PODPIS ZAUFANY
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ATTISANO
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Rada Naukowa Muzeum i Instytutu Zoologii
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za pośrednictwem:
Rady Doskonałości Naukowej
pl. Defilad 1
00-901 Warszawa
(Pałac Kultury i Nauki, p. XXIV, pok. 2401)

Alfredo Attisano
……………………………………………………………………
(imię i nazwisko wnioskodawcy)

Muzeum i Instytut Zoologii Polskiej Akademii Nauk
……………………………………………………………………
(miejsce pracy/jednostka naukowa)

Wniosek

z dnia ……23.01.2026…………..

o przeprowadzenie postępowania w sprawie nadania stopnia doktora habilitowanego w dziedzinie **nauki ścisłe i przyrodnicze** w dyscyplinie **nauki biologiczne.**
Osiągnięcie naukowe uprawniające do wszczęcia postępowania o nadanie stopnia naukowego doktora habilitowanego:
osiągnięcie naukowe pt. „Koewolucyjny wyścig zbrojeń i zmienność fenotypowa piskląt w układzie pasożyt lęgowy – żywiciel z Nowej Kaledonii" obejmuje cykl tematyczny pięciu artykułów opublikowanych w recenzowanych międzynarodowych czasopismach naukowych. Łączny współczynnik wpływu czasopism, w których opublikowano artykuły, wynosi **15,079**, a łączna liczba punktów według listy ministerialnej wynosi **620**.

Wnioskuję – na podstawie art. 221 ust. 10 ustawy z dnia 20 lipca 2018 r. Prawo o szkolnictwie wyższym i nauce – aby komisja habilitacyjna podejmowała uchwałę w sprawie nadania stopnia doktora habilitowanego w głosowaniu **jawnym**

Zostałem poinformowany, że: Administratorem w odniesieniu do danych osobowych pozyskanych w ramach postępowania w sprawie nadania stopnia doktora habilitowanego jest Przewodniczący Rady Doskonałości Naukowej z siedzibą w Warszawie (pl. Defilad 1, XXIV piętro, 00-901 Warszawa). Kontakt za pośrednictwem e-mail: kancelaria@rdn.gov.pl , tel. 22 656 60 98 lub w siedzibie organu. Dane osobowe będą przetwarzane w oparciu o przesłankę wskazaną w art. 6 ust. 1 lit. c) Rozporządzenia UE 2016/679 z dnia z dnia 27 kwietnia 2016 r. w związku z art. 220 - 221 oraz art. 232 – 240 ustawy z dnia 20 lipca 2018 roku - Prawo o szkolnictwie wyższym i nauce, w celu przeprowadzenie postępowania o nadanie stopnia doktora habilitowanego oraz realizacji praw i obowiązków oraz środków odwoławczych przewidzianych w tym postępowaniu.Szczegółowa informacja na temat przetwarzania danych osobowych w postępowaniu dostępna jest na stronie www.rdn.gov.pl/klauzula-informacyjna-rodo.html

Alfredo Attisano
……………………………………..
(podpis wnioskodawcy)

Załączniki:

Załącznik 1. Dane wnioskodawcy
Załącznik 2. Potwierdzenie uzyskania stopnia doktora
Załącznik 3. Autoreferat
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TŁUMACZENIE POŚWIADCZONE Z JĘZYKA ANGIELSKIEGO

[godło]

UNIVERSITY OF EXETER
[UNIWERSYTET EXETER]

My, niżej podpisani, niniejszym poświadczamy, że

Alfredo Attisano

zrealizował zatwierdzony program studiów
i spełniwszy wymogi Rozporządzeń i Regulaminów Uniwersytetu
uzyskał Tytuł

Doktora filozofii

nadany przez Senat Uniwersytetu w dniu
4 marca 2013 roku.

*[hologram z godłem
Uniwersytetu]*
/-/ nieczytelny podpis
KANCLERZ

/-/ nieczytelny podpis
WICEKANCLERZ

/-/ nieczytelny podpis
PREZES

Ja niżej podpisana, Biruta Gruszecka, tłumacz przysięgły języka angielskiego, wpisana na listę tłumaczy przysięgłych przy Ministerstwie Sprawiedliwości pod numerem TP/1740/06, oświadczam, że treść powyższego tłumaczenia jest zgodna z treścią przedstawionego mi oryginału dokumentu w języku angielskim. ----------------
Wpisano do repertorium pod numerem: 185/2026--
Toruń, 21 stycznia 2026---

UNIVERSITY OF EXETER
[UNIWERSYTET EXETER]

SUPLEMENT DO DYPLOMU WYKAZ OCEN

Nr odniesienia Uniwersytetu	590047993/1	Data urodzenia	10 sierpnia 1979
Nazwisko	ATTISANO	Nr odniesienia HESA	0911190067725
Imiona	ALFREDO	Data wpisu	5 października 2009
Nazwa kwalifikacji:		Doktor filozofii	
Dziedzina naukowa:		Zróżnicowanie historii życia i ewolucyjna reakcja na stres pokarmowy u Oncopeltus Fasciatus (Hemiptera: Lygaeidae)	
		Tytuł nadany 4 marca 2013 roku	
Język wykładowy		Angielski	

Dane dotyczące programu studiów (dalsze dane dotyczące stosownych specyfikacji programowych można uzyskać na stronie pod adresem www.exeter.ac.uk/progspecs/).

Podejście ECTS Punkty Ocena

2009/0 PHD *[doktor filozofii]* w dziedzinie nauk biologicznych – C
Etap 1 dzienne

Postęp: Zaliczenie 30 września 2010

2010/1 PHD *[doktor filozofii]* w dziedzinie nauk biologicznych – C
Etap 2 dzienne

Postęp: Zaliczenie 30 września 2011

2011/2 PHD *[doktor filozofii]* w dziedzinie nauk biologicznych – C
Etap 3 dzienne

Postęp: Zaliczenie 11 października 2012

2012/3 PHD *[doktor filozofii]* w dziedzinie nauk biologicznych – C
Etap 4 Oczekiwanie na przyznanie tytułu (dzienne), bez rejestracji

Postęp: Ukończenie 4 marca 2013

*= Zwolnienie z modułu, ścieżki lub tytułu. C = Akceptacja

Data wystawienia wykazu ocen: 5 marca 2013

BIRUTA GRUSZECKA

Oceny i wyniki nie mogą być wydawane stronie trzeciej bez pisemnej zgody studenta.

/-/ nieczytelny podpis
M. Shoebridge
Dyrektor ds. Usług Akademickich
Uniwersytet Exeter

Informacje dotyczące przyznawania tytułów i instytucji przyznającej tytułu znajdują się na odwrocie wykazu ocen.

[hologram z godłem Uniwersytetu]

* * *

Ja niżej podpisana, Biruta Gruszecka, tłumacz przysięgły języka angielskiego, wpisana na listę tłumaczy przysięgłych przy Ministerstwie Sprawiedliwości pod numerem TP/1740/06, oświadczam, że treść powyższego tłumaczenia jest zgodna z treścią przedstawionego mi oryginału dokumentu w języku angielskim. ----------------
Wpisano do repertorium pod numerem: 186/2026---
Toruń, 21 stycznia 2026---

BIRUTA GRUSZECKA
NR TP/1740/06

Autoreferat

1. Imię i nazwisko.

Alfredo Attisano

2. Posiadane dyplomy, stopnie naukowe lub artystyczne – z podaniem podmiotu nadającego stopień, roku ich uzyskania oraz tytułu rozprawy doktorskiej.

2007 – tytuł magistra Nauk Przyrodniczych, Wydział Zoologii na Uniwersytecie w Neapolu „Federico II", Włochy. Tytuł pracy magisterskiej: „Narzędzia genetyczne dla ochrony i zarządzania populacjami ptaków w Kampanii, w południowych Włoszech", promotorzy: prof. Maria Filomena Caliendo, dr Daniela Rippa.

2013 – doktorat z Nauk Biologicznych, Centrum Ekologii i Ochrony Środowiska, Wydział Nauk Biologicznych, Uniwersytet Exeter, Wielka Brytania. Tytuł rozprawy doktorskiej: „Zróżnicowanie historii życia i ewolucyjna reakcja na stres pokarmowy u *Oncopeltus fasciatus (Hemiptera:Lygaeidae)"*, promotorzy: prof. Patricia J. Moore, prof. Allen J. Moore, prof. Tom Tregenza.

3. Informacja o dotychczasowym zatrudnieniu w jednostkach naukowych lub artystycznych.

09.2005 – 04.2007 - Asystent. Laboratorium Genetyki Populacyjnej, Katedra Zoologii, Uniwersytet w Neapolu „Federico II", Włochy

09.2009 – 03.2013 - Doktorant. Centrum Ekologii i Ochrony Przyrody, Wydział Nauk Biologicznych, Uniwersytet Exeter, Wielka Brytania.

09.2010 – 05.2012 - Asystent. Centrum Ekologii i Ochrony Przyrody, Wydział Nauk Biologicznych, Uniwersytet Exeter, Wielka Brytania.

03.2013 – 11.2014 – Post-doc. Grupa ekologii behawioralnej, Wydział Zoologii, Uniwersytet Cambridge, Wielka Brytania.

05.2015 – obecnie - adiunkt. Muzeum i Instytut Zoologii PAN.

4. Omówienie osiągnięć, o których mowa w art. 219 ust. 1 pkt. 2 ustawy z dnia 20 lipca 2018 r.

4.1 Cykl pięciu artykułów naukowych opublikowanych w latach 2018–2025, stanowiących moje osiągnięcie pt. „Koewolucyjny wyścig zbrojeń i zmienność fenotypowa piskląt w układzie pasożyt lęgowy – żywiciel z Nowej Kaledonii”.

1. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports*, 8: 1–10. https://doi.org/10.1038/s41598-018-28710-5 [IF$_{2018}$ = 4.011; Q1; MNiSW punktów = 140]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
2. **Attisano, A.,** Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021). Threat recognition and response in an avian brood-parasite host from New Caledonia. *Current Zoology*, 67: 255–262. https://doi.org/10.1093/cz/zoaa061 [IF$_{2021}$ = 2.734; Q1; MNiSW punktów = 100]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
3. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Current Zoology*, 67: 653–663. https://doi.org/10.1093/cz/zoab066 [IF$_{2021}$ = 2.734; Q1; MNiSW punktów = 100]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
4. **Attisano, A.,** Gill, B.J., Anderson, M.G., Gula, R., Langmore, N.E., Okahisa, Y., Sato, N.J., Tanaka, K., Thorogood, R., Ueda, K., Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Journal of Animal Ecology* 93: 30-43, https://doi.org/10.1111/1365-2656.13849 [IF$_{2023}$ = 3.5; Q1; MNiSW punktów = 140]

   Oświadczam, że mój wkład w powyższy artykuł obejmował organizację i zarządzanie danymi dostarczonymi przez wszystkich współautorów, przeprowadzenie analizy statystycznej, przygotowanie rysunków i tabel oraz napisanie pierwszej wersji manuskryptu.

W odniesieniu do sekcji z Nowej Kaledonii w artykule mój wkład polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie i przeprowadzeniu analizy statystycznej. Jestem pierwszym autorem i autorem korespondencyjnym.

5. **Attisano, A.,** Anderson M.G., Langmore N.E., Gula, R., Theuerkauf J. (2025). Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo *Chalcites lucidus*. *Animal Behaviour* 221:123083, https://doi.org/10.1016/j.anbehav.2025.123083 [IF_{2025} = 2.3; Q1; MNiSW punktów = 140]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uporządkowaniu i zarządzaniu danymi dostarczonymi przez wszystkich współautorów, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. W odniesieniu do sekcji z Nowej Kaledonii w artykule mój wkład polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie i przeprowadzeniu analizy statystycznej. Jestem pierwszym autorem i autorem korespondencyjnym

Łączna wartość współczynnika wpływu (IF) czasopism, w których opublikowałem prace, wynosi 15,079, a łączna liczba punktów MNiSW 620. Publikacje uwzględnione na liście osiągnięć są rezultatem prac finansowanych w ramach grantów nr 2012/05/E/NZ8/02694 i 2016/23/B/NZ8/03082 (publikacje nr 1, 3, 4), 2016/23/B/NZ8/03082 (publikacja nr 2) oraz 2022/45/B/NZ8/03740 (publikacja nr 5). Jestem kierownikiem projektu w dwóch ostatnich grantach. Projekt 2016/23/B/NZ8/03082 został ukończony 05.07.2021, natomiast projekt 2022/45/B/NZ8/03740 jest w trakcie realizacji i zakończy się 07.01.2027. Dwie publikacje zawarte w tym osiągnięciu są efektem współpracy ornitologów z Polski i Japonii (publikacje 1 i 3), a publikacje 4 i 5 powstały w wyniku współpracy z ornitologami z Polski, Japonii, Australii i Nowej Zelandii (publikacje 4 i 5).

4.1.1 Wprowadzenie

Pasożyty lęgowe ptaków składają jaja w gniazdach innych ptaków, zwanych żywicielami. Żywiciele opiekują się potomstwem pasożyta, co wiąże się z wysokimi kosztami energetycznymi i obniżonym sukcesem reprodukcyjnym (Soler 2017). Presja selekcyjna działa na żywicieli prowadzi do wykształcenia obrony przed pasożytnictwem, co z kolei sprzyja selekcji strategii pozwalających unikać tej obrony. Te interakcje mogą skutkować koewolucyjnym wyścigiem zbrojeń między żywicielami a pasożytami lęgowymi (Dawkins & Krebs 1979; Davies 2011).

Wiele gospodarzy potrafi rozpoznać jaja pasożytów lęgowych w swoim gnieździe, a mechanizmy tej dyskryminacji i odrzucania jaj pasożytów są przedmiotem wielu programów badawczych (Brooke & Davies 1988; Antonov et al. 2009; Spottiswoode & Stevens 2011; Caves et al. 2015; Hanley et al. 2021; Marchetti 2000; Spottiswoode & Stevens 2010; Honza & Cherry 2017; Ruiz-Raya & Soler 2020; Samaš et al. 2021). Wiadomo także, że wyścig zbrojeń na etapie jaja może prowadzić do zmienności wyglądu jaj zarówno u gospodarza, jak i pasożyta lęgowego (Takasu 2003; Spottiswoode & Stevens 2012; Medina et al. 2020; Yang et al. 2020). Dlatego też, wiele badań przeprowadzonych w ciągu 40 lat dała nam ugruntowaną wiedzę na temat ewolucji interakcji pasożyt legowy-gospodarz na etapie jaja (Davies 2015; Soler 2017).

Z drugiej strony, obrona gospodarza przed pisklętami pasożytów lęgowych jest rzadka (Soler 2009; Grim 2011). Bezpośrednie dowody obrony gospodarza przed pisklętami pasożytów znaleziono u żywicieli z Oceanii (Langmore et al. 2003; Sato et al. 2010, 2015; Tokue & Ueda 2010), podczas gdy w innych rejonach świata żywiciele zawsze akceptują pisklęta pasożytów (Grim 2017) lub mogą odrzucać pasożyta tylko na etapie podlota (Grim et al. 2003; De Mársico et al. 2012). W rezultacie nasza wiedza na temat czynników selektywnych napędzających interakcje na wczesnym etapie wyścigu zbrojeń jest ograniczona (Grim 2017).

W moim osiągnięciu habilitacyjnym skupiam się na koewolucyjnych interakcjach zachodzących na etapie pisklęcia w układzie pasożyt lęgowy – gospodarz z odległego archipelagu Nowej Kaledonii. Na tej wyspie Pacyfiku krzakówka wachlarzowata (*Gerygone flavolateralis*) jest wyłącznym gospodarzem kukułeczki jarzębatej (*Chalcites lucidus*). Krzakówki nie odrzucają jaj pasożyta, tylko odrzucają pisklęta pasożyta, usuwając je z gniazda, zwykle w ciągu 24 godzin od wyklucia. W tym systemie dyskryminacja pisklęcia pasożyta przez gospodarza promuje selekcję na mimikrę piskląt żywiciela przez kukułkę, aby uniknąć odrzucenia (Sato et al. 2015). Ponadto zarówno pisklęta gospodarza i pasożyta mają dwie formy fenotypowe - jasną i ciemną, co wskazuje na dalszą selekcję na w kierunku zmienności fenotypowej w wyglądzie piskląt (Sato et al. 2015). Lęgi gospodarza – krzakówki mogą być monomorficzne (jasne lub ciemne) lub mieszane, z dwoma fenotypami piskląt współistniejącymi w tym samym gnieździe. Pomimo zmienności fenotypowej i wewnątrz lęgowej, krzakówki zawsze odrzucają pisklęta kukułek niezależnie od typu lęgu, ale nigdy nie odrzucają własnych piskląt przez pomyłkę. Zmienność fenotypowa piskląt jest rzadka u ptaków (Kilner 2006), a żaden inny system na świecie nie osiągnął poziomu złożoności w wyglądzie piskląt podobnego do obserwowanego na Nowej Kaledonii. Dlatego system pasożytnictwa lęgowego z Nowej Kaledonii oferuje wyjątkową okazję do zbadania interakcji pasożyt-gospodarz na etapie pisklęcia i zrozumienia mechanizmów selekcji dyskryminacji piskląt pasożytów i zmienności fenotypowej piskląt w ramach koewolucyjnego wyścigu zbrojeń.

Cykl artykułów stanowiący moją rozprawę habilitacyjną opisuje modalności mimikry piskląt gospodarzy (publikacja 1) i pokazuje, jak słabe lub nieobecne są mechanizmy obrony przed pasożytem na wcześniejszych etapach cyklu rozrodczego żywiciela mogły promować selekcję na rzecz udoskonalonych strategii obrony na późniejszych etapach wyścigu zbrojeń w tym systemie (artykuły 2, 3). Zbadałem również, jakich cech używają rodzice żywiciele, aby odróżnić pisklę kukułki od swoich własnych (artykuł 3). Na koniec, przyglądając się wzorcom zmienności fenotypowej piskląt i mimikry piskląt w całym zasięgu występowania lśniącej brązowej kukułki w regionie Pacyfiku, pokazałem, jak koewolucyjne interakcje z jej żywicielami promowały dywersyfikację piskląt i przyczyniły się do ewolucji geograficznie i genetycznie odseparowanych podgatunków kukułki (artykuły 4, 5).

4.1.2 Wyniki

1. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports*, 8: 1–10.

Celem badań było zrozumienie, w jaki sposób pisklęta kukułeczki jarzębatej naśladują wygląd piskląt krzakówki wachlarzowatej. Podczas sezonów 2013–2014 (finansowanych z grantu 2012/05/E/NZ8/02694) badacze z Pracowni Ekologii Behawioralnej MiIZ PAN i oraz Grupy Ekologii Behawioralnej na Uniwersytecie Rikkyo w Tokio zaobserwowali dwa wyraźne fenotypy piskląt krzakówki wachlarzowatej, jasny i ciemny, podczas gdy pisklęta kukułeczki wykazywały wyłącznie fenotyp jasny. Analiza widm reflektancji wykazała, że jasne pisklęta kukułeczki bardziej przypominają jasny fenotyp gospodarza, co sugeruje naśladowanie jasnych piskląt gospodarza przez kukułkę (Sato et al., 2015). Jednak widma reflektancji nie uwzględniają złożonych powierzchni, takich jak całe ciało pisklęcia, dlatego wyniki Sato et al. (2015) dostarczyły jedynie częściowej interpretacji mechanizmów naśladowania piskląt gospodarza przez pisklęta kukułki brązowej.

W 2015 roku dołączyłem do Pracowni Ekologii Behawioralnej w Muzeum i Instytucie Zoologii PAN jako adiunkt, aby dalej badać mechanizmy naśladowania piskląt gospodarza przez pisklęta kukułeczki jarzębatej. Wykorzystałem fotografię wielospektralną piskląt, która umożliwia analizę informacji wizualnych z większych obszarów ciała pisklęcia, co pozwala na bardziej wszechstronną i szczegółową analizę wizualną w porównaniu do widm reflektancji. Użyłem zdjęć zebranych przez moich kolegów i mnie w latach 2013–2015 (w ramach grantu 2012/05/E/NZ8/02694, w którym byłem wykonawcą) oraz przeze mnie w 2017 roku (w ramach grantu 2016/23/B/NZ8/03082, w którym byłem kierownikiem). Analizowałem obrazy piskląt, stosując modele widzenia ptaków, aby zanalizować, jak pisklęta wyglądają w oczach rodziców-gospodarzy. Następnie porównałem trzy typy piskląt (jasny gospodarz, ciemny gospodarz i jasna kukułka) pod kątem komponentów chromatycznych (kolor) i achromatycznych (luminancja) trzech obszarów ciała piskląt: grzbietu (cały obszar grzbietowy, w tym skóra i pióra puchowe), bocznych kołnierzy (mięsistych bocznych części dzioba pisklęcia) oraz samej skóry. Wykazałem, że dwa fenotypy piskląt gospodarza różnią się od siebie bardziej niż od piskląt kukułeczki, a jasne pisklęta kukułeczki naśladują kilka cech wizualnych, zarówno chromatycznych, jak i achromatycznych, obu form gospodarza. W rezultacie jasne pisklęta kukułeczki wydają się pośrednie między dwoma morfami gospodarza, zamiast być idealnym odwzorowaniem jedynie jasnego fenotypu gospodarza. Wyniki tych badań sugerują, że jasne pisklęta kukułeczki podlegają selekcji w kierunku naśladowania pośredniej formy, co zwiększa szanse na akceptację przez gospodarza niezależnie od fenotypu lęgu (jasny, ciemny lub mieszany), w którym się wykluwają. Jednocześnie względna częstość fenotypów lęgów gospodarza na naszych stanowiskach badawczych może tworzyć scenariusz selekcji zależnej od zagęszczenia, w którym ciemne pisklęta kukułeczki są mniej przystosowane niż fenotyp jasny i mogą stopniowo zanikać w lokalnej populacji, co tłumaczy rzadkość tego fenotypu na naszych terenach badawczych.

2. **Attisano, A.,** Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021a). Threat recognition and response in an avian brood-parasite host from New Caledonia. *Current Zoology*, 67: 255–262

Celem badań było ustalenie, czy dorosłe krzakówki wachlarzowate rozpoznają dorosłe kukułeczki jarzębate w pobliżu gniazda i czy wykazują adaptacyjne reakcje obronne, aby zmniejszyć ryzyko pasożytnictwa. Pary krzakówek wachlarzowatych mogą rozpoznawać dorosłe kukułeczki w okolicy gniazda jako pasożyta lęgowego, który zagraża przetrwaniu ich jaj, i w związku z tym stosować obronne mechanizmy przeciwpasożytnicze przed złożeniem jaja przez kukułkę w gnieździe gospodarza (Feeney et al., 2012). Spodziewalibyśmy się, że krzakówki atakują kukułeczki zbliżające się do aktywnych gniazd, że ataki są częstsze w okresie inkubacji oraz, że osobniki narażone na pasożyty lęgowe mają wyższe wskaźniki pasożytnictwa i odrzucania piskląt. Jednak kukułeczka jarzębata usuwa jaja lub pisklęta z około

13% aktywnych gniazd gospodarza bez ich pasożytowania, działając tym samym jako drapieżnik gniazdowy (Attisano et al., 2020). W związku z tym pary krzakówek mogą rozpoznawać kukułeczki jako małego drapieżnika gniazdowego, który zagraża lęgom lub jajom, ale nie ich życiu. W takim przypadku oczekiwalibyśmy, że krzakówki atakują kukułki zbliżające się do aktywnych gniazd, ale bez różnic w częstotliwości ataków między okresem inkubacji a wychowywania piskląt oraz bez różnic we wskaźnikach pasożytnictwa i odrzucania piskląt między osobnikami atakującymi kukułkę a tymi, które tego nie robią. Jeśli mechanizmy obronne na etapie pierwszej linii są nieobecne lub nieskuteczne w zapobieganiu pasożytnictwu, może to prowadzić do zwiększonej selekcji na rozwój lepszych mechanizmów obronnych na późniejszych etapach cyklu rozrodczego gospodarza.

Umieściliśmy modele: 1) dorosłej kukułeczki jarzębatej jako pasożyta lęgowego i małego drapieżnika gniazdowego, 2) wrony jako dużego drapieżnika gniazdowego oraz 3) zięby jako nieznanego gatunku ptaka w pobliżu aktywnych gniazd krzakówek i określiliśmy ich reakcje behawioralne na te trzy modele. Krzakówki wachlarzowate atakowały tylko model kukułki, zbliżały się, ale nie atakowały modelu zięby, a zawsze unikały modelu wrony. Gniazda par, które atakowały model kukułki, miały podobne wskaźniki pasożytnictwa jak gniazda par, które nie atakowały modelu kukułki. Częstotliwość ataków była podobna w okresie inkubacji i wychowywania piskląt. Wreszcie, wskaźniki odrzucania piskląt nie wzrosły po ekspozycji na model kukułki.

Wyniki pokazują, że krzakówki rozpoznają dorosłe kukułeczki spośród innych ptaków. Jednak ich zachowanie bardziej odpowiada założeniom reakcji na małego drapieżnika gniazdowego niż na pasożyta lęgowego. W związku z tym mechanizmy obronne pierwszej linii u krzakówek wachlarzowatych są nieobecne lub nieskuteczne w zapobieganiu pasożytnictwu, co sprzyja selekcji na lepsze mechanizmy obronne gospodarza na późniejszych etapach wyścigu zbrojeń w tym systemie.

3. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021b). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Current Zoology*, 67: 653–663.

Celem badań było ustalenie, czy krzakówka wachlarzowata potrafi rozróżniać i usuwać jaja kukułeczki jarzębatej z gniazda oraz, jakie cechy wykorzystują rodzice krzakówki do rozpoznawania piskląt kukułeczki od własnych. Brązowo-oliwkowe jaja kukułeczki jarzębatej są około 20% większe i wyraźnie różnią się od białawo-brązowo nakrapianych jaj krzakówki wachlarzowatej. Pomimo tych różnic, nigdy nie zaobserwowaliśmy, by krzakówki odrzucały jaja kukułeczki. Brak odrzucania jaj może wynikać z tego, że jaja kukułeczki: 1) unikają wykrycia przez gospodarza dzięki ciemnemu ubarwieniu (Langmore et al. 2009) lub 2) są zbyt duże, by mały gospodarz mógł je chwycić (Marchetti 2000). Przetestowałem te hipotezy, wprowadzając do aktywnych gniazd krzakówek w okresie inkubacji sztuczne jaja o różnych kolorach (przypominające jaja kukułeczki, gospodarza lub niebieskie) oraz rozmiarach (50% mniejsze od jaj krzakówek, tej samej wielkości co prawdziwe jaja kukułeczki i krzakówek). Odkryłem, że dorosłe krzakówki chwytały i odrzucały sztuczne jaja niezależnie od ich koloru, ale tylko wtedy, gdy były mniejsze od prawdziwych jaj. Nigdy nie odrzucały sztucznych jaj o rozmiarze odpowiadającym prawdziwym jajom kukułeczki lub krzakówek. W związku z tym krzakówki rozpoznają brązowo-oliwkowe jaja kukułeczki w swoim gnieździe, ale są one zbyt duże, by je chwycić i odrzucić.

Dodatkowo zbadałem, jakie sygnały wykorzystują rodzice krzakówek do rozróżniania piskląt kukułeczki od własnych. Testowałem rozpoznawanie piskląt na podstawie koloru, wprowadzając sztuczne pisklęta imitujące ubarwienie prawdziwych piskląt krzakówek (jasne, ciemne). Testowałem także rozpoznawanie piskląt na podstawie puchu natalnego i czasu wyklucia, wprowadzając pisklęta adoptowane, które: 1) miały puch natalny obecny lub usunięty oraz 2) były wprowadzane przed lub po wykluciu pierwszego pisklęcia gospodarza w lęgu. Ponadto nagrałem odgłosy żebrania piskląt krzakówek i kukułeczek podczas karmienia przez rodziców krzakówek w aktywnych gniazdach. Stwierdziłem, że sztuczne pisklęta były odrzucane rzadziej niż prawdziwe, a ich kolor nie wpływał na stopień odrzucania. Stopień odrzucania adoptowanych piskląt był wyższy, gdy brakowało im puchu natalnego i były wprowadzane do gniazda przed wykluciem lęgu w gnieździe eksperymentalnym. Odgłosy żebrania różniły się znacząco między pisklętami pasożyta a gospodarza przez cały okres pisklęcy.

Wyniki pokazują, że mechanizmy obronne na etapie jaj u krzakówki wachlarzowatej są nieskuteczne w zapobieganiu pasożytnictwu lęgowemu, podobnie jak mechanizmy na etapie pierwszej linii (Attisano et al., 2021a). Wyniki tych dwóch badań sugerują zwiększoną presję selekcyjną na ewolucję mechanizmów obronnych na etapie pisklęcym u krzakówki jako jedynej skutecznej metody znacznego zmniejszenia negatywnego wpływu pasożytnictwa lęgowego. Selekcja na mechanizmy obronne na etapie pisklęcym jest wspierana przez fakt, że pisklęta dostarczają wielu sygnałów ułatwiających rozróżnianie przez rodziców gospodarzy, co potwierdzają moje wyniki, wskazujące, że rodzice krzakówek mogą rozróżniać pisklęta na podstawie puchu natalnego, kolejności wyklucia, odgłosów żebrania i wyglądu wizualnego.

4. **Attisano, A.,** Gill, B.J., Anderson, M.G., Gula, R., Langmore, N.E., Okahisa, Y., Sato, N.J., Tanaka, K., Thorogood, R., Ueda, K., Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Journal of Animal Ecology* 93: 30-43

Celem badań było opisanie, jak wyścig zbrojeń między kukułeczką jarzębatą (*Chalcites lucidus*) a jej gospodarzami w Australii, Nowej Kaledonii i Nowej Zelandii doprowadziły do dywersyfikacji fenotypowej na etapie pisklęcym oraz jak przyczyniło się to do rozdzielności różnych podgatunków kukułek. W każdym regionie kukułeczka pasożytuje na gospodarzach z rodziny *Acanthizidae*, którzy mają podobne zwyczaje lęgowe i gniazdowe. Niektórzy gospodarze mają jedynie umiarkowanie skuteczne mechanizmy obronne na etapie pierwszej linii i jaj, podczas gdy inni odrzucają pisklęta kukułek zaraz po wykluciu. Pisklęta trzech podgatunków kukułeczki jarzębatej różnią się wizualnie między sobą i bardziej przypominają fenotyp piskląt lokalnego gospodarza w każdym regionie. Zaobserwowaliśmy również zmienność fenotypową piskląt kukułek i gospodarzy w niektórych regionach, ale nie we wszystkich. Wzorce mechanizmów obronnych gospodarzy i zmienności fenotypowej piskląt w różnych regionach sugerują różne etapy ewolucyjne wyścigu zbrojeń, w których raz kukułka, a raz gospodarz ma przewagę. Gospodarze z umiarkowanymi mechanizmami obronnymi na etapach pierwszej linii i jaj nie wykazują obrony na etapie pisklęcym, i odwrotnie. W regionach, gdzie pisklę pasożyta lepiej wizualnie pasuje do piskląt gospodarza, odrzucanie piskląt kukułek nie występuje lub jest zbyt rzadkie, by je wykryć podczas badań terenowych.

Badania te jako pierwsze pokazują, jak interakcje na etapie pisklęcym między kukułką a jej gospodarzami mogą prowadzić do specjalizacji na gospodarza i zmienności fenotypowej piskląt na dużej skali geograficznej. Podkreśla również znaczenie pasożytnictwa lęgowego w promowaniu dywersyfikacji fenotypowej i przyczynianiu się do procesu specjacji poprzez tworzenie oddzielnych podgatunków.

5. **Attisano, A.,** Anderson M.G., Langmore N.E., Gula, R., Theuerkauf J. (2025) Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo, Chalcites lucidus. *Animal Behaviour* 221:123083

Celem tych badań, wraz z moim wcześniejszym badaniami nad mimikrą wizualną (Attisano et al., 2023), było znalezienie dowodów na hipotezę, że pisklęta trzech podgatunków kukułeczki jarzębatej wyewoluowały multimodalną mimikrę piskląt swoich gospodarzy. Pasożyty lęgowe mogą różnicować się w populacje specyficzne dla gospodarza, naśladując wizualne cechy potomstwa gospodarza, takie jak wygląd jaj i piskląt (Medina et al. 2020). Jednak dowody na mimikrę odgłosów żebrania i specjalizację akustyczną u pasożytów lęgowych są nadal rzadkie (Jamie & Kilner 2017). Badania te opierają się na podobnych przesłankach co badana nr 4 z tej listy osiągnięć, tj. wykrycie mimikry lokalnego gospodarza przez każdy z podgatunków kukułeczki jarzębatej, a tym samym dowodów na specjalizację na gospodarza. Podczas gdy badania nr 4 miało na celu wykrycie i opisanie mimikry wizualnej podgatunków kukułeczki jarzębatej, te badania testuje obecność mimikry akustycznej między każdym podgatunkiem kukułki a odpowiednim lokalnym gospodarzem w ich zasięgu występowania w regionie Pacyfiku.

Odkryłem, że pisklęta podgatunków kukułeczki jarzębatej z Australii, Nowej Kaledonii i Nowej Zelandii wydają odgłosy żebrania odpowiadające tym, jakie wydają pisklęta ich głównego gospodarza w każdym regionie, co wskazuje na akustyczną specjalizację na gospodarza. Dopasowanie jest bardziej precyzyjne w obszarach, gdzie gospodarz nie odrzuca piskląt kukułek. Ponadto odgłosy żebrania każdego podgatunku kukułki są bardziej podobne do odgłosów ich odpowiednich gospodarzy niż do siebie nawzajem. W związku z tym koewolucyjne interakcje, a nie związki filogenetyczne, napędzają selekcję na akustyczną dywersyfikację struktury odgłosów żebrania kukułek.

Badania 4 i 5 z tej listy osiągnięć pokazują, że koewolucyjne interakcje w tych systemach gospodarz-kukułka promowały wyrafinowaną mimikrę wizualną i akustyczną gospodarza przez pisklęta kukułeczki jarzębatej. Te systemy gospodarz-kukułka są doskonałymi modelami do badania mechanizmów koewolucyjnych i zrozumienia ich roli w dywersyfikacji fenotypowej oraz tworzenia geograficznie izolowanych jednostek ewolucyjnych w regionie południowego Pacyfiku.

4.1.3 Streszczenie

Wyniki przedstawione w mojej rozprawie habilitacyjnej pokazują, że:

- jasne pisklęta kukułeczki jarzębatej *(Chalcites lucidus)* z Nowej Kaledonii naśladują oba morfotypy piskląt swojego gospodarza, krzakówki wachlarzowatej *(Gerygone flavolateralis).* Sugeruje to selekcję na morfotyp pośredni, który zwiększa prawdopodobieństwo akceptacji pisklęcia kukułki przez rodziców gospodarza niezależnie od fenotypu lęgu gospodarza (Attisano et al. 2018)
- nieskuteczne mechanizmy obronne na etapach pierwszej linii i jaj w cyklu lęgowym gospodarza promowały selekcję na obronę przed pisklęciem pasożyta u krzakówki wachlarzowatej. Gospodarz ten nie może uniknąć pasożytnictwa na etapach składania jaj

(Attisano et al. 2021a) i nie jest w stanie odrzucić jaj kukułki z powodu ograniczeń morfologicznych (Attisano et al. 2021b). Dlatego jedyną skuteczną obroną przed pasożytnictwem dla tego gospodarza jest odrzucanie pisklęcia pasożyta. Pisklęta pasożyta dostarczają rodzicom gospodarza wielu sygnałów w porównaniu z dorosłymi osobnikami i jajami pasożyta, co ułatwia rozróżnianie piskląt i ewolucję strategii odrzucania piskląt (Attisano et al. 2021b)

- kukułeczka jarzębata wykazuje specjalizację na jednego gospodarza w swoim zasięgu występowania w regionie południowego Pacyfiku, przy czym pisklęta pasożyta naśladują wizualne i akustyczne cechy piskląt odpowiednich lokalnych gospodarzy w każdym regionie (Attisano et al. 2023, 2025). Koewolucyjne interakcje promowały dywersyfikację fenotypową w tych systemach pasożyt-gospodarz i przyczyniły się do powstania izolowanych podgatunków kukułeczki jarzębatej.

