial eggs (Figure 1B): parasite-like (brown, mimicking the parasite egg), host-like (whitish-grey with brown speckles, mimicking the host egg), and blue (novel visual stimulus to the host as no other passerine in New Caledonia lays blue eggs). We hand-rolled the clay into an egg shape and painted it with nontoxic paints (Turner Color Works Ltd, Osaka, Japan). The parasite-like and host-like eggs mimicked as close as possible the color of cuckoo and gerygone eggs, respectively, whereas the color of the blue model was highly dissimilar from both cuckoo and gerygone eggs. The artificial eggs had a standardized size of 10×7 mm, which is about 50% of the length and width of an average gerygone egg. The primary reason for this experiment was to test if gerygones would remove foreign eggs that are much easier to grasp compared with eggs of normal size (Table 1). The second aspect was to test if the frequency of ejection depended on the color of the model. If the cuckoo eggs were cryptic, we would expect a lower ejection rate of parasite-like artificial eggs compared with blue or host-like artificial eggs (Table 1).

For Experiment 2, we used 4 types of artificial eggs differing in luminance and size (Figure 1C): high luminance combined with large size, high luminance and medium size, low luminance and large size, low luminance, and medium size. We chose the size of these artificial eggs to match the size range of real eggs encountered by gerygones in their nest. Thus, the large artificial eggs matched the size of a cuckoo egg (22×14 mm), which is the largest egg possible in this system, and the medium-sized artificial eggs matched the size of the smallest gerygone egg that we measured in the field (15×11 mm). We molded the clay into an egg shape using a custom-made plastic

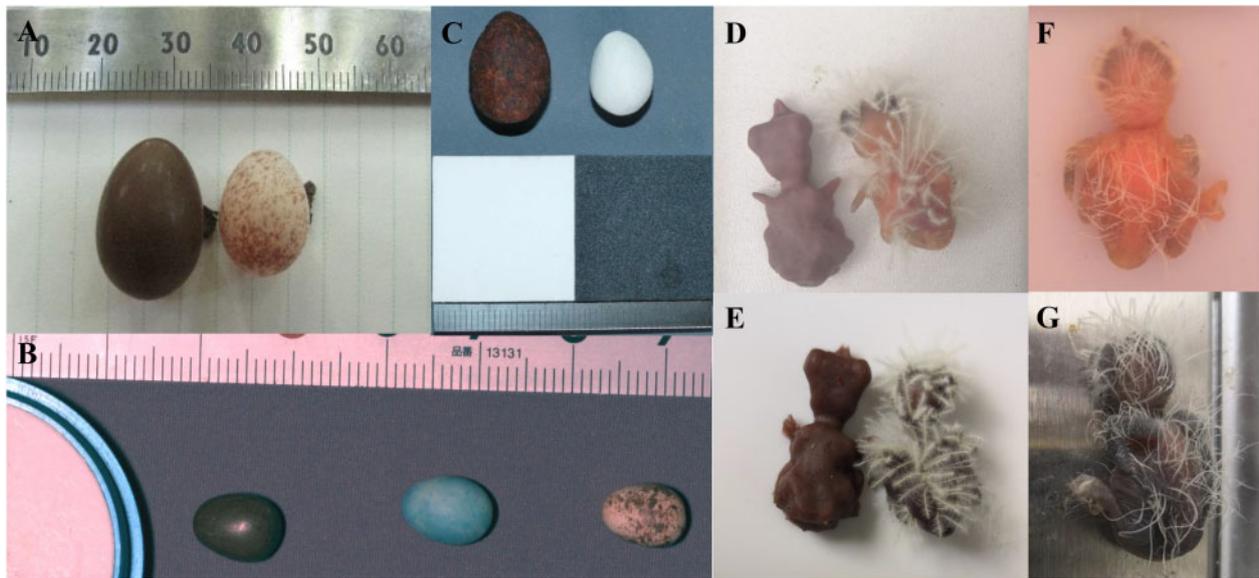**Figure 1.** (**A**) Eggs of shining bronze-cuckoo (left) and fan-tailed gerygone (right). (**B**) Artificial eggs for Experiment 1: parasite-like brown (left), blue (center), and host-like whitish-gray with brown speckles (right). (**C**) Artificial eggs for Experiment 2: low reflectance (left, only large size shown) and high reflectance (right, only small size shown). (**D**) Bright artificial nestling (left) with bright fan-tailed gerygone nestling (right). (**E**) Dark artificial nestling (left) with dark fan-tailed gerygone nestling (right). (**F**) Bright shining bronze-cuckoo nestling. (**G**) Dark shining bronze-cuckoo nestling. All nestlings in the photos are newly hatched (Day 0). Gerygone and cuckoo nestlings are not at the same scale.

mold to achieve artificial eggs of consistent size. We painted the low luminance models with 2 layers of nontoxic paint (Copic Ciao Marker E57, walnut brown) to mimic as closely as possible the luminance of a dark-brown shining bronze-cuckoo egg, whereas the high luminance models kept the original white color of the modeling clay to achieve higher luminance than both gerygone and cuckoo eggs. The first aim of this experiment was to test if the gerygones ejected artificial eggs within the size range of real eggs (Table 1). The second aim was to test if the frequency of ejection depended on the luminance of the model. If the low luminance model was cryptic then we would expect it to be less often ejected than the high luminance model irrespective of the size (Table 1).