4.1.4 Referencje

Antonov A, Stokke BG, Moksnes A, Røskaft E, 2009. Evidence for egg discrimination preceding failed rejection attempts in a small cuckoo host. *Biol Lett* 5:169–171.

Attisano A, Anderson MG, Langmore NE, Gula R, Theuerkauf J, 2025. Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo, Chalcites lucidus. *Anim Behav* 221:123083.

Attisano A, Gill BJ, Anderson MG, Gula R, Langmore NE, Okahisa Y, Sato NJ, Tanaka KD, Thorogood R, Ueda K, Theuerkauf J, 2023. Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *J Anim Ecol* 92:30–43.

Attisano A, Groß LB, Sato NJ, Okahisa Y, Tanaka KD, Gula R, Ueda K, Theuerkauf J, 2020. Impact of brood parasitism and predation on nest survival of the fan-tailed gerygone in New Caledonia. *J Avian Biol* 51:e02476.

Attisano A, Hlebowicz K, Gula R, Theuerkauf J, 2021a. Threat recognition and response in an avian brood-parasite host from New Caledonia. *Curr Zool*:255–262.

Attisano A, Sato NJ, Tanaka KD, Okahisa Y, Kuehn R, Gula R, Ueda K, Theuerkauf J, 2018. Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Sci Rep* 8:1–10.

Attisano A, Sato NJ, Tanaka KD, Okahisa Y, Ueda K, Gula R, Theuerkauf J, 2021b. Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Curr Zool* 67:653–663.

Brooke MDL, Davies NB, 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 335:630–632.

Caves EM, Stevens M, Iversen ES, Spottiswoode CN, 2015. Hosts of avian brood parasites have evolved egg signatures with elevated information content. *Proc R Soc B* 282:20150598.

Davies NB, 2011. Cuckoo adaptations: trickery and tuning. *J Zool* 284:1–14.

Davies NB, 2015. *Cuckoo: Cheating by Nature*. Bloomsbury Publishing

Dawkins R, Krebs JR, 1979. Arms races between and within species. *Proc Roy Soc B* 205:489–511.

De Mársico MC, Gantchoff MG, Reboreda JC, 2012. Host–parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proc Roy Soc B* 279:3401–3408.

Feeney WE, Welbergen JA, Langmore NE, 2012. The frontline of avian brood parasite–host coevolution. *Anim Behav* 84:3–12.

Grim T, 2011. Ejecting chick cheats: a changing paradigm? *Front Zool* 8:14.

Grim T, 2017. Host defence against brood parasite nestlings: theoretical expectations and empirical evidence. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Soler M. Springer International Publishing, 539–556.

Grim T, Kleven O, Mikulica O, 2003. Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism? *Biol Lett* 270:S73–S75.

Hanley D, Rutledge SL, Villa J, 2021. The perceptual and cognitive processes that govern egg rejection in hosts of avian brood parasites. *Front Ecol Evol* 9.

Honza M, Cherry M, 2017. Egg characteristics affecting egg rejection. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Springer International Publishing, 401–419.

Jamie GA, Kilner RM, 2017. Begging call mimicry by brood parasite nestlings: adaptation, manipulation and development. In: Soler M (ed.). *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Cham: Springer International Publishing, 517–538.

Kilner RM, 2006. Function and evolution of color in young birds. *Bird Coloration Volume II: Function and Evolution*. Hill GE, McGraw KJ. Harvard University Press, 201–232.

Langmore NE, Hunt S, Kilner RM, 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422:157–160.

Langmore NE, Stevens M, Maurer G, Kilner RM, 2009. Are dark cuckoo eggs cryptic in host nests? *Anim Behav* 78:461–468.

Marchetti K, 2000. Egg rejection in a passerine bird: size does matter. *Anim Behav* 59:877–883.

Medina I, Kilner RM, Langmore NE, 2020. From micro- to macroevolution: brood parasitism as a driver of phenotypic diversity in birds. *Curr Zool* 66:515–526.

Ruiz-Raya F, Soler M, 2020. Signal detection and optimal acceptance thresholds in avian brood parasite–host systems: implications for egg rejection. *Phil Trans R Soc B* 375:20190477.

Samaš P, Hauber ME, Honza M, 2021. A meta-analysis of avian egg traits cueing egg-rejection defenses against brood parasitism. *Front Ecol Evol* 9:551.

Sato NJ, Tanaka KD, Okahisa Y, Yamamichi M, Kuehn R, Gula R, Ueda K, Theuerkauf J, 2015. Nestling polymorphism in a cuckoo-host system. *Curr Biol* 25:R1164–R1165.

Sato NJ, Tokue K, Noske RA, Mikami OK, Ueda K, 2010. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biol Lett* 6:67–69.

Soler M, 2009. Co-evolutionary arms race between brood parasites and their hosts at the nestling stage. *J Avian Biol* 40:237–240.

Soler M, 2017. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Springer International Publishing

Spottiswoode CN, Stevens M, 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc Natl Acad Sci USA* 107:8672–8676.

Spottiswoode CN, Stevens M, 2011. How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proc R Soc B* 278:3566–3573.

Spottiswoode CN, Stevens M, 2012. Host-parasite arms races and rapid changes in bird egg appearance. *Am Nat* 179:633–648.

Takasu F, 2003. Co-evolutionary dynamics of egg appearance in avian brood parasitism. *Evol Ecol Res* 5:345–362.

Tokue K, Ueda K, 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* 152:835–839.

Yang C, Si X, Liang W, Møller AP, 2020. Spatial variation in egg polymorphism among cuckoo hosts across 4 continents. *Curr Zool* 66:477–483.

4.2 Inne wybrane osiągnięcia naukowe

Innym moim wybranym osiągnięciem jest seria trzech artykułów opublikowanych w latach 2013–2015, w których opracowałem technikę badania lotu owadów w warunkach laboratoryjnych i wykorzystałem ją do analizy fizjologicznych czynników wpływających na zachowanie migracyjne u dużego pluskwiaka mlecznego oraz wpływu rodzicielskiego na morfologię skrzydeł i wydajność lotu u chrząszcza grabarza. Artykuły te należą do najczęściej cytowanych z mojej listy osiągnięć naukowych. Wszystkie prace zostały opublikowane po uzyskaniu stopnia doktora.

1. **Attisano, A.,** Tregenza, T., Moore, A. J., & Moore, P. J. (2013). Oosorption and migratory strategy of the milkweed bug, *Oncopeltus fasciatus*. *Animal Behaviour*, 86: 651–657. https://doi.org/10.1016/j.anbehav.2013.07.013 [IF$_{2013}$ = 3.068; Q1; MNiSW punktów = 140]

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy, zaprojektowaniu i wdrożeniu metodologii, zebraniu danych w terenie i w laboratorium, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym i korespondencyjnym autorem.

W tym badaniu wykorzystałem opracowaną przeze mnie technikę pomiaru lotu owadów w warunkach laboratoryjnych (numer 3 na tej liście osiągnięć), aby zbadać interakcję między fizjologią rozrodu a zachowaniem migracyjnym u dużego pluskwiaka mlecznego (*Oncopeltus fasciatus*). Owad ten ma częściową strategię migracyjną, tj. w obrębie populacji niektóre osobniki migrują, a inne nie. Odkryłem, że fizjologiczne dostosowania układu rozrodczego w odpowiedzi na niedobory pożywienia korelują z różnicami w zachowaniu migracyjnym, łącząc w ten sposób fizjologię rozrodu z adaptacjami behawioralnymi w celu radzenia sobie z niekorzystnymi warunkami środowiskowymi.

2. **Attisano, A.**, & Kilner, R. M. (2015). Parental effects and flight behaviour in the burying beetle, *Nicrophorus vespilloides*. *Animal Behaviour*, 108: 91–100. https://doi.org/10.1016/j.anbehav.2015.07.020 [IF$_{2015}$ = 3.169; Q1; MNiSW punktów = 140]

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy, zaprojektowaniu i wdrożeniu metodologii, zebraniu danych w terenie i w laboratorium, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym i korespondencyjnym autorem.

W tym badaniu wykorzystałem zmodyfikowaną wersję opracowanych przeze mnie młynów lotu (artykuł 3), aby zbadać, w jaki sposób opieka rodzicielska wpływa na morfologię potomstwa i zachowania behawioralne u chrząszcza grabarza (*Nicrophorus vespilloides*). Odkryłem, że różne reżimy opieki rodzicielskiej (pełna opieka, brak opieki) mają istotny wpływ na morfologię skrzydeł potomstwa w wieku dorosłym. Różnice w morfologii skrzydeł są związane ze zmiennością zachowań lotnych i ostatecznie wpływają na zdolność osobników do konkurowania o zasoby w wieku dorosłym.

3. **Attisano, A.,** Murphy, J. T., Vickers, A., & Moore, P. J. (2015). A Simple flight mill for the study of tethered flight in insects. *JoVE (Journal of Visualized Experiments)*, 106: e53377. https://doi.org/10.3791/53377 [IF$_{2015}$ = 1.113; Q2; MNiSW punktów = 70]

Oświadczam, że mój wkład w powyższy artykuł polegał na zaprojektowaniu i zbudowaniu młynów lotu, napisaniu i przetestowaniu kodu, zebraniu danych, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem.

W tym artykule opisuję młyny lotu, które opracowałem podczas doktoratu, aby analizować lot owadów w warunkach laboratoryjnych. Artykuł zawiera przewodnik krok po kroku, jak zbudować młyn lotu na podstawie mojego projektu. Artykuł zawiera również pełny kod, który napisałem w Pythonie, aby analizować indywidualne dane lotu i wyodrębniać statystyki dotyczące wydajności lotu.

5. Informacja o wykazywaniu się istotną aktywnością naukową albo artystyczną realizowaną w więcej niż jednej uczelni, instytucji naukowej lub instytucji kultury, w szczególności zagranicznej

5.1 Działalność badawcza

Swoją działalność naukową prowadziłem w placówkach badawczych w Polsce i za granicą: University of Exeter, University of Cambridge, University of Naples oraz Muzeum i Instytut Zoologii PAN. Współpracowałem również z naukowcami z wielu placówek badawczych na całym świecie, takich jak Australian National University (Australia), University of Vienna (Austria), University of Helsinki (Finlandia), Technical University of Munich (Niemcy), Max Planck Institute for Ornithology (Niemcy), University of Giessen (Niemcy), University of Bielefeld (Niemcy), IRD Noumea (Nowa Kaledonia), Auckland Museum (Nowa Zelandia), Massey University (Nowa Zelandia), Doñana Biological Station (Hiszpania), University of Stockholm (Szwecja), University of Zurich (Szwajcaria), University of Lausanne (Szwajcaria), Rikkyo University (Tokio), University of Georgia (USA), University of Exeter (Wielka Brytania), University of Cambridge (Wielka Brytania) i inne.

Jestem autorem 22 artykułów badawczych w specjalistycznych i interdyscyplinarnych czasopismach międzynarodowych wymienionych w Web of Science. Jestem pierwszym autorem w 11 publikacjach i autorem korespondencyjnym w 8. Pełna lista moich artykułów badawczych znajduje się w załączniku 4, sekcji II.8. Moje badania skupiają się na ekologii behawioralnej i ewolucyjnej owadów i ptaków, w szczególności na reakcjach fizjologicznych i behawioralnych na trudne środowiska, wpływie rodzicielstwa i zmianach ewolucyjnych, pasożytnictwie lęgowym, fenologii rozrodu i ochronie.

Przed uzyskaniem stopnia doktora

W latach 2006–2007 pracowałem jako asystent naukowy i brałem udział w kilku projektach monitoringu dzikiej przyrody w Laboratorium Genetyki Populacyjnej na Wydziale Zoologii Uniwersytetu w Neapolu. W tym okresie zdobyłem ważne umiejętności terenowe i laboratoryjne, które bardzo mi pomogły w mojej dotychczasowej karierze akademickiej.

W 2009 roku otrzymałem stypendium doktoranckie w Centrum Ekologii i Ochrony Przyrody Uniwersytetu w Exeter, finansowane przez Europejski Fundusz Społeczny (ESF). W mojej rozprawie doktorskiej skupiłem się na fizjologii rozrodu dużego pluskwiaka mlecznego *(Oncopeltus fasciatus)* jako mechanizmie radzenia sobie z trudnymi warunkami środowiskowymi. Podczas doktoratu opublikowałem dwa artykuły skupiające się na fizjologii rozrodu (Moore & Attisano, 2011), jakości pożywienia jako mediatorze kompromisu między rozrodem a długowiecznością (Attisano et al., 2012). Trzeci artykuł skupiał się na powiązaniu między fizjologią rozrodu a częściowym zachowaniem migracyjnym u owadów jako mechanizmem adaptacyjnym do radzenia sobie z niepewnością środowiskową (Attisano et al., 2013) i został opublikowany po ukończeniu doktoratu. Podczas doktoratu zaprojektowałem i zbudowałem młynek do lotów do badanialotu u owadów w warunkach laboratoryjnych i opisałem metodologię w artykule, który opublikowałem po uzyskaniu doktoratu (Attisano et al., 2015).

Po uzyskaniu doktoratu

W latach 2013–2014 zajmowałem stanowisko podoktorskie w Grupie Ekologii Behawioralnej na Wydziale Zoologii Uniwersytetu Cambridge, współpracując z prof. Rebeccą Kilner. Pracowałem nad opieką rodzicielską jako mediatorem zmian ewolucyjnych, wykorzystując jako gatunek modelowy chrząszcza grabarza *(Nicrophorus vespilloides).* Wykorzystałem młyny lotu, które zaprojektowałem podczas doktoratu, aby zbadać, w jaki sposób wpływ rodzicielski wpływa na rozwój skrzydeł i zachowanie podczas lotu u potomstwa (Attisano & Kilner, 2015). Brałem również udział w badaniach nad tym w jaki sposób reżimy opieki rodzicielskiej w trakcie rozwoju wywołują zmiany w zachowaniu rodzicielskim potomstwa w wieku dorosłym (Kilner et al., 2015) oraz w roli interakcji międzygatunkowych między chrząszczami a ich roztoczami foretycznymi w wywoływaniu reakcji plastycznych na niepewność środowiskową (De Gasperin et al., 2019).

W 2015 roku dołączyłem do Pracowni Ekologii Behawioralnej w Muzeum i Instytucie Zoologii PAN jako adiunkt, aby pracować nad polimorfizmem ubarwienia piskląt i koewolucyjnymi interakcjami między pasożytniczą kukułeczką jarzębatą *(Chalcites lucidus)* a jej żywicielem, krzakówką wachlarzowatą *(Gerygone flavolateralis)* z Nowej Kaledonii. Stanowisko to było częścią międzynarodowej współpracy badaczy z Muzeum i Instytutu Zoologii (Polska), Rikkyo University (Japonia) i Technische Universität München (Niemcy). Wyniki tej pracy zostały opublikowane w dwóch artykułach, w których przyjrzałem się sposobom mimikry wizualnej pisklęcia kukułki żywiciela krzakówki (Attisano et al., 2018, włączonym do cyklu tematycznego mojego głównego osiągnięcia naukowego) oraz wpływowi ojcostwa na determinację zmienności fenotypowej u piskląt krzakówki wachlarzowatej (Bojarska et al., 2018).

W latach 2017–2021 byłem kierownikiem projektu (PI) w projekcie finansowanym przez Narodowe Centrum Nauki (łączne dofinansowanie 842 200 zł). Celem projektu było zbadanie koewolucyjnych interakcji i mechanizmów dyskryminacji piskląt kukułeczki jarzębatej przez żywiciela krzakówkę wachlarzowatą z Nowej Kaledonii. Jeden z aspektów tych badań koncentrował się na zrozumieniu aspektów biologii rozrodu krzakówki wachlarzowatej i określeniu wskaźników przeżywalności gniazd w odniesieniu do pasożytnictwa i presji drapieżnictwa (Attisano et al., 2019, 2020). Drugi aspekt skupiał się na badaniu strategii obrony gniazda u żywiciela krzakówki wachlarzowatej przed pasożytami lęgowymi i drapieżnikami gniazdowymi oraz mechanizmów rozróżniania jaj i piskląt pasożyta lęgowego (Attisano et al., 2021a, 2021b, oba artykuły są zawarte w cyklu tematycznym mojego głównego osiągnięcia naukowego). Kierowałem również analizą wykorzystującą trzy długoterminowe badania naukowe obejmujące 40 lat badań terenowych z Australii, Nowej Kaledonii i Nowej Zelandii, aby wyjaśnić czynniki selekcyjne napędzające interakcje koewolucyjne i dywersyfikację fenotypową między trzema podgatunkami lśniącej kukułeczki jarzębatej i jej żywicielami w Oceanii (Attisano et al., 2023, zawarte w cyklu tematycznym mojego głównego osiągnięcia naukowego).

W 2019 roku byłem członkiem-założycielem Gondwanan Ornithology Working Group w International Ornithologists Union, której celem jest gromadzenie ornitologów pracujących na półkuli południowej oraz wspieranie współpracy i wymiany wiedzy. Opublikowaliśmy artykuł w Trends in Ecology and Evolution, w którym pokazaliśmy w badaniach nad biologią behawioralną, ekologiczną i ewolucyjną między obiema półkulami i zaproponowaliśmy sposoby na przezwyciężenie tej luki w wiedzy (Theuerkauf et al., 2022).

Od 2023 roku jestem kierownikiem projektu (PI) w projekcie finansowanym przez Narodowe Centrum Nauki w Polsce (całkowite dofinansowanie 2 058 660 zł). Celem projektu jest dalsze badanie koewolucyjnych interakcji na etapie pisklęcia między kukułeczką jarzębatą a krzakówką wachlarzowatą na Nowej Kaledonii i zrozumienie czynników selekcyjnych determinujących zmienność fenotypową piskląt u tych gatunków. Projekt jest w toku i zakończy się w styczniu 2027 r. Pierwsze wyniki tego pokazują, w jaki sposób naśladowanie żebrzących odgłosów żywiciela przez pisklęta kukułeczki jarzębatej może napędzać specjalizację u tego pasożyta lęgowego i prowadzić do powstania odrębnych podgatunków (Attisano et al., 2025, zawarte w cyklu tematycznym głównego osiągnięcia naukowego).

W latach 2024–2025 brałem udział w badaniach mających na celu opracowanie metodologii szacowania liczebności populacji skrytych gatunków ptaków tropikalnych lasów deszczowych (Theuerkauf et al., 2025a) oraz planowaniem ochrony zagrożonych gatunków ptaków w Nowej Kaledonii (Theuerkauf et al., 2025b). Współpracowałem również z ornitologami z całego świata, aby zbadać ogólnoświatowe wzorce wokalizacji ptaków, w szczególności strukturę odgłosów alarmowych w odpowiedzi na pasożyty lęgowe i drapieżniki gniazd (Feeney et al., 2025) oraz metodologie dokładnego rozpoznawania gatunków ptaków na całym świecie na podstawie ich wokalizacji (Perez-Granados et al., 2025a, 2025b; Funosas et al., 2026).

5.2 Recenzje czasopism naukowych

Recenzowałem 66 manuskryptów dla międzynarodowych czasopism naukowych, w tym: Animal Behaviour (9), Animals (26), Avian Research (2), Behavioural Ecology (1), Behavioural Ecology and Sociobiology (3), Behavioural Processes (1), Biological Journal of the Linnean Society (1), Biology (2), Current Zoology (1), Diversity (1), Ecology and Evolution (2), Ecological Informatics (7), Ethology Ecology and Evolution (1), European Zoological Journal (1), Frontiers in Zoology (1), Forests (3), Integrative Zoology (1), Journal of Animal Ecology (1), Philosophical Transactions of the Royal Society B (1), Polish Journal of Ecology (1).

5.3 Projekty badawcze

Po uzyskaniu stopnia doktora brałem udział w 5 projektach badawczych: 2 jako kierownik projektu (PI), 2 jako post-doc i 1 jako współpracownik.

1) Projekt finansowany przez European Research Council (ERC). Tytuł projektu: The origin of the fittest: canalization, plasticity and selection as a consequence of provisioning during development. Okres realizacji: 05.03.2013 – 30.11.2014. Stanowisko: post-doc.
2) Projekt finansowany przez Narodowe Centrum Nauki, Polska, Sonata Bis 1. Tytuł projektu: Czy mechanizm epigenetyczny eskaluje koewolucyjny wyścig zbrojeń w układach pasożytniczych ptaków i żywicieli?. Okres realizacji: 05.05.2015 – 25.07.2017. Stanowisko: adiunkt.
3) Projekt finansowany przez Narodowe Centrum Nauki, Polska, OPUS 12. Tytuł projektu: Polimorfizm fenotypowy piskląt i koewolucyjny wyścig zbrojeń w układzie żywiciel-pasożyt w Nowej Kaledonii. Okres realizacji: 06.07.2017 – 05.07.2021. Rola: Kierownik projektu.
4) Projekt finansowany przez Narodowe Centrum Nauki, Polska, OPUS 15. Tytuł projektu: Wybór partnera i zakładanie rodziny u ptaka współwystępującego w rozrodzie. Okres realizacji: 09.01.2019 – 08.01.2024. Rola: wykonawca.
5) Projekt finansowany przez Narodowe Centrum Nauki, Polska, OPUS 23. Tytuł projektu: Rola wczesnego środowiska i fizjologii w zmienności fenotypowej piskląt w

koewolucyjnym wyścigu zbrojeń u ptaków. Okres realizacji: 27.01.2023 – 26.01.2027. Stanowisko: Kierownik projektu.

5.4 Konferencje naukowe

Uczestniczyłem w kilku konferencjach naukowych, na których wygłaszałem referaty i prezentowałem plakaty, jako autor lub współautor. Pełna lista konferencji, w których uczestniczyłem, znajduje się w Załączniku 4, sekcja II.2.

5.5 Stypendia

1) Stypendium doktoranckie na Uniwersytecie w Exeter finansowane przez European Social Fund. Tytuł: Geographic variation and evolved response to food stress. Okres: 01.10.2009 – 30.09.2012.

6. Informacja o osiągnięciach dydaktycznych, organizacyjnych oraz popularyzujących naukę lub sztukę

6.1 Osiągnięcia dydaktyczne

Przed uzyskaniem stopnia doktora

Podczas studiów doktoranckich, jako asystent, udzielałem pomocy w wykładach i opiece nad studentami studiów licencjackich na kierunkach: Ekologia ewolucyjna, Rozwój i różnorodność, Ekologia i ochrona, Trendy w ekologii i ewolucji, Analiza danych biologicznych. W 2010 r. ukończyłem kurs nauczania w szkolnictwie wyższym i uzyskałem certyfikat LTHE (Learning and Teaching in Higher Education) fazy 1. Nadzorowałem również trzech studentów studiów licencjackich podczas realizacji ich projektu badawczego.

Po uzyskaniu doktoratu

W latach 2013–2014, na stanowisku post-doc w Department of Zoology Uniwersytetu Cambridge, nadzorowałem projekty licencjackie dwóch studentów.

W latach 2017–2018 pełniłem funkcję opiekuna badań terenowych magistranta z Uniwersytetu w Bremie w Niemczech. Tytuł pracy magisterskiej brzmiał: „Głównymi drapieżnikami krzakówki wachlarzowatej (*Gerygone flavolateralis*) w Nowej Kaledonii są rodzime ptaki, ale nie inwazyjne gryzonie”.

Od 2022 roku koordynuję i prowadzę kurs ekologii behawioralnej w Szkole Doktorskiej BioPlanet działającej przy Muzeum i Instytucie Zoologii PAN w Warszawie.

W latach 2023–2024 opiekowałem się magistrantem z Uniwersytetu w Getyndze w Niemczech. Tytuł pracy magisterskiej brzmiał: „Zasięg występowania i zachowanie terytorialne krzakówki wachlarzowatej (*Gerygone flavolateralis*) z Nowej Kaledonii”.

Od 2023 roku jestem promotorem pomocniczym doktoranta z Muzeum i Instytutu Zoologii PAN. Tytuł projektu doktorskiego brzmi: „Ekologiczne i fizjologiczne skutki zmienności fenotypowej piskląt”.

Ponadto prowadziłem zajęcia dla uczniów szkół średnich. W 2009 r., będąc zatrudnionym jako asystent badawczy w MATER Soc.Cons. w Neapolu we Włoszech, zorganizowałem i przeprowadziłem kursy z zakresu Użytkowania gruntów i zarządzania nimi, Recyklingu i zrównoważonego rozwoju oraz Ryzyka środowiskowego dla uczniów szkół średnich. W latach 2018–2022 udzielałem korepetycji uczniom szkół średnich i prowadziłem moduły z zakresu pisania tekstów naukowych i umiejętności komunikacji naukowej w ramach programu stypendialnego finansowanego przez Adamed Group w Polsce. W latach 2022–2023 prowadziłem kurs z zakresu analizy danych i programowania w języku R dla uczniów szkoły średniej z Akademia High School w Polsce.

6.2 Popularyzacja nauki

6.2.1 Wykłady i krótkie referaty

Zostałem zaproszony do wygłoszenia seminariów i krótkich referatów 6 razy w Polsce i Wielkiej Brytanii:

1. Center for Ecology and Evolution, University of Exeter. Seminarium doktoranckie. Tytuł: Reproductive physiology and evolution of a partial migratory strategy. 26.04.2011.
2. Department of Zoology, University of Cambridge. Seminarium. Tytuł: Parental effects and flight behaviour in the burying beetle. 20.10.2013.
3. Muzeum i Instytut Zoologii, PAN. Seminarium. Tytuł: The coevolutionary arms race in an avian host-parasite system from New Caledonia. 17.03.2016.
4. Dzień Włoskich Badań Naukowych w Polsce, Ambasada Włoch, Warszawa. Seminarium. Tytuł: Behavioural ecology of birds from New Caledonia. 22.06.2022.
5. Muzeum i Instytut Zoologii PAN. Seminarium. Tytuł: Nestling phenotypic variation in a brood parasite-host system from New Caledonia. 07.02.2023.
6. Uniwersytet im. Adama Mickiewicza w Poznaniu. Seminarium. Tytuł: Coevolution and nestling phenotypic variation in an avian brood parasite-host system from New Caledonia. 19.03.2025.

6.2.2 Wywiady dla mediów

W 2018 roku współpracowałem jako konsultant naukowy przy produkcji filmu dokumentalnego o dzikiej przyrodzie na temat ekologii behawioralnej ptaków z Nowej Kaledonii dla NHK (Nippon Hōsō Kyōkai - głównego krajowego kanału telewizyjnego w Japonii). Część godzinnego filmu dokumentalnego skupiała się na moich badaniach nad krzakówką wachlarzowatą i lśniącą kukułeczką jarzębatą, a także zawierała wywiad i dokumentację moich badań terenowych. Film dokumentalny został zaprezentowany w ramach cyklu filmów dokumentalnych o dzikiej przyrodzie, który jest jednym z programów telewizyjnych o największej widowni w Japonii.

Moje badania zostały omówione w magazynach internetowych takich jak: Gazeta Wyborcza (2022), Nauka w Polsce (2025), Świat Nauki (2017).

7. Oprócz kwestii wymienionych w pkt. 1-6, wnioskodawca może podać inne informacje, ważne z jego punktu widzenia, dotyczące jego kariery zawodowej.

Podnosiłem swoje kwalifikacje zawodowe poprzez uczestnictwo w warsztatach i kursach doskonalenia zawodowego:

1. Certyfikat PolLASA, praca ze zwierzętami laboratoryjnymi, 2022
2. Machine learning. Stanford University Online course, 2021
3. Signal extraction, cluster analysis and acoustic indices in Kaleidoscope Pro. Wildlife Acoustics Training, Online course. 2021
4. R programming. John Hopkins University, Online course, 2015
5. R-objected programming and package development. University of Cambridge Bioinformatics Training. 2014
6. Programming with Python 3. University of Cambridge Training, 2014
7. Open source tools for GIS analysis and data processing. University of Exeter, 2012
8. Learning and Teaching in Higher Education, LTHE Phase 1. University of Exeter, 2010

(podpis wnioskodawcy)

Alfredo Attisano

Wykaz osiągnięć naukowych albo artystycznych, stanowiących znaczny wkład w rozwój określonej dyscypliny

I. WYKAZ OSIĄGNIĘĆ NAUKOWYCH ALBO ARTYSTYCZNYCH, O KTÓRYCH MOWA W ART. 219 UST. 1. PKT 2 USTAWY

2. Cykl powiązanych tematycznie artykułów naukowych, zgodnie z art. 219 ust. 1. pkt 2b ustawy

Wszystkie artykuły zostały opublikowane po uzyskaniu stopnia doktora.

1. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports*, 8: 1–10. https://doi.org/10.1038/s41598-018-28710-5 [IF$_{2018}$ = 4.011; Q1; MNiSW punktów = 140]
   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
2. **Attisano, A.,** Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021). Threat recognition and response in an avian brood-parasite host from New Caledonia. *Current Zoology*, 67: 255–262. https://doi.org/10.1093/cz/zoaa061 [IF$_{2021}$ = 2.734; Q1; MNiSW punktów = 100]
   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
3. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Current Zoology*, 67: 653–663. https://doi.org/10.1093/cz/zoab066 [IF$_{2021}$ = 2.734; Q1; MNiSW punktów = 100]
   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem i autorem korespondencyjnym.
4. **Attisano, A.,** Gill, B.J., Anderson, M.G., Gula, R., Langmore, N.E., Okahisa, Y., Sato, N.J., Tanaka, K., Thorogood, R., Ueda, K., Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Journal*

of Animal Ecology, 93: 30-43, https://doi.org/10.1111/1365-2656.13849 [IF$_{2023}$ = 3.5; Q1; MNiSW punktów = 140]

Oświadczam, że mój wkład w powyższy artykuł obejmował organizację i zarządzanie danymi dostarczonymi przez wszystkich współautorów, przeprowadzenie analizy statystycznej, przygotowanie rysunków i tabel oraz napisanie pierwszej wersji manuskryptu. W odniesieniu do sekcji z Nowej Kaledonii w artykule mój wkład polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie i przeprowadzeniu analizy statystycznej. Jestem pierwszym autorem i autorem korespondencyjnym.

5. **Attisano, A.,** Anderson M.G., Langmore N.E., Gula, R., Theuerkauf J. (2025). Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo *Chalcites lucidus*. *Animal Behaviour*, 221:123083, https://doi.org/10.1016/j.anbehav.2025.123083 [IF$_{2025}$ = 2.3; Q1; MNiSW punktów = 140]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uporządkowaniu i zarządzaniu danymi dostarczonymi przez wszystkich współautorów, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel oraz napisaniu pierwszej wersji manuskryptu. W odniesieniu do sekcji z Nowej Kaledonii w artykule mój wkład polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zaplanowaniu metodologii, zebraniu danych w terenie i przeprowadzeniu analizy statystycznej. Jestem pierwszym autorem i autorem korespondencyjnym.

4. Osiągnięcia naukowe lub artystyczne inne niż wymienione w pkt I.2

Artykuły zostały opublikowane po uzyskaniu stopnia doktora.

1) **Attisano, A.,** Tregenza, T., Moore, A. J., & Moore, P. J. (2013). Oosorption and migratory strategy of the milkweed bug, Oncopeltus fasciatus. *Animal Behaviour*, 86: 651–657. https://doi.org/10.1016/j.anbehav.2013.07.013 [IF$_{2013}$ = 3.068; Q1; MNiSW punktów = 140]

   Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy, zaprojektowaniu i wdrożeniu metodologii, zebraniu danych w terenie i w laboratorium, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym i korespondencyjnym autorem.

2) **Attisano, A.,** & Kilner, R. M. (2015). Parental effects and flight behaviour in the burying beetle, Nicrophorus vespilloides. *Animal Behaviour*, 108: 91–100.

https://doi.org/10.1016/j.anbehav.2015.07.020 [IF_{2015} = 3.169; Q1; MNiSW punktów = 140]

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy, zaprojektowaniu i wdrożeniu metodologii, zebraniu danych w terenie i w laboratorium, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym i korespondencyjnym autorem.

3) **Attisano, A.,** Murphy, J. T., Vickers, A., & Moore, P. J. (2015). A Simple flight mill for the study of tethered flight in insects. JoVE (Journal of Visualized Experiments), 106: e53377. https://doi.org/10.3791/53377 [IF_{2015} = 1.113; Q2; MNiSW punktów = 70]

Oświadczam, że mój wkład w powyższy artykuł polegał na zaprojektowaniu i zbudowaniu młynów lotu, napisaniu i przetestowaniu kodu, zebraniu danych, przeprowadzeniu analizy statystycznej, przygotowaniu rysunków i tabel, napisaniu pierwszej wersji manuskryptu. Jestem pierwszym autorem.

II. WYKAZ AKTYWNOŚCI NAUKOWEJ ALBO ARTYSTYCZNEJ

2. Wykaz wystąpień na krajowych lub międzynarodowych konferencjach naukowych lub artystycznych, z wyszczególnieniem przedstawionych wykładów na zaproszenie i wykładów plenarnych.

** autor prezentujący*

Przed uzyskaniem stopnia doktora

1) ***Attisano. A.,** Tregenza T., Moore A.J., Moore P.J. *Reproductive physiology and evolution of a partial migratory system* (poster). Meeting of the International Society for Behavioural Ecology, Lund, 12-17 August 2012

Po uzyskaniu stopnia doktora

1) Theuerkauf J., Gula. R., Sato N.J., Tanaka K.D, Okahisa Y., Kuehn R., Gazda M.A., **Attisano A.** *Escalation of the co-evolutionary arms race in an avian host-parasite system in New Caledonia* (prezentacja ustna). Polish Evolutionary Conference, Poznań, 24–26 September 2015
2) Gazda M. A., Kuehn R., Sato N. J., Tanaka K. D., Ueda K., Okahisa Y., **Attisano A.,** Gula R., Theuerkauf J. *Mating system of the fan-tailed gerygone (Gerygone flavolateralis) and its role in a co-evolutionary host-cuckoo arms race* (poster). Polish Evolutionary Conference, Poznań, 24–26 September 2015

3) ***Attisano A.,** Sato N. J., Tanaka K. D., Okahisa Y., Kuehn R., Gula R., Ueda K., Theuerkauf J. *Visual discrimination of parasitic nestlings in a cuckoo-host polymorphic system* (prezentacja ustna). Polish Evolutionary Conference, Białystok, 25–27 September 2016
4) De Gasperin O., Duarte A., English, S., **Attisano A.,** Kilner R. *The early life environment pre-determines individual plasticity in a life history strategy* (poster). Meeting of the European Society for Evolutionary Biology, Groningen, 20–25 August 2017
5) ***Attisano A.,** Sato N. J., Tanaka K. D., Okahisa Y., Kuehn R., Gula R., Ueda K., Theuerkauf J. *Co-evolutionary arms race and visual discrimination of polymorphic nestlings in a cuckoo-host system of New Caledonia* (prezentacja ustna). International Ornithological Congress, Vancouver, 19–26 August 2018
6) Theuerkauf J., **Attisano A.,** Gula R. *Cooperative breeding, clannish organisation, coevolutionary arms race, and other unique adaptations of birds in New Caledonia* (prezentacja ustna). International Ornithological Congress, Vancouver, 19-26 August 2018
7) Walesiak M., Theuerkauf J., **Attisano A.,** Gula R. *Biogeographical analysis of the cuckoo-host relationships in New Caledonia* (poster). Polish Evolutionary Conference, Warsaw, 26–28 September 2018
8) Gula R., Kuehn R., Zagalska-Neubauer M., **Attisano A.,** Theuerkauf J. *Sex ratios and cooperative polyandry in the endangered Kagu of New Caledonia* (prezentacja ustna). International Ornithological Congress, Virtual congress, 15–19 August 2022
9) ***Attisano A.,** Gula R., Theuerkauf J. *Do early environment or physiology determine nestling phenotypic variation?* (prezentacja ustna). Meeting of the International Society for Behavioural Ecology, Melbourne, 29 September – 4 October 2024
10) **Attisano A.,** Anderson M.G., Langmore N.E., Gula R., Theuerkauf J. *Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo* (prezentacja ustna). New Zealand Bird Conference 2025, Auckland, 31 May – 2 June 2025

3. Wykaz udziału w komitetach organizacyjnych i naukowych konferencji krajowych lub międzynarodowych, z podaniem pełnionej funkcji.