We then investigated if fan-tailed gerygone parents ejected foreign nestlings that did not match the color of their own brood (Table 1). We used artificial nestlings made out of soft (to mimic the skin of newly hatched nestlings) silicone rubber (Ecoflex 00-30, Smooth-on), casted in a custom-made mold allowing us to produce models of standardized size (27×12 mm) and mass (1.2 g) similar to newly hatched gerygone and cuckoo nestlings. We painted the artificial nestlings with non-toxic silicone paint (Silk-pig, Smooth-on) to obtain 2 types, bright and dark, which mimicked as closely as possible the 2 morphs of both gerygone and cuckoo nestlings (Figure 1, D–G).

We measured color and luminance of the artificial eggs and nestlings using multispectral images taken with a Fuji IS-Pro full-spectrum digital photo camera. We used the MICA Image Analysis Toolbox plugin (Troscianko and Stevens 2015) for ImageJ (Schneider et al. 2012) to convert the multispectral images to cone catch using the peacock violet sensitive (VS) visual model (Hart 2002) as both the parasite and host in New Caledonia are predicted to have a VS visual system (Aidala et al. 2012a, 2012b). We verified that the artificial eggs mimicked as closely as possible the color (Experiment 1) and luminance (Experiment 2) of cuckoo and gerygone eggs and that artificial nestlings (Experiment 3) mimicked as

closely as possible the color and luminance of the respective cuckoo and gerygone nestling morphs (Supplementary materials S1 and S2).

Ejection of artificial eggs

We introduced artificial eggs in active non-parasitized nests at laying or early incubation (<5 days after first egg laying) stages that we randomly assigned to a treatment. On Day 1, we randomly chose one host egg from the nest, temporarily placed it in an incubator, and replaced it with the first artificial egg of the treatment. For Experiment 1, the treatment was one of the 6 possible presentation sequences (consecutive combinations of the 3 artificial egg colors). The complete egg presentation lasted for 6 days during which we introduced at 2-day intervals the 3 (either blue, parasite-like, or host-like) artificial egg types to the nest. We used 15 nests at 2 sites (PGF, Farino) for a total of 44 model presentations (at one nest we could not introduce the host-like egg because of depredation). For Experiment 2, we assigned each nest to a size treatment (either large or medium) and introduced the 2 egg types (a low-luminance and a high-luminance type) at 2-day intervals in the nest. We randomized the presentation order for each nest. We used 14 nests at all 3 sites for a total of 25 egg presentations (at 3 nests we could not introduce the second artificial egg in the sequence because of depredation or adverse weather conditions).

We confirmed acceptance or ejection of the artificial egg at each nest check and replaced it (if still present) with the next one in the treatment sequence. We checked for the presence of bill marks or scratches on the surface of accepted models to monitor unsuccessful ejection attempts (failed puncture- or grasp-ejection) by the host. On the final day of the experiment, we removed the last artificial egg in the sequence (if still in the nest) and returned the host egg from the incubator to the nest. In case the original nest was meanwhile depredated, we introduced the egg to the next available gerygone nest that was not used for the experiments and in a similar developmental stage.

Ejection of artificial nestlings

We introduced artificial nestlings into 30 nests (23 nonparasitized and 7 parasitized) at all 3 sites. We randomized the color of the artificial nestling introduced into the nest, thus resulting in 2 experimental combinations: model matching the host brood color (match of the whole host brood in monomorphic broods or of at least one host nestling in mixed broods, $n = 19$) and model not matching the host brood color ($n = 11$). We introduced the artificial nestlings into the nest after at least one host nestling had hatched (range 0–6 days of age), so that we knew the skin color of the first hatchling. We checked all nests 2–4 days after the introduction of the artificial nestling to determine the complete host brood color composition, to confirm the acceptance or ejection of the model, and to remove accepted artificial nestlings from the nest. As we were not able to keep nestlings in captivity for the duration of the presentation, we did not replace one of the host nestlings with the models, thus artificial and host nestlings co-existed in the nest.

Ejection of cross-fostered gerygone nestlings

We occasionally had gerygone nestlings hatching in incubators that we could not reintroduce into their original nests, because these were meanwhile lost to depredation. As hand-raising was not possible, we introduced these hatchlings into other available gerygone nests, where they had at least a chance of survival. This allowed us to conduct quasi-experimental observations using cross-fostering.

We conducted observations at 14 nonparasitized nests at 2 sites (PGF, Farino). The nests were between 4 days before to 4 days after hatching and contained at least one unhatched host egg (infertile eggs or undeveloped embryos), thus we could replace this egg with the cross-fostered nestling and avoid an increase in brood size. We introduced the nestlings randomly in respect to the foster brood color, thus the cross-fostered nestlings were either matching ($n = 11$) or not matching ($n = 3$) the foster brood color, and in relation to the time of hatching of the foster brood, thus the cross-fostered nestlings were introduced either before hatching of the foster brood ($n = 7$) or after at least one of the foster host nestlings had hatched ($n = 7$). Cuckoo nestlings have a sparser and less conspicuous natal down than gerygone nestlings (Figure 1, D–G), thus host parents might use this as a visual cue for the discrimination of the parasite. Therefore, we manipulated the appearance of some cross-fostered nestlings by trimming their natal down with fine forceps so that the introduced nestlings either had ($n = 8$) or lacked ($n = 6$) down feathers to verify if this increased or decreased chances of acceptance. We checked each nest after 2 days to confirm acceptance or ejection of the cross-fostered nestling.

Tomial ratio and grasp index

We caught adult fan-tailed gerygones using mist nets and measured bill length as the distance from the commissural point to the tip of the upper mandible and bill width as the distance between the commissural points. We compared the calculated tomial ratio and grasp index with respective measurements obtained from common hosts of the brown-headed cowbird (Rasmussen et al. 2010) and common cuckoo (Moksnes et al. 1991) to understand if bill size of the fan-tailed gerygone might constrain egg ejection.

Begging calls

We recorded begging calls of cuckoo and gerygone nestlings from the day of hatching (Day 0) until Day 13 of 27 nests at all 3 sites at about 2-day intervals between recording sessions for each given nest (depending on weather conditions). We inserted a Shure SM93 micro condenser microphone into the external bottom layer of the nest at a distance of 1–2 cm from the floor of the incubation chamber thus allowing us to record the faint begging calls of newly hatched chicks with a Tascam DR-40 digital recorder. From the recordings, it was possible to determine when the parents landed on the nest (marked by a loud thump) and called their chicks causing a begging response from the nestlings. Starting from this point, we extracted 5-s long audio tracks of the begging calls and visualized them in a spectrogram (Hann window, 3 dB bandwidth 135 Hz, 90% overlap, Hop size 51 samples, DFT 512 samples, Grid spacing 93.8 Hz). We defined a call as a single uninterrupted trace on the spectrogram. We measured the number of calls produced by the nestlings within the 5-s period, the time interval between calls, call duration, lowest frequency, highest frequency, frequency bandwidth, peak frequency (frequency at which the highest amplitude occurs), and call entropy (amount of disorder in the call, with 0 being a call of constant frequency) in Raven Pro version 1.6 (Center for Conservation Bioacustics 2019). We used the nest as the sample unit and averaged the measurements for each parameter across the recordings at each nest. Some of the nests contained several fan-tailed gerygone nestlings during the recording sessions (as the brood size can range from 1 to 3 chicks), and in these cases, we measured all the begging calls in the recordings and obtained an average value for each call parameter. We recorded cuckoo nestlings ($n = 7$) only when they were the only chick in the nest, that is, before any of the host eggs hatched or when reared alone in the nest.

Nest illumination

We measured illumination within the incubation chamber of 68 nests (of which 21% were parasitized) at all 3 sites using a Sanwa LX2 illuminance meter. We collected measurements between 800 and 1,600 h during sunny days with no cloud cover. For each nest, we took 3 measurements by placing the meter's sensor inside the incubation chamber and averaged the measurements for each nest. We conducted egg ejection tests (with artificial eggs from Experiment 2) at 8 and nestling ejection tests (with artificial nestlings from Experiment 3) at 14 of the 68 measured nests.

Stats

We conducted the experiments over multiple breeding seasons, but we found that year was not an influential factor and thus removed it from the analyses. We then investigated which variables contributed to the ejection of artificial eggs, artificial nestlings, and cross-fostered nestlings by building models in which the response variable was the ejection of the focal egg or nestling (0 = accepted, 1 ejected). For the egg ejection experiments, we used generalised linear mixed models (GLMMs) that included type of artificial egg, site (to account for a population effect on ejection), and day of the season (range 1–130, 1 = 9th September, to account for a temporal effect on ejection) as fixed effects and nest ID as a random effect (to account for multiple egg presentations at the same nest). We tested for the effect of egg size on ejection with a generalised linear model (GLM) that included size of all experimental eggs (small, medium, and large) as a fixed effect. For ejection of the artificial nestlings, we used a GLM that included color-match of the artificial and the host nestlings (0 = no match, 1 = match), parasitism (0 = nonparasitized, 1 = parasitized), site and day of the season as fixed effects. For the ejection of cross-fostered nestlings, we used a GLM that included color-match of the cross fostered nestling with the foster brood

(0 = no match, 1 = match), presence of down feathers (0 = present, 1 = lacking), and timing of introduction into the nest (before hatching of host nestlings, after hatching of host nestlings) as fixed effects. In addition, we investigated the influence of nest illumination on ejection of cuckoo and artificial nestlings using 2 GLMs that included ejection of either the cuckoo or artificial nestling as a binomial response variable and average nest illumination as a fixed effect.

Fan-tailed gerygone host parents usually eject the cuckoo nestling within the first 24–48 h after hatching and we never observed ejection or nest abandonment by host parents later than 4 days after hatching (Attisano et al. 2019). We thus divided the recordings of begging calls into 3 age groups based on chick development, begging call structure, and probability of ejection of the parasite chick: 0–3 days (early nestling period, hatchlings and young chicks, quiet begging calls with simple structure, very high probability of ejection of the parasite), 4–7 days (mid nestling period, begging calls beginning to present a defined structure, low probability of ejection of the parasite), 8–13 days (late nestling period, loud begging calls with a complete defined structure, no ejection, and no abandonment of the nest). We obtained an average value for each nest in each developmental group using multiple calls from the same nest (range 1–4 recordings) and used these values in a discriminant analysis. We first tested if a discriminant model could differentiate among host, accepted cuckoo, and ejected cuckoo nestlings based on the measurements collected during 0–3 days from hatching. We then used the begging call measurements collected during the early, mid, and late nestling periods to check if the discriminant model was able to differentiate between species according to the developmental stages of the chicks (i.e., if the cuckoo nestlings mimicked the hosts at any stage of the nestling period). Finally, we built mixed models to test for the effect of species and nestling age on the 8 measured call parameters using the full dataset of the recordings of begging calls collected from Days 0 to 13 from hatching (i.e., the average value from all the recording sessions from each nest within each day). We checked if begging call parameters followed a normal distribution and then used each parameter as a response variable in either a LMM or GLMM which included species (cuckoo, gerygone), chick age (range 0–13 days), and their interaction as fixed effects and nest ID as random effect to account for repeated measures on the same nest.