Członek założyciel – Gondwanan Ornithology Working Group, International Ornithologists Union, 2019

4. Wykaz uczestnictwa w pracach zespołów badawczych realizujących projekty finansowane w drodze konkursów krajowych lub zagranicznych, z podziałem na projekty zrealizowane i będące w toku realizacji, oraz z uwzględnieniem informacji o pełnionej funkcji w ramach prac zespołów.

Przed uzyskaniem stopnia doktora

1) Okres: 01.10.2009 – 30.09.2012
Rola: Student doktorancki
Finasowanie: European Social Fund (ESF)
Tytuł projektu: Geographic variation and evolved response to food stress

Po uzyskaniu stopnia doktora

Projekty ukończone:

1) Okres: 05.03.2013 – 30.11.2014
Role: asystent badawczy podoktorancki
Finasowanie: European Research Council (ERC)
Tytuł projektu: The origin of the fittest: canalization, plasticity and selection as a consequence of provisioning during development
2) Okres: 05.05.2015 – 25.07.2017
Rola: wykonawca
Finasowanie: Sonata Bis 1, National Science Center (NCN)
Tytuł projektu: Czy mechanizm epigenetyczny intensyfikuje ewolucyjny wyścig zbrojeń między pasożytami lęgowymi i ich gospodarzami?
3) Okres: 06.07.2017 – 05.07.2021
Rola: kierownik projektu
Finasowanie: Opus 12, National Science Center (NCN)
Tytuł projektu: Rola warunków rozwoju i fizjologii piskląt w kształtowaniu ich fenotypowej zmienności w systemie pasożytnictwa lęgowego
4) Okres: 09.01.2019 – 08.01.2024
Rola: wykonawca
Finansowanie: Opus 15, National Science Center (NCN)

Tytuł projektu: Wybór partnera i tworzenie się rodzin u kooperatywnego gatunku ptaków

Projekt w trakcie realizacji:

1) Okres: 27.01.2023 – 26.01.2027
   Rola: kierownik projektu
   Finansowanie: Opus 23, National Science Center (NCN)
   Tytuł projektu: Fenotypowy polimorfizm piskląt i ko-ewolucyjny wyścig zbrojeń między gospodarzem i pasożytem lęgowym na Nowej Kaledonii

5. Wykaz członkostwa w międzynarodowych lub krajowych organizacjach i towarzystwach naukowych wraz z informacją o pełnionych funkcjach.

European Society for Evolutionary Biology - członek zwyczajny od 2013
International Ornithological Union - członek zwyczajny od 2018
International Society Behavioural Ecology - członek zwyczajny od 2012
European Ornithologists' Union - członek zwyczajny od 2017

8. Wykaz recenzowanych prac naukowych lub artystycznych, w szczególności publikowanych w czasopismach międzynarodowych.

Przed uzyskaniem stopnia doktora

1. Moore, P. J., & **Attisano, A.** (2011). Oosorption in response to poor food: Complexity in the trade-off between reproduction and survival. *Ecology and Evolution*, 1: 37–45 https://doi.org/10.1002/ece3.4 [IF_{2011} = 1.2; Q3; MNiSW punktów = 100]
2. **Attisano, A.,** Moore, A. J., & Moore, P. J. (2012). Reproduction-longevity trade-offs reflect diet, not adaptation. *Journal of Evolutionary Biology*, 25: 873–880 https://doi.org/10.1111/j.1420-9101.2012.02476.x [IF_{2012} = 3.5; Q1; MNiSW punktów = 70]

Po uzyskaniu stopnia doktora

1. **Attisano, A.,** Tregenza, T., Moore, A. J., & Moore, P. J. (2013). Oosorption and migratory strategy of the milkweed bug, Oncopeltus fasciatus. *Animal Behaviour*, 86: 651–657 https://doi.org/10.1016/j.anbehav.2013.07.013 [IF_{2013} = 3.1; Q1; MNiSW punktów = 140]
2. Kilner, R. M., Boncoraglio, G., Henshaw, J. M., Jarrett, B. J., De Gasperin, O., **Attisano, A.,** & Kokko, H. (2015). Parental effects alter the adaptive value of an adult behavioural

trait. *eLife*, 4: e07340 https://doi.org/10.7554/eLife.07340 [IF$_{2015}$ = 8.3; Q1; MNiSW punktów = 200]

3. **Attisano, A.,** & Kilner, R. M. (2015). Parental effects and flight behaviour in the burying beetle, Nicrophorus vespilloides. *Animal Behaviour*, 108: 91–100 https://doi.org/10.1016/j.anbehav.2015.07.020 [IF$_{2015}$ = 3.2; Q1; MNiSW punktów = 140]
4. **Attisano, A.,** Murphy, J. T., Vickers, A., & Moore, P. J. (2015). A Simple Flight Mill for the Study of Tethered Flight in Insects. *JoVE (Journal of Visualized Experiments)*, 106: e53377 https://doi.org/10.3791/53377 [IF$_{2015}$ = 1.1; Q2; MNiSW punktów = 70]
5. Bojarska, K., Kuehn, R., Gazda, M. A., Sato, N. J., Okahisa, Y., Tanaka, K. D., **Attisano, A.,** Gula, R., Ueda, K., & Theuerkauf, J. (2018). Mating system and extra-pair paternity in the Fan-tailed Gerygone *Gerygone flavolateralis* in relation to parasitism by the Shining Bronze-cuckoo *Chalcites lucidus. PLoS ONE*, 13: e0194059 https://doi.org/10.1371/journal.pone.0194059 [IF$_{2018}$ = 2.8; Q2; MNiSW punktów =100]
6. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports*, 8: 1–10 https://doi.org/10.1038/s41598-018-28710-5 [IF$_{2018}$ = 4.0; Q1; MNiSW punktów = 140]
7. Gasperin, O. D., Duarte, A., English, S., **Attisano, A.,** & Kilner, R. M. (2019). The early-life environment and individual plasticity in life-history traits. *Ecology and Evolution*, 9: 339–351 https://doi.org/10.1002/ece3.4749 [IF$_{2019}$ = 2.4; Q2; MNiSW punktów = 100]
8. **Attisano, A.,** Thiel, F., Sato, N., Okahisa, Y., Bolopo, D., Tanaka, K. D., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2019). Breeding biology of the fan-tailed gerygone *Gerygone flavolateralis* in relation to parasitism by the shining bronze-cuckoo *Chalcites lucidus*. *Journal of Ornithology*, 160: 91–103 https://doi.org/10.1007/s10336-018-1592-6 [IF$_{2019}$ = 1.3; Q2; MNiSW punktów = 140]
9. **Attisano, A.,** Groß, L. B., Sato, N. J., Okahisa, Y., Tanaka, K. D., Gula, R., Ueda, K., & Theuerkauf, J. (2020). Impact of brood parasitism and predation on nest survival of the fan-tailed gerygone in New Caledonia. *Journal of Avian Biology*, 51: e02476 https://doi.org/10.1111/jav.02476 [IF$_{2020}$ = 2.4; Q1; MNiSW punktów = 100]
10. **Attisano, A.,** Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021). Threat recognition and response in an avian brood-parasite host from New Caledonia. *Current Zoology*, 67: 255–262 https://doi.org/10.1093/cz/zoaa061 [IF$_{2021}$ = 2.7; Q1; MNiSW punktów = 100]
11. **Attisano, A.,** Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from

New Caledonia. *Current Zoology*, 67: 653–663 https://doi.org/10.1093/cz/zoab066 [IF$_{2021}$ = 2.7; Q1; MNiSW punktów = 100]

12. Theuerkauf, J., Villaviciencio, C. P., Adreani, N. M., **Attisano, A.,** Craig, A., D’Amelio, P. B., Gula, R., Lee, A. T. K., Mentesana, L., Quillfeldt, P., Quirici, V., Quispe, R., Vasquez, R. A., Wingfield, J. C., & Masello, J. F. (2022). Austral birds offer insightful complementary models in ecology and evolution. *Trends in Ecology & Evolution*, 37: 759-767, https://doi.org/10.1016/j.tree.2022.05.003 [IF$_{2022}$ = 16.8; Q1; MNiSW punktów = 200]
13. **Attisano, A.,** Gill, B.J., Anderson, M.G., Gula, R., Langmore, N.E., Okahisa, Y., Sato, N.J., Tanaka, K., Thorogood, R., Ueda, K., Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Journal of Animal Ecology* 93: 30-43, https://doi.org/10.1111/1365-2656.13849 [IF$_{2023}$ = 3.5; Q1; MNiSW punktów = 140]
14. **Attisano, A.,** Anderson M.G., Langmore N.E., Gula, R., Theuerkauf J. (2025) Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo, *Chalcites lucidus*. *Animal Behaviour*, 221:123083 https://doi.org/10.1016/j.anbehav.2025.123083 [IF$_{2025}$ = 2.3; Q1; MNiSW punktów = 140]
15. Theuerkauf, J., Bloc, H., **Attisano, A.,** Gula, R., Jourdan, H, Masello, J. (2025). Combining distance sampling and triangulation to estimate density of elusive rainforest vertebrates. *Biological Conservation*, 306:111133 https://doi.org/10.1016/j.biocon.2025.111133 [IF$_{2025}$ = 4.9; Q1; MNiSW punktów = 140]
16. Theuerkauf, J., Okahisa, Y., Hunt, G.R., Rouys, S., Boissenin, M., Bloc, H., Ugolini, D., Chartendrault, V., Duval, T., Angin, B., Desmoulins, F., Barré, N., Kuehn, R., Quin, D., **Attisano, A.,** Gula, R (2025). Density distribution of the flightless charismatic Kagu to inform conservation of endangered endemic rainforest species in New Caledonia. *Journal of Ornithology*, https://doi.org/10.1007/s10336-025-02318-9 [IF$_{2025}$ = 1.3; Q1; MNiSW punktów = 140]
17. Feeney, W.E., Kennerley, J.A., Wheatcroft, D., Liang, W., Lamb, J.B., Teunissen, N., Lawson, S.L., Enos, J.K., Zhou, B., Poje, C., Richardson, N.M., Ryan, T.A., Cowan, Z., Brooker, R.M., Attwood, M., Boersma, J., Zamora, M., **Attisano, A.,** Gula, R., Theuerkauf, J., Gloag, R., Fiorini, V.D., Gill, S.A., Peters, A., Honza, M., Spottiswoode C.N., Hauber, M.E., Manica, A., Webster, M.S., Blasi, D.E. (2025). Learned use of an innate sound-meaning association in birds. *Nature Ecology and Evolution*, https://doi.org/10.1038/s41559-025-02855-9 [IF$_{2025}$ = 14.1; Q1; MNiSW punktów = 100]
18. Perez-Granados, C., Funosas, D., Morant., J., Marin, O.H., Mendoza, I., …. Dehwal, A.,

Attisano, A., Theuerkauf, J., Oliveira-Junior, D.D., Lima-Santos, C.S., Salustio-Gomes, C., da Paz, R.C., Pichorim, M., Goodale, E., Sebastián-González, E. (2025). Optimization of passive acoustiv bird surveys: a global assessment of BirdNET settings. *Ibis*, https://doi.org/10.1111/ibi.70013 [IF_{2025} = 1.8; Q1; MNiSW punktów = 100]

19. Pérez-Granados, C., Morant, J., Darras, KFA, Marín-Gómez, MG, Mendoza, I., Muñoz-Mohedano, MA. …. **Attisano, A.,** Theuerkauf, J., E., Sebastián-González, E. (2025). WABAD: a world annotated bird acoustic dataset for passive acoustic monitoring. *Ecology*, in press [IF_{2025} = 4.4; Q1; MNiSW punktów = 200]
20. Funosas, D., Sebastián-González, E., Morant, J., Marín-Gómez, MG, …., **Attisano, A.**, Theuerkauf, J., Goodale, E., Darras, KFA, Pérez-Granados, C. (2026) A global assessment of BirdNET performance: differences among continents, biomes and species. *Ecological Indicators*, 182: 114550, https://doi.org/10.1016/j.ecolind.2025.114550 [IF_{2025} = 7.4; Q1; MNiSW punktów = 200]

10. Wykaz udziału w zespołach badawczych, realizujących projekty inne niż określone w pkt. II.4.

1) Okres: 02.03.2021 – do teraz
   Rola: wykonawca
   Finansowanie: Fundacja SAVE
   Tytuł projektu: Monitoring i ochrona wilka *Canis lupus* w centralnej Polsce
2) Okres: 01.01.2023 – 01.01.2024
   Rola: wykonawca
   Finansowanie: Province Sud, New Caledonia
   Tytuł projektu: Utworzenie metody liczenia do oceny wielkości populacji zagrożonego *Ducula goliath*

IV. DANE NAUKOMETRYCZNE

Dane na dzień 22.01.2026

1. Całkowita wartość Impact Factor opublikowanych artykułów: 95,05
2. Proporcje kwartylów czasopism: 77% Q1, 18% Q2, 5% Q3
3. Liczba cytowań publikacji wnioskodawcy:
   a. Web of Science: 230 (z autocytowaniami), 198 (bez autocytowań)
   b. Scopus: 224 (z autocytowaniami), 192 (bez autocytowań)

    c. Google Scholar: 341
    d. ResearchGate: 301

4. h-index
    a. Web of Science: 9
    b. Scopus: 9
    b. Google Scholar: 9
    c. ResearchGate: 10
5. Całkowita liczba punktów przyznanych przez MNiSW: 2900

(podpis wnioskodawcy)

SCIENTIFIC REPORTS

Visual discrimination of polymorphic nestlings in a cuckoo-host system

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Mimicry by avian brood parasites favours uniformity over variation within a breeding attempt as host defence against parasitism. In a cuckoo-host system from New Caledonia, the arms race resulted in both host (*Gerygone flavolateralis*) and parasite (*Chalcites lucidus*) having nestlings of two discrete skin colour phenotypes, bright and dark. In our study sites, host nestlings occurred in monomorphic and polymorphic broods, whereas cuckoo nestlings only occurred in the bright morph. Irrespective of their brood colour, host parents recognised and ejected parasite nestlings but never ejected their own. We investigated whether host parents visually recognised their own nestlings by using colour, luminance and pattern of multiple body regions. We found that the parasite mimicked multiple visual features of both host morphs and that the visual difference between host morphs was larger than the difference between the parasite and the mimicked host morph. Visual discrimination alone may result in higher chances of recognition errors in polymorphic than in monomorphic host broods. Host parents may rely on additional sensorial cues, not only visual, to assess nestling identity. Nestling polymorphism may be a trace of evolutionary past and may only have a marginal role in true-recognition of nestlings in the arms race in New Caledonia.

The interactions between brood parasites and their hosts are a classic example of a co-evolutionary process in which adaptation on one side leads to counter-adaptation on the other and so on[1]. Phenotypic polymorphism is an example of such an adaption with an important role in the host-parasite co-evolutionary arms race[2]. For example, European Cuckoo *Cuculus canorus* females have two alternative plumage phenotypes that can help evading detection by the host[3–5], while polymorphism in egg appearance may allow hosts to escape brood parasitism[6,7]. The evolution of successful host defences against brood parasitism, which involve the ability to detect and discriminate the brood parasite, is the fundamental driver in the arms race[1]. Thus, cognitive and perceptual abilities of the host are essential in the evolution and maintenance of phenotypic variation in both the host and parasite[2]. Variation in egg colour and pattern is an example of such defence strategy. In response to egg discrimination by hosts, brood parasites evolve egg mimicry[8–12], which in turn favours the evolution of distinct egg signatures[13–15] or distinct polymorphism in host clutches[6,7,16,17]. However, in a given host population, the success of such a defence strategy depends on phenotypic variation among clutches, which makes it difficult for the parasite to target a particular egg type, and on egg uniformity within clutches, which allows host parents to better discriminate a parasite against their own egg template[18–23].

In some host-cuckoo systems the arms race has reached the nestling stage, and host parents discriminate parasite nestlings from their own[24–33], which led to improved mimicry by cuckoo nestlings[34,35] (but see[36]). In theory, the same mechanisms that determine egg polymorphism should also apply to nestling polymorphism[2] and a recent study showed that polymorphism does indeed occur at the nestling stage in a cuckoo-host system in New Caledonia[37]. In this Pacific island, the local subspecies of the Fan-tailed Gerygone, *Gerygone flavolateralis flavolateralis*, is the exclusive host of the local subspecies of the Shining Bronze-cuckoo, *Chalcites lucidus layardi*. Mimicry by bronze-cuckoo nestlings is common in *Chalcites*–*Gerygone* systems[34,38] and it also occurs in New Caledonia[37]. Despite the mimicry, two Australian *Gerygone* species[25,26] and the Fan-tailed Gerygone from New

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Caledonia[37] are able to recognise and eject the cuckoo nestling from their nest before it can evict any host egg or nestling.

In contrast to Australian *Gerygone* species, Fan-tailed Gerygone have two distinct nestling morphs, with a pinkish-grey (bright) or a darkish-brown (dark) skin, which can occur in monomorphic and polymorphic broods[37,39]. Brood colouration can vary within broods of the same parents, however it is most often constant for the same pair across multiple breeding attempts and extra-pair copulations do not influence the proportions of bright, dark or polymorphic broods[39]. The Shining Bronze-cuckoo from New Caledonia also has two nestling morphs, dark and bright[37]. Two nestling morphs, in this case however yellow and black, are also known to occur in the Australian Shining Bronze-cuckoo subspecies *C. l. plagosus*[34]. In general, nestling polymorphism is rare in birds[40] and its occurrence within a brood parasite-host arms race is likely the result of strong selective pressure. Polymorphism in Shining Bronze-cuckoo nestlings may be an adaptation to mimic different hosts[34], whereas the two host nestling morphs may have originated as a host defence strategy caused by the strong selection imposed by parasitism.

Polymorphic broods in a cuckoo host increase phenotypic variation and contradicts the principle of intra-nest uniformity[23]. This in theory should increase the likelihood of recognition errors by host parents. Within monomorphic broods, a cuckoo nestling might be accepted only if it matches the host nestling appearance and ejected if it does not, whereas in polymorphic broods a cuckoo nestling might always be accepted, because it matches one or the other host nestling morph. Moreover, in non-parasitised polymorphic broods, both host nestling morphs might sometimes be mistaken for a parasite and ejected from the nest. If nestling appearance is a cue for the recognition of the parasite, then polymorphic broods should decrease host fitness due to high chances of recognition errors. In our study sites, we only encountered the bright cuckoo morph and Fan-tailed Gerygone parents recognised and ejected the cuckoo nestling in both bright and dark monomorphic broods[37]. However, in our former research[37], we were not able to confirm ejection of the parasite in polymorphic broods because none of the polymorphic broods in the previous study was parasitised.

It is also unclear how Fan-tailed Gerygone parents recognise the parasite nestlings. Some hosts of bronze-cuckoos discriminate the begging calls of the parasite from their own nestlings[24,29]. Although vocal learning can start in the pre-hatching period[29], host parents can only discriminate nestlings once they emit begging calls with a definite structure, which usually forms around the age of 3–4 days[24,29,38,41]. Fan-tailed Gerygone host parents usually eject the parasite within 24 hours from hatching[37] thus a similar auditory recognition based on properly structured nestling begging calls seems unlikely. Visual cues may be the main source of information for recognition. Fan-tailed Gerygone nestlings are covered by a dense layer of white multi-barbed down distributed over the head, back, rump, thighs and side areas, whereas Shining Bronze-cuckoo nestlings from New Caledonia have a sparser bristle-like down over the head, rump, thighs and side areas plus two dense layers of short white multi-barbed down around the orbital area[37]. The bristle-like down is unusual for parasite cuckoo nestlings[42] and absent in the Australian Shining Bronze-cuckoo subspecies[34], but bronze-cuckoos species that parasitise *Gerygone* hosts may present sparse down over some body areas[26,34,43].

In this study, we investigated if visual cues are sufficient for host parents to obtain reliable information regarding nestling identity. Visual recognition of nestlings in the New Caledonian cuckoo–host system is a challenging cognitive task because host parents must recognise a parasite in either a monomorphic or a polymorphic brood and recognise the two host nestling morphs in any brood as their own offspring. Thus, visual cues alone may allow nestling recognition in all type of broods if, based on one or multiple visual features, the two host nestling morphs appear more similar to each other than to a parasite nestling. On the other hand, visual cues alone may not be sufficient to avoid recognition errors if, based on one or multiple visual features, the two host morphs appear more different to each other than to a parasite nestling. In this case, the recognition of the parasite may involve other sensorial cues, for example auditory or olfactory, or a combination of multiple sensorial cues.

We analysed the visual information available to Fan-tailed Gerygone parents from newly hatched parasite and host nestlings. This represents the time when the ejection occurs under natural conditions (usually within 24 hours from hatching). We quantified skin colour and luminance, nestling dorsal region colour and luminance (with skin and down combined as a unique visual stimulus), colour and luminance of rictal flanges and the influence of down on nestling visual pattern and contrast. We then compared the measured values between host morphs and cuckoo nestlings and between bright and dark host morphs. Finally, we quantified age-related changes in skin luminance of the two host nestling morphs by measuring skin luminance from hatching until the appearance of juvenile plumage. The main objectives of our study were to (1) verify that ejection of the parasite occurs in any type of gerygone brood, (2) assess the visual mimicry of the host morph by cuckoo nestlings, (3) quantify the effect of down on the overall colour, luminance, pattern and contrast compared to bare skin areas, (4) identify which visual cues may convey "host" vs. "non-host" information and (5) measure changes in skin colouration of host nestlings over time.

Methods

Study area and field methodology. We conducted field work at four sites on the main island (Grande Terre) of New Caledonia during six breeding seasons (September-January) in 2011/2012-2015/16 and 2017/2018: Parc provincial des Grandes Fougères (main study site) and near surroundings (21°37′39.44″ S, 165°45′41.75″ E), approx. 40 km west (21°35′58.89″ S, 165°23′55.61″ E) of the main study site, approx. 90 km southeast (22°9′36.96″S, 166°25′24.11″ E) of the main study site and approx. 130 km northwest (20°41′45.55″ S, 164°59″38.41″ E) of the main study site. Field sites included areas of tropical rainforest (main study site) and savannah composed of grasslands and small patches of secondary forest (other sites). We located Fan-tailed Gerygone nests by following host parents returning to their nests. We found 190 active (containing at least one egg) nests of Fan-tailed Gerygones of which 30 contained cuckoo eggs, resulting in an overall parasitism rate of 16%. Is unlikely that the parasitism rate was influenced by early ejection of the cuckoo egg as the Fan-tailed

Gerygone always accepted cuckoo eggs during our study, similar to other *Gerygone* hosts[44,45]. Upon finding an active nest, we monitored egg development by candling until the day of hatching. Due to high predation rates, we enclosed nests with eggs older than 7 days in chicken-wire fences, which allowed host parents to pass through, but kept the nest out of reach of the main avian predators. We took photos of nestlings on the day of hatching (defined as day 0). Fan-tailed Gerygone parents rarely abandon their own nestlings but may abandon an empty nest. Therefore, we always removed one nestling at a time from the nest. In case of a single nestling, one person stayed at the nest to prevent parents returning to the empty nest while another took the photos. No pair abandoned an active nest at the nestling stage due to this manipulation. We limited handling of nestlings to 3 minutes and returned gerygone nestlings to their nest immediately after taking the photos.

Because host parents usually ejected cuckoo nestlings soon after hatching[37], we replaced the cuckoo eggs of 8 nests with model eggs resembling size and colour of the real cuckoo eggs. We then artificially incubated the cuckoo eggs and took photos of the hatchlings. We returned the artificially incubated cuckoo hatchlings into their nests of origin and video recorded the behaviour of host parents. If the original nest was predated, we introduced the cuckoo hatchling into a suitable active non-parasitised Fan-tailed Gerygone nest and recorded the behaviour of host parents. In these cases, we introduced an artificial cuckoo egg in the non-parasitised nest a few days before and successively exchanged it with the cuckoo hatchling. Artificially incubated cuckoo hatchlings were always returned to or introduced in the host nests on the day of hatching.

Nestling photos. During four field seasons (2013/14, 2014/15, 2015/16, 2017/18), we took photos of gerygone and cuckoo nestlings on the day of hatching. The two Fan-tailed Gerygone nestling morphs are easily distinguishable at hatching, thus we categorised them as bright or dark by visual inspection, whereas we only found cuckoo nestlings of the bright morph in our field sites. Nests of Fan-tailed Gerygone are dome shaped and with a narrow entrance, which restricted the possibility of taking standardised photos of the nestlings inside the nest. We therefore placed the nestlings in a shaded area outside the nest to avoid heat shock by direct sunlight exposure and took the photos using natural illumination. Each nestling was placed in a standardised natural resting position into a rectangular open box (50 × 20 × 10 mm) padded with cotton and lined with a grey photographic mat background (ca. 18% reflectance). We placed the camera approximately 40 cm vertically above the nestling to include head, nape, back and rump areas. Each photo included a 98% optical PTFE white reflectance standard (Ocean optics WS-1). During the 2013/14 and 2014/15 field seasons we used an Olympus E-5 digital camera equipped with a Zuiko 35 mm macro lens and took photos using standardised settings (shutter priority mode, ISO 200, 1/60). We used these photos for visual analysis of nestlings in the human visible (VIS) light spectrum (400–700 nm). During the 2015/16 and 2017/18 field seasons, we took photos with a Fuji IS-PRO ultraviolet (UV) sensitive digital camera equipped with a Coastal Optic 60 mm UV macro lens (Coastal Optic Systems). We took ultraviolet photos using a UV pass filter (Baader UV filter, transmitting between 320 and 380 nm), and VIS photos using a UV and infrared (IR) cut filter (Hoya UV & IR cut filter, transmitting between 390 and 700 nm). A custom-built filter holder allowed quickly swapping UV and VIS filters on the camera lens between shots of each nestling. We used a Nikon SB-80DX flashlight unit with the UV filter removed when taking UV photos. This provided additional ultraviolet light, decreased the exposure time for the UV photos, avoided blurred images and decreased manipulation time of nestlings. We used standardised camera settings for the Fuji IS-Pro in all photos (VIS: ISO 100, f8, variable shutter speed in aperture priority mode; UV: ISO 100, f8, 1/125).

Colour, luminance and pattern analyses. We linearised the red, green and blue camera sensor responses, standardised the digital photos in respect to light intensity using the pixel values of the 98% white standard and transformed pixel values to reflectance values[46]. Over-exposed or not correctly linearised photos were excluded from the analysis. We aligned, scaled and combined images from 2015/16 and 2017/18 to multispectral images including the UV and VIS visual information. Based on the spectral sensitivities of the Fuji IS-Pro UV camera, we converted the multispectral images from camera colour space to relative photon catches of avian shortwave (SW), mediumwave (MW), longwave (LW) and UV sensitive cone photoreceptors. Both the Shining Bronze-cuckoo and the Grey Warbler *Gerygone igata* from New Zealand, a close relative of the Fan-tailed Gerygone from New Caledonia, have a violet sensitive (VS) visual system[47]. We therefore used the spectral sensitivity of the most commonly used violet sensitive bird model, the peafowl *Pavo cristatus*[48].

Following the methodology described by Troscianko & Stevens[49], we generated polynomial models that translated the camera sensor response into peafowl cone-catch quanta by comparing the predicted camera and peafowl responses to a list of thousands of natural reflectance spectra. From calibrated multispectral images, we selected four regions per each focal nestling using the polygon selection tool in ImageJ[50]. We selected each region to include the most evident visual features of the nestling that host parents might use to recognise nestlings. For each region, we generated an average photon catch value (amount of photons that reach the retina) according to the cone response of the peafowl visual system. This allowed us to quantify how Fan-tailed Gerygone host parents perceive the visual features of nestlings.

We selected two regions of bare skin from head and rump of the focal nestling and averaged the values to a single ***skin*** value. The third region, ***dorsum***, included the entire dorsal region of the nestling in a natural resting position and thus combined bare skin and down. The fourth region, ***flanges***, included the lateral rictal flanges of the focal nestling. We measured colour and luminance of all selected regions, but measured pattern differences using only the ***skin*** and ***dorsum*** regions. We then compared these values between pairs of nestling types (bright host, dark host, parasite). We performed the skin colour and luminance analysis on multispectral images of 22 nestlings (15 bright host, 4 dark host, 3 parasite). Colour differences were calculated using the log version of the Vorobyev – Osorio receptor noise model[51], which generated "just noticeable differences" (JND) values. This predicts whether two colours are discriminable in sufficiently good light conditions based on the signal-to-noise ratio of the focal visual system. A JND value below 1 means two colours are not discriminable, values between 1 and 3 mean two colours are difficult to discriminate except under optimal viewing conditions, values above 3 mean colours are increasingly easier to discriminate.

We measured achromatic (luminance) differences as described in Siddiqi *et al.*[52]. We calculated Weber fractions from the single cone ratios of the peafowl visual system (1: 1.9: 2.2: 2.1)[48] and used a noise-to-signal ratio of 0.05 for the most abundant cone type. We compared each individual nestling with all nestlings of a different type to obtain three groups of JND values: Cuckoo-Bright (cuckoo nestlings compared to the bright gerygone morph), Cuckoo-Dark (cuckoo nestlings compared to the dark gerygone morph) and Bright-Dark (bright compared to dark gerygone morph). Thus, our analysis included absolute comparisons of nestling pairs (JND values for each group) and relative differences between groups (JND comparisons between groups) in monomorphic and polymorphic host broods.

To measure the effect of down on the visual appearance of nestlings compared to bare skin areas, we used pattern difference analysis. We used VIS photos of 78 nestlings: 8 cuckoo, 59 bright and 11 dark host. We linearised images and converted them to reflectance values (RGB-equalised). However, we did not convert them into the predicted response of the peafowl visual system because we did not know the sensor spectral sensitivity of the Olympus camera. We thus obtained measurements as camera response objective values in the VIS spectrum (400–700 nm). We followed the Fourier analysis and bandpass filtering approach used in previous studies of animal markings and patterns[53,54]. We generated pattern differences using a Fast Fourier Transform bandpass filter at 17 levels (from 2 pixels, increasing exponentially with $\sqrt{2}$ up to 350 pixels) and calculated spatial frequency differences between the two focal nestlings at each spatial scale by summing the absolute difference in energy. Such pattern difference describes the degree to which the nestling patterns match each other in terms of size, spacing and contrast. We used the same three groups as in the colour and luminance analysis to obtain the absolute comparison between pairs of nestlings (pattern difference value for each group) and relative differences between groups (pattern difference comparisons between groups).

In 2014/15 and 2015/16, we took photos of the ventral side of the focal nestling each day from day 0 (hatching day) until day 11. We chose the ventral side of the focal nestlings because it was featherless until the age of 13–14 days and thus allowed us to isolate skin areas to follow changes in skin luminance. We collected photos from 73 bright and 17 dark host nestlings. As we took photos with two different cameras, we only used objective reflectance measurements in camera colour space and linearised and standardised the photos relative to the 98% white standard. Markings and patterns are mainly encoded by achromatic information, thus we used the green camera sensor as this more closely corresponds to the avian luminance channel[55]. We then converted measured reflectance values into proportions relative to the 98% white standard.

Statistical analyses. We ran mixed models to analyse the difference in colour JND, luminance JNDs and pattern difference within each region (***skin, flanges, dorsum***). We used GLMMs with a log link function to analyse colour and luminance JNDs and a LMM to analyse the pattern difference. We applied log transformation of the pattern difference values to achieve normally distributed residuals. The models included comparison (Bright-Dark, Cuckoo-Dark, Cuckoo-Bright) as main effect and site and pair ID as crossed random effects. We did not have cases of multiple breeding by the same pair (in the same or different years) in the used data set. Upon finding a significant effect, we ran a post-hoc pairwise comparisons between pairs of groups within each region. We quantified the rate of change in luminance during development of the two host morphs with an LMM for repeated measures that included site, nestling age, skin colour and the interaction age*skin as fixed effects and nestling ID (nested within age) as random effect. We used the Image Analysis Toolbox in ImageJ[49] to prepare the multispectral images, convert them into cone catches and obtain colour and luminance JNDs and pattern difference values. All statistical analyses were run in R 3.2.1[56].

Data availability. All data generated or analysed during this study are included as Supplementary Information files.

Ethical statement. The Province Sud of New Caledonia issued all permits (3045-2011, 2437-2012, 2532-2013, 2801-2014, 2476-2015, 2372-2017). Handling and collection of the nestlings was performed in accordance with the guidelines and regulations outlined in the permits. The 1st Warsaw Local Ethics Committee for Animal Experimentation approved the experimental procedures.

Results

Ejection of the parasite. In 30 parasitised breeding attempts, 15 cuckoo nestlings hatched, whereas in the other 15 cases the cuckoo did not hatch (3 cases), predators destroyed the nest (8) or we could not follow the nest until hatching (4). In all 15 cases of cuckoo hatching, the host parents ejected the parasite within 24 hours from hatching in all brood types (Table 1). We never observed Fan-tailed Gerygone host parents ejecting a Shining Bronze-cuckoo egg or one of their own nestlings in any brood type. We observed 9 cases of nest desertion at the egg stage (5% of 190 active nests) in 8 unparasitised nests and in 1 parasitised nest. The unparasitised nests were deserted in 7 cases due to unintended disturbance caused by the nest checks or placing of the video cameras and once after disturbance by predators. The parasitised nest was deserted 1 day after host parents ejected the cuckoo nestling, most likely as a consequence of human disturbance (placement of the protective fence) rather than parasitism. Thus, none of the nest desertion we observed seemed to be a direct consequence of brood parasitism, but rather an involuntary consequence of our research activities.