We built GLMMs in R version 3.6.3 (R Core Team 2019) using the package lme4 (Bates et al. 2015) and extracted *P*-values for the variables in each model using the function *ANOVA* from the package car (Fox and Weisberg 2019). We used additional nonparametric tests when variables did not meet the assumption of a normal distribution and report averages with 95% CIs.

Results

Ejection of artificial eggs

Fan-tailed gerygone ejected only the small artificial eggs from Experiment 1 (10×7 mm), but accepted all medium and large artificial eggs from Experiment 2 (15×11 mm and 22×14 mm). In Experiment 1, gerygones ejected 73% of the blue eggs compared with 53% of the parasite-like and 43% of the host-like eggs (Figure 2A) and we confirmed by video recording that they removed eggs by grasp-ejection (Supplementary material S4). For this egg ejection experiment, we found that neither egg type (GLMM; $\chi^2 = 2.562$, $df = 2$, $P = 0.278$), day of the season (GLMM; $\chi^2 = 2.525$, $df = 1$, $P = 0.112$) nor site (GLMM; $\chi^2 = 3.762$, $df = 1$, $P = 0.052$) had an
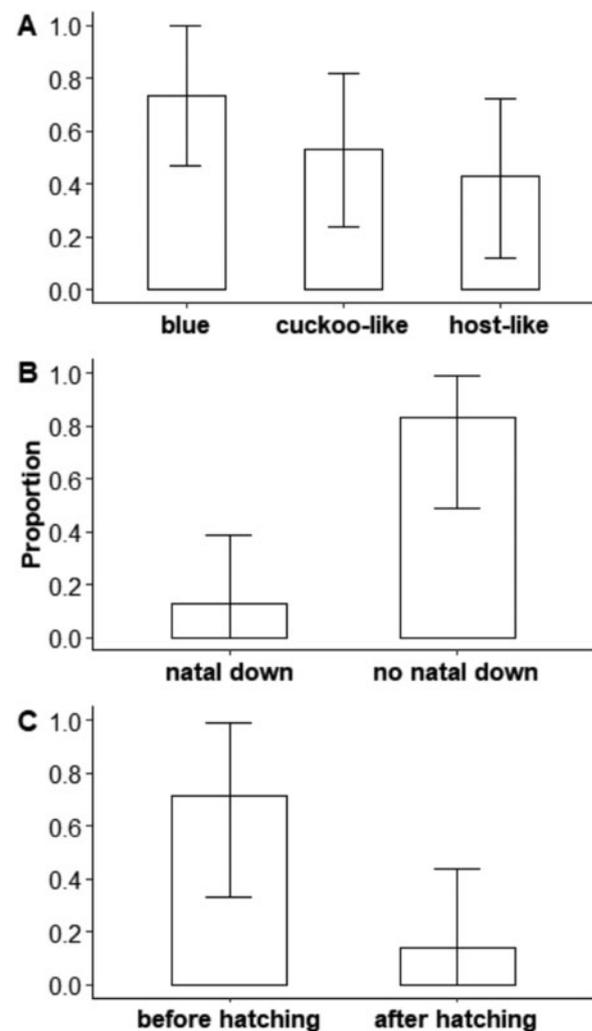

Figure 2. Proportion (with 95% Bonferroni CIs) of ejected artificial eggs in Experiment 1 (**A**, $n = 15$ blue, $n = 15$ parasite-like, $n = 14$ host-like) and ejected cross-fostered nestlings according to presence/absence of natal down (**B**, $n = 8$ natal down present, $n = 6$ natal down absent) and timing of introduction to the foster brood (**C**, $n = 7$ before hatching of the foster brood, $n = 7$ after hatching).

effect on the ejection of the egg models. The presentation sequence of the egg models also had no influence on ejection rates ($\chi^2 = 4.374$, $df = 5$, $P = 0.497$). The size of the artificial eggs was the only factor determining the ejection response, with small eggs often ejected but medium and large eggs always accepted (GLM; $\chi^2 = 32.806$, $df = 2$, $P < 0.001$). All the accepted eggs showed no presence of scratches or marks, suggesting that the host did not attempt to pierce or grasp them.