Successful parasitism was too rare to be detected with only 30 parasitised and monitored breeding attempts, which means that in our sites the parasite success should be lower than 3% (i.e. 1/30). We however observed four

Brood type	Number of broods	Parasitised nests	Cuckoo nestlings	Ejection events**
Bright	66	7	7	7
Dark	13	3	3	3
Polymorphic	8	1	1	1
unknown brood type*	104	19	4	4
	191	30	15	15

Table 1. Total number of Fan-tailed Gerygone broods, nests parasitised by Shining Bronze-cuckoo, number of cuckoo hatchlings and number of parasite nestling ejection events observed during the period 2011/12-2015/16 and 2017/18. *We could not determine the brood phenotype due to predation, hatching failure or accidental damage of the eggs. **In 11 naturally parasitised nests (5 bright monomorphic broods, 2 dark monomorphic, 1 polymorphic and 3 broods of unknown nestling composition) and in 4 nests (2 bright, 1 dark and 1 unknown) to which we introduced artificially incubated cuckoo nestlings.

cases of successful parasitism at other sites: one observation of a cuckoo nestling (about 11 days old) and three observations of a cuckoo fledgling fed by both Fan-tailed Gerygone host parents. In none of these four cases, we could determine the original host brood phenotype or if the cuckoo nestling had evicted host eggs or nestlings. Cuckoos hatched earlier than host eggs but gerygone parents did not always eject the cuckoo nestling before their own offspring hatched. Thus, Shining Bronze-cuckoo nestlings coexisted with Fan-tailed Gerygone nestlings in 6 broods (4 bright, 2 dark and 1 polymorphic) before being ejected by host parents.

Colour and luminance differences. Cuckoo nestlings mimicked the colour of both host morphs (Fig. 1a). The bright and dark host morphs had a relatively larger colour difference in the ***skin*** region than the cuckoo and both host morphs (Fig. 1a). All nestling groups had similar colour differences in the ***dorsum*** and ***flanges*** regions (Fig. 1a). The colour of the ***skin*** region was generally discriminable among nestlings in good light conditions whereas mean colour JND values were around the discrimination threshold of 3 JNDs for all nestling groups in the ***dorsum*** and ***flanges*** regions (Fig. 1a). The presence of down decreased the colour differences compared to bare skin areas (***dorsum*** vs. ***skin***, mean JNDs ± 95% CI: 3.16 ± 0.30 vs. 5.09 ± 0.46).

Cuckoo nestlings mimicked skin luminance of both host morphs, in particular the bright morph, whereas the bright and dark host morphs had a relatively larger skin luminance difference than the cuckoo compared to both host morphs (Fig. 1b). Cuckoo nestlings were also more similar to dark host morphs in the ***dorsum*** region (Fig. 1b). Down of nestlings decreased achromatic differences compared to bare skin areas (***dorsum*** vs. ***skin***, mean JNDs ± 95% CI, 7.48 ± 0.79 vs. 11.54 ± 1.49). There was no difference between nestling groups in the ***flanges*** region (Fig. 1b). With the exception of the ***flanges*** region, all mean luminance JND values were above the discrimination threshold of 3 JNDs for all groups within each region.

Skin of bright Fan-tailed Gerygones darkened as the nestlings grew older, whereas the dark nestlings kept their luminance (Linear mixed model, age*skin, $n = 90$, Wald $\chi^2 = 5.32$, d.f. = 1, $P = 0.021$; Fig. 2).

Pattern differences. The presence of down increased the pattern difference between nestlings in the ***dorsum*** region compared to the bare areas of the ***skin*** region (Fig. 3). Within the ***dorsum*** region, cuckoo chicks had lower pattern differences with bright host morphs than with dark host morphs (Fig. 3). Moreover, bright host morphs had a similar pattern difference with cuckoo chicks and dark host morphs (Fig. 3). There was no pattern difference between groups in the ***skin*** region (all pairwise comparisons $P > 0.1$; Fig. 3).

Discussion

We found that visual mimicry by Shining Bronze-cuckoo nestlings from New Caledonia was based on the mimicking of multiple visual features of the host, similar to bronze-cuckoos from Australia[34,42]. We expected an improved mimicry of the respective similar host morph, i.e. bright cuckoo nestlings would better mimic bright host nestlings and dark cuckoo nestlings would better mimic dark host nestlings. However, we found only a bright cuckoo morph with features that improve mimicry with both host morphs rather than expressly mimicking only the bright host morph. The most conspicuous of these features is the presence of the white down. Host parents may use these features to visually recognise their nestlings, but cuckoo nestlings might also evade detection by the host because they are more similar to either host morphs when down and skin are combined as a single visual stimulus. More specifically, the down makes bright cuckoo nestlings more similar to both host morphs in terms of colour and more similar to dark host morphs in terms of luminance. The down also creates a high visual contrast with bare skin areas that increases the cuckoo mimicry with the bright host morph, whereas the dark morph has a higher contrast difference with both the cuckoo and the bright host morph. Similar to other brood parasites[57,58], cuckoo nestlings mimic the colour and luminance of the rictal flanges of host nestlings, as these are almost completely indistinguishable among all nestlings.

Although the Shining Bronze-cuckoo from New Caledonia parasitises a single host, it seems to have a mimicry strategy comparable with a generalist brood parasite. Its bright nestlings have features that closely resemble the preferred host, in this case the more frequent bright morph, but also general features that allow exploiting a "secondary host", in this case the dark morph of the same host species. Generalist brood parasites exploiting different hosts are known to employ "average appearance" strategies. For example, genetic races (gentes) of the Common Cuckoo mimic eggs of their favourite hosts but also have "average" egg appearance that can facilitate

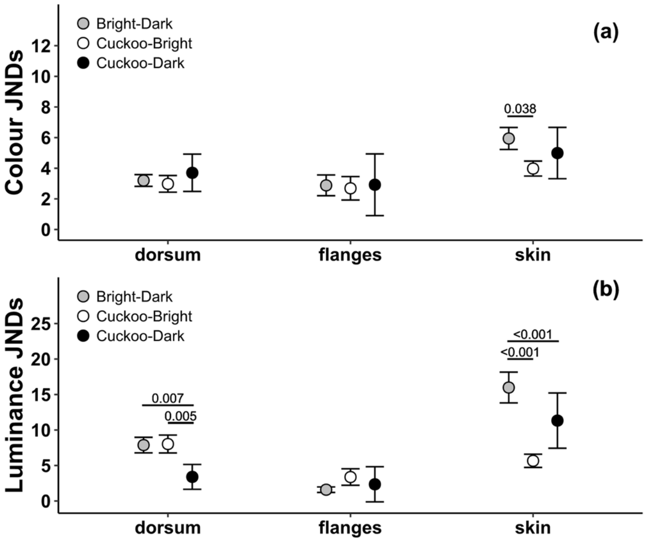

Figure 1. Colour (**a**) and luminance (**b**) just noticeable differences (JND, mean ± 95% CI). Horizontal bars with P values indicate pairwise comparisons between groups or regions. Higher JND values indicates higher colour differences in the eyes of host parents between nestling types in each group. Sample size (number of comparisons) for ***dorsum*** and ***skin*** regions are Bright-Dark = 60, Cuckoo-Bright = 45, Cuckoo-Dark = 12 and for the ***flanges*** region are Bright-Dark = 27, Cuckoo-Bright = 18, Cuckoo-Dark = 6.

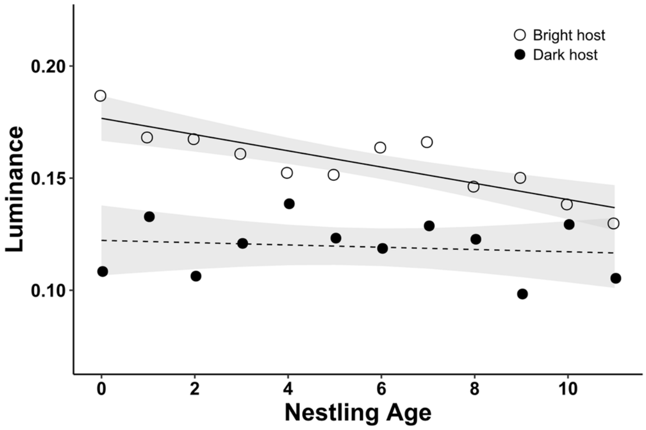

Figure 2. Regressions lines (with 95% CI as shaded area) of skin luminance in relation to age for the bright (solid line) and dark (dashed line) morphs of Fan-tailed Gerygone nestlings.

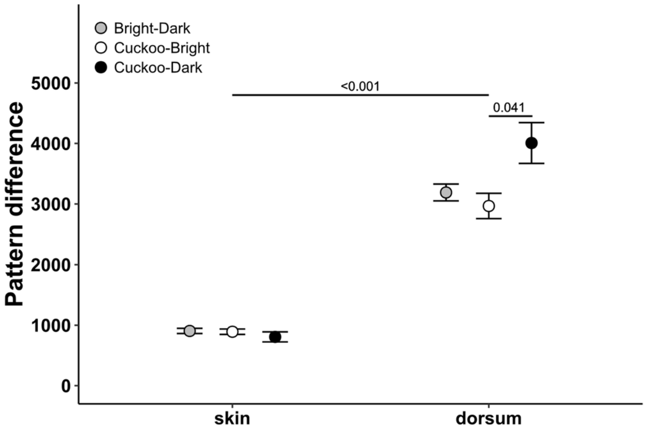

Figure 3. Mean pattern differences (pattern size, spacing and contrast) with 95% CI between nestling types in each group for each region of interest. Horizontal bars with P values indicate pairwise comparisons between groups or regions.

the use of secondary hosts[53]. Similarly, the generalist Horsfield's Bronze-cuckoo *Chalcites basalis* lays eggs that are intermediate in appearance with the eggs of its various hosts[59]. Nestlings of the Horsfield's Bronze-cuckoo also have a skin colouration that facilitates mimicry of their various host nestlings[34]. The Shining Bronze-cuckoo subspecies from Australia, *C. l. plagosus*, has two nestling morphs that may depend on the presence of gentes specialised on particular hosts[34,43]. In New Caledonia, the occurrence of possible gentes of the Shining Bronze-cuckoo subspecies *C. l. layardi* with bright or dark nestlings might depend on local frequencies of the host phenotypes. The relatively high frequency of bright host broods in our study sites may thus have led to low frequencies, or even disappearance, of the dark cuckoo morph which would explain why we never found a dark cuckoo morph during our study. In this case, there would only be selection acting on an average appearance of the bright cuckoo morph rather than on the frequencies of two contrasting cuckoo morphs.

The two host nestling phenotypes differ from each other in skin colour and luminance. In most cases, the dark host morph was as different from the cuckoo nestling as it was from the bright host morph. Luminance of the rictal flanges appeared to be the only feature with low visual difference between the two host morphs thus offering the only visual signals that could potentially allow distinguishing host from parasite. However, the use of the rictal flanges as a discriminatory cue may prove unreliable as the comparisons of colour and luminance between host and parasite nestlings showed low or no differences, meaning that cuckoo nestlings may exploit this visual signal to their advantage. Despite the striking visual difference between the two host morphs, we confirmed that ejection of the parasite occurred in the two monomorphic and in the polymorphic broods, extending previous observations on the ejection behaviour in Fan-tailed Gerygone[37]. A single host-specific visual signal is unlikely to be a reliable discriminator between "host" and "non-host" as none of the visual signals taken singly may offer certainty of reliable recognition. Rather, host parents must combine multiple visual features of the nestlings to achieve discrimination of the parasite. Nevertheless, the recognition of the parasite by host parents is easier in monomorphic broods. In this case, cuckoo nestlings should be accepted 1) if all visual features are perfectly matched or 2) if host parents have low discrimination ability for one or multiple visual features. In polymorphic broods, the recognition process is far more complex because in parasitised broods, the dark host morph is the odd-looking one and thus it should more likely be recognised as "non-host". Moreover, in non-parasitised polymorphic broods, the two host nestling morphs appear different from each other, thus one morph should theoretically be recognised as "non-host" and ejected. However, this did not happen during our research. This raises the question of how host parents identify both host morphs as their own offspring and do not eject one as "non-host" by mistake.

Several studies showed that egg ejector hosts are able to recognise the parasite by discordancy with the majority of the clutch. For example, host parents may compare size[60] or colour and pattern[61–63] of a foreign egg against the majority of the eggs in the clutch. Alternatively, host parents can recognise the parasite via true-recognition by comparing eggs to a learned template[64,65]. In some cases, the two strategies can be used in conjunction[66]. A recognition by discordancy seems unlikely in Fan-tailed Gerygone because of its low average clutch size of 2 eggs[37] and because Shining Bronze-cuckoo females usually remove one of the host eggs before laying their own[67]. In an average parasitised Fan-tailed Gerygone brood, the ratio between host and parasite is therefore 1:1, which makes it impossible to compare one nestling against a majority. In addition, because the two host morphs greatly differ from each other, a recognition by discordance may lead to the ejection of one of the host nestlings in polymorphic broods despite the presence of the parasite. Our observations that ejection of the parasite can occur before hatching of host nestlings suggest that Fan-tailed Gerygone parents achieve true-recognition via a comparison with a cognitive template. The true-recognition of the parasite in Fan-tailed Gerygone is thus a more refined behaviour than other forms of advanced discrimination described in various cuckoo hosts[24,28,36]. True-recognition and ejection of a parasite mimicking host nestlings requires high cognitive abilities from host parents, which may explain why such host defence behaviour is rare[33]. It will take further research to find out whether the template is innate or learned in Fan-tailed Gerygone parents (see[24,41]).

Although visual cues may have an important role in the parasite recognition process, their reliability may be limited by low light conditions in the incubation chamber of dome-shaped nests compared to open cup nests[68]. Thus, the true-recognition by Fan-tailed Gerygone host parents might be based on a combination of multiple sensorial cues. Auditory cues may have an important role in the recognition of a foreign nestling. For example, Superb Fairy-wrens *Malurus cyaneus* can discriminate Horsfield's Bronze-cuckoo nestlings by the different structure of their begging calls[24,41]. In addition, bronze-cuckoo nestlings mimic the begging calls of their main host[38,41]. However, nestlings may not produce proper begging calls until 3–4 days of age[38,41], whereas Fan-tailed Gerygone host parents eject the parasite nestling within 24 hours from hatching. In addition, ejection can occur before hatching of the host nestlings thus host parents cannot always compare, or do not need to compare, begging calls of the parasite and host. Another possibility is that true-recognition involves olfactory cues. For example, European Magpies *Pica pica* can discriminate foreign eggs in their clutch via odour cues[69] and experimental evidence seems to indicate that at least some birds may be capable of odour self-recognition[70]. Olfactory cues may be particularly useful in a dome-shaped nest where volatile compounds may concentrate in a restricted space. Low light conditions in the nest may thus favour the use of auditory and olfactory cues for discrimination when visual cues becomes unreliable.

Nestling polymorphism is a rare occurrence in birds[40], thus the polymorphism of host and parasite in the New Caledonia system likely originated because of strong selective pressures imposed by the arms race. Bronze-cuckoo nestlings are known for their plasticity to mimic the preferred host[34], similar to host-specific races of the Common Cuckoo mimicking eggs of different hosts in Europe and Asia[71]. On the other hand, host nestling polymorphism should rarely occur because it would increase the likelihood of committing recognition errors[23]. To our knowledge, only two cases of nestling polymorphism in hosts of brood parasites have been described and both involve a *Gerygone* host: the Fan-tailed Gerygone[37] from New Caledonia and the Grey Gerygone[72] from New Zealand. However, while the Fan-tailed Gerygone is a nestling ejector, the Grey Gerygone is neither an egg[44] nor a nestling Briskie, pers. comm. ejector. Other nestling ejecting *Gerygone* species seem to have only monomorphic broods with either dark or bright nestlings[25,26]. In the Fan-tailed Gerygone, there are two possible scenarios to explain the colour of nestlings at hatching. In the first scenario, the dark morph is ancestral and a down-regulation mechanism of the melanocortin system suppresses the melanin synthesis with a consequent appearance of a bright morph at hatching. In the second scenario, the bright morph is ancestral and an up-regulation mechanism of the melanocortin system causes a dark morph to appear at hatching. A recent phylogenetic analysis[73] shows that the Fan-tailed Gerygone is most closely related to *Gerygone* species with dark nestlings[26], and in this study, we show that the bright host morph progressively darkens with age, whereas no change occurs in the dark morph. This suggests that the dark host morph is ancestral and that cuckoos probably mimicked it in the initial phases of the arms race. Mimicry by Shining Bronze-cuckoo nestlings then probably promoted polymorphism in the host with the appearance of a bright host morph that increased in frequency in the population under negative frequency selection. This in turn likely promoted polymorphism in cuckoo nestlings with the appearance of a bright cuckoo morph. Thus, host nestling polymorphism was probably favoured as host defence in the first stages of the arms race if the same evolutionary mechanisms as for egg polymorphism apply to nestling polymorphism[2]. However, egg phenotype solely depends on the mother[74], whereas nestling phenotypes depend on the genetic background of both parents[75]. Thus, nestling phenotypes may change if parents exchange partners or incur in extra-pair copulations and this may strongly constrain the selective advantage of nestling polymorphism as a host defence. In the Fan-tailed Gerygone, extra-pair copulations had however no impact on the frequency of nestling or brood types[39]. Nevertheless, polymorphic broods may have further promoted the arms race, which involves generalist mimicry by the parasite and true-recognition based on multiple sensorial cues by the host.

References

1. Davies, N. B. Cuckoo adaptations: trickery and tuning. *J. Zool.* **284**, 1–14 (2011).
2. Tanaka, K. D. Polymorphism in avian brood parasitism: a coevolutionary perspective. *Ornith. Sci.* **15**, 133–140 (2016).
3. Davies, N. B. & Welbergen, J. A. Cuckoo–hawk mimicry? An experimental test. *Proc. R. Soc. B* **275**, 1817–1822 (2008).
4. Honza, M., Šicha, V., Procházka, P. & Ležalová, R. Host nest defense against a color-dimorphic brood parasite: great reed warblers (*Acrocephalus arundinaceus*) versus common cuckoos (Cuculus canorus). *J. Ornith.* **147**, 629–637 (2006).
5. Trnka, A., Trnka, M. & Grim, T. Do rufous common cuckoo females indeed mimic a predator? An experimental test. *Biol. J. Linn. Soc.* **116**, 134–143 (2015).
6. Lee, J. W. & Yoo, J. C. Effect of host egg color dimorphism on interactions between the vinous-throated parrotbill (*Paradoxornis webbianus*) and common cuckoo (*Cuculus canorus*). *Korean J. Biol. Sci.* **8**, 77–80 (2004).
7. Yang, C. *et al*. Coevolution in action: disruptive selection on egg colour in an avian brood parasite and its host. *Plos One* **5**, e10816 (2010).
8. Cherry, M. I., Bennett, A. T. & Moskát, C. Host intra-clutch variation, cuckoo egg matching and egg rejection by great reed warblers. *Naturwissenschaften* **94**, 441–447 (2007).
9. Honza, M., Šulc, M., Jelínek, V., Požgayová, M. & Procházka, P. Brood parasites lay eggs matching the appearance of host clutches. *Proc. R. Soc. B.* **281**, 20132665 (2014).
10. Liang, W., Yang, C. & Takasu, F. Modeling the cuckoo's brood parasitic behaviour in the presence of egg polymorphism. *J. Ethol.* **34**, 127–132 (2016).
11. Avilés, J. M. *et al*. Rapid increase in cuckoo egg matching in a recently parasitized reed warbler population. *J. Evol. Biol.* **19**, 1901–1910 (2006).
12. Attard, M. R. G., Medina, I., Langmore, N. E. & Sherratt, E. Egg shape mimicry in parasitic cuckoos. *J. Evol. Biol.* **30**, 2079–2084 (2017).
13. Spottiswoode, C. N. & Stevens, M. How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proc. R. Soc. B* **278**, 3566–3573 (2011).
14. Caves, E. M., Stevens, M., Iversen, E. S. & Spottiswoode, C. N. Hosts of avian brood parasites have evolved egg signatures with elevated information content. *Proc. R. Soc. B* **282**, 20150598 (2015).
15. Stoddard, M. C., Kilner, R. M. & Town, C. Pattern recognition algorithm reveals how birds evolve individual egg pattern signatures. *Nat. Comm.* **5**, 4117 (2014).
16. Liang, W. *et al*. Modelling the maintenance of egg polymorphism in avian brood parasites and their hosts. *J. Evol. Biol.* **25**, 916–929 (2012).
17. Yang, C. *et al*. Egg polymorphism and egg discrimination in the Daurian Redstart *Phoenicurus auroreus*, a host of the Common Cuckoo *Cuculus canorus*. *Ornithol. Sci.* **15**, 127–132 (2016).
18. Øien, I. J., Moksnes, A. & Røskaft, E. Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo. *Cuculus canorus. Behav. Ecol.* **6**, 166–174 (1995).
19. Wang, L. *et al*. Egg rejection and clutch phenotype variation in the plain prinia *Prinia inornata*. *J. Avian Biol.* **47**, 788–794 (2016).
20. Landstrom, M. T., Heinsohn, R. & Langmore, N. E. Clutch variation and egg rejection in three hosts of the Pallid Cuckoo. *Cuculus pallidus. Behaviour* **147**, 19–36 (2010).
21. Peer, B. D., Rothstein, S. I. & McCleery, R. A. Intraclutch variation in egg appearance constrains rejection of Brown-headed Cowbird (*Molothrus ater*) eggs in Common Grackles (*Quiscalus quiscula*). *Auk* **127**, 759–764 (2010).
22. Stokke, B. G., Moksnes, A. & Røskaft, E. Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution* **56**, 199–205 (2002).
23. Moskát, C., Avilés, J. M., Bán, M., Hargitai, R. & Zölei, A. Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behav. Ecol. Sociobiol.* **62**, 1885–1890 (2008).
24. Langmore, N. E., Hunt, S. & Kilner, R. M. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160 (2003).
25. Sato, N. J., Tokue, K., Noske, R. A., Mikami, O. K. & Ueda, K. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biol. Lett.* **6**, 67–69 (2010).
26. Tokue, K. & Ueda, K. Mangrove Gerygones *Gerygone laevigaster* eject Little Bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* **152**, 835–839 (2010).
27. Shizuka, D. & Lyon, B. E. Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature* **463**, 223–226 (2010).
28. Soler, M., Martinez, J. G., Soler, J. J. & Møller, A. P. Chick recognition and acceptance: a weakness in magpies exploited by the parasitic great spotted cuckoo. *Behav. Ecol. Sociobiol.* **37**, 243–248 (1995).
29. Colombelli-Négrel, D. *et al*. Embryonic learning of vocal passwords in Superb Fairy-wrens reveals intruder cuckoo nestlings. *Curr. Biol.* **22**, 2155–2160 (2012).
30. Lichtenstein, G. Low success of Shiny Cowbird chicks parasitizing Rufous-bellied Thrushes: chick–chick competition or parental discrimination? *Anim. Behav.* **61**, 401–413 (2001).

31. Yasukawa, K., Berrios, H. K. & Johannes, A. W. A test of the nestling discrimination hypothesis for parasitism of Red-winged Blackbirds (*Agelaius phoeniceus*) by Brown-headed Cowbirds (*Molothrus ater*). *Wilson J. Ornith.* **128**, 437–441 (2016).
32. Grim, T. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evol. Ecol. Res.* **8**, 785–802 (2006).
33. Grim, T. Ejecting chick cheats: a changing paradigm? *Front. Zool.* **8**, 14 (2011).
34. Langmore, N. E. *et al*. Visual mimicry of host nestlings by cuckoos. *Proc. R. Soc. B* **278**, 2455–2463 (2011).
35. De Mársico, M. C., Gantchoff, M. G. & Reboreda, J. C. Host–parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proc. R. Soc. B* **279**, 3401–3408 (2012).
36. Grim, T. Experimental evidence for chick discrimination without recognition in a brood parasite host. *Proc. R. Soc. B* **274**, 373–381 (2007).
37. Sato, N. J. *et al*. Nestling polymorphism in a cuckoo-host system. *Curr. Biol.* **25**, R1164–R1165 (2015).
38. Anderson, M. G., Ross, H. A., Brunton, D. H. & Hauber, M. E. Begging call matching between a specialist brood parasite and its host: a comparative approach to detect coevolution. *Biol. J. Linn. Soc.* **98**, 208–216 (2009).
39. Bojarska, K. *et al*. Mating system and extra-pair paternity in the Fan-tailed Gerygone *Gerygone flavolateralis* in relation to parasitism by the Shining Bronze-cuckoo *Chalcites lucidus*. *Plos One* **13**, e0194059 (2018).
40. Kilner, R. M. Function and evolution of color in young birds. In: Hill, G. E. & McGraw, K. J. (eds) *Bird Coloration volume II: Function and Evolutio*n. pp. 201–232. Harvard University Press, Cambridge, MA (2006).
41. Langmore, N. E., Maurer, G., Adcock, G. J. & Kilner, R. M. Socially acquired host-specific mimicry and the evolution of host races in Horsfield's Bronze-cuckoo *Chalcites basalis*. *Evolution* **62**, 1689–1699 (2008).
42. Payne, R. B. & Sorensen, M. D. *The cuckoos* (Vol. 15). Oxford University Press (2005).
43. Gill, B. J. Notes on the Shining Cuckoo (*Chrysococcyx lucidus*) in New Zealand. *Notornis* **29**, 215–227 (1982).
44. Thorogood, R., Kilner, R. M. & Rasmussen, J. L. Grey Gerygone hosts are not egg rejecters, but Shining Bronze-cuckoos lay cryptic eggs. *Auk* **134**, 340–349 (2017).
45. Gloag, R., Keller, L. A. & Langmore, N. E. Cryptic cuckoo eggs hide from competing cuckoos. *Proc. R. Soc. B* **281**, 20141014 (2014).
46. Stevens, M., Parraga, C. A., Cuthill, I. C., Partridge, J. C. & Troscianko, T. S. Using digital photography to study animal coloration. *Biol. J. Linn. Soc.* **90**, 211–237 (2007).
47. Aidala, Z. *et al*. Ultraviolet visual sensitivity in three avian lineages: paleognaths, parrots, and passerines. *J. Comp. Physiol. A* **198**, 495–510 (2012).
48. Hart, N. S. *Vision in the peafowl (Aves: Pavo cristatus). J. Exp. Biol.* **205**, 3925–3935 (2002).
49. Troscianko, J. & Stevens, M. Image calibration and analysis toolbox–a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol. Evol.* **6**, 1320–1331 (2015).
50. Schneider, C. A., Rasband, W. S. & Eliceiri, K. W. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* **9**, 671 (2012).
51. Vorobyev, M. & Osorio, D. Receptor noise as a determinant of colour thresholds. *Proc. R. Soc. B* **265**, 351–358 (1998).
52. Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M. & Summers, K. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* **207**, 2471–2485 (2004).
53. Stoddard, M. C. & Stevens, M. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc. R. Soc. B* **277**, 1387–1393 (2010).
54. Troscianko, J., Wilson-Aggarwal, J., Stevens, M. & Spottiswoode, C. N. Camouflage predicts survival in ground-nesting birds. *Sci. Rep.* **6**, 19966 (2016).
55. Spottiswoode, C. N. & Stevens, M. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc. Natl. Acad. Sci. USA* **107**, 8672–8676 (2010).
56. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/ (2015)
57. Schuetz, J. G. Reduced growth but not survival of chicks with altered gape patterns: implications for the evolution of nestling similarity in a parasitic finch. *Anim. Behav.* **70**, 839–848 (2005).
58. Nicolai, J. Mimicry in parasitic birds. *Sci. Am.* **231**, 92–99 (1974).
59. Feeney, W. E., Stoddard, M. C., Kilner, R. M. & Langmore, N. E. "Jack-of-all-trades" egg mimicry in the brood parasitic Horsfield's Bronze-cuckoo? *Behav. Ecol.* **6**, 1365–1373 (2014).
60. Marchetti, K. Egg rejection in a passerine bird: size does matter. *Anim. Behav.* **59**, 877–883 (2000).
61. Avilés, J. M., Soler, J. J., Soler, M. & Møller, A. P. Rejection of parasitic eggs in relation to egg appearance in magpies. *Anim. Behav.* **67**, 951–958 (2004).
62. Cassey, P., Honza, M., Grim, T. & Hauber, M. E. The modelling of avian visual perception predicts behavioural rejection responses to foreign egg colours. *Biol. Lett.* **4**, 515–517 (2008).
63. Stevens, M., Troscianko, J. & Spottiswoode, C. N. Repeated targeting of the same hosts by a brood parasite compromises host egg rejection. *Nat. Commun.* **4**, 2475 (2013).
64. Lotem, A., Nakamura, H. & Zahavi, A. Constraints on egg discrimination and cuckoo-host co-evolution. *Anim. Behav.* **49**, 1185–1209 (1995).
65. Bán, M., Moskát, C., Barta, Z. & Hauber, M. E. Simultaneous viewing of own and parasitic eggs is not required for egg rejection by a cuckoo host. *Behav. Ecol.* **4**, 1014–1021 (2013).
66. Moskát, C. *et al*. Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. *J. Exp. Biol.* **213**, 1976–1983 (2010).
67. Briskie, J. V. Direct observations of Shining Cuckoos (*Chrysococcyx lucidus*) parasitising and depredating Grey Warbler (*Gerygone igata*) nests. *Notornis* **54**, 15–19 (2007).
68. Langmore, N. E. *et al*. The evolution of egg rejection by cuckoo hosts in Australia and Europe. *Behav. Ecol.* **16**, 686–692 (2005).
69. Soler, J. J. *et al*. Recognizing odd smells and ejection of brood parasitic eggs. An experimental test in magpies of a novel defensive trait against brood parasitism. *J. Evol. Biol.* **27**, 1265–1270 (2014).
70. De León, A., Mínguez, E. & Belliure, B. Self-odour recognition in European storm-petrel chicks. *Behaviour* **140**, 925–933 (2003).
71. Gibbs, H. L. *et al*. Genetic evidence for female host-specific races of the common cuckoo. *Nature* **407**, 183–186 (2000).
72. Gill, B. J. Breeding habits of the Grey Warbler (*Gerygone igata*). *Notornis* **30**, 137–165 (1983).
73. Nyári, Á. S. & Joseph, L. Evolution in Australasian mangrove forests: multilocus phylogenetic analysis of the Gerygone warblers (Aves: Acanthizidae). *Plos One* **7**, e31840 (2012).
74. Gosler, A. G., Barnett, P. R. & Reynolds, S. J. Inheritance and variation in eggshell patterning in the great tit *Parus major*. *Proc. R. Soc. B* **267**, 2469–2473 (2000).
75. Roulin, A. & Dijkstra, C. Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity* **90**, 359–364 (2003).

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Author Contributions

A.A., N.J.S., K.D.T., R.K., R.G., K.U. and J.T. designed the study. A.A., N.J.S. and Y.O. conducted fieldwork. A.A. ran the analyses and wrote the first draft. All co-authors revised the manuscript.

Additional Information

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Threat recognition and response in an avian brood-parasite host from New Caledonia

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Abstract

Nest predation and avian brood parasitism are the main sources of nest failure in many passerine birds. Large predators threaten both brood and parents, whereas brood parasites pose only a danger to eggs or nestlings. The fan-tailed gerygone *Gerygone flavolateralis* from New Caledonia is subjected to high rates of nest predation by the New Caledonian crow *Corvus moneduloides* (responsible for about 20–40% of predation) and moderate rates of brood parasitism by the shining bronze-cuckoo *Chalcites lucidus* (parasitizing about 18% of nests), which also depredates nests that are too advanced for parasitism (13% of nests). To test if fan-tailed gerygones are able to discriminate predators from brood parasites, we presented 3 bird models at active gerygone nests: a brood parasite/small nest predator (shining bronze-cuckoo), a large nest predator (crow), and a small non-native bird (common chaffinch *Fringilla coelebs*), which is unknown to the gerygone, as a control. We assessed the response of adult gerygones to the presentation of each model by measuring the minimum approach distance, number of alarm calls, number of attacks, and time to first nest visit after the presentation (latency). Adult gerygones often attacked the cuckoo, approached but never attacked the chaffinch and always avoided the crow. Latency was shorter after an attack response and during brooding, but similar among models. We did not find any link between the cuckoo model presentation and later ejection of cuckoo nestlings. We conclude that adult fan-tailed gerygones discriminate between different models and respond accordingly to the level of threat, but do not show awareness of parasitism risk and increase of nestling ejection rates following exposure to the cuckoo model.

Key words: brood parasitism, enemy recognition, frontline defense, mobbing, nest defense, nest predation

Predation and brood parasitism are major sources of nest failure, thus many small passerines defend their nest against potential threats (Schmidt and Whelan 1999; Caro 2005). However, the impact of brood parasites and nest predators are different for nesting birds as brood parasites only threaten the brood, whereas a predator might also be dangerous to the adults. Therefore, threat recognition is crucial for the nest owners because it allows them to assess the relative risk and respond with a specific defense (Caro 2005).

Large reproductive losses caused by brood parasites to their hosts lead to a host–parasite co-evolutionary arms race (Davies 2015). Discrimination of the parasite eggs or nestlings is a defense in many hosts (Stokke et al. 2002; Moskát et al. 2008; Sato et al. 2010; Spottiswoode and Stevens 2010; Tokue and Ueda 2010; Attisano et al. 2018; Noh et al. 2018), however, an even more effective defense would be to prevent the brood parasite from approaching the nest and laying an egg altogether (Feeney et al. 2012). Several studies showed that some hosts mob experimental models of brood parasites placed at the nest (Mclean 1987; Moksnes et al. 1991; Davies et al. 2003; Dyrcz and Hałupka 2006) and often the response suggests recognition of the brood parasites (Neudorf and Sealy 1992; Gill and Sealy 1996; Welbergen and Davies 2008; Feeney et al. 2015). Hosts that are exposed to cuckoo models can perceive a higher risk of parasitism leading to increased nest guarding (Medina and Langmore 2016a) or a higher rejection rate of foreign eggs (Moksnes et al. 1993; Davies et al. 1996) and parasitized broods (Langmore et al. 2009). Host discrimination of the parasite can be influenced by the local variation of exposure likelihood to brood parasites (Lindholm and Thomas 2000; Welbergen and Davies 2009) or by spreading information about the risk of brood parasitism among members of the social group (Feeney and Langmore 2013), neighboring conspecifics (Welbergen and Davies 2008) or other host species (Yu et al. 2019). Brood parasites might represent a higher risk for their host than just parasitism as some can also be important nest predators (Soler et al. 2017) and cause high reproductive losses (Arcese et al. 1996). Nest predation by avian brood parasites is a strategy to increase the chances of parasitism by forcing hosts to lay a new clutch after depredating their nests that were in an advanced developmental stage unsuitable for parasitism (Soler et al. 2017).

The body size difference between nest owners and either a predator or a brood parasite could also play an important role in the adoption of a specific defense response. For small passerines, nest predators are usually larger and better armed and thus might threaten both adult and offspring survival (Caro 2005). The difference in size is less pronounced between avian brood parasites and their hosts, particularly in brood parasites that specialize on a small range of hosts (Medina and Langmore 2016b). A brood parasite might be perceived by nest owners as a direct threat to nest survival but not as a danger to adult survival. If the nest owner recognizes the adult cuckoo at the nest as a parasite and associates it with the later occurrence of cuckoo eggs or hatchlings in the nest, we would expect higher rates of ejection or higher levels of other anti-parasite behavior.

In the remote archipelago of New Caledonia, the fan-tailed gerygone *Gerygone flavolateralis* is the sole host of the obligate brood-parasitic shining bronze-cuckoo *Chalcites lucidus* and their interactions resulted in an arms race that escalated to the nestling stage (Sato et al. 2015). Gerygone parents accept the cuckoo egg, despite being larger and odd-looking compared to gerygone eggs, but eject newly hatched cuckoo nestlings from their nest even though cuckoo nestlings mimic the appearance of the host nestlings (Attisano et al. 2018). Nests of fan-tailed gerygone suffer high rates of predation by native birds (about 45% of nests), in particular the New Caledonian crow *Corvus moneduloides* and the white-bellied goshawk *Accipiter haplochrous* (Attisano et al. 2020). The shining bronze-cuckoo parasitizes 18% of the nests on average, but it also depredates about 13% of the active nests by removing whole host clutches or broods (Attisano et al. 2020). A few gerygone species have been observed to mob a cuckoo at the nest (Briskie 2007; Gloag et al. 2014; Attisano et al. 2019). However, none of these observations clarifies if mobbing is due to recognition of the brood parasite per se or rather is a generalized response against a potential enemy approaching the nest.

In this study, we tested the anti-predator/parasite response of adult fan-tailed gerygones by presenting at the nest 3 bird models: a shining bronze-cuckoo as their brood parasite and at the same time small nest predator, a crow as a large nest predator that can also be a risk for adults, and a common chaffinch *Fringilla coelebs* as an non-native unknown bird, which is neither a parasite nor a predator and thus used as a control. We quantified the perceived risk posed by the models for the nest owners by assessing the response to the respective models and measuring the time to first nest visit after the model presentation (latency). We expected the gerygone parents to react more aggressively toward the cuckoo and the chaffinch because they should perceive these models as less threatening than the crow. If gerygones perceive the cuckoo as a parasite, we would also expect to observe higher aggressiveness toward the cuckoo model during earlier stages of the breeding cycle, when the risk of parasitism is higher. Finally, we assessed if the anti-parasite defense of the gerygone, i.e. ejection of parasite nestlings, was associated with an earlier aggressive response to the cuckoo model.

Material and Methods

Field sites and study species

We conducted fieldwork at three sites on the main island (Grande Terre) of New Caledonia from October to December 2019: Parc des Grandes Fougères (PGF, 21°37' S, 165°45' E), Farino and surroundings (Farino, 21°39' S, 165°46' E) and Domaine de Deva (Deva, 21°35' S, 165°22' E). The field sites included areas of forest, thicket and savannah. The fan-tailed gerygone is a small insectivorous bird (adult mass 6.0–6.2 g, length 10 cm), which breeds from September to January with a peak in October/November (Attisano et al. 2019). The nest is dome-shaped and attached to small branches in trees, bushes, or ferns. Gerygone pairs are socially monogamous, form long-term bonds and use the same territory over several breeding seasons (Gazda et al. 2015; Bojarska et al. 2018; Attisano et al. 2019).

We searched for active nests by following adults flying to their nests or by directly searching for nests in known territories. Nests can be located at various heights (range 0.4–20 m), but for practical reasons, we restricted our study to nests lower than 3 m. Upon finding an active nest we recorded the GPS coordinates and determined the stage of the nest by egg candling (Lokemoen and Koford 1996) or by ageing nestlings based on their development stage. This allowed us to estimate the nest age by counting an average of 4 days for laying, 18 days of incubation, and 14 days of brooding (Attisano et al. 2019).

Experimental trials

We presented 3 bird models at active nests (containing at least one egg or nestling) of fan-tailed gerygones. In previous studies with similar experimental designs as ours, researchers used a single model of a brood-parasite (Moksnes et al. 1993; Dyrcz and Hałupka 2006; Langmore et al. 2012), 2 models (Neudorf and Sealy 1992; Gill and Sealy 1996; Davies et al. 2003) or multiple replicates of each model (Grim 2005; Welbergen and Davies 2008; Feeney and Langmore 2013; Feeney et al. 2015; Medina and Langmore 2016a; Yu et al. 2020). We decided to use a single replicate of each model and, to validate the assumption that models represented different levels of threat to adults and nests of fan-tailed gerygones, compared the response to models with the reaction to 9 nest approach events by live shining bronze-cuckoos and 12 predation events by live predators that we recorded by video monitoring of active nests from 2011 to 2019 (Attisano et al. 2020).

As models, we used a stuffed female shining bronze-cuckoo, a stuffed male common chaffinch and a plastic model of a crow resembling a New Caledonian crow with black feathers (goose, New Caledonian crow) glued onto it (Figure 1). The shining bronze-cuckoo is smaller (mass 21–22 g, length 15–17 cm: Payne 2005) than the other major nest predators and is easily distinguishable from any other sympatric bird species due to its unique plumage coloration with golden green upperparts and barred brown belly. We used the chaffinch and the plastic crow model because we had no access to other stuffed species of New Caledonian birds. We used the common chaffinch (mass 17–29 g, length 14–18 cm: Clement 2020) as a novel and nonthreatening bird because it was similar in size to an adult shining bronze-cuckoo, but different in appearance to any New Caledonian passerine. The plastic crow model resembled overall size, color and appearance of a New Caledonian crow, which is one of the largest (mass 280–355 g, length 40–43 cm: Debus 2020) and most important nest predators of fan-tailed gerygones in New Caledonia (Attisano et al. 2020). Although we never observed predation of adult gerygones, New Caledonian crows are likely to depredate on fledglings, and their large size and predatory behavior might cause adult gerygones to see them as a direct threat to both the nest and their own survival.

We presented the models at 30 active nests (6 parasitized and 24 non-parasitized) during the incubation or brooding stage. Each nest was subjected to one experimental trial, except for 2 nests where we presented models once during incubation and once during brooding. We performed trials in the morning from 7:00 to 13:00 h between the 1st and the 14th day of incubation or between the 1st and 7th day after the first chick hatched. We did not conduct trials during laying as during this period fan-tailed gerygone parents spend little time attending the nest and are susceptible to disturbance which may lead to nest abandonment. Shining bronze-cuckoos can parasitize host nests during early incubation (Gill 1983), meaning this is still a sensitive period for the host and the reaction to a cuckoo should not differ from the laying period. In addition, we were also interested in the variation in response between incubation and brooding periods to understand if hosts were more aggressive toward the cuckoo during early breeding stages (more sensitive to parasitism) or during later stages (more sensitive to depredation; see Briskie and Sealy 1989; Gill and Sealy 1996).

We fixed models to a small wooden square base (5 × 5 cm for cuckoo and chaffinch, 8 × 8 cm for crow) and placed them with Velcro tape on a mount consisting of a larger square wooden base (14 × 14 cm) attached on top of a 1-m wooden pole (Figure 1). We approached the focal nests with the models concealed in a box. We then checked from a safe distance for the presence of adult birds around the nest and if the female was incubating or brooding. If the female was inside the nest, we observed the nest from a hidden location about 10 m away until the end of the incubation/brooding bout. Once the female left the nest and neither parent was around, we first placed the presentation mount (without models) at a distance of about 2 m from the nest, directly facing the entrance. We then observed the nest from the hidden location, waiting for the parents to return and become habituated to the presence of the mount and let the female to resume incubation/brooding. We considered the parents to be habituated to the mount when both adults approached the nest showing no agitated behavior, females resumed a normal incubation/brooding behavior, males showed no signs of alertness (no alarm calls, no approach to the mount) and when both parents left the nest with no sign of alertness when leaving for the successive foraging trip. Habituation to the mount took less than 1 min and the mount never caused an alert reaction by any of the parents.

The average interval female fan-tailed gerygones spend away from the nest is 14 min (Attisano et al. 2019). When the female left the nest for the second time, we waited an additional 8 min before placing the first model on the mount to start the presentation trial. We left the mount in place and only swapped models between presentation trials. We randomized the presentation order of the models for each trial and presented the models at least one hour apart from each other to allow for any carry-over effect to be minimized. We presented each model on the mount for a maximum period of 10 minutes, however if gerygone adults responded to the model within this time interval, we limited the presentation time to 2 minutes from the start of the response to minimize stress for the parents and decrease the chances that a predator would notice the nest due to the additional activity. We video- and audio-recorded (Nikon D5100 with Nikkor 70-300mm f/4.5-5.6G IF-ED lens, digital recorder Tascam DR-05 with directional microphone Rode NTG-2) the reaction by the gerygones from the hidden location. We categorized the response to the models as "no approach" (parents staying > 5 m from the model, no mobbing), "approach"

Figure 1. Models on the mount used for the trials (from top to bottom): shining bronze-cuckoo, common chaffinch, crow.

(parents approaching < 2 m from the mount, no physical contact with the model, alarm calls) or "attack" (physical contact with the model, alarm calls). If the parents did not return to the nest within 10 min of model presentation, we removed the model and categorized the trial as "no response." We defined latency as the period of time between the end of the presentation trial (model removed from the mount) and the first nest visit of one of the parents after the model removal. In total, we performed 95 presentation trials, 32 with the chaffinch, 32 with the cuckoo and 31 with the crow (heavy rain terminated one trial), during incubation ($n = 74$) or brooding ($n = 21$). We counted the number of attacks and alarm calls directed to the models during the 2-min presentation time using the video and audio recordings. We visualized the audio recordings of alarm calls in Raven Pro 1.6.1 (Center for Conservation Bioacustics 2019) using spectrograms with a Hann window, 1000 samples, 63.4 filter bandwidth and 80% overlap. We isolated single alarm call phrases and counted number of elements in the phrase, total phrase duration, highest frequency, and peak power.

Response to models and nestling ejection

We checked if the exposure to the cuckoo model triggered a lasting response of gerygone parents leading to later nestling ejection. We ran presentation trials during incubation at 6 parasitized nests and checked the nests 1 day after hatching of the cuckoo for ejection or acceptance of the cuckoo nestling. In addition, we opportunistically presented the cuckoo model for 2 min at one nest containing an about 15-day old cuckoo nestling accepted by its foster parents and assessed the response of adult gerygones to the cuckoo model.

Statistical analyses

We ran all analyses in R 3.6.3 (R Core Team 2019). We considered only the cases for which we observed an active response to the models and excluded from the statistical analysis the "no response" trials and classified the response to models as an ordinal variable (Response) with values "no approach" (1), "approach" (2) and "attack" (3). We used Response as the dependent variable with the categorical variables Model (chaffinch, crow, cuckoo), Site (Deva, Farino, PGF), Stage (incubation, brooding) and Order (presentation order of the models coded as 1, 2 and 3) as fixed effects and the metric variables Nest Age (age of the nest when the trial was conducted, with 0 = day of first egg laid and 36 = fledging day, range during trials: 5–30) and Day Season (day of the season when the trial was conducted, with $1 = 1^{st}$ October, range during trials: 3–74) as covariates to include temporal effects of nest age and season on the response to the bird models. We included Nest ID as random effects to control for individual variation in response. We also analyzed which factors influenced the latency to return to the nest following the model presentation. Some adult gerygones returned to the nest before removal of the model leading to negative values for Latency (ranging from −1.4 to 30.2 min). We therefore added the absolute value of the minimum Latency (1.4 min) plus 1 min to each Latency value to obtain a log-normal distribution. We used Latency as the dependent variable with Model, Site, Stage and Response as fixed effects and Nest ID as a random effect. The variable Response was not independent from the variables Model and Stage, thus to avoid collinearity effects we did not include models that included a combination of these factors. We built ordinal logistic regression mixed models with the function *clmm* from the package *ordinal* (Christensen 2019) to analyze Response and general linear mixed models with log-link function using the function *glmer* from the package *lme4* (Bates et al. 2015) to analyze Latency. We built all models that included simple combinations of the main factors and ranked them based on their AICc values using the function *aictab* from the package *AICcmodavg* (Mazerolle 2019). We included all trials with active responses to models in the analyses, including the two nests at which trials were repeated at the incubation and brooding stage because the inclusion or exclusion of these nests did not change the results. Finally, we compared the number of alarm calls and attacks by linear mixed models using the number of attacks or alarm calls as the dependent variable, Model, Site and Stage as fixed effects, and Nest ID as a random effect. We report all means with 95% confidence intervals and percentages with Bonferroni confidence intervals (Byers et al. 1984).

Ethical standards

The Province Sud of New Caledonia issued the permit (2720-2019) for fieldwork. The Province Nord of New Caledonia allowed us to stuff a shining bronze-cuckoo found dead in Hienghène in 2011. The stuffed chaffinch model was obtained from the collection of the Ornithological Station of the Museum and Institute of Zoology, Polish Academy of Sciences.

Results

Response to models

Out of 95 trials, adult gerygones responded to the three bird models in 69 cases (73%). The response of adult gerygones strongly depended on the model type (Figure 2A, Supplementary Material S2). When excluding the "no response" cases, gerygones attacked the cuckoo model in 57 ± 25% ($n = 23$) of trials, whereas they never attacked the chaffinch ($n = 22$) or crow ($n = 24$) model. Gerygones approached the chaffinch model in 82 ± 18% ($n = 22$) of trials, which is more often than they did with the cuckoo (26 ± 22%, $n = 23$) or the crow model (17 ± 17%, $n = 24$). Gerygones avoided ("no approach") the crow model in 83 ± 17% ($n = 24$) of trials, which is more often than they did with the chaffinch (18 ± 18%, $n = 22$) or the cuckoo model (17 ± 19%, $n = 23$). The behavioral response of gerygone pairs to the experimental models was consistent with what we observed during video monitoring of live shining bronze-cuckoos or predators approaching active nests. In the 9 cases of video monitored visits of female cuckoos to active nests, the gerygone parents either were not near the nest ($n = 7$) or attacked the cuckoo at the nest in the same way gerygone pairs did with the experimental cuckoo model ($n = 2$). In 7 cases of predation by New Caledonian crows and 5 cases of predation by the white-bellied goshawk, the adult gerygones did not alarm, approach or mob the predators.

The AICc ranking suggested a strong effect of Model on the response of adult gerygones whereas Stage was less important, and Order only had a minor effect (Table 1, Supplementary Material S2). Adult gerygones approached the models (all combined) more frequently during incubation (47 ± 17%, $n = 49$) than during brooding (25 ± 23%, $n = 20$), whereas they did not approach or attack the models more frequently during brooding (no approach: 50 ± 27%; attack: 25 ± 23%; $n = 20$) than during incubation (no approach: 37 ± 16%; attack: 16 ± 13%; $n = 49$).

Mobbing and nest fate

Gerygones produced a clearly higher number of alarm calls during the 2-min presentation trials in response to the cuckoo compared to

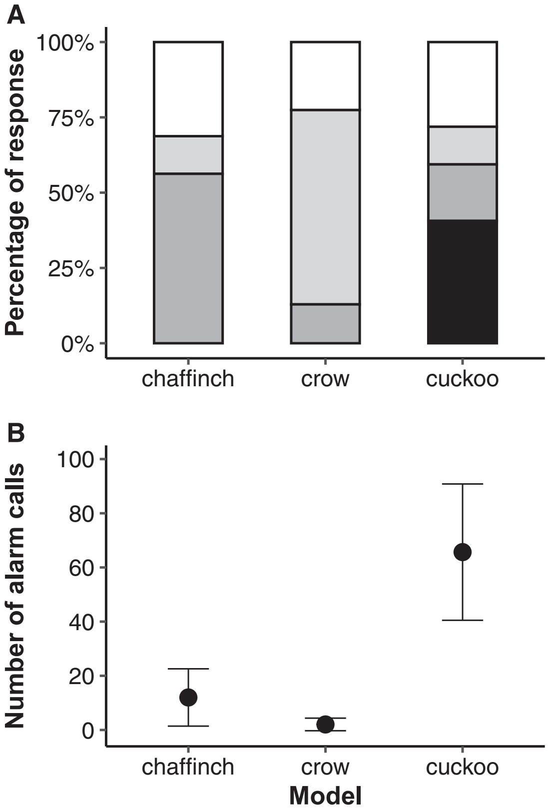

Figure 2. (A) Percentages of responses by fan-tailed gerygone adults to each model presented at active nests. Fillings in bars represent: Response: open = no response, light grey = no approach, dark grey = approach, black = attack (chaffinch: $n = 32$; crow: $n = 31$; cuckoo: $n = 32$). (B) Average ± 95% CI number of alarm calls directed to the experimental models by adult gerygones during 2 min of presentation (chaffinch: $n = 22$; crow: $n = 24$; cuckoo: $n = 23$).

the other models (Figure 2B). They also attacked only the cuckoo model (mean number of attacks: 11 ± 5, $n = 16$), whereas they swooped the chaffinch only occasionally and never approached the crow. Alarm calls of fan-tailed gerygones consisted of repeated phrases uttered in unison (39 ± 2 dB at a distance of 10 m, $n = 27$). There was no difference in the structure of alarm calls (phrase duration, number of elements in the phrase, highest frequency, peak power) to different models or type of response (Supplementary Material S2). Alarm calls to any of the models ($n = 30$) were given in 20% of the cases with no approach, in 37% with approach and in 43% with a direct attack (only to the cuckoo model). In 28 of the 30 mobbing cases, the nest owners alone responded to the model in front of their nest. In the two other cases at two different nests, conspecific neighbors were attracted by the alarm calls of the nest owners and briefly participated in mobbing the cuckoo model together with the resident pair. In both cases, the neighbor intervention was shorter (<20 s) and less intense (only approach and alarm, no attack) than that of the nest owners. We identified the individual that attacked the cuckoo model in 12 cases by colored plastic leg bands: in 6 cases only the male, in 1 case only the female and in 5 cases both sexes attacked the model.

We could determine the nest fate in 28 of the 30 nests: 19 were depredated, 3 were successful and 6 failed for other reasons (heavy rain, parasitism, dead chicks for unknown reasons). Nests at which parents mobbed at least one model during the trials, were not more often depredated (59 ± 27%, $n = 17$) than nests at which parents did not mob any of the models during the trials (82 ± 26%, $n = 11$; Supplementary Material S2). Adult gerygones produced a similar number of alarm calls at nests that were depredated (65 ± 35, $n = 19$) compared to nests that were successful (74 ± 56, $n = 3$; Supplementary Material S2). No nest was abandoned due to presentation of the model.

Table 1. Models ranked by AICc for effect on response to bird models and latency of first nest visit by adult gerygones after the model removal ($n = 69$ trials, excluding "no response" cases)

Parameter in model	K	AICc	ΔAICc	*w*
Response				
Model	8	113.17	0	0.67
Model + Stage	7	115.33	2.16	0.23
Model + Order	7	117.75	4.58	0.07
Model + Stage + Order	8	120.06	6.89	0.02
Model + Site + Order	9	122.17	9.00	0.01
Model + Stage + Site + Order	10	124.82	11.65	0.00
Model + Stage + Site + Order + Nest Age + Day Season	12	128.97	15.80	0.00
Nest Age	4	152.71	39.54	0.00
Day Season	4	152.82	39.65	0.00
Stage	4	152.87	39.70	0.00
Site	5	153.27	40.10	0.00
Order	5	154.80	41.63	0.00
Latency				
Response	5	521.87	0	0.63
Response + Site	7	525.69	3.82	0.09
Stage	4	526.02	4.15	0.08
Model + Stage	6	526.33	4.47	0.07
Model	5	527.39	5.52	0.04
Nest Age + Day Season	5	527.68	5.81	0.03
Stage + Site	6	528.20	6.33	0.03
Model + Stage + Site	8	529.08	7.21	0.02
Site	5	530.52	8.65	0.01

Latency

Latency of the first nest visit after presentation tended to be shorter in parents that attacked the model (Figure 3A) and those that were brooding (Figure 3C), but was on average similar for the different models presented at the nest (Figure 3B). The model ranking indicated that Latency was mainly dependent on Response of adult gerygones, whereas the other parameters had low rankings (Table 1, Supplementary Material S2).

Cuckoo nestling ejection

In nests at which we presented models, 5 out of 6 cuckoo eggs hatched. Including the nest containing a 15-day old cuckoo nestling where we only presented the cuckoo model, we recorded 4 cases of ejection within 1 day from hatching and 2 cases of acceptance by the host parents (the 15–day old cuckoo nestling fledged later, the other was depredated when 16 days old). In both nests in which the gerygone parents accepted the cuckoo nestling, they attacked the cuckoo model. In the 4 nests where the gerygone parents ejected the cuckoo hatchling, they either attacked the cuckoo model (1 nest), only approached it (2 nests), or did not respond (1 nest).

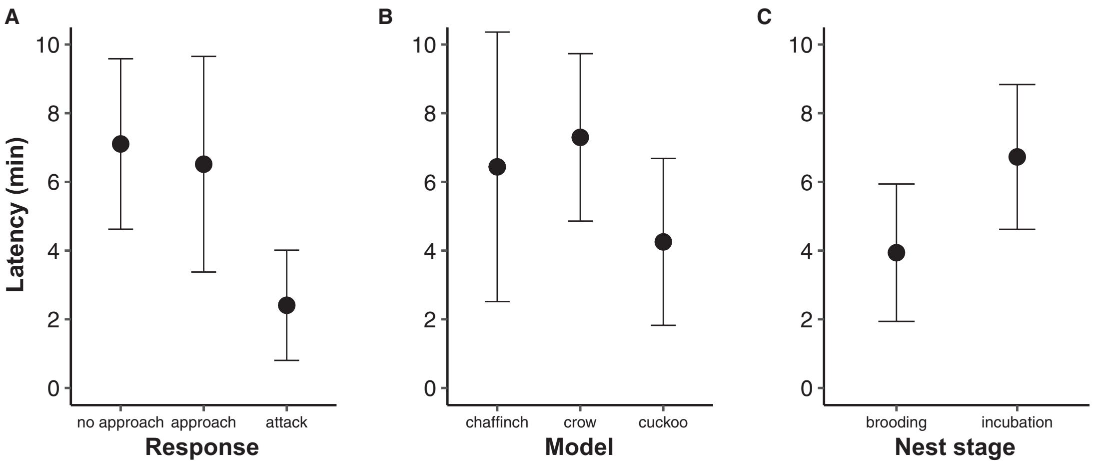

Figure 3. Latency to the first nest visit (mean ± 95% CI) after removal of the model at the nest depending on (A) response to the model (no approach: $n = 27$; approach: $n = 27$; attack: $n = 12$), (B) model presented at the nest (chaffinch: $n = 21$; crow: $n = 23$; cuckoo: $n = 22$) and (C) nest stage (brooding: $n = 17$; incubation: $n = 49$).

Discussion

We found that fan-tailed gerygones discriminated among bird models presented at their nest and responded differently. Adult gerygones clearly recognized the cuckoo model as a threat as they usually attacked it, whereas they never attacked the chaffinch and always avoided the crow. This is consistent with the observation that many hosts of brood parasites discriminate among models presented at the nest (Gill and Sealy 1996; Welbergen and Davies 2008; Feeney et al. 2015). The discrimination ability of the fan-tailed gerygone is not surprising because the shining bronze-cuckoo has a very different appearance than any other New Caledonian bird and is smaller than other common nest predators on the island. This eliminates confounding effects such as resemblance to other sympatric birds (Grim 2005; Davies and Welbergen 2008; Trnka et al. 2012; Feeney and Langmore 2013). However, many hosts experiencing a brood parasite in the proximity of their nest show awareness to the risk of parasitism by increasing nest guarding (Medina and Langmore 2016a) or mobbing the brood parasite when vulnerability to parasitism is the highest during the nesting cycle (Briskie and Sealy 1989; Gill and Sealy 1996). We cannot unequivocally clarify whether the cuckoo is perceived only as a predator or also as a parasite by adult gerygones. However, we found no evidence that exposure to the adult cuckoo model caused anti-parasite responses by the gerygones, suggesting no awareness of parasitism risk. Therefore, our results rather suggest that the fan-tailed gerygone response to the cuckoo model is an immediate anti-predator defense.

Many hosts defend their nest by mobbing both brood parasites and predators (Gill and Sealy 1996; Lindholm and Thomas 2000; Avilés and Parejo 2006); however, fan-tailed gerygones often mobbed the cuckoo model but never even approached the crow model. The response to the crow model suggests that parents rather lower their activity around the nest to avoid nest detection by the predator (Martin et al. 2000). Because nest concealment has no effect on predation rates and parasitism in the fan-tailed gerygone (Attisano et al. 2020), being inconspicuous around the nest might be the best strategy against predation. However, the response to the cuckoo and chaffinch models also indicate that parents might take the risk of disclosing the nest in some cases, most likely because neither cuckoo nor chaffinch are perceived as dangerous to their own survival, whereas the crow likely is. The size difference between the models may not be the sole factor affecting the risk assessment, as fan-tailed gerygones also approach and alarm when humans approach their nest, a behavior that in many cases helped us locating the nest. The "no approach" and "no alarm" response suggests therefore that crows are perceived as a danger for adults. The response to a potential nest predator depends on the trade-off between nest survival and adult survival (Montgomerie and Weatherhead 1988). Fan-tailed gerygones might prioritize nest survival if a cuckoo is approaching the nest, but own survival if a crow is approaching because mobbing a larger and better armed predator could result in injuries or death (Sordahl 1990). The survival of the parents should have priority over nest survival if a predator is perceived as dangerous for adults. The avoidance of the crow model was indeed consistent across nest age and stage, suggesting that adult survival was always prioritized over the survival of eggs or nestlings. Avoidance, mostly associated with presentation of the crow model, was also associated with a longer latency to the first nest visit after model presentation, implying that adult gerygones were more aware of a potential risk in these occasions.

Gerygones recognized the adult cuckoo model at the nest as a low threat to themselves as they attacked this model and had shorter latency to the first nest visit after an attack response. This is likely an anti-predator defense toward a nondangerous nest predator rather than an anti-parasite response. The shining bronze-cuckoo parasitizes fan-tailed gerygone nests mainly during the short laying period (4 days on average), but this is also the time when parents leave the nest unattended for the longest periods (Attisano et al. 2019). We observed several instances of cuckoos approaching nests during laying but never observed gerygone parents attacking the cuckoos at this stage. Nest parasitism can occur after host incubation has begun (Gill 1983); however, shining bronze-cuckoos are also major predators of fan-tailed gerygone nests during the incubation and brooding stages (Attisano et al. 2020). Therefore, cuckoos approaching the nest are attacked because they directly threaten the nest but are not dangerous for the adult gerygones. Similarly, pied flycatchers *Ficedula hypoleuca* would not attack a Eurasian sparrowhawk *Accipiter nisus* as it is dangerous for the adults, but attack great spotted woodpeckers *Dendrocopos major* as they endanger offspring but not adults (Dale et al. 1996). We did not find any indication that a mobbing response would increase the risk of nest predation, thus attacking the cuckoo might not be a risky strategy to save the nest. In addition, the response to the cuckoo model did not differ between incubation and brooding, thus fan-tailed gerygone adults seem to perceive the cuckoo as a permanent predation threat across the nesting period. Briskie and Sealy (1989) also suggested that the aggressive response of least flycatcher *Empidonax minimus* towards brown-headed cowbirds *Molothrus ater* does not vary during the entire nesting period because cowbirds depredate on eggs and nestlings.

Finally, although based on a small sample size, we found no clear association between response to the cuckoo model and ejection of cuckoo nestlings. We suggest that the lack of such association is likely caused by the time lag between presentation of the adult cuckoo model and the hatching of the parasite nestling. As shown in egg ejector hosts, observing an adult cuckoo at the nest leads to high egg rejection rates of foreign eggs because these two stimuli occur within a short time period (Moksnes et al. 1993; Davies et al. 1996; Bártol et al. 2002; Langmore et al. 2009). Fan-tailed gerygones on the other hand do not reject shining bronze-cuckoo eggs, thus they would observe a cuckoo hatchling in the nest much later after having been exposed to an adult cuckoo parasitizing their nest. It thus seems unlikely that exposure to a cuckoo might lead to lasting anti-parasite responses in fan-tailed gerygones.

Although the mobbing response by fan-tailed gerygones was different toward each model, there was no difference in the vocal structure of the alarm calls across models and thus no evidence of referential meaning specific to a particular threat in contrast to what is observed in other species (Gill and Sealy 2004). During the presentation trials, neighboring conspecifics were rarely attracted by the calls of the nest owners in response to the cuckoo model presentation. In reed warblers *Acrocephalus scirpaceus* alarm calls attract conspecific neighbors spreading the message that a brood parasite is present in the area (Welbergen and Davies 2008), but in fan-tailed gerygone we only rarely observed conspecific neighbors approaching a pair while mobbing a cuckoo model. Rather, alarm calls of the fan-tailed gerygones seem to be mainly aimed at increasing the attention of the breeding partner toward an approaching danger, as the alarm call phrase has a similar structure to the contact calls used by the pair during foraging (authors' unpublished data). Thus, the alarm calls might have a social function, as in the splendid fairy-wren *Malurus cyaneus*, in which naïve family members identify a parasite by observing more experienced conspecifics mobbing the cuckoo (Feeney and Langmore 2013).

In a previous study, we showed that fan-tailed gerygone parents spend long periods away from the nest during laying (Attisano et al. 2019). Although this behavior might decrease nest predation, it allows enough time for the shining bronze-cuckoo to parasitize the nest without detection by the host. In this study we show that fan-tailed gerygones responded to different levels of threat to the nest and to their own survival. Adult gerygones defend their nest from a predatory shining bronze-cuckoo because attacking this small nest predator bears a low risk for the adults' own survival. Thus, they do not seem to have developed a frontline anti-parasite response but rather an anti-predator defense against their brood parasite. Ultimately, because parasitism by an adult cuckoo cannot be avoided, the nestling ejection response is the better option to decrease brood losses due to parasitism. This promoted a refined recognition ability of the alien nestling with very low rates of recognition errors but that is not associated with an awareness of parasitism risk by host parents.

Author contributions

A.A. conceived the study, designed the experiment, conducted fieldwork, analyzed the data and wrote the first draft. K.H. designed the experiment and conducted fieldwork. R.G. conceived the study. J.T. conceived the study and designed the experiment. All authors provided advice to the analyses and edited the article.

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Supplementary material

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

Conflict of interest

We declare that we have no competing interest.

References

Arcese P, Smith JN, Hatch MI, 1996. Nest predation by cowbirds and its consequences for passerine demography. *Proc Natl Acad Sci USA* **93**:4608.

Attisano A, Groß LB, Sato NJ, Okahisa Y, Tanaka KD et al. 2020. Impact of brood parasitism and predation on nest survival of the fan-tailed gerygone in New Caledonia. *J Avian Biol* **51**:e02476.

Attisano A, Sato NJ, Tanaka KD, Okahisa Y, Kuehn R et al. 2018. Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Sci Rep* **8**:10.

Attisano A, Thiel F, Sato N, Okahisa Y, Bolopo D et al. 2019. Breeding biology of the fan-tailed gerygone *Gerygone flavolateralis* in relation to parasitism by the shining bronze-cuckoo Chalcites lucidus. *J Ornithol* **160**:91–103.

Avilés JM, Parejo D, 2006. Nest defense by Iberian azure-winged magpies *Cyanopica cyanus*: do they recognize the threat of brood parasitism? *Ethol Ecol Evol* **18**:321–333.

Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T, 2002. Responses of great reed warblers Acrocephalus arundinaceus to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *J Avian Biol* **33**:420–425.

Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**:1–48.

Bojarska K, Kuehn R, Gazda MA, Sato NJ, Okahisa Y et al. 2018. Mating system and extra-pair paternity in the Fan-tailed Gerygone Gerygone flavolateralis in relation to parasitism by the shining bronze-cuckoo *Chalcites lucidus*. *PLoS One* **13**. DOI: 10.1371/journal.pone.0194059.

Briskie JV, 2007. Direct observations of shining cuckoos *Chrysococcyx lucidus* parasitising and depredating grey warbler *Gerygone igata* nests. *Notornis* **54**:15–19.

Briskie JV, Sealy SG, 1989. Changes in nest defense against a brood parasite over the breeding cycle. *Ethology* **82**:61–67.

Byers CR, Steinhorst RK, Krausman PR, 1984. Clarification of a technique for analysis of utilization-availability data. *J Wildl Manag* **48**:1050–1053.

Caro T, 2005. *Antipredator Defenses in Birds and Mammals*. Chicago (IL): University of Chicago Press.

Center for Conservation Bioacustics, 2019. *Raven Pro: Interactive Sound Analysis Software (Version 1.6.1)*. Ithaca (NY): The Cornell Lab of Ornithology.

Christensen RHB, 2019. Regression Models for Ordinal Data. Available from: https://CRAN.R-project.org/package=ordinal

Clement P, 2020. Common chaffinch Fringilla coelebs, version 1.0. In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. *Birds of the World*. Ithaca: Cornell Lab of Ornithology. Available from: 10.2173/bow.comcha.01.

Dale S, Gustavsen R, Slagsvold T, 1996. Risk taking during parental care: a test of three hypotheses applied to the pied flycatcher. *Behav Ecol Sociobiol* **39**:31–42.

Davies NB, 2015. *Cuckoo: Cheating by Nature*. London (UK): Bloomsbury Publishing.

Davies NB, Brooke MDL, Kacelnik A, 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc Roy Soc B* **263**:925–931.

Davies NB, Butchart SHM, Burke TA, Chaline N, Stewart IRK, 2003. Reed warblers guard against cuckoos and cuckoldry. *Anim Behav* **65**:285–295.

Davies NB, Welbergen JA, 2008. Cuckoo-hawk mimicry? An experimental test. *Proc Roy Soc B* **275**:1817–1822.

Debus S, 2020. New Caledonian Crow Corvus moneduloides, version 1.0. In: del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E, editors. *Birds of the World*. Ithaca: Cornell Lab of Ornithology. Available from: 10.2173/bow.neccro1.01

Dyrcz A, Hałupka L, 2006. Great reed warbler *Acrocephalus arundinaceus* and reed warbler *Acrocephalus scirpaceus* respond differently to cuckoo dummy at the nest. *J Ornithol* **147**:649–652.

Feeney WE, Langmore NE, 2013. Social learning of a brood parasite by its host. *Biol Lett* **9**:20130443.

Feeney WE, Troscianko J, Langmore NE, Spottiswoode CN, 2015. Evidence for aggressive mimicry in an adult brood parasitic bird, and generalized defences in its host. *Proc Roy Soc B* **282**:20150795.

Feeney WE, Welbergen JA, Langmore NE, 2012. The frontline of avian brood parasite - host coevolution. *Anim Behav* **84**:3–12.

Gazda MA, Kuehn R, Sato NJ, Tanaka KD, Okahisa Y et al. 2015. Establishment of microsatellite markers to assess the mating system of the fan-tailed gerygone *Gerygone flavolateralis* for studying cuckoo-host arms race. *Ann Zool Fennici* **52**:280–284.

Gill BJ, 1983. Brood-parasitism by the shining cuckoo chrysococcyx lucidus at Kaikoura, New Zealand. *Ibis* **125**:40–55.

Gill SA, Sealy SG, 1996. Nest defence by yellow warblers: recognition of a brood parasite and an avian nest predator. *Behaviour* **133**:263–282.

Gill SA, Sealy SG, 2004. Functional reference in an alarm signal given during nest defence: seet calls of yellow warblers denote brood-parasitic brown--headed cowbirds. *Behav Ecol Sociobiol* **56**:71–80.

Gloag R, Keller LA, Langmore NE, 2014. Cryptic cuckoo eggs hide from competing cuckoos. *Proc Roy Soc B* **281**:20141014.

Grim T, 2005. Host recognition of brood parasites: implications for methodology in studies of enemy recognition. *Auk* **122**:530–543.

Langmore NE, Cockburn A, Russell AF, Kilner RM, 2009. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behav Ecol* **20**:978–984.

Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM et al. 2012. Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behav Ecol* **23**:798–805.

Lindholm A, Thomas R, 2000. Between populations of reed warblers in defences against brood parasitism. *Behaviour* **137**:25–42.

Lokemoen JT, Koford RR, 1996. Using candlers to determine the incubation stage of passerine eggs. *J Field Ornith* **67**:660–668.

Martin TE, Scott J, Menge C, 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc Roy Soc B* **267**: 2287–2293.