Ejection of artificial nestlings

Fan-tailed gerygones accepted 23 (77%) and ejected 7 (23%) artificial nestlings. For comparison, during 8 field seasons, gerygones accepted 4 (12%), and ejected 29 (88%) cuckoo hatchlings. At the 8 parasitized experimental nests gerygones ejected 1 and accepted 7 artificial nestlings, whereas gerygones ejected the cuckoo nestlings in 6 occasions within 1–2 days from hatching (in 2 nests the cuckoo egg did not hatch). The ejection of the artificial nestling was not influenced by color-matching of the host brood (GLM; $\chi^2 = 0.303$,
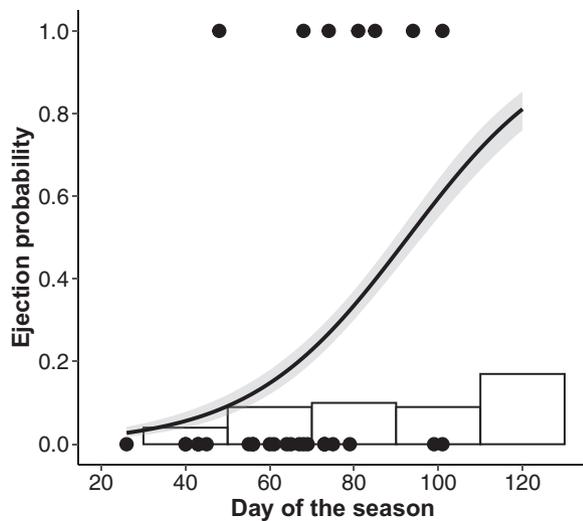
Figure 3. Logistic regression (estimate = 0.053, SE = 0.028) for the probability of fan-tailed gerygones to accept (0) or eject (1) the artificial nestling in relation to day of the season (1 = 9th September). Black points are artificial nestling ejection trials and the gray area around the regression line is the 95% confidence band. Vertical bars are the proportions of cuckoo nestlings ejected by host parents observed within 20-day periods during the 8 breeding seasons.

$df = 1$, $P = 0.582$), site (GLM; $\chi^2 = 3.405$, $df = 2$, $P = 0.182$), or the nest being parasitized (GLM; $\chi^2 = 1.119$, $df = 1$, $P = 0.290$). The probability of ejection of artificial nestlings increased as the season progressed (GLM; $\chi^2 = 6.119$, $df = 1$, $P = 0.013$) along with the proportion of nests with cuckoo nestling ejections (Figure 3).

Ejection of cross-fostered gerygone nestlings

Fan-tailed gerygone foster parents accepted 8 (57%) and ejected 6 (43%) cross-fostered gerygone nestlings. The ejection response was best explained by the lack of down (GLM; $\chi^2 = 11.345$, $df = 1$, $P = 0.001$; Figure 2B) and timing of introduction of the cross-fostered nestling to the foster brood (GLM; $\chi^2 = 6.453$, $df = 1$, $P = 0.011$; Figure 2C), whereas there was no influence of color-match of the foster brood (GLM; $\chi^2 = 3.819$, $df = 1$, $P = 0.051$). We also found no influence of day of the season (logistic regression; $\chi^2 = 2.598$, $df = 1$, $P = 0.107$) nor site ($\chi^2 = 1.027$, $df = 1$, $P = 0.311$) on the ejection of cross-fostered nestlings.

Tomial ratio and grasp index

Bills of adult fan-tailed gerygones ($n = 71$) were on average 12.7 ± 0.1 mm long and 4.0 ± 0.03 mm wide. The average fan-tailed gerygone had a tomial ratio of 0.88 ± 0.02 and a grasp index of 51.2 ± 1.5 mm^2.

Begging calls

The discriminant model was able to differentiate among gerygone nestlings, accepted cuckoo nestlings and ejected cuckoo nestlings that were no more than 3 days old (Figure 4). The model correctly identified the species of the nestling (as belonging to cuckoo or gerygone) in 91% of the cases ($n = 22$, 1 accepted cuckoo misidentified as a gerygone and 1 gerygone misidentified as an ejected cuckoo) when the nestlings were between 0 and 3 days old, 86% of the cases ($n = 14$, 1 cuckoo misidentified as a gerygone and 1 gerygone misidentified as a cuckoo) when the nestlings were 4 to 7 days old and 83% of the cases ($n = 6$, 1 cuckoo misidentified as a gerygone) when
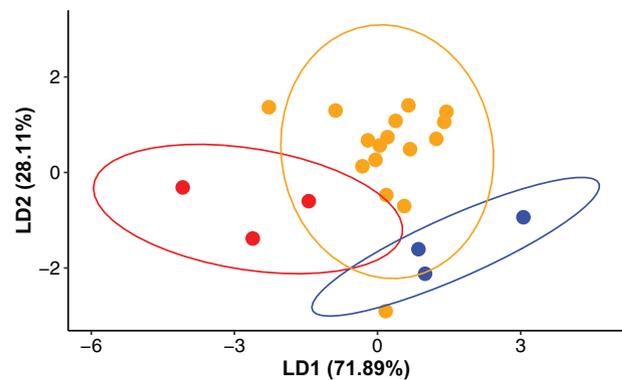

Figure 4. Canonical plot of the first and second linear discriminant functions for the 8 measured parameters of the begging calls in 0–3 days old nestlings. Orange dots are fan-tailed gerygone nestlings, red dots are shining bronze-cuckoo nestlings accepted by host parents and blue dots are shining bronze-cuckoo nestlings ejected by their host parents within 1–2 days from hatching. Ellipses are 95% CIs around the centroid of the distribution for each nestling type.

the nestlings were 8 to 13 days old. The species were defined by significant differences in lowest, highest, and peak frequencies of the begging calls, whereas all begging parameters, with the exception of entropy, varied with the nestling age (Table 2; Figure 5; Supplementary material S3).