Mazerolle MJ, 2019. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). Available from: https://cran.r-project.org/package=AICcmodavg

Mclean IG, 1987. Response to a dangerous enemy: should a brood parasite be mobbed? *Ethol* **75**:235–245.

Medina I, Langmore NE, 2016a. Batten down the thatches: front-line defences in an apparently defenceless cuckoo host. *Anim Behav* **112**:195–201.

Medina I, Langmore NE, 2016b. The evolution of host specialization in avian brood parasites. *Ecol Lett* **19**:1110–1118.

Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe HM et al. 1991. Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116**:64–89.

Moksnes A, Røskaft E, Korsnes L, 1993. Rejection of cuckoo *Cuculus canorus* eggs by meadow pipits *Anthus pratensis*. *Behav Ecol* **4**:120–127.

Montgomerie RD, Weatherhead PJ, 1988. Risks and rewards of nest defence by parent birds. *Q Rev Biol* **63**:167–187.

Moskát C, Avilés JM, Bán M, Hargitai R, Zölei A, 2008. Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behav Ecol Sociobiol* **62**:1885–1890.

Neudorf DL, Sealy SG, 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? *Behaviour* **123**:84–105.

Noh H, Gloag R, Langmore NE, 2018. True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proc Roy Soc B* **285**:20180726.

Payne RB, 2005. *The Cuckoos*. Oxford (UK): Oxford University Press.

R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Sato NJ, Tanaka KD, Okahisa Y, Yamamichi M, Kuehn R et al. 2015. Nestling polymorphism in a cuckoo-host system. *Curr Biol* **25**: R1164–R1165.

Sato NJ, Tokue K, Noske RA, Mikami OK, Ueda K, 2010. Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour. *Biol Lett* **6**: 67–69.

Schmidt KA, Whelan CJ, 1999. The relative impacts of nest predation and brood parasitism on seasonal fecundity in songbirds. *Conserv Biol* **13**: 46–57.

Soler M, Pérez-Contreras T, Soler JJ, 2017. Brood parasites as predators: farming and mafia strategies. In: Soler M, editor. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. Berlin (DE): Springer International Publishing. 271–286.

Sordahl TA, 1990. The risks of avian mobbing and distraction behavior: an anecdotal review. *Wilson Bull* **102**:349–352.

Spottiswoode CN, Stevens M, 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc Natl Acad Sci USA* **107**:8672–8676.

Stokke BG, Moksnes A, Røskaft E, 2002. Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution* **56**: 199–205.

Tokue K, Ueda K, 2010. Mangrove gerygones *Gerygone laevigaster* eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis* **152**:835–839.

Trnka A, Prokop P, Grim T, 2012. Uncovering dangerous cheats: how do avian hosts recognize adult brood parasites? *PLoS One* **7**. DOI: 10.1371/journal.pone.0037445.

Welbergen JA, Davies NB, 2008. Reed warblers discriminate cuckoos from sparrowhawks with graded alarm signals that attract mates and neighbours. *Anim Behav* **76**:811–822.

Welbergen JA, Davies NB, 2009. Strategic variation in mobbing as a front line of defense against brood parasitism. *Curr Biol* **19**:235–240.

Yu J, Lu H, Sun W, Liang W, Wang H, Møller AP, 2019. Heterospecific alarm-call recognition in two warbler hosts of common cuckoos. *Anim Cogn* **22**:1149–1157.

Yu JEM, Sun W, Liang W, Wang H, Møller AP, 2020. Differently sized cuckoos pose different threats to hosts. *Curr Zool* **66**:247–253.

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Article

Article

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 ± 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

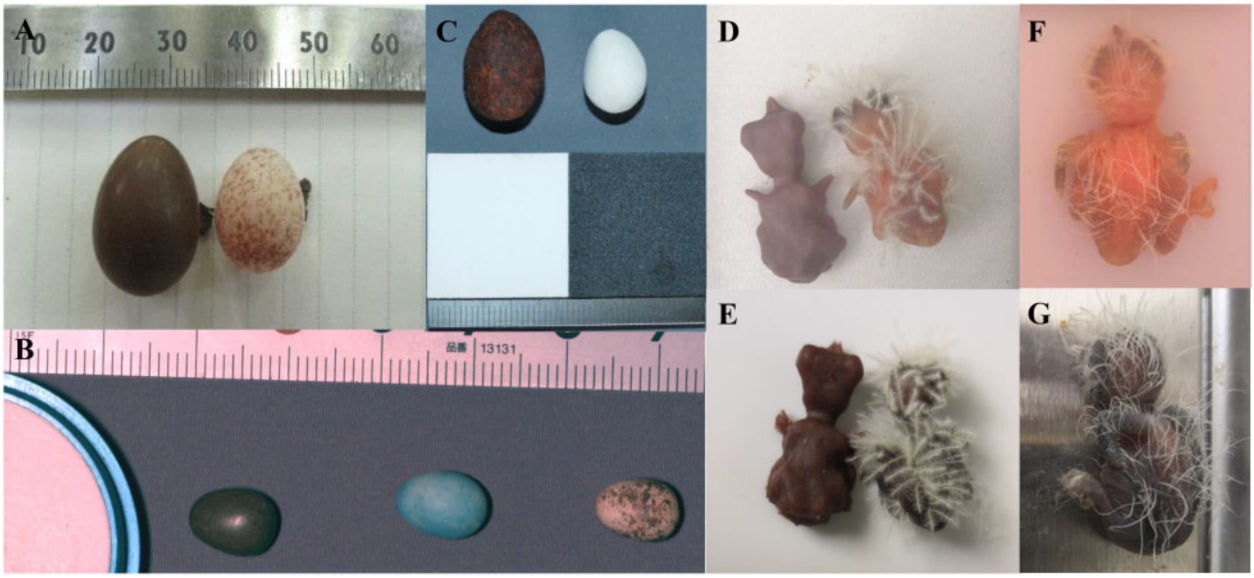

Figure 1. (**A**) Eggs of shining bronze-cuckoo (left) and fan-tailed gerygone (right). (**B**) Artificial eggs for Experiment 1: parasite-like brown (left), blue (center), and host-like whitish-gray with brown speckles (right). (**C**) Artificial eggs for Experiment 2: low reflectance (left, only large 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 Bioacoustics 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 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.

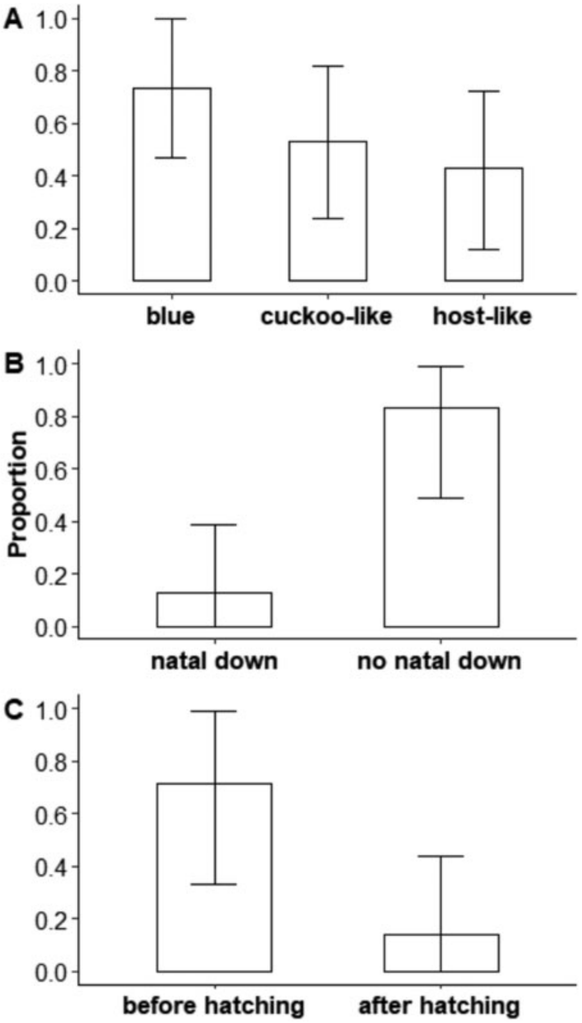

Figure 2. Proportion (with 95% Bonferroni CIs) of ejected artificial eggs in Experiment 1 (**A**, $n = 15$ blue, $n = 15$ parasite-like, $n = 14$ host-like) and ejected cross-fostered nestlings according to presence/absence of natal down (**B**, $n = 8$ natal down present, $n = 6$ natal down absent)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

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; $\chi^2 = 0.303$,

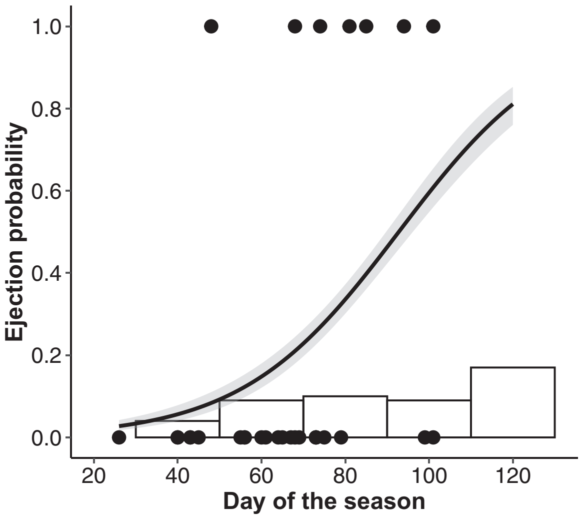

Figure 3. Logistic regression (estimate = 0.053, SE = 0.028) for the probability of fan-tailed gerygones to accept (0) or eject (1) the artificial nestling in relation to day of the season (1 = 9th September). Black points are artificial nestling ejection trials and the gray area around the regression 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 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).

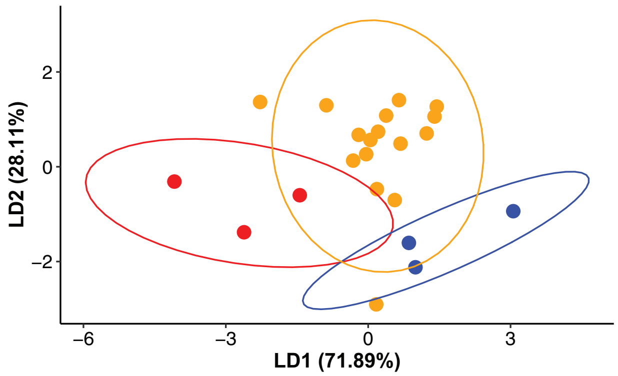

Figure 4. Canonical plot of the first and second linear discriminant functions for the 8 measured parameters of the begging calls in 0–3 days old nestlings. Orange dots are fan-tailed gerygone nestlings, red dots are shining bronze-cuckoo nestlings accepted by host parents and blue dots are shining bronze-cuckoo 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.

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

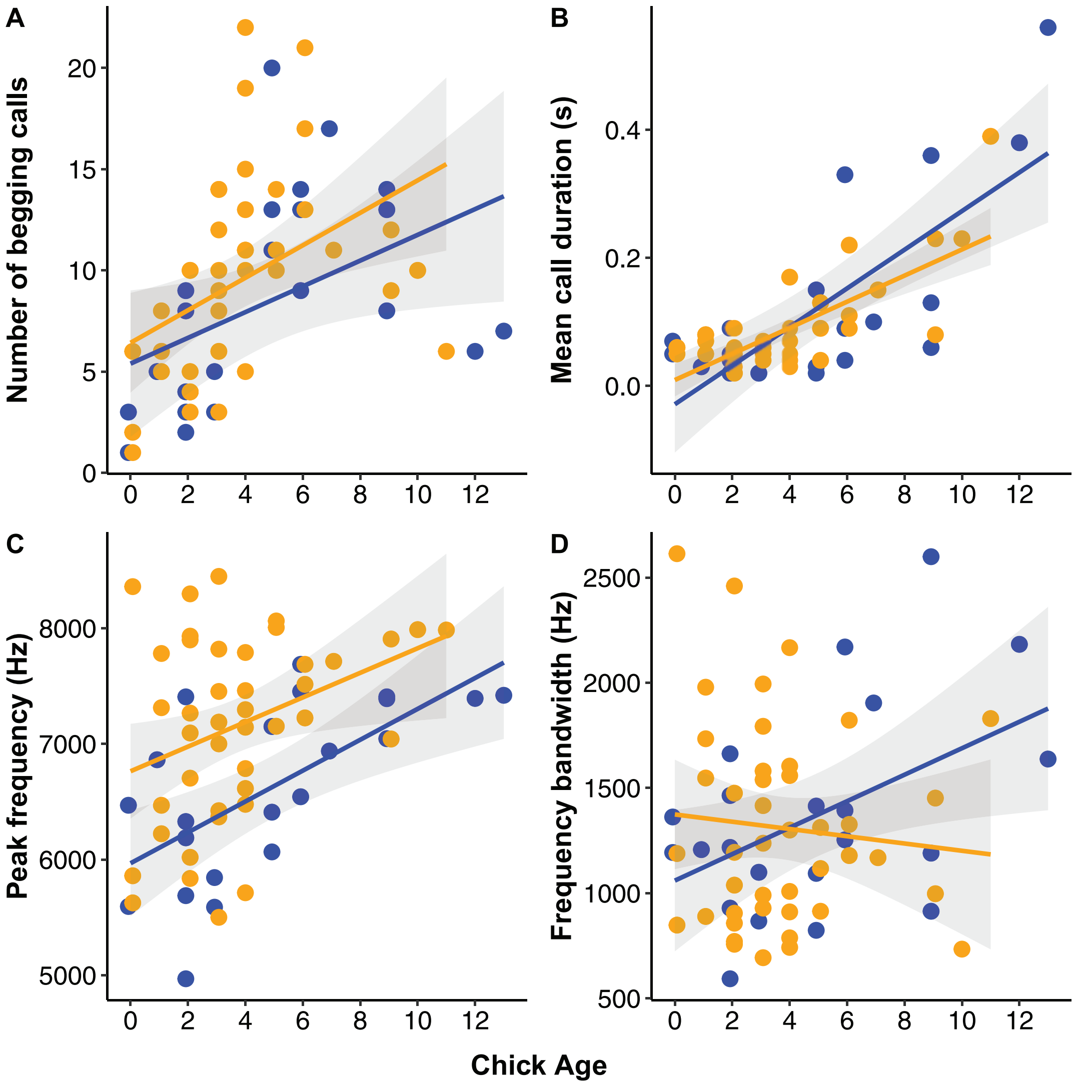

Figure 5. Variation of begging call parameters in relation to age of fan-tailed gerygone (orange) and shining bronze-cuckoo (blue) nestlings. The grey shaded areas around the regression lines are the 95% confidence bands.

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.

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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".

References

Aidala Z, Chong N, Anderson MG, Hauber ME, 2012a. Predicted visual sensitivity for short-wavelength light in the brood parasitic cuckoos of New Zealand. *Chin Birds* **3**:295–301.

Aidala Z, Huynen L, Brennan PLR, Musser J, Fidler A et al., 2012b. Ultraviolet visual sensitivity in three avian lineages: paleognaths, parrots, and passerines. *J Comp Physiol A* **198**:495–510.

Anderson MG, Brunton DH, Hauber ME, 2010. Species specificity of grey warbler begging solicitation and alarm calls revealed by nestling responses to playbacks. *Anim Behav* **79**:401–409.

Attisano A, Sato NJ, Tanaka KD, Okahisa Y, Kuehn R et al., 2018. Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Sci Rep* **8**:1–10.

Attisano A, Thiel F, Sato N, Okahisa Y, Bolopo D et al., 2019. Breeding biology of the fan-tailed gerygone *Gerygone flavolateralis* in relation to parasitism by the shining bronze-cuckoo *Chalcites lucidus*. *J Ornithol* **160**:91–103.

Avilés JM, Parejo D, 2006. Nest defense by Iberian azure-winged magpies (Cyanopica cyanus): do they recognize the threat of brood parasitism? *Ethol Ecol Evol* **18**:321–333.

Avilés JM, Soler JJ, Pérez-Contreras T, 2006. Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. *Proc R Soc B* **273**:2821–2829.

Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T, 2002. Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *J Avian Biol* **33**:420–425.

Bates D, Mächler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. *J Stat Softw* **67**:1–48.

Bojarska K, Kuehn R, Gazda MA, Sato NJ, Okahisa Y et al., 2018. Mating system and extra-pair paternity in the Fan-tailed Gerygone Gerygone flavolateralis in relation to parasitism by the Shining Bronze-cuckoo Chalcites lucidus. PLoS One **13**: e0194059

Briskie JV, Sealy SG, 1989. Changes in nest defense against a brood parasite over the breeding cycle. *Ethology* **82**:61–67.

Britton NF, Planqué R, Franks NR, 2007. Evolution of defence portfolios in exploiter - victim systems. *Bull Math Biol* **69**:957–988.

Caves EM, Stevens M, Iversen ES, Spottiswoode CN, 2015. Hosts of avian brood parasites have evolved egg signatures with elevated information content. *Proc R Soc B* **282**:20150598.

Center for Conservation Bioacustics, 2019. *Raven Pro: Interactive Sound Analysis Software (Version 1.6.1)*. Ithaca (NY): The Cornell Lab of Ornithology.

Colombelli-Négrel D, Hauber ME, Robertson J, Sulloway FJ, Hoi H et al., 2012. Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Curr Biol* **22**:2155–2160.

Davies NB, 2015. *Cuckoo: Cheating by Nature*. London: Bloomsbury Publishing.

Davies NB, Brooke MDL, Kacelnik A, 1996. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc Roy Soc B* **263**:925–931.

Dawkins R, 1982. *The Extended Phenotype*. Oxford: Oxford University Press.

De Mársico MC, Gantchoff MG, Reboreda JC, 2012. Host - parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proc Roy Soc B* **279**:3401–3408.

Fox J, Weisberg S, 2019. *An R Companion to Applied Regression*. Thousand Oaks (CA): Sage.

Gibbs HL, Sorenson MD, Marchetti K, Brooke M de L, Davies NB et al., 2000. Genetic evidence for female host- specific races of the common cuckoo. *Nature* **407**:183–186.

Gloag R, Keller LA, Langmore NE, 2014. Cryptic cuckoo eggs hide from competing cuckoos. *Proc Roy Soc B* **281**:20141014.

Grim T, 2006. The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evol Ecol Res* **8**:785–802.

Grim T, 2007. Equal rights for chick brood parasites. *Ann Zool Fennici* **44**:8.

Grim T, 2017. Host defence against brood parasite nestlings: theoretical expectations and empirical evidence. In: Soler M, editor. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. New York (NY): Springer International Publishing. 539–556.

Guigueno MF, Sealy SG, 2012. Nest sanitation in passerine birds: implications for egg rejection in hosts of brood parasites. *J Ornithol* **153**:35–52.

Guigueno MF, Sealy SG, Westphal AM, 2014. Rejection of parasitic eggs in passerine hosts: size matters more for a non-ejecter. *Auk* **131**:583–594.

Hart NS, 2002. Vision in the peafowl. *J Exp Biol* **205**:3925–3935.

Honza M, Cherry M, 2017. Egg characteristics affecting egg rejection. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. New York (NY): Springer International Publishing. 401–419.

Kilner RM, 2006. Function and evolution of color in young birds. In: Hill GE, McGraw KJ, editors. *Bird Coloration Volume II: Function and Evolution*. Cambridge (MA): Harvard University Press. 201–232.

Langmore NE, Cockburn A, Russell AF, Kilner RM, 2009a. Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behav Ecol* **20**:978–984.

Langmore NE, Hunt S, Kilner RM, 2003. Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**:157–160.

Langmore NE, Kilner RM, Butchart SHM, Maurer G, Davies NB et al., 2005. The evolution of egg rejection by cuckoo hosts in Australia and Europe. *Behav Ecol* **16**:686–692.

Langmore NE, Maurer G, Adcock GJ, Kilner RM, 2008. Socially aquired host-specific mimicry and the evolution of host races in Horsfield's bronze cuckoo *Chalcites basalis*. *Evolution* **62**:1689–1699.

Langmore NE, Stevens M, Maurer G, Kilner RM, 2009b. Are dark cuckoo eggs cryptic in host nests? *Anim Behav* **78**:461–468.

Liang W, Yang C, Takasu F, 2017. How can distinct egg polymorphism be maintained in the rufescent prinia *Prinia rufescens* - plaintive cuckoo *Cacomantis merulinus* interaction-a modeling approach. *Ecol Evol* **7**:5613–5620.

Lokemoen JT, Koford RR, 1996. Using candlers to determine the incubation stage of passerine eggs. *J Field Ornith* **67**:660–668.

Marchetti K, 2000. Egg rejection in a passerine bird: size does matter. *Anim Behav* **59**:877–883.

Medina I, Langmore NE, 2016. Batten down the thatches: front-line defences in an apparently defenceless cuckoo host. Anim Behav **112**: 195–201.

Medina I, Langmore NE, 2019. Nest illumination and the evolution of egg rejection in hosts of brood parasites. *Auk* **136**:1–6.

Moksnes A, Røskaft E, Braa AT, 1991. Rejection behavior by common cuckoo hosts towards artificial brood parasite eggs. *Auk* **108**:348–354.

Moskát C, Avilés JM, Bán M, Hargitai R, Zölei A, 2008. Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behav Ecol Sociobiol* **62**:1885–1890.

Noh HJ, Gloag R, Langmore NE, 2018. True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proc Roy Soc B* **285**:20180726.

R Core Team, 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing

Rasmussen JL, Underwood TJ, Sealy SG, 2010. Functional morphology as a barrier to the evolution of grasp-ejection in hosts of the Brown-headed cowbird *Molothrus ater*. *Can J Zool* **88**:1210–1217.

Rohwer S, Spaw CD, 1988. Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evol Ecol* **2**:27–36.

Rothstein SI, 1975. An experimental and teleonomic investigation of avian brood parasitism. *Condor* **77**:250–271.

Sato NJ, Mikami OK, Ueda K, 2010. The egg dilution effect hypothesis: a condition under which parasitic nestling ejection behaviour will evolve. *Ornithol Sci* **9**:115–121.

Sato NJ, Tanaka KD, Okahisa Y, Yamamichi M, Kuehn R et al., 2015. Nestling polymorphism in a cuckoo-host system. *Curr Biol* **25**:R1164–R1165.

Schneider CA, Rasband WS, Eliceiri KW, 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* **9**: 671–675.

Soler M, 2017. *Avian Brood Parasitism: Behaviour, Ecology, Evolution and Coevolution*. New York (NY): Springer International Publishing

Spottiswoode CN, Stevens M, 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc Natl Acad Sci USA* **107**:8672–8676.

Tanaka KD, Morimoto G, Stevens M, Ueda K, 2011. Rethinking visual supernormal stimuli in cuckoos: visual modeling of host and parasite signals. *Behav Ecol* **22**:1012–1019.

Taylor CJ, Langmore NE, 2020. How do brood-parasitic cuckoos reconcile conflicting environmental and host selection pressures on egg size investment? *Anim Behav* **168**:89–96.

Thorogood R, Kilner RM, Rasmussen JL, 2017. Grey Gerygone hosts are not egg rejecters, but shining bronze-cuckoos lay cryptic eggs. *Auk* **134**:340–349.

Troscianko J, Stevens M, 2015. Image calibration and analysis toolbox: a free software suite for objectively measuring reflectance, colour and pattern. *Methods Ecol Evol* **6**:1320–1331.

Underwood TJ, Sealy SG, 2006. Grasp-ejection in two small ejecters of cowbird eggs: a test of bill-size constraints and the evolutionary equilibrium hypothesis. *Anim Behav* **71**:409–416.

Yang C, Li Z, Zhang Y, Wang H, Liang W et al., 2016. Egg polymorphism and egg discrimination in the Daurian redstart *Phoenicurus auroreus*, a host of the common cuckoo *Cuculus canorus*. *Ornithol Sci* **15**:127–132.

Yang C, Si X, Liang W, Møller AP, 2020. Spatial variation in egg polymorphism among cuckoo hosts across 4 continents. *Curr Zool* **66**:477–483.

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LONG TERM STUDY

Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race

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Abstract

1. Decades of research have shown that the coevolutionary arms race between avian brood parasites and their hosts can promote phenotypic diversification in hosts and brood parasites. However, relatively little is known about the role of brood parasitism in promoting phenotypic diversification of nestlings.
2. We review field data collected over four decades in Australia, New Caledonia and New Zealand to assess potential for coevolutionary interactions between the shining bronze-cuckoo (*Chalcites lucidus*) and its hosts, and how diversification at the nestling stage may be generating different subspecies.
3. The shining bronze-cuckoo is a specialist parasite of a few hosts in the family Acanthizidae. It has diversified into subspecies, of which the nestlings closely mimic the respective host nestlings in each region. Additionally, some cuckoo subspecies have polymorphic nestlings.
4. The Acanthizidae hosts have similar breeding and nesting habits and only moderately effective frontline defences against parasitism at cuckoo egg laying or at the egg stages. However, some hosts have developed highly effective defences at the nestling stage by recognising and ejecting cuckoo nestlings from the nest. As with the cuckoo nestlings, some hosts have polymorphic nestlings.
5. The coevolutionary interactions in each region suggest different evolutionary stages of the arms race in which either the parasite or the host is currently in the lead. The presence of moderately effective defences at the egg laying and egg stages might explain why some hosts do not have defences at the nestling stage.
6. The south-Pacific cuckoo – host systems are excellent models to explore the evolutionary mechanisms driving the diversification at the nestling stage in the coevolutionary arms race between avian brood parasites and their hosts.

KEYWORDS
Chalcites, coevolution, Cuculiformes:Cuculidae, geographic variation, nestling polymorphism, Passeriformes:Acanthizidae

1 | INTRODUCTION

Obligate brood parasites lay their eggs in nests of other species, their hosts, which are left to care for the foreign nestlings incurring a considerable fitness cost (Davies, 2015; Soler, 2017). This can induce an evolutionary arms race in which hosts are under selection to evolve defences against parasitism while brood parasites are under selection to evolve improved strategies to evade host defences (Dawkins & Krebs, 1979). Antagonistic behavioural interactions can often lead to phenotypic diversification (Vamosi, 2011; Yoder & Nuismer, 2010), and indeed decades of research have shown that brood parasitism can promote phenotypic diversification in several aspects of the biology of brood parasites and their hosts (reviewed in Medina et al., 2020). For example, a brood-parasitic lifestyle is associated with traits that facilitate successful parasitism, such as small body size and small eggs (Davies, 2011; Krüger & Davies, 2002), thick eggshells (Stokke et al., 2002) and plastic mating systems (Louder et al., 2019). Similarly, brood parasitism can influence the evolution of host traits such as egg (Caves et al., 2015; Øien et al., 1995; Soler & Møller, 1996) and nestling (Hauber & Kilner, 2007) phenotypes and breeding systems (Feeney et al., 2013).

Polymorphism is a common outcome of the arms race and is generally thought to result from negative frequency-dependent selection driven by host discrimination of the parasite (Cook et al., 2012; Spottiswoode & Stevens, 2012; Takahashi et al., 2010; Tanaka, 2016). For example, a common parasite morph resembling that of the host is an effective way to escape host detection, however a rare parasite morph could also escape detection if the host has not yet learned to recognise it as a parasite. Relative morph frequencies can thus oscillate over time depending on the host's discrimination ability or perception of local risk (Davies et al., 1996; Ruiz-Raya & Soler, 2020). For example, there is experimental evidence from adult common cuckoos *Cuculus canorus* that negative frequency dependent selection occurs on polymorphisms in parasite plumage (Mappes & Lindström, 2012). Females have two distinct plumage phenotypes, a grey and a rufous or hepatic form (Honza et al., 2006; Thorogood & Davies, 2012). Hosts react more aggressively towards the locally-common morph (Honza et al., 2006; Trnka & Grim, 2013), but can be induced to switch their behaviour if the alternate form becomes less rare (Thorogood & Davies, 2012). Similar plumage polymorphisms are common across Cuculidae but are more likely to occur in species that are brood parasites, suggesting that this is an adaptation to facilitate successful parasitism (Thorogood & Davies, 2013).

The factors underlying the evolution of egg polymorphism are also well understood (Honza & Cherry, 2017). A great number of host species across different avian clades recognise and reject (either by ejection or nest abandonment) the parasite egg (Medina & Langmore, 2015; Yang et al., 2020), which leads to egg mimicry by the parasite (Brooke & Davies, 1988; Stoddard & Stevens, 2010). Host egg polymorphism can thus evolve in response to parasite mimicry because it facilitates recognition of the parasite egg (Medina & Langmore, 2016; Takasu, 2003; Yang et al., 2020). Host egg polymorphism can occur as variation between clutches (Moskát et al., 2008; Øien et al., 1995; Stokke et al., 2002), discrete polymorphism (two or more discrete egg morphs) within a host population (Liang et al., 2017; Yang et al., 2016) or as a variation in multiple egg features (eggshell colour, luminance and spot patterns) acting as individual signatures (Caves et al., 2015; Spottiswoode & Stevens, 2011). Egg polymorphism in brood parasites can occur when generalist brood parasites exploiting multiple host species specialise into host-specific lineages whose egg phenotype is a close match of the specific host they parasitise (Abernathy & Liang, 2020; Brooke & Davies, 1988; Gibbs et al., 2000; Spottiswoode et al., 2011; Starling et al., 2006; Stoddard & Stevens, 2010).

Despite decades of research, we still do not fully understand the coevolution between host and parasite nestlings. One reason for this is that much of the empirical and theoretical research has historically focused on few well-known avian parasite–host systems such as the common cuckoo from Europe and the cowbirds, genus *Molothrus*, from the Americas and their respective hosts (Kennerley et al., 2022). Many hosts in these systems have well-developed defences at the frontline (before the cuckoo egg is laid, for example mobbing the adult parasite) or egg (after the cuckoo egg is laid, for example rejection of the cuckoo egg or nest desertion) stages, but always accept the parasite nestlings (but see De Mársico et al., 2012 and Grim et al., 2003 for rejection of parasite fledglings). Therefore, nestling discrimination was assumed to be a costly defence due to the high risk of misrecognising own chicks as a parasite (Lotem, 1993). Additionally, hosts encounter parasite nestlings at lower frequencies than parasite eggs, which might relax selection for the development of host defences at the nestling stage (Britton et al., 2007; Grim, 2006). As a consequence, the nestling stage of the arms race has been less studied than the frontline and egg stages (Grim, 2011, 2017) and the selective factors and evolutionary outcomes underlying phenotypic diversification at the nestling stage of the arms race are less understood.

An example of nestling mimicry and diversification comes from the parasitic *Vidua* finches and their hosts. *Vidua* nestlings mimic gape colour and patterns, begging calls and begging postures of their estrildid hosts (Jamie et al., 2020; Payne, 2005a). However, they do not evict host nestlings or affect their survival rates (Schuetz, 2005a) and the hosts do not discriminate *Vidua* nestlings (Schuetz, 2005a, 2005b). Therefore, in these systems nestling mimicry is not the result of coevolutionary interactions between host and parasite but rather appears to be due to nestling competition to stimulate parental provisioning (Hauber & Kilner, 2007; Kilner et al., 1999). The

Australasian bronze-cuckoos (genus *Chalcites*) and their hosts, on the other hand, show evidence of a coevolutionary arms race at the nestling stage. Some hosts of bronze-cuckoos recognise and reject (Langmore et al., 2003) or eject the parasite nestling from the nest (Sato et al., 2015; Sato, Tokue, et al., 2010; Tokue & Ueda, 2010). Correspondingly, bronze-cuckoo nestlings mimic host nestlings in traits such as colour and luminance of skin, flanges and gape and presence and distribution of down feathers (Attisano et al., 2018; Langmore et al., 2011; Noh et al., 2018). Hosts discriminate the parasite nestlings via cues such as natal down, hatching order or begging calls (Attisano, Sato, et al., 2021; Langmore et al., 2003; Noh et al., 2018, 2021). Host breeding experience and risk of parasitism can also influence rejection of the parasite nestling (Langmore, Cockburn, et al., 2009). Remarkably, some of these systems also present polymorphism in both the host and parasite nestlings (Attisano, Sato, et al., 2021; Langmore et al., 2011; Sato et al., 2015).

We present a synthesis based on 40 years of studies on the biology of the shining bronze-cuckoo (*Chalcites lucidus*) and its hosts conducted in Australia, New Caledonia and New Zealand. We first describe the biology of the shining bronze-cuckoo and its hosts, highlighting commonalities and differences across the range by reviewing key aspects of these parasite–host relationships. We continue by describing host nestling mimicry by the shining bronze-cuckoo, nestling polymorphism and host defences at the nestling stage. Finally, we discuss the role of brood parasitism in promoting nestling phenotypic diversification and the evolutionary implications of nestling polymorphism in the arms race between the shining bronze-cuckoo and its hosts. The field work in New Caledonia was conducted with permits from the Province Sud Nouvelle Calédonie (3045–2011, 2437–2012, 2532–2013, 2801–2014, 2476–2015, 2372–2017, 3469–2018 and 2720–2019) and did not require ethical approval. Field work in New Zealand was conducted with permits from The Wildlife Service, Marlborough Catchment Board, The University of Canterbury Animal Ethics Committee (AEC 2010/24R) and the New Zealand Department of Conservation, *Te Papa Atawhai* (AK/15301/RES). Field work in Australia was conducted under the approval of the Australian National University Animal Experimentation Ethics Committee (Protocol Numbers F.BTZ.99.99, A2012/47 and F.BTZ.61.03, A2021/37), and Environment ACT (Licence numbers LT1999021, LT200340, LT2004112, LT2005164, LT2006229, LT2007266, LT2011509, LT2012589, LT2013667, LT2014776, LT2015842 and LT2016895).

2 | MODEL SPECIES

2.1 | The shining bronze-cuckoo

Four subspecies of the shining bronze-cuckoo are currently recognised (Payne, 2005b). The migratory *C. l. plagosus* breeds in Tasmania, south-east and south-west Australia and overwinters in the Lesser Sunda Islands and New Guinea (Friedman, 1968; Gill, 1983a). The migratory subspecies *C. l. lucidus* breeds in New Zealand and the Chatham Islands and overwinters in the Solomon Islands and Bismarck Archipelago (Fell, 1947; Friedman, 1968). These two subspecies might come into contact during migration in Queensland outside the breeding season (Gill, 1983a; Noske, 2019), but genetic admixture is unlikely. The subspecies *C. l. layardi* forms resident populations in New Caledonia and Vanuatu. The fourth subspecies *C. l. harterti* is resident on Rennell and Bellona Islands, however little is known about its behavioural ecology, and we exclude it from our synthesis. There is no evidence of contact between migratory and resident subspecies (Friedman, 1968).

The shining bronze-cuckoo is a specialist parasite of a small group of closely related hosts in the family Acanthizidae, all of which build suspended, dome-shaped nests. The subspecies on the New Zealand mainland exclusively parasitises the grey warbler, *Gerygone igata* (Gill, 1983b, 1998), the subspecies from New Caledonia exclusively parasitises the fan-tailed gerygone, *G. flavolateralis* (Sato et al., 2015) and the subspecies from Australia is a specialist parasite of thornbills (*Acanthiza* species), particularly the yellow-rumped thornbill *A. chrysorroa* (Brooker & Brooker, 1989a). Although historical nest records in Australia reported also superb fairy-wrens *Malurus cyaneus* and splendid fairy-wrens *M. splendens* as hosts of *C. l. plagosus* (Brooker & Brooker, 1989b), multiple field studies found no parasitism of fairy-wrens (Brooker & Brooker, 1989a, 1992; Langmore & Kilner, 2007). Field experiments additionally showed that all shining bronze-cuckoo chicks transferred from thornbill nests to superb fairy-wren nests resulted in rejection of the cuckoo chicks by the fairy-wren hosts (Langmore et al., 2003). Historical records of shining bronze-cuckoo nestlings being reared by superb fairy-wrens were probably misidentifications of Horsfield's bronze-cuckoos *C. basalis*, the primary brood parasite of fairy-wrens (Payne, 2005b).