Nest illumination

Nests of fan-tailed gerygone had a mean illuminance of 656 ± 170 lux (range 11–3,365 lux). Nests from which gerygones ejected cuckoo nestlings ($n = 9$) had similar illuminance to non-parasitized nests ($n = 47$; GLM, $\chi^2 = 0.013$, $df = 1$, $P = 0.909$). Similarly, nests from which artificial nestlings were ejected ($n = 2$) had similar illuminance to nests in which the artificial nestlings were accepted ($n = 12$; GLM, $\chi^2 = 0.707$, $df = 1$, $P = 0.4$). Nest illumination was neither affected by site (Kruskal–Wallis $\chi^2 = 2.134$, $df = 2$, $P = 0.344$) nor part of the day (morning versus afternoon; Kruskal–Wallis $\chi^2 = 0.705$, $df = 1$, $P = 0.401$).

Discussion

Our results showed that the fan-tailed gerygone does not eject eggs based on their appearance. The gerygones only removed artificial eggs that were small enough to be grasped irrespective of their color, whereas they always accepted artificial eggs matching the size range of gerygone and cuckoo eggs irrespective of their luminance. Thus, egg size, rather than its appearance, is likely to constrain egg ejection in this host. Similarly, the ejection of foreign nestlings (gerygone or cuckoo) is not based on cues such as nestling skin color, but is rather based on other visual cues such as the presence of natal down as well as the timing of introduction. Begging calls might also be used as an additional cue for the discrimination of foreign nestlings. Therefore, fan-tailed gerygones always accept eggs within a natural size range and discriminate eggs and nestlings by using different cues.

We found that the fan-tailed gerygone did also not reject foreign eggs by deserting parasitized clutches as other hosts do (Langmore et al. 2003; Medina and Langmore, 2016). Instead, nest abandonment in the fan-tailed gerygone is rare and is not linked to the presence of a cuckoo egg in the nest. The reason might be that female gerygones invest large resources into egg production (over 20% of the female body mass per egg) and that a pair completes a breeding

Table 2 Average (with 95% CI) parameters of begging calls for cuckoo nestlings accepted by the host parents ($n = 3$), cuckoo nestlings ejected by the host parents ($n = 3$), and gerygone nestlings ($n = 16$) with P-values of mixed models of the difference in begging call parameters between species (gerygone, cuckoo), age of the chick (0–13) and their interaction. Statistically significant results at $P < 0.05$ are in bold

|	Cuckoo accepted	Cuckoo ejected	Gerygone	Species	Age	Species*Age
Number of calls in 5 s	4.33 ± 5.02	4.83 ± 8.98	6.93 ± 1.66	0.168	**< 0.001**	0.218
Interval between calls (s)	1.19 ± 2.54	0.67 ± 1.17	0.75 ± 0.20	0.682	**0.005**	0.931
Call duration (s)	0.03 ± 0.03	0.07 ± 0.07	0.05 ± 0.01	0.763	**< 0.001**	0.162
Lowest frequency (kHz)	5.38 ± 1.72	5.19 ± 1.02	6.05 ± 0.35	**0.005**	**< 0.001**	0.831
Highest frequency (kHz)	6.41 ± 2.41	6.57 ± 1.15	7.41 ± 0.53	**0.005**	**< 0.001**	**0.046**
Peak frequency (kHz)	6.06 ± 2.33	6.06 ± 1.04	6.96 ± 0.47	**0.011**	**< 0.001**	0.270
Frequency bandwidth (kHz)	1.03 ± 0.75	1.38 ± 0.62	1.36 ± 0.31	0.096	**< 0.001**	**< 0.001**
Entropy	2.86 ± 1.38	2.77 ± 0.66	2.89 ± 0.38	0.322	0.753	0.043
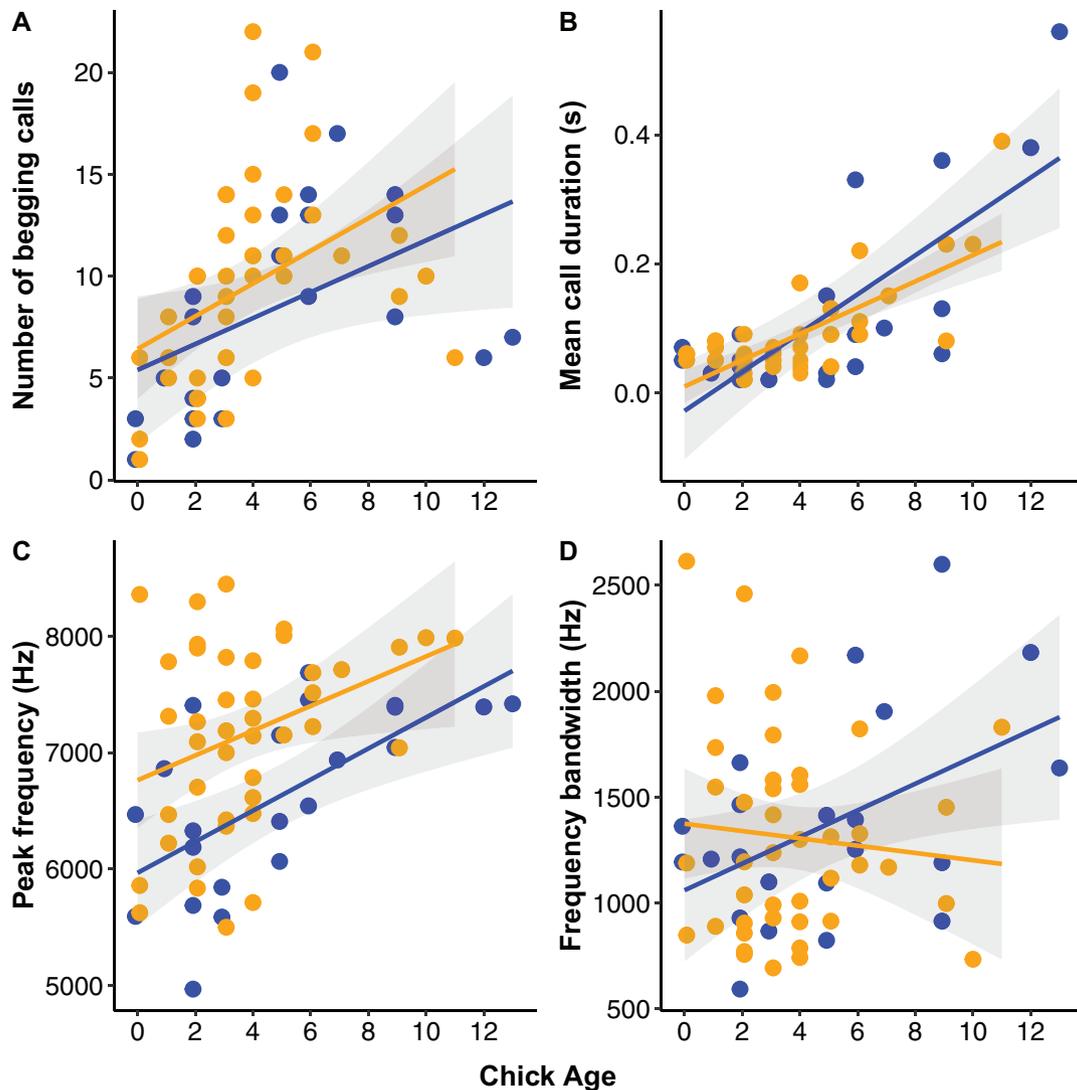
Figure 5. Variation of begging call parameters in relation to age of fan-tailed gerygone (orange) and shining bronze-cuckoo (blue) nestlings. The grey shaded areas around the regression lines are the 95% confidence bands.