Female shining bronze-cuckoos produce dark unmarked eggs with colours ranging from olive-green to dark brown (Figure 1), which have been assumed to be cryptic in the poorly illuminated hosts' domed nests (Langmore et al., 2005; Langmore, Stevens, et al., 2009). The contrast with the host eggs is striking. All exploited hosts have eggs that are either immaculate white or whitish with brown speckles (Figure 1), but hosts usually accept foreign eggs irrespective of their coloration (Attisano, Sato, et al., 2021; Thorogood et al., 2017). Female bronze-cuckoos always remove one egg from the nest before laying their own and sometimes they can remove an egg laid by a previous cuckoo female (Gloag et al., 2014). Therefore, the dark coloration might decrease the chances of detection by other competing female cuckoos, rather than by the host (Brooker et al., 1990; Gloag et al., 2014; Thorogood et al., 2017).

The duration of the cuckoo laying season is 18–19 weeks (August – December) in Australia (Brooker & Brooker, 1989b), 13–15 weeks (October – January) in New Caledonia (Attisano et al., 2019) and 10–12 weeks (October – December) in New Zealand (Gill, 1983b). Parasitism rates vary across the three regions (Table 1) and increase over the breeding season in Australia and in New Zealand's South Island (Gill, 1983b, 1998; Medina & Langmore, 2016) are low throughout the season in New Zealand's North Island (Anderson et al., 2013) and relatively constant throughout the breeding season

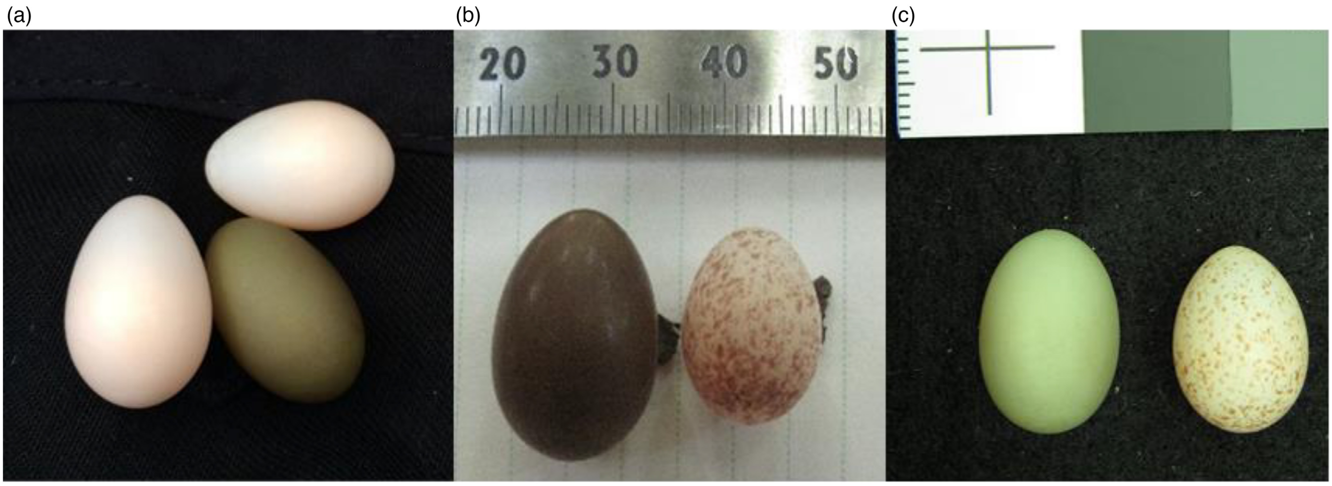

FIGURE 1 Eggs of shining bronze-cuckoos and their hosts from (a) Australia (cuckoo: olive green; yellow-rumped thornbill: unspotted white; photo by N. Langmore), (b) New Caledonia (cuckoo: dark brown; fan-tailed gerygone: whitish grey with brown speckles; photo by N. Sato) and (c) New Zealand (cuckoo: olive-green; grey warbler: whitish with brown speckles; photo by R. Thorogood).

in New Caledonia (Table 1). Multiple parasitism (i.e. when multiple cuckoo females lay single eggs in the same host nest) is common in some bronze-cuckoos (e.g. *C. minutillus*, Gloag et al., 2014). However, it is rare in the shining bronze-cuckoo: instances of two cuckoo eggs being laid in the same gerygone nest have been reported only once in New Caledonia (Attisano et al., 2019) and once in New Zealand (Briskie, 2007). The average incubation period of the cuckoo egg is shorter than that of the hosts' eggs (Attisano et al., 2019; Brooker & Brooker, 1989a; Gill, 1983b; Table 1); therefore, cuckoo nestlings usually hatch earlier than host nestlings. However, mis-timed laying can result in the cuckoo chicks hatching after the host chicks, a relatively frequent occurrence in New Zealand (Table 1). The shining bronze-cuckoo chick usually evicts all host eggs or nestlings within 1–2 days after hatching (Brooker & Brooker, 1989a; Sato et al., 2015), but eviction can occur as late as 7 days after hatching (Gill, 1983b; Table 1).

2.2 | The hosts

The nests of the Acanthizidae hosts of the shining bronze-cuckoo have a distinctive dome-shaped structure and are suspended in various trees and shrubs at heights ranging from ground level to 20 m in the canopy (Attisano et al., 2019; Ebert, 2004; Gill, 1982). *G. igata* and *G. flavolateralis* are the only species building such nests in New Zealand (mainland) and New Caledonia, respectively, and no evidence of parasitism by shining bronze-cuckoos has been found in other common sympatric open-cup nesters that are potentially suitable hosts in these regions (Briskie, 2003; Gill, 1983b). In Australia, the number of potential hosts with open and domed nests is higher, however the shining bronze-cuckoo targets thornbill hosts, in particular the yellow-rumped thornbill *A. chrysorrhoa*, the nests of which closely resemble gerygone nests (Brooker & Brooker, 1989a; Medina & Langmore, 2016). Therefore, host nest location and structure might have more influence than host density or diet in determining host choice by the shining bronze-cuckoo.

The yellow-rumped thornbill from Australia is a facultative cooperative breeder and does not defend exclusive breeding territories (Ebert, 2004). On the other hand, the gerygones from New Zealand and New Caledonia form monogamous pairs and defend their breeding territory against conspecific trespassers (Attisano et al., 2019; Gill, 1982). Nest predation is the major cause of nest loss in all the hosts, with predation rates ranging from about 30% in New Zealand (Gill, 1982) to over 80% in New Caledonia and Australia (Attisano et al., 2020; Ebert, 2004). Besides nest losses due to host egg and chick eviction by the cuckoo nestling, adult female shining bronze-cuckoos also destroy 13%–16% of the active non-parasitised nests by removing host eggs or killing host nestlings (Attisano et al., 2020; Briskie, 2007). This behaviour targets nests that are too advanced in the breeding cycle and stimulates re-nesting in the hosts, thereby increasing the availability of new nests for parasitism ('farming strategy'; Soler, 2017).

The clutch size is significantly smaller in the New Caledonian host than in the hosts from New Zealand and Australia (Table 1). All the hosts lay eggs at 2-day intervals; thus, the host laying period is between 4 and 6 days in New Caledonia and 6–8 days in New Zealand and Australia. Female cuckoos increase the survival chances of their nestling by laying their egg during the host incubation period (Davies, 2015). The laying window is thus significantly shorter for the New Caledonian cuckoo, which might help explain the strong synchronicity with the host laying period (Table 1). Re-nesting after nest failure occurs in all hosts, however consecutive successful breeding attempts within the same season have been observed only in Australia and in New Zealand's South Island, whereas in the North Island and in New Caledonia host pairs have typically only one successful breeding attempt per season (Anderson et al., 2013; Attisano et al., 2019; Ebert, 2004; Gill, 1982).

All the hosts show some defences at the frontline stage. They react aggressively to adult shining bronze-cuckoos approaching the nest (Briskie, 2007) as well as to stuffed specimens of shining bronze-cuckoos presented at the nest (Attisano, Hlebowicz, et al., 2021;

TABLE 1 Details of the shining bronze-cuckoo – host systems in Australia (Brooker & Brooker, 1989a; Ebert, 2004), New Caledonia (Attisano et al., 2018, 2019; Sato et al., 2015) and New Zealand (Anderson et al., 2013; Gill, 1982, 1983b; Thorogood et al., 2017). All averages with CI.

	Australia	**New Caledonia**	**New Zealand**
Shining bronze-cuckoo subspecies	***C. l. plagosus***	***C. l. layardi***	***C. l. lucidus***
Secondary hosts	*A. reguloides*	No	No
Migratory	Yes	No	Yes
Host nestling mimicry	Yes	Yes	Yes
Nestling polymorphism (bright: dark)	91:9 (*n* = 22)	94:6 (*n* = 26)	Only dark (*n* = 20)
Average incubation (days)	13 ± 1	16 ± 1	16 ± 5
Average nestling period (days)	20 ± 1	19 ± 1	20 ± 1
Cuckoo laying relative to host laying (nests)			
Before	40%	0	0
During	53% (*n* = 15)	100% (*n* = 26)	37% (*n* = 8)
After	7%	0	63%
Cuckoo hatching relative to first host hatching (nests)			
Before	83%	80%	58%
Same day	0 (*n* = 6)	10% (*n* = 19)	0 (*n* = 12)
After	17%	10%	42%
Eviction of host eggs/nestlings relative to cuckoo hatching (nests)			
Day 1 from hatching	0	25%	0
≥ Day 2 from hatching	100% (*n* = 7)	75% (*n* = 4)	100% (*n* = 12)
Cuckoo nestlings rejected by hosts	0	86% (*n* = 28)	0
Cuckoo fledglings	92% (*n* = 24)	7% (*n* = 28)	65% (*n* = 20)
Main host	***A. chrysorrhoa***	***G. flavolateralis***	***G. igata***
Breeding system	Facultatively cooperative	Socially monogamous	Socially monogamous
Territorial	No	Yes	Yes
Rejects cuckoo eggs (ejection or nest abandonment)	Only if cuckoo laying mis-timed	No	No
Ejects cuckoo chicks	No	Yes	No
Nestling polymorphism (bright: dark)	No	75:25 (*n* = 222)	66:34 (*n* = 192)
Brood ratio (bright:dark:mixed)	All bright (*n* = 40)	69:23:8 (*n* = 132)	43:15:42 (*n* = 65)
Mean clutch size	3.2 ± 0.1 (*n* = 51)	2.0 ± 0.1 (*n* = 223)	3.5 ± 0.1 (*n* = 117)
Average incubation length (days)	17 ± 1	17 ± 1	20 ± 1
Average nestling period (days)	19 ± 1	15 ± 1	18 ± 1
Parasitism rate	30% (*n* = 106)	20% (*n* = 344)	26% (*n* = 138)
Nests with multiple parasitism	0	1	0[a]

[a] Briskie (2007) reported a case of multiple parasitism in a different field study.

Medina & Langmore, 2016). The yellow-rumped thornbill begins nesting in mid-winter, substantially earlier than congeneric and sympatric insectivorous species and before migratory cuckoos arrive in their breeding ground, which is consistent with selection for earlier breeding to escape parasitism (Medina & Langmore, 2016). A similar process might occur in the grey warbler as in the South Island breeding begins before arrival of migratory cuckoos (although not earlier than sympatric insectivores that are not parasitised); thus, earlier clutches suffer lower parasitism rates than later ones (Anderson et al., 2013).

Yellow-rumped thornbills sometimes reject cuckoo eggs laid before the host starts laying by burying these in the nest lining or they might abandon the nest if the cuckoo lays after the host has started incubation (N. Langmore, pers. obs.). They also show low rejection rates of blue artificial eggs introduced in the nest (Medina & Langmore, 2019). By contrast, gerygone hosts always accept cuckoo and artificial eggs mimicking size and colour of real host and cuckoo eggs (Attisano, Sato, et al., 2021; Gloag et al., 2014; Thorogood et al., 2017). A possible explanation for gerygone hosts being egg acceptors is that they might be unable to grasp and eject the large cuckoo egg (Gill, 1998; Guigueno et al., 2014; Moksnes et al., 1991). In New Caledonia, the cuckoo egg is about 50% larger in volume than the host egg (Figure 1) and the fan-tailed gerygone host has a bill size comparable with small acceptor hosts of the common cuckoo in Europe and cowbirds in North America (Moksnes et al., 1991; Rasmussen et al., 2010). Indeed, fan-tailed gerygones always accept artificial eggs matching the size of real eggs but frequently eject artificial eggs smaller than real eggs even if these mimic the colour of host or parasite eggs, thus suggesting that the small bill size might prevent ejection of the large cuckoo eggs (Attisano, Sato, et al., 2021). Another explanation is that by accepting the cuckoo egg the host reduces the chances of losing an additional host egg during multiple parasitism attempts by different cuckoo females (Sato, Mikami, & Ueda, 2010).

Frontline and egg defences in these hosts are thus only partly or not at all effective in preventing parasitism. This might have been instrumental in promoting an escalation to the nestling stage as the next step in these arms races (Grim, 2017; Langmore et al., 2003).

3 | NESTLING MIMICRY, POLYMORPHISM AND DISCRIMINATION

3.1 | Nestling mimicry and polymorphism in parasite nestlings

Discrimination of the parasite egg by the hosts favours selection of host egg mimicry in brood parasites (Honza & Cherry, 2017). Similarly, discrimination of the parasite nestling by hosts of bronze-cuckoos (Langmore et al., 2003; Sato, Tokue, et al., 2010; Tokue & Ueda, 2010) has favoured selection of host nestling mimicry in several bronze-cuckoo species (Langmore et al., 2011). Some hosts of bronze-cuckoos also discriminate the begging call of the parasite nestling (Colombelli-Négrel et al., 2012; Langmore et al., 2003; McLean & Waas, 1987), which in turn has favoured selection of begging call mimicry by the parasite (Anderson et al., 2009; Langmore et al., 2008; Noh et al., 2021; Ranjard et al., 2010).

The shining bronze-cuckoo also has geographic variation in visual mimicry with nestlings of each subspecies closely resembling the respective local host in traits such as colour and luminance of the skin and mouth flanges (Figure 2 and Supplementary Material). McGill and Goddard (1979) found a similar difference in cuckoo nestling coloration among subspecies of the little bronze-cuckoo *C. minutillus*. Besides coloration, the shining bronze-cuckoo nestlings of each subspecies also usually mimic their respective hosts in regard to the presence of natal down; cuckoo nestlings from New Caledonia and New Zealand have sparse down feathers which mimic the natal down of the host nestlings (Figure 3). However, cuckoo nestlings in Australia are usually naked or have a small number of short, fine filaments on the head, whereas host nestlings have a longer, fine down on the head and back (Langmore et al., 2011). Usually, Cuculinae nestlings are naked at hatching (Payne, 2005b), however natal down is a common trait of bronze-cuckoos parasitising gerygone hosts (Langmore et al., 2011; Tokue & Ueda, 2010). Remarkably, shining bronze-cuckoo nestlings can also occur in two distinct skin colour morphs within a subspecies, typically a common 'bright' and a rare 'dark' (melanic) morph (Figure 3). The occurrence of polymorphism in shining bronze-cuckoos varies across its range, as it has been observed only in Australia and New Caledonia (Langmore et al., 2011; Sato et al., 2015), but not in New Zealand where Gill (1983b) only observed a dark morph (Table 1). There is therefore evidence of the formation of host-specific lineages in the shining bronze-cuckoo,

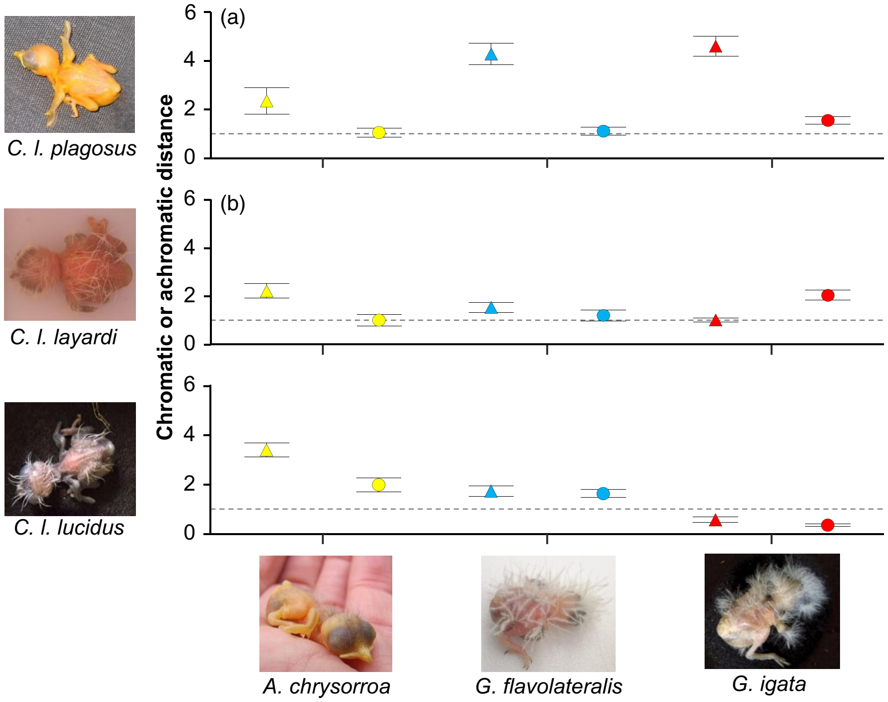

FIGURE 2 Chromatic (triangle) and achromatic (circle) distances between the most common morphs of shining bronze-cuckoo subspecies (bright morph in AU and NC, dark morph in NZ) and the most common morphs of hosts (all bright) from Australia (*A. chrysorroa*, yellow), New Caledonia (*G. flavolateralis*, light blue) and New Zealand (*G. igata*, red). Visual distances were calculated using the peafowl vision model, with larger distances indicating larger visual differences between nestlings. The dashed horizontal lines indicate the threshold value below which two objects cannot be discriminated by an observer under high-light levels. See the attached Supporting Information for a description of the methodology for the visual modelling analysis.

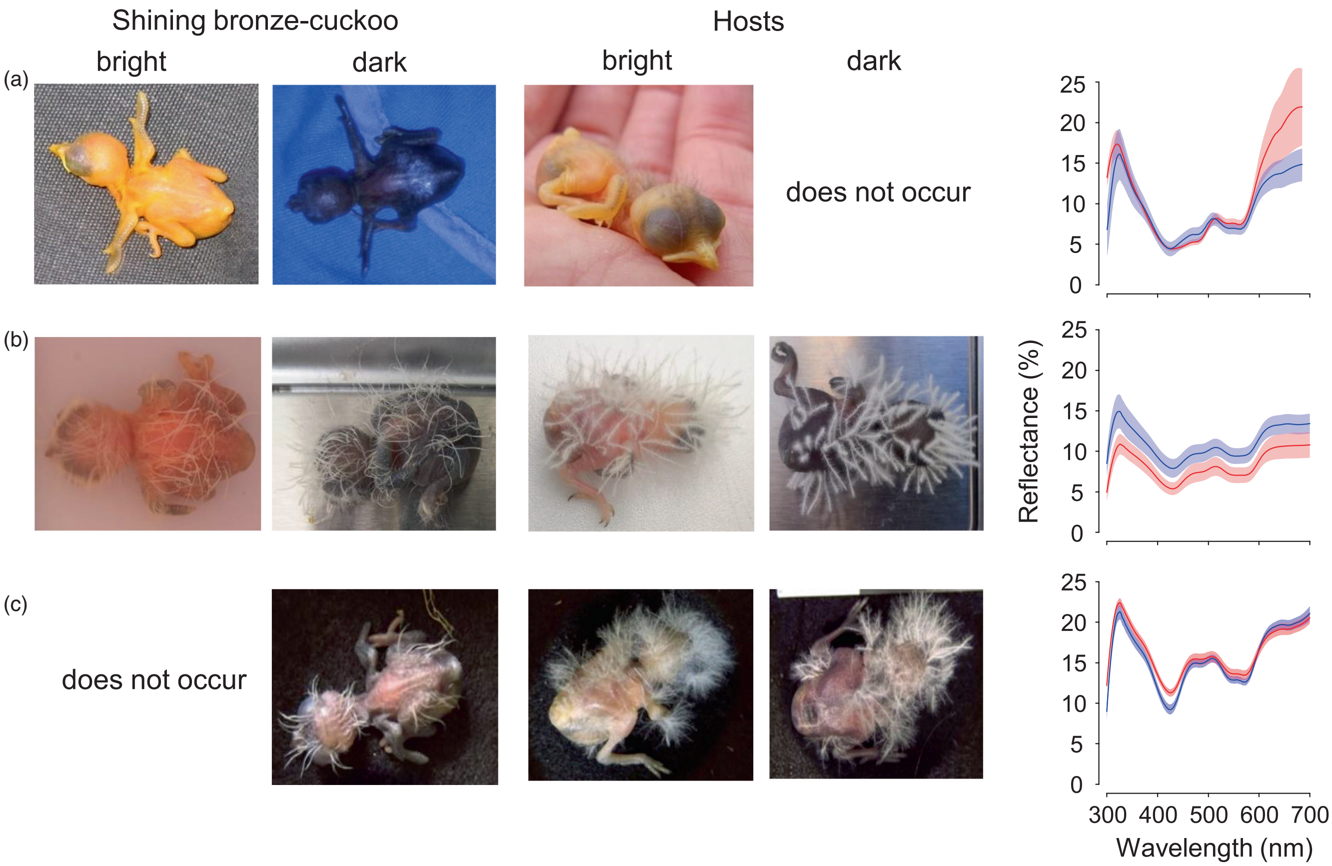

FIGURE 3 Representative photos and reflectance spectra showing the phenotypic variation in nestlings of shining-bronze cuckoos and their hosts in (a) Australia (modified from Langmore et al., 2011; photos by N. E. Langmore), (b) New Caledonia (modified from Sato et al., 2015; photos by A. Attisano) and (c) New Zealand (data from M. G. Anderson and R. Thorogood, photos by R. Thorogood). All nestlings were newly hatched (day 0–1), except (c) in which host nestlings were 4 days old. Lines in graphs are mean reflectance spectra (shaded areas are 95% CI) of the most common morph of nestlings of the shining-bronze cuckoo (red lines, bright morph in AU and NC, dark morph in NZ) and the respective host (blue lines, all bright morphs) from each region.

as the nestlings of each cuckoo subspecies appear more similar to their main hosts than they are to each other (Figures 2 and 3 and Supplementary Material).

3.2 | Polymorphism in host nestlings

One of the most intriguing aspects of the shining bronze-cuckoo – host systems is that hosts also have polymorphic nestlings with a common 'bright' and a rare 'dark' (melanic) morph (Figure 3). As with the cuckoo, polymorphism varies regionally: gerygone hosts from New Caledonia and New Zealand have polymorphic nestlings, whereas yellow-rumped thornbill nestlings from Australia are monomorphic (Figure 3). In addition, while the New Caledonian host is distinctly dimorphic, colour variation in the New Zealand host is less evident yet clearly noticeable to a human observer. In New Zealand, the two host nestling morphs progressively darken with age (Gill, 1983c), whereas in New Caledonia only the bright morph becomes progressively darker until the two morphs are indistinguishable from each other around the age of 9–10 days (Attisano et al., 2018). The two morphs of the New Caledonian host also have similar growth and survival rates, with no evident effect of skin coloration on nestling condition (Attisano et al., 2019).

The two nestling morphs can co-exist in the same brood (Gill, 1983c; Sato et al., 2015). The overall ratio of bright to dark host nestlings is similar in New Caledonia and New Zealand, but mixed broods are relatively more common in the New Zealand host and the brood coloration varies across sites within both regions (Table 1 and Supplementary material). At least for the New Caledonian host, extra-pair copulation does not influence the proportion of mixed broods (Bojarska et al., 2018) and population genetic analyses confirm that the observed host chick polymorphism does not diverge from a Hardy–Weinberg equilibrium, particularly when assuming a dominant dark-morph allele (Sato et al., 2015).

3.3 | Host defences at the nestling stage

In Australia, all cuckoo nestlings that hatched in nests of yellow-rumped thornbills evicted host eggs or nestlings and were reared by the hosts. There is thus no indication of discrimination of the parasite nestling (Table 1).

In New Zealand, a total of 20 cuckoo nestlings hatched in nests of grey warblers and evicted host eggs or nestlings, and 13 cuckoos were reared by the host (Table 1). Of the seven cuckoo nestlings that failed to fledge, four died from nest depredation but the cause of death of the other three cuckoo nestlings was uncertain. In one case, a cuckoo nestling was dead in the nest after a sudden change to cold and wet weather and with no signs of injury, however we cannot rule out that the death resulted from nest abandonment by host parents. Finally, two other nests, each previously containing a cuckoo nestling (3–7 days old), were found intact but empty at last inspection. It is possible that these nestlings were depredated by adult shining bronze-cuckoos (Briskie, 2007), but we also cannot exclude the possibility that host parents removed the parasite from the nest. In summary, field data show that the grey warbler host does not usually discriminate and eject the cuckoo nestling, but any rejection of the cuckoo nestling cannot yet be ruled out without an experiment manipulating nestling mimicry.

By contrast, in New Caledonia most cuckoo nestlings that hatched in fan-tailed gerygone nests were ejected by the host within 24–48 h from hatching before they could evict any host eggs or nestlings (Table 1). The discrimination ability of the host is very accurate: they ejected the parasite even when it was the only chick in the nest and never ejected host chicks in non-parasitised or parasitised nests (Attisano et al., 2018; Sato et al., 2015). Both parents can eject the parasite nestling: in three cases, this was the host mother, in another three cases the host father and in one case both parents seemingly collaborated in ejecting the parasite nestling. The parasite nestling was ejected whether or not it matched the host brood colour (Attisano et al., 2018; Sato et al., 2015). Field experiments show that nestling down, hatching order and begging calls might be more important cues for the recognition of the parasite than chick colour (Attisano, Sato, et al., 2021). Host acceptance of the shining bronze-cuckoo nestlings in New Caledonia is relatively low, as only 14% of the cuckoo hatchlings ($n = 28$) were accepted by the host parents, of which only two fledged (Table 1).

4 | DISCUSSION

4.1 | Host-specific lineages in the shining bronze-cuckoo

Chalcites bronze-cuckoos are already known for the exquisite mimicry exhibited by their nestlings (Langmore et al., 2011), but our synthesis adds a further level of complexity in these intriguing arms races by highlighting the remarkable phenotypic diversification of the shining bronze-cuckoo's nestlings across its range. The shining bronze-cuckoo is a specialist brood parasite of a small number of passerines, some of which discriminate and reject the parasite nestling. The choice of hosts might be constrained by their availability, for example only one host exists in New Caledonia and mainland New Zealand, by competition for hosts with other bronze-cuckoo species, for example between *C. minutillus* and *C. basalis* in Australia, or by specific habitat or diet requirements (Payne, 2005b). It is well known that discrimination of the parasite egg by the host can lead to parasite egg mimicry and diversification into host-egg-specific lineages (Abernathy & Liang, 2020; Gibbs et al., 2000; Spottiswoode et al., 2011; Starling et al., 2006). Therefore, the shining bronze-cuckoo – host systems fulfil the expectations of selection for the evolution of specialised host-specific lineages at the nestling stage of the arms race much in the same way that host discrimination drives parasite egg mimicry and diversification.

No study yet has looked at the genetic relationships among the shining bronze-cuckoo subspecies, whereas the population genetic structure and host-specific lineages of two closely related species, the Horsfield's bronze-cuckoo (*C. basalis*) and the little-bronze-cuckoo (*C. minutillus*), have received more attention. The Horsfield's bronze-cuckoo shows no evidence of host-specific diversification (Joseph et al., 2002). It has instead evolved a 'Jack-of-all-trades' strategy that appears to have relaxed selection for host-specific lineages: it has evolved an egg that is somewhat similar to the eggs of several hosts (Feeney et al., 2014), a two-tone nestling colour that is somewhat similar to nestlings of various hosts (Langmore et al., 2011) and a begging call that can be modified to match that of the relevant host (Langmore et al., 2008). Australian populations of the little bronze-cuckoo are not completely genetically separated (Joseph et al., 2011), but present nestling diversification that suggests the presence of host-specific lineages (McGill & Goddard, 1979). The shining bronze-cuckoo has a wider geographic range and subspecies that are spatially separated in distinct geographic regions, which could result in genetic isolation and a more marked differentiation than in other closely related species.

4.2 | Coevolutionary arms race and nestling polymorphism

Mimicry and host-specific lineages at the egg and nestling stages might be shaped by similar selective factors and have similar roles in the coevolutionary interactions between brood parasites and their hosts (Honza & Cherry, 2017; Tanaka, 2016). However, the role of nestling polymorphism in the arms race is not as clear as that of egg polymorphism. Nestling polymorphism is rare in birds (Kilner, 2006), whereas egg polymorphism is relatively common (Yang et al., 2020). A few studies have reported discrete polymorphism in melanin or carotenoid-based plumage coloration in older nestlings or juveniles (Galván et al., 2010; Kapun et al., 2011; Rohwer et al., 2012; Roulin et al., 2016), however, the case of shining bronze-cuckoos and their gerygone hosts is, to our knowledge, the only known example of discrete skin, but not plumage, polymorphism in hatchlings, and of nestling polymorphism occurring in both the brood parasite and the host.

Phenotypic diversification and polymorphism are known in brood parasites as a consequence of their parasitic habits (Medina & Langmore, 2015). The rare dark morph of the Australian cuckoo subspecies might indicate a specialisation to a host with unknown nestling colour (e. g. Tasmanian thornbill, *Acanthiza ewingii*). The

New Caledonian cuckoo subspecies started parasitising its single host within the last 1.7 my (Nyári & Joseph, 2012) and the nestling polymorphism might have originated before the separation from the Australian subspecies or have parallelly been developed in more recent times. The absence of polymorphism in the New Zealand cuckoo might be due to the loss of a second morph or because this was not observed during field studies due to small samples and its rarity. However, in all regions we found that nestlings of each cuckoo subspecies have a remarkable resemblance to the main host (Figures 2 and 3 and Supplementary Material). Furthermore, the common bright cuckoo morph in New Caledonia mimics several visual features of both host morphs (Attisano et al., 2018), which might indicate selection for an intermediate parasite morph similar to the intermediate egg and nestling phenotypes of the generalist common cuckoo (Stoddard & Stevens, 2010) and Horsfield's bronze-cuckoo (Feeney et al., 2014; Langmore et al., 2011). Such a strategy should return higher pay-offs due to the overall high frequency of bright host nestlings, of which the bright cuckoo is a closer match, and still offer some competitive advantage when the parasite does not match the host brood colour. Therefore, the rarity of the dark morphs in Australia and New Caledonia and the monomorphism in New Zealand might indicate selection towards improved mimicry of the host nestlings rather than polymorphism.

Host nestling polymorphism fits with theoretical predictions that offspring phenotypes dissimilar from the mimetic parasite should improve the capability for discrimination by the host (Takasu, 2003; Tanaka, 2016); however, the nestling phenotype might be a less reliable discrimination cue than the egg phenotype. First, the egg phenotype is maternally inherited (Gosler et al., 2000), whereas the nestling phenotype is a result of the genetic contribution of both parents (Roulin & Dijkstra, 2003). For example, in New Caledonia each adult host can experience a brood colour change across seasons due to partner replacement or extra-pair copulations (Bojarska et al., 2018), which also means that the frequency of mixed broods can be low but cannot reach zero in this host. Second, egg discrimination in rejector hosts is improved by increased within-nest uniformity and between-nest variability of egg phenotypes (Moskát et al., 2008; Stokke et al., 2002), however mixed broods of the two gerygone hosts challenge this assumption and should in theory lead to more recognition errors and rejection of own offspring by mistake. The frequency of mixed broods varies among and within regions which might suggest a disadvantage of mixed broods in areas with high parasitism pressure and thus selection for monomorphic broods of either morph. Third, the female is usually the sex responsible for the discrimination and rejection of the parasite egg as she can imprint on her own egg phenotype or compare the foreign egg with her own (Davies, 2015; Grim, 2017). However, in the fan-tailed gerygone both sexes can discriminate and eject the parasite nestling. Thus, imprinting on their own nestling phenotype is advantageous only if the pair produces the same nestling phenotype, which is not always the case in this host. Therefore, nestling coloration should not be the main cue for the discrimination of the parasite. Experimental evidence indeed shows that fan-tailed gerygones discriminate foreign nestlings mainly based on cues such as down feathers, hatching order and begging calls (Attisano, Sato, et al., 2021).

Nestling polymorphism might also be related to environmental factors, for example skin coloration might be influenced by UV radiation levels that are potentially harmful for the nestlings. Testing this hypothesis will require more work as little is known about the possible protective role of skin melanisation against UV radiation in nestlings (Galván & Solano, 2016). Melanisation is also linked to immune response and fitness in birds (Chakarov et al., 2008; Gangoso et al., 2015), however the condition of nestlings does seem to be unrelated to skin melanisation in the fan-tailed gerygone (Attisano et al., 2019). Further work is thus needed to understand if and how environmental factors and physiology contribute to nestling polymorphism in these host species.

In New Caledonia, nestling polymorphism might have decreased the rate of recognition errors of the parasite during early stages of the arms race. However, it gradually lost its importance as the main discrimination cue due to the cuckoo achieving improved mimicry and polymorphism, leading to a finer discrimination based on a combination of multiple cues (Attisano et al., 2018; Attisano, Sato, et al., 2021). Polymorphism can then persist in the host population because it bears no additional costs to nestling growth and survival. In New Zealand, the arms race might be at an early stage as the host morphs are not yet sufficiently dissimilar from the parasite nestling to allow host parents to reliably discriminate the parasite (Figure 3 and Supplementary Material). Further support for different evolutionary stages of the arms race also come from the fact that the cuckoo accurately mimics the begging calls of the grey warbler in New Zealand (Anderson et al., 2009; McLean & Waas, 1987; Ranjard et al., 2010), whereas the mimicry is imperfect in New Caledonia (Attisano, Sato, et al., 2021).

4.3 | Host defences at the nestling stage

The nestling mimicry by the Australian cuckoo subspecies suggests the possibility that a thornbill host was able to discriminate the parasite nestling at some point in the past but nowadays it can no longer accurately discriminate the parasite from its own chicks. Instead, it developed moderately effective anti-parasitism defences at the nest-building and egg stages (Medina & Langmore, 2016), which might have further relaxed selection for improved nestling recognition (Britton et al., 2007; Grim, 2006).

Besides the fan-tailed gerygone from New Caledonia, two other gerygone species from Australia, the large-billed *G. magnirostris* and the mangrove gerygone, *G. laevigaster*, which are parasitised by the little bronze-cuckoo, recognise and eject parasite nestlings (Sato, Tokue, et al., 2010; Tokue & Ueda, 2010). These three gerygone nestling ejector species belong to the same evolutionary branch (Nyári & Joseph, 2012), thus suggesting a common origin for this host defence behaviour. True recognition of the parasite occurs in the large-billed gerygone and fan-tailed gerygone hosts (Attisano, Sato, et al., 2021; Noh et al., 2018).

However large-billed gerygones sometimes eject their own nestlings by mistake (Noh et al., 2018; Sato, Tokue, et al., 2010; Tokue & Ueda, 2010), whereas fan-tailed gerygones do not (Attisano et al., 2018; Sato et al., 2015). The misrecognition errors of the large-billed gerygone host might depend on the fact that the little bronze-cuckoo is the gerygone specialist in Australia and nestling mimicry can be so accurate as to sometimes fool the host. On the other hand, the shining bronze-cuckoo is not a gerygone specialist in its Australian range meaning the fan-tailed gerygone might only be a suboptimal host, yet the only one building a dome-shaped nest in New Caledonia, and the less accurate mimicry allows the host to always recognise its own nestlings. The New Caledonian cuckoo subspecies is also a year-round resident; thus the parasitism pressure is evenly spread across the entire breeding season and the host cannot escape parasitism via changes in the breeding phenology. Coupled with the lack of effective defences at the egg laying stage, these factors might have strengthened selection for accurate nestling discrimination in the fan-tailed gerygone host.

The grey warbler from New Zealand is closely related to the three gerygone ejector species and separated from them about 100,000 years ago (Nyári & Joseph, 2012). Therefore, the arms race in New Zealand might be at a relatively early stage in which enough selective pressure promoted the parasite's visual and auditory mimicry but not nestling dimorphism and recognition of the parasite nestling by the host. It is also possible that grey warblers have some defences at the nestling stage that do not involve ejection of the parasite, for example they might abandon nests containing a single parasite nestling as other bronze-cuckoo hosts do (Langmore, Cockburn, et al., 2009), but our field evidence does not conclusively support this. Grey warblers also escape parasitism thanks to their breeding phenology as populations on the North Island and earlier breeders in the South Island of New Zealand suffer low parasitism rates (Anderson et al., 2013; Gill, 1983b). This might suggest relaxed selection for nestling discrimination in this host.

5 | CONCLUSIONS

The shining bronze-cuckoo – host systems are promising models for coevolutionary research as they can contribute to significant advancements of current theories of the nestling stage of the arms race. We suggest some possible research avenues that could contribute greatly to our understanding of these systems. First, there is the need to clarify the phylogenetic relationships within the shining bronze-cuckoo clade and understand if the variation in nestling appearance is due to the presence of host-specific lineages or to genetically distinct cuckoo species. Second, detailed field studies of other members of the *Gerygone* clade are needed to assess the variation in host defences and the occurrence of nestling polymorphism across members of the group. The ancestral nature of the parasite ejection behaviour can only be supported by confirming its occurrence in a larger number of *Gerygone* species. Additionally, gerygones show specialisation to different types of habitats over their wide geographic range (Keast & Recher, 1997), thus factors dependent on local ecological conditions (for example temperature, solar radiation or nest microclimate environment) could potentially influence the nestling phenotype. Therefore, gerygones are excellent models for comparative analyses of the wider ecological factors shaping the evolution of nestling polymorphism and defences at the nestling stage of the arms race. Third, the study of the genetic and physiological mechanisms underlying nestling skin polymorphism could help in understanding the selective factors contributing to the expression of the trait. Molecular (genomics, proteomics) and physiological (stress response assays) techniques have so far been employed in the study of nestling plumage polymorphism (Gangoso et al., 2015; Roulin & Dijkstra, 2003), yet no study has been published on species with skin polymorphic nestlings. Finally, a more careful investigation on the presence of nestling polymorphism in hosts, including those not belonging to the genus *Gerygone*, and non-hosts is also needed. Nestling polymorphism might have been overlooked due to an historical imbalance of studies focusing on the egg stage rather than the nestling stage of the arms race. Examples of host defences at the nestling stage have been found in multiple hosts (reviewed in Grim, 2017), thus researchers should be aware that nestling polymorphism could be a possible outcome of the arms race. At the same time, evidence of nestling polymorphism in non-hosts would allow to confirm or deny its role within an arms race and better understand its evolutionary causes.

AUTHOR CONTRIBUTIONS

Alfredo Attisano, Brian J. Gill, Michael G. Anderson, Roman Gula, Naomi E. Langmore, Nozomu J. Sato, Keita D. Tanaka, Rose Thorogood, Keisuke Ueda and Jörn Theuerkauf designed the studies; Alfredo Attisano, Brian J. Gill, Michael G. Anderson, Naomi E. Langmore, Yuji Okahisa, Nozomu J. Sato, Rose Thorogood collected the data; Alfredo Attisano led the writing of the manuscript; Alfredo Attisano, Brian J. Gill, Michael G. Anderson, Roman Gula, Naomi E. Langmore, Keita D. Tanaka, Rose Thorogood and Jörn Theuerkauf contributed to the writing; all authors gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

Data used to generate Figures 2 and 3 and additional figures and tables in the Supporting Information is available from Dryad Digital Repository https://doi.org/10.5061/dryad.95x69p8pf (Attisano et al., 2022).

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REFERENCES

Abernathy, V. E., & Liang, W. (2020). Empirical evidence of different egg morphs that match host eggs in the brush cuckoo (*Cacomantis variolosus*). *Emu - Austral Ornithology*, *120*(4), 322–332. https://doi.org/10.1080/01584197.2020.1856686

Anderson, M. G., Gill, B. J., Briskie, J. V., Brunton, D. H., & Hauber, M. E. (2013). Latitudinal differences in the breeding phenology of Grey Warblers covary with the prevalence of parasitism by Shining Bronze-Cuckoos. *Emu - Austral Ornithology*, *113*(2), 187–191. https://doi.org/10.1071/MU12086

Anderson, M. G., Ross, H. A., Brunton, D. H., & Hauber, M. E. (2009). Begging call matching between a specialist brood parasite and its host: A comparative approach to detect coevolution. *Biological Journal of the Linnean Society*, *98*(1), 208–216. https://doi.org/10.1111/j.1095-8312.2009.01256.x

Attisano, A., Gill, B. J., Anderson, M. G., Gula, R., Langmore, N. E., Okahisa, Y., Sato, N. J., Tanaka, K. D., Thorogood, R., & Theuerkauf, J. (2022). Data from: Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.95x69p8pf

Attisano, A., Groß, L. B., Sato, N. J., Okahisa, Y., Tanaka, K. D., Gula, R., Ueda, K., & Theuerkauf, J. (2020). Impact of brood parasitism and predation on nest survival of the fan-tailed gerygone in New Caledonia. *Journal of Avian Biology*, *51*(7), e02476. https://doi.org/10.1111/jav.02476

Attisano, A., Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021). Threat recognition and response in an avian brood-parasite host from New Caledonia. *Current Zoology*, *67*, 255–262. https://doi.org/10.1093/cz/zoaa061

Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-28710-5

Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Current Zoology*, *67*(6), 653–663. https://doi.org/10.1093/cz/zoab066

Attisano, A., Thiel, F., Sato, N., Okahisa, Y., Bolopo, D., Tanaka, K. D., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2019). Breeding biology of the fan-tailed gerygone *Gerygone flavolateralis* in relation to parasitism by the shining bronze-cuckoo *Chalcites lucidus*. *Journal of Ornithology*, *160*(1), 91–103. https://doi.org/10.1007/s10336-018-1592-6

Bojarska, K., Kuehn, R., Gazda, M. A., Sato, N. J., Okahisa, Y., Tanaka, K. D., Attisano, A., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Mating system and extra-pair paternity in the Fan-tailed Gerygone Gerygone flavolateralis in relation to parasitism by the Shining Bronze-cuckoo *Chalcites lucidus*. *PLoS ONE*, *13*(3), e0194059. https://doi.org/10.1371/journal.pone.0194059

Briskie, J. V. (2003). Frequency of egg rejection by potential hosts of the New Zealand cuckoos. *The Condor*, *105*, 719–727.

Briskie, J. V. (2007). Direct observations of shining cuckoos (*Chrysococcyx lucidus*) parasitising and depredating grey warbler (*Gerygone igata*) nests. *Notornis*, *54*, 15–19.

Britton, N. F., Planqué, R., & Franks, N. R. (2007). Evolution of defence portfolios in exploiter–victim systems. *Bulletin of Mathematical Biology*, *69*(3), 957–988. https://doi.org/10.1007/s11538-006-9178-5

Brooke, M. D. L., & Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, *335*(6191), 630–632. https://doi.org/10.1038/335630a0

Brooker, L. C., Brooker, M. G., & Brooker, A. M. H. (1990). An alternative population/genetics model for the evolution of egg mimesis and egg crypsis in cuckoos. *Journal of Theoretical Biology*, *146*(1), 123–143. https://doi.org/10.1016/S0022-5193(05)80048-7

Brooker, M. G., & Brooker, L. C. (1989a). The comparative breeding behaviour of two sympatric cuckoos, Horsfield's Bronze-Cuckoo Chrysococcyx basalis and the Shining Bronze-Cuckoo *C. lucidus*, in Western Australia: A new model for the evolution of egg morphology and host specificity in avian brood. *Ibis*, *131*(4), 528–547. https://doi.org/10.1111/j.1474-919X.1989.tb04789.x

Brooker, M. G., & Brooker, L. C. (1989b). Cuckoo hosts in Australia. *Australian Zoological Reviews*, *2*, 1–67.

Brooker, M. G., & Brooker, L. C. (1992). Evidence for individual female host specificity in two Australian Bronze-cuckoos (*Chrysococcyx* spp.). *Australian Journal of Zoology*, *40*, 485–493. https://doi.org/10.1071/ZO9920485

Caves, E. M., Stevens, M., Iversen, E. S., & Spottiswoode, C. N. (2015). Hosts of avian brood parasites have evolved egg signatures with elevated information content. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1810), 20150598. https://doi.org/10.1098/rspb.2015.0598

Chakarov, N., Boerner, M., & Krüger, O. (2008). Fitness in common buzzards at the cross-point of opposite melanin-parasite interactions. *Functional Ecology*, *22*(6), 1062–1069. https://doi.org/10.1111/j.1365-2435.2008.01460.x

Colombelli-Négrel, D., Hauber, M. E., Robertson, J., Sulloway, F. J., Hoi, H., Griggio, M., & Kleindorfer, S. (2012). Embryonic learning of vocal passwords in superb fairy-wrens reveals intruder cuckoo nestlings. *Current Biology*, *22*(22), 2155–2160. https://doi.org/10.1016/j.cub.2012.09.025

Cook, L. M., Grant, B. S., Saccheri, I. J., & Mallet, J. (2012). Selective bird predation on the peppered moth: The last experiment of Michael Majerus. *Biology Letters*, *8*(4), 609–612. https://doi.org/10.1098/rsbl.2011.1136

Davies, N. B. (2011). Cuckoo adaptations: Trickery and tuning. *Journal of Zoology*, *284*(1), 1–14. https://doi.org/10.1111/j.1469-7998.2011.00810.x

Davies, N. B. (2015). *Cuckoo: Cheating by nature*. Bloomsbury Publishing.

Davies, N. B., Brooke, M. D. L., & Kacelnik, A. (1996). Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *263*(1372), 925–931. https://doi.org/10.1098/rspb.1996.0137

Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *205*(1161), 489–511. https://doi.org/10.1098/rspb.1979.0081

De Mársico, M. C., Gantchoff, M. G., & Reboreda, J. C. (2012). Host–parasite coevolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1742), 3401–3408. https://doi.org/10.1098/rspb.2012.0612

Ebert, D. (2004). *Social behaviour and breeding biology of the yellow-rumped thornbill* (PhD thesis). Australian National University.

Feeney, W. E., Medina, I., Somveille, M., Heinsohn, R., Hall, M. L., Mulder, R. A., Stein, J. A., Kilner, R. M., & Langmore, N. E. (2013). Brood parasitism and the evolution of cooperative breeding in birds. *Science*, *342*(6165), 1506–1508. https://doi.org/10.1126/science.1240039

Feeney, W. E., Stoddard, M. C., Kilner, R. M., & Langmore, N. E. (2014). "Jack-of-all-trades" egg mimicry in the brood parasitic Horsfield's bronze-cuckoo? *Behavioral Ecology*, *25*(6), 1365–1373. https://doi.org/10.1093/beheco/aru133

Fell, H. B. (1947). The migration of the New Zealand bronze cuckoo, *Chalcites lucidus lucidus* (Gmelin). *Transactions of the Royal Society of New Zealand*, *76*, 504–515.

Friedman, H. (1968). *The evolutionary history of the avian genus Chrysococcyx*. Smithsonian Institution Press.

Galván, I., Gangoso, L., Grande, J. M., Negro, J. J., Rodríguez, A., Figuerola, J., & Alonso-Alvarez, C. (2010). Antioxidant machinery differs between melanic and light nestlings of two polymorphic raptors. *PLoS ONE*, *5*(10), e13369. https://doi.org/10.1371/journal.pone.0013369

Galván, I., & Solano, F. (2016). Bird integumentary melanins: Biosynthesis, forms, function and evolution. *International Journal of Molecular Sciences*, *17*(4), 520. https://doi.org/10.3390/ijms17040520

Gangoso, L., Roulin, A., Ducrest, A.-L., Grande, J. M., & Figuerola, J. (2015). Morph-specific genetic and environmental variation in innate and acquired immune response in a color polymorphic raptor. *Oecologia*, *178*(4), 1113–1123. https://doi.org/10.1007/s00442-015-3306-6

Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M.d. L., Davies, N. B., & Nakamura, H. (2000). Genetic evidence for female host- specific races of the common cuckoo. *Nature*, *407*, 183–186. https://doi.org/10.1038/35025058

Gill, B. J. (1982). Breeding of the grey warbler Gerygone igata at Kaikoura, New Zealand. *Ibis*, *124*(2), 123–147. https://doi.org/10.1111/j.1474-919X.1982.tb03752.x

Gill, B. J. (1983a). Morphology and migration of *Chrysococcyx lucidus*, an Australasian cuckoo. *New Zealand Journal of Zoology*, *10*(4), 371–381. https://doi.org/10.1080/03014223.1983.10423932

Gill, B. J. (1983b). Brood-parasitism by the Shining Cuckoo *Chrysococcyx lucidus* at Kaikoura. *New Zealand. Ibis*, *125*(1), 40–55. https://doi.org/10.1111/j.1474-919X.1983.tb03082.x

Gill, B. J. (1983c). Breeding habits of the Grey Warbler (*Gerygone igata*). *Notornis*, *30*(2), 137–165.

Gill, B. J. (1998). Behavior and ecology of the shining cuckoo *Chrysococcyx lucidus*. In S. I. Rothstein & S. K. Robinson (Eds.), *Parasitic birds and their hosts. Studies in coevolution* (pp. 143–151). Oxford University Press.

Gloag, R., Keller, L. A., & Langmore, N. E. (2014). Cryptic cuckoo eggs hide from competing cuckoos. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1792), 20141014. https://doi.org/10.1098/rspb.2014.1014

Gosler, A. G., Barnett, P. R., & James Reynolds, S. (2000). Inheritance and variation in eggshell patterning in the great tit *Parus major*. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1461), 2469–2473. https://doi.org/10.1098/rspb.2000.1307

Grim, T. (2006). The evolution of nestling discrimination by hosts of parasitic birds: Why is rejection so rare? *Evolutionary Ecology Research*, *8*, 785–802.

Grim, T. (2011). Ejecting chick cheats: A changing paradigm? *Frontiers in Zoology*, *8*(1), 14. https://doi.org/10.1186/1742-9994-8-14

Grim, T. (2017). Host defence against brood parasite nestlings: Theoretical expectations and empirical evidence. In M. Soler (Ed.), *Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 539–556). Springer International Publishing.

Grim, T., Kleven, O., & Mikulica, O. (2003). Nestling discrimination without recognition: A possible defence mechanism for hosts towards cuckoo parasitism? *Biology Letters*, *270*, S73–S75. https://doi.org/10.1098/rsbl.2003.0017

Guigueno, M. F., Sealy, S. G., & Westphal, A. M. (2014). Rejection of parasitic eggs in passerine hosts: Size matters more for a non-ejecter. *The Auk*, *131*(4), 583–594. https://doi.org/10.1642/AUK-14-36.1

Hauber, M. E., & Kilner, R. M. (2007). Coevolution, communication, and host chick mimicry in parasitic finches: Who mimics whom? *Behavioral Ecology and Sociobiology*, *61*(4), 497–503. https://doi.org/10.1007/s00265-006-0291-0

Honza, M., & Cherry, M. (2017). Egg characteristics affecting egg rejection. In *Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 401–419). Springer International Publishing.

Honza, M., Šicha, V., Procházka, P., & Ležalová, R. (2006). Host nest defense against a color-dimorphic brood parasite: Great reed warblers (*Acrocephalus arundinaceus*) versus common cuckoos (*Cuculus canorus*). *Journal of Ornithology*, *4*(147), 629–637. https://doi.org/10.1007/s10336-006-0088-y

Jamie, G. A., Belleghem, S. M. V., Hogan, B. G., Hamama, S., Moya, C., Troscianko, J., Stoddard, M. C., Kilner, R. M., & Spottiswoode, C. N. (2020). Multimodal mimicry of hosts in a radiation of parasitic finches. *Evolution*, *74*(11), 2526–2538. https://doi.org/10.1111/evo.14057

Joseph, L., Wilke, T., & Alpers, D. (2002). Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-Cuckoo Chalcites basalis of Australia. *Molecular Ecology*, *11*(4), 829–837. https://doi.org/10.1046/j.1365-294X.2002.01481.x

Joseph, L., Zeriga, T., Adcock, G. J., & Langmore, N. E. (2011). Phylogeography and taxonomy of the Little Bronze-Cuckoo (*Chalcites minutillus*) in Australia's monsoon tropics. *Emu*, *111*(2), 113–119. https://doi.org/10.1071/MU10050

Kapun, M., Darolová, A., Krištofik, J., Mahr, K., & Hoi, H. (2011). Distinct colour morphs in nestling European Bee-eaters Merops apiaster: Is there an adaptive value? *Journal of Ornithology*, *152*(4), 1001–1005. https://doi.org/10.1007/s10336-011-0688-z

Keast, A., & Recher, H. F. (1997). The adaptive zone of the genus Gerygone (Acanthizidae) as shown by morphology and feeding habits. *Emu - Austral Ornithology*, *97*(1), 1–17. https://doi.org/10.1071/MU97001

Kennerley, J. A., Somveille, M., Hauber, M. E., Richardson, N. M., Manica, A., & Feeney, W. E. (2022). The overlooked complexity of avian brood parasite–host relationships. *Ecology Letters*, *25*(8), 1889–1904. https://doi.org/10.1111/ele.14062

Kilner, R. M. (2006). Function and evolution of color in young birds. In G. E. Hill & M. G. KJ (Eds.), *Bird coloration volume II: Function and evolution* (pp. 201–232). Harvard University Press.

Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature*, *397*(6721), 667–672. https://doi.org/10.1038/17746

Krüger, O., & Davies, N. B. (2002). The evolution of cuckoo parasitism: A comparative analysis. *Proceedings of the Royal Society of London*.

Series B: Biological Sciences, *269*(1489), 375–381. https://doi.org/10.1098/rspb.2001.1887

Langmore, N. E., Cockburn, A., Russell, A. F., & Kilner, R. M. (2009). Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behavioral Ecology*, *20*(5), 978–984. https://doi.org/10.1093/beheco/arp086

Langmore, N. E., Hunt, S., & Kilner, R. M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*, *422*(6928), 157–160. https://doi.org/10.1038/nature01460

Langmore, N. E., & Kilner, R. M. (2007). Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalis*. *Animal Behaviour*, *74*(4), 995–1004. https://doi.org/10.1016/j.anbehav.2007.02.028

Langmore, N. E., Kilner, R. M., Butchart, S. H. M., Maurer, G., Davies, N. B., Cockburn, A., Macgregor, N. A., Peters, A., Magrath, M. J. L., & Dowling, D. K. (2005). The evolution of egg rejection by cuckoo hosts in Australia and Europe. *Behavioral Ecology*, *16*(4), 686–692. https://doi.org/10.1093/beheco/ari041

Langmore, N. E., Maurer, G., Adcock, G. J., & Kilner, R. M. (2008). Socially aquired host-specific mimicry and the evolution of host races in Horsfield's bronze cuckoo *Chalcites basalis*. *Evolution*, *62*(7), 1689–1699. https://doi.org/10.1111/j.1558-5646.2008.00405.x

Langmore, N. E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M. L., Peters, A., & Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), 2455–2463. https://doi.org/10.1098/rspb.2010.2391

Langmore, N. E., Stevens, M., Maurer, G., & Kilner, R. M. (2009). Are dark cuckoo eggs cryptic in host nests? *Animal Behaviour*, *78*(2), 461–468. https://doi.org/10.1016/j.anbehav.2009.06.003

Liang, W., Yang, C., & Takasu, F. (2017). How can distinct egg polymorphism be maintained in the rufescent prinia (*Prinia rufescens*)-plaintive cuckoo (*Cacomantis merulinus*) interaction-a modeling approach. *Ecology and Evolution*, *7*(15), 5613–5620. https://doi.org/10.1002/ece3.3090

Lotem, A. (1993). Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature*, *362*, 743–745. https://doi.org/10.1038/362743a0

Louder, M. I. M., Hauber, M. E., Louder, A. N. A., Hoover, J. P., & Schelsky, W. M. (2019). Greater opportunities for sexual selection in male than in female obligate brood parasitic birds. *Journal of Evolutionary Biology*, *32*(11), 1310–1315. https://doi.org/10.1111/jeb.13537

Mappes, J., & Lindström, L. (2012). How did the cuckoo get its polymorphic plumage? *Science*, *337*(6094), 532–533. https://doi.org/10.1126/science.1225997

McGill, I., & Goddard, M. (1979). The little bronze-cuckoo in New South Wales. *Australian Birds*, *14*, 23–24.

McLean, I. G., & Waas, J. R. (1987). Do cuckoo chicks mimic the begging calls of their hosts? *Animal Behaviour*, *35*(6), 1896–1898. https://doi.org/10.1016/S0003-3472(87)80083-0

Medina, I., Kilner, R. M., & Langmore, N. E. (2020). From micro- to macroevolution: Brood parasitism as a driver of phenotypic diversity in birds. *Current Zoology*, *66*(5), 515–526. https://doi.org/10.1093/cz/zoaa033

Medina, I., & Langmore, N. E. (2015). The costs of avian brood parasitism explain variation in egg rejection behaviour in hosts. *Biology Letters*, *11*(7), 20150296. https://doi.org/10.1098/rsbl.2015.0296

Medina, I., & Langmore, N. E. (2016). Batten down the thatches: Front-line defences in an apparently defenceless cuckoo host. *Animal Behaviour*, *112*, 195–201. https://doi.org/10.1016/j.anbehav.2015.12.006

Medina, I., & Langmore, N. E. (2019). Nest illumination and the evolution of egg rejection in hosts of brood parasites. *The Auk*, *136*(1), 1–6. https://doi.org/10.1093/auk/uky002

Moksnes, A., Røskaft, E., & Braa, A. T. (1991). Rejection behavior by common cuckoo hosts towards artificial brood parasite eggs. *The Auk*, *108*(2), 348–354. https://doi.org/10.1093/auk/108.2.348

Moskát, C., Avilés, J. M., Bán, M., Hargitai, R., & Zölei, A. (2008). Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behavioral Ecology and Sociobiology*, *62*(12), 1885–1890. https://doi.org/10.1007/s00265-008-0618-0

Noh, H. J., Gloag, R., & Langmore, N. E. (2018). True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20180726. https://doi.org/10.1098/rspb.2018.0726

Noh, H.-J., Gloag, R., Leitão, A. V., & Langmore, N. E. (2021). Imperfect mimicry of host begging calls by a brood parasitic cuckoo: A cue for nestling rejection by hosts? *Current Zoology*, *67*(6), 665–674. https://doi.org/10.1093/cz/zoab056

Noske, R. (2019). New Zealand shining bronze-cuckoo *Chalcites lucidus* are regular visitors to Southeast Queensland. *The Sunbird*, *48*, 149–158.

Nyári, Á. S., & Joseph, L. (2012). Evolution in Australasian mangrove forests: Multilocus phylogenetic analysis of the Gerygone warblers (Aves: Acanthizidae). *PLoS ONE*, *7*(2), e31840. https://doi.org/10.1371/journal.pone.0031840

Øien, I., Moksnes, A., & Røskaft, E. (1995). Evolution of variation in egg color and marking pattern in European passerines: Adaptations in a coevolutionary arms race with the cuckoo, *Cuculus canorus*. *Behavioral Ecology*, *6*, 166–174. https://doi.org/10.1093/beheco/6.2.166

Payne, R. B. (2005a). Nestling mouth markings and colors of Old World finches Estrildidae: Mimicry and coevolution of nesting finches and their Vidua brood parasites. Miscellaneous Publications, Museum of Zoology, University of Michigan, no. 194, Ann Arbor.

Payne, R. B. (2005b). *The cuckoos*. OUP Oxford.

Ranjard, L., Anderson, M. G., Rayner, M. J., Payne, R. B., McLean, I., Briskie, J. V., Ross, H. A., Brunton, D. H., Woolley, S. M. N., & Hauber, M. E. (2010). Bioacoustic distances between the begging calls of brood parasites and their host species: A comparison of metrics and techniques. *Behavioral Ecology and Sociobiology*, *64*(11), 1915–1926. https://doi.org/10.1007/s00265-010-1065-2

Rasmussen, J. L., Underwood, T. J., & Sealy, S. G. (2010). Functional morphology as a barrier to the evolution of grasp-ejection in hosts of the Brown-headed Cowbird (*Molothrus ater*). *Canadian Journal of Zoology*, *88*(12), 1210–1217. https://doi.org/10.1139/Z10-088

Rohwer, V. G., Bonier, F., & Martin, P. R. (2012). Juvenal plumage polymorphism in Yellow Warblers is not associated with sex. *The Condor*, *114*(2), 407–411. https://doi.org/10.1525/cond.2012.110086

Roulin, A., & Dijkstra, C. (2003). Genetic and environmental components of variation in eumelanin and phaeomelanin sex-traits in the barn owl. *Heredity*, *90*(5), 359–364. https://doi.org/10.1038/sj.hdy.6800260

Roulin, A., Monstiers, B. D., Ifrid, E., Silva, A. D., Genzoni, E., & Dreiss, A. N. (2016). Reciprocal preening and food sharing in colour-polymorphic nestling barn owls. *Journal of Evolutionary Biology*, *29*(2), 380–394. https://doi.org/10.1111/jeb.12793

Ruiz-Raya, F., & Soler, M. (2020). Signal detection and optimal acceptance thresholds in avian brood parasite–host systems: Implications for egg rejection. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*(1802), 20190477. https://doi.org/10.1098/rstb.2019.0477

Sato, N. J., Mikami, O. K., & Ueda, K. (2010). The egg dilution effect hypothesis: A condition under which parasitic nestling ejection behaviour will evolve. *Ornithological Science*, *9*(2), 115–121. https://doi.org/10.2326/osj.9.115

Sato, N. J., Tanaka, K. D., Okahisa, Y., Yamamichi, M., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2015). Nestling polymorphism in a cuckoo-host system. *Current Biology*, *25*(24), R1164–R1165. https://doi.org/10.1016/j.cub.2015.11.028

Sato, N. J., Tokue, K., Noske, R. A., Mikami, O. K., & Ueda, K. (2010). Evicting cuckoo nestlings from the nest: A new anti-parasitism behaviour. *Biology Letters*, *6*(1), 67–69. https://doi.org/10.1098/rsbl.2009.0540

Schuetz, J. G. (2005a). Reduced growth but not survival of chicks with altered gape patterns: Implications for the evolution of nestling similarity in a parasitic finch. *Animal Behaviour*, *70*(4), 839–848. https://doi.org/10.1016/j.anbehav.2005.01.007

Schuetz, J. G. (2005b). Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of defences against parasitism. *Evolution*, *59*(9), 2017–2024. https://doi.org/10.1111/j.0014-3820.2005.tb01070.x

Soler, J. J., & Møller, A. P. (1996). A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behavioral Ecology*, *7*(1), 89–94. https://doi.org/10.1093/beheco/7.1.89

Soler, M. (2017). *Avian brood parasitism: Behaviour, ecology, evolution and coevolution*. Springer International Publishing.

Spottiswoode, C. N., & Stevens, M. (2011). How to evade a coevolving brood parasite: Egg discrimination versus egg variability as host defences. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1724), 3566–3573. https://doi.org/10.1098/rspb.2011.0401

Spottiswoode, C. N., & Stevens, M. (2012). Host-parasite arms races and rapid changes in bird egg appearance. *The American Naturalist*, *179*(5), 633–648. https://doi.org/10.1086/665031

Spottiswoode, C. N., Stryjewski, K. F., Quader, S., Colebrook-Robjent, J. F. R., & Sorenson, M. D. (2011). Ancient host specificity within a single species of brood parasitic bird. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(43), 17738–17742. https://doi.org/10.1073/pnas.1109630108

Starling, M., Heinsohn, R., Cockburn, A., & Langmore, N. E. (2006). Cryptic gentes revealed in pallid cuckoos *Cuculus pallidus* using reflectance spectrophotometry. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1596), 1929–1934. https://doi.org/10.1098/rspb.2006.3490

Stoddard, M. C., & Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1686), 1387–1393. https://doi.org/10.1098/rspb.2009.2018

Stokke, B. G., Moksnes, A., & Røskaft, E. (2002). Obligate brood parasites as selective agents for evolution of egg appearance in passerine birds. *Evolution*, *56*(1), 199–205. https://doi.org/10.1111/j.0014-3820.2002.tb00861.x

Takahashi, Y., Yoshimura, J., Morita, S., & Watanabe, M. (2010). Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution*, *64*(12), 3620–3628. https://doi.org/10.1111/j.1558-5646.2010.01083.x

Takasu, F. (2003). Co-evolutionary dynamics of egg appearance in avian brood parasitism. *Evolutionary Ecology Research*, *5*(3), 345–362.

Tanaka, K. D. (2016). Polymorphism in avian brood parasitism: A coevolutionary perspective. *Ornithological Science*, *15*(2), 133–140. https://doi.org/10.2326/osj.15.133

Thorogood, R., & Davies, N. B. (2012). Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science*, *337*(6094), 578–580. https://doi.org/10.1126/science.1220759

Thorogood, R., & Davies, N. B. (2013). Hawk mimicry and the evolution of polymorphic cuckoos. *Chinese Birds*, *4*(1), 39–50. https://doi.org/10.5122/cbirds.2013.0002

Thorogood, R., Kilner, R. M., & Rasmussen, J. L. (2017). Grey Gerygone hosts are not egg rejecters, but Shining Bronze-Cuckoos lay cryptic eggs. *The Auk*, *134*(2), 340–349. https://doi.org/10.1642/AUK-16-128.1

Tokue, K., & Ueda, K. (2010). Mangrove gerygones Gerygone laevigaster eject little bronze-cuckoo *Chalcites minutillus* hatchlings from parasitized nests. *Ibis*, *152*(4), 835–839. https://doi.org/10.1111/j.1474-919X.2010.01056.x

Trnka, A., & Grim, T. (2013). Color plumage polymorphism and predator mimicry in brood parasites. *Frontiers in Zoology*, *10*(1), 25. https://doi.org/10.1186/1742-9994-10-25

Vamosi, S. M. (2011). On the role of enemies in divergence and diversification of prey: A review and synthesis. *Canadian Journal of Zoology*, *83*, 894–910. https://doi.org/10.1139/z05-063

Yang, C., Li, Z., Zhang, Y., Wang, H., Liang, W., & Møller, A. P. (2016). Egg polymorphism and egg discrimination in the Daurian Redstart *Phoenicurus auroreus*, a host of the Common Cuckoo *Cuculus canorus*. *Ornithological Science*, *15*(2), 127–132. https://doi.org/10.2326/osj.15.127

Yang, C., Si, X., Liang, W., & Møller, A. P. (2020). Spatial variation in egg polymorphism among cuckoo hosts across 4 continents. *Current Zoology*, *66*(5), 477–483. https://doi.org/10.1093/cz/zoaa011

Yoder, J. B., & Nuismer, S. L. (2010). When does coevolution promote diversification? *The American Naturalist*, *176*(6), 802–817. https://doi.org/10.1086/657048

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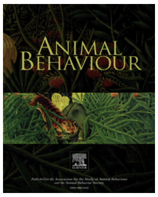

Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo, *Chalcites lucidus*

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Antagonistic coevolutionary interactions between avian brood parasites and their hosts can lead to selection for the discrimination of parasites by their host via visual or acoustic signals. Therefore, nestlings of some brood parasites may be under selection to evolve visual and vocal mimicry of host nestlings to avoid discrimination by host parents. Some brood parasites diversify into host-specific populations by mimicking visual features of the host offspring (either eggs or nestlings). However, whether a similar mechanism applies to the begging calls of their hosts remains unclear. In this study, we analysed the begging calls of three subspecies of the shining bronze-cuckoo, which present visual mimicry of three different host species (family Acanthizidae) that vary in their ability to discriminate parasite nestlings. We found that the begging calls of each cuckoo subspecies match the respective host more closely than any of the other cuckoo subspecies. Therefore, selection for coevolutionary diversification appears to overcome phylogenetic constraints on cuckoo begging call structure. The coevolutionary interactions in these parasite–host systems have promoted the selection for refined host mimicry by the cuckoo and the formation of geographically isolated evolutionary units across the range of the species.

Obligate avian brood parasites lay their eggs in nests of other species, their hosts, which are left to care for foreign nestlings, thereby incurring high fitness costs (Soler, 2017a). Hosts and parasites can be involved in a coevolutionary arms race in which host discrimination of the parasite can lead to adaptations by the parasite to exploit the host, followed by adaptations by the host to avoid parasitism (Davies, 2011; Dawkins & Krebs, 1979). Agonistic interactions within the arms race can occur at all stages of the host breeding cycle, starting from before the parasites laid eggs to the fledging stage (Soler, 2017a). These agonistic coevolutionary interactions can lead to phenotypic diversification (Langmore et al., 2024), and several studies have shown that the arms race has promoted phenotypic diversification in several aspects of the biology of hosts and parasites (Medina et al., 2020). Still little is know about diversification occurring at the nestling stage, as this has received relatively little attention compared to other stages of the host breeding cycle (Grim, 2017). However, in a few host–parasite systems, the arms race has reached remarkable levels of sophistication in the ability of hosts to discriminate parasite nestlings and in the ability of parasites to accurately mimic young hosts (Attisano et al., 2023; De Mársico et al., 2019; Jamie et al., 2020; Langmore et al., 2003; Sato et al., 2015).

Begging by nestlings plays a fundamental role in offspring–parent communication by signalling nestling needs, thereby influencing parental provisioning (Kilner, 2002). Nestlings of brood parasites can break into this communication system by either exploiting host preferences for certain nestling signals such as loud begging or by mimicking the structure of the host begging calls (Soler, 2017b). The selective factors determining the strategy of parasites depend on the lifestyle of parasites and the ability of hosts to discriminate the parasite nestling (Jamie & Kilner, 2017). Nestlings of generalist brood parasites exploiting non-discriminating hosts produce exaggerated begging calls that tune into the foster parents' sensorial biases of providing food to chicks with a larger size or louder calls, for example, common cuckoo, *Cuculus canorus* (Kilner et al., 1999; Samaš et al., 2020), great spotted cuckoo, *Clamator glandarius* (Roldán et al.,

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2013), or shiny cowbird, *Molothrus bonariensis* (Gloag & Kacelnik, 2013; Tuero et al., 2016). Nestlings of specialist brood parasites