cycle in about 10–12 weeks (including nest building, laying, incubation, brooding, and raising the fledglings) which is about half the length of the breeding season. Therefore, nest abandonment might reduce the chances of a successful reproduction within the same

breeding season and thus be too costly as a form of egg rejection strategy in this host.

A possible reason why gerygones never ejected artificial eggs that were at least the size of their own eggs might be that they were not

able to puncture–eject the models because these were made of clay. However, we think that this form of egg ejection is unlikely as we never observed any egg removal by this host, neither indirectly via a reduction in clutch size nor directly on camera despite intensive video monitoring. In addition, we never recorded beak marks on any artificial egg. Another reason for the acceptance might be that fan-tailed gerygones produce small clutches of 2 eggs on average (Attisano et al. 2019), thus accepting the cuckoo egg might prevent further reduction of the host clutch by multiple parasitizing cuckoo females (egg dilution effect in Sato et al. 2010). Alternatively, a strategy of removing eggs from the nest might result in ejection errors and lead to a costly reduction of their own clutch (Davies et al. 1996). Similar rejection experiments conducted on the grey gerygone *Gerygone igata* and the yellow-rumped thornbill *Acanthiza chrysorroa*, which are closely related to the fan-tailed gerygone and are also hosts of the shining bronze-cuckoo, confirm that also these hosts are acceptors of naturally sized artificial eggs (Thorogood et al. 2017; Medina and Langmore 2019). However, our result that fan-tailed gerygones frequently ejected small eggs suggests that another reason why fan-tailed gerygones accept natural eggs (of both host and parasite) might be that the eggs are too large to be grasped and removed from the nest. The tomial ratio and grasp index, which are important indicators for grasp-ejector hosts, would indeed place the fan-tailed gerygone in the group of small hosts from Europe and North America that accept foreign eggs (tomial ratio: 0.62–1.14, Rothstein 1975; grasp index: 53.4–285.0, Rohwer and Spaw 1988; Moksnes et al. 1991; Underwood and Sealy 2006). Therefore, the absence of ejection of eggs of natural size in this host is most likely explained by a combination of the high cost of ejecting the eggs and by physical limitations preventing grasp-ejection of a foreign egg.

Although we did not specifically test for nest sanitation behavior using additional non-egg shaped objects, we think it is unlikely that the small artificial eggs might have been removed because they were seen solely as foreign material. First, studies linking nest sanitation and egg rejection consistently showed that hosts respond differently to non-egg shaped and egg shaped models, suggesting that the latter, even when smaller than real eggs, are likely to be regarded as real eggs by the hosts (Guigueno and Sealy 2012; Honza and Cherry 2017). In our case, the artificial eggs resembled the shape of a gerygone egg and the host ejected all types, not just the alien-looking blue one, at relatively high rates. Second, the dome-shaped nest might prevent foreign material to fall into the nest, thus sanitation in the form of removal of foreign nonegg objects in this host is a much rarer behavior than in open cup nesters. Third, egg discrimination by size and shape does occur in some hosts of brood parasites (Marchetti 2000; Langmore et al. 2003; Guigueno et al. 2014; Taylor and Langmore 2020), and the gerygones frequently removed the small artificial eggs but did not remove artificial eggs matching the size of real eggs. It is thus likely that the fan-tailed gerygone was not physically able to remove eggs of medium or large size, but they were able to grasp-eject the small eggs.

Closed nests have generally lower illumination than open nests (Langmore et al. 2005; Avilés et al. 2006); therefore, Langmore et al. (2009a) hypothesized that dark bronze-cuckoo eggs might escape detection because they are cryptic in this type of nest. Our observation that fan-tailed gerygones frequently ejected the parasite-like small artificial eggs would rather suggest that these were not cryptic because the hosts detected the parasite-like eggs as well as they detected the blue and host-like eggs. However, some gerygone nests have relatively low illumination values meaning that light availability might sometimes be a limiting factor. Superb fairy-wren *Malurus*

spendens build similar dome-shaped nests and reject foreign eggs based on their size rather than color, suggesting they might use tactile cues to discriminate foreign eggs (Langmore et al. 2003). Therefore, the relatively similar ejection rates of small artificial eggs of various colors could also be explained by the fan-tailed gerygone using tactile cues to detect artificial eggs.

There are several possible explanations why fan-tailed gerygones do not rely on the skin color of the artificial nestlings and cross-fostered nestlings as a discrimination cue. First, low illumination within the nests might make color cues less effective. Second, extra-pair copulations and partner changes across multiple seasons could cause variation in the brood coloration and increase the chances that the same parent will encounter both host nestling morphs during its lifetime (Bojarska et al., 2018). Third, cuckoo nestlings also occur in 2 morphs (Sato et al. 2015), thus increasing the phenotypic variation of nestlings, which could lead to higher chances of misidentification. Therefore, skin color alone cannot be a reliable cue for the discrimination of the parasite nestling. However, cuckoo nestlings have a sparser natal down than the host and always hatch earlier than the host chicks, which mean that these can be more reliable cues for the discrimination of the parasite nestling than skin color. Similar results were also found in other hosts that reject bronze-cuckoo nestlings using either hatching order or natal down as cues (Langmore et al. 2009a; Noh et al. 2018). In addition, we found that the shining bronze-cuckoo nestlings only imperfectly mimic the host begging calls, thus gerygone host parents might use sound cues for the discrimination, similarly to other hosts that discriminate the parasite nestlings via their begging calls (Langmore et al. 2003; Colombelli-Négrel et al. 2012).

The relatively low rate of ejection of the artificial nestlings might have been the consequence of lack of additional cues, besides color, required to trigger an ejection response. Shining bronze-cuckoo nestlings constantly move after they hatch, likely an adaptation to help them remove host eggs or nestlings. In contrast, the artificial nestlings were inanimate and lacked auditory cues in the form of begging calls. In addition, the timing of hatching of the nestlings has an effect on the ejection response of the host (Figure 2C) and the low ejection rate of the artificial nestlings might have been a consequence of the introduction of artificial nestlings in the nest after hatching of the host brood. The probability of ejection of artificial nestlings increased along with the frequency of ejection of cuckoo nestlings toward the end of the breeding season. This pattern suggests that nestling ejection might be a direct response to the seasonally increased presence of parasite nestlings and not the result of a parasitism risk perceived in the past, for example, due to previous experience of adult parasites approaching the nest or presence of parasite eggs in the nest, as it commonly occurs in other hosts (Briskie and Sealy 1989; Bártol et al. 2002; Avilés and Parejo 2006; Langmore et al. 2009b).

We conclude that egg and nestling ejection strategies are unlikely to co-exist as host defense behaviors in the fan-tailed gerygone. Potential visual cues such as color and luminance are not effective for the discrimination of eggs and nestlings. The evolution of an egg ejection strategy might be constrained by high costs and by physical limitations forcing acceptance of the large cuckoo egg. However, a nestling ejection strategy could have evolved because cuckoo nestlings can be more easily grasped and ejected than a large cuckoo egg. Discrimination of foreign nestlings can also be based on a combination of multiple cues such as natal down, timing of hatching, and begging calls, which further facilitates the evolution of a nestling ejection over an egg ejection strategy. Our study highlights the

importance of studying multiple cues at multiple stages of the arms race to better understand the evolution of discrimination of the brood parasite by the host.

Author Contributions

A.A., N.J.S., K.D.T., K.U., R.G., and J.T. conceived the study. A.A., N.J.S., and K.D.T. designed the experiments. A.A., N.J.S., Y.O., and K.D.T. conducted fieldwork. A.A. analyzed the data and wrote the first draft. All authors commented on the analyses and edited the manuscript.

Ethical Standards

The Province Sud of New Caledonia issued all permits (3045-2011, 2437-2012, 2532-2013, 2801-2014, 2476-2015, 2372-2017, 3469-2018, and 2720-2019) for fieldwork. The first Warsaw Local Ethics Committee for Animal Experimentation approved the field work methods.

Conflict of Interest Statement

We declare that we have no competing interests.

Supplementary Material

"Supplementary material can be found at https://academic.oup.com/cz".

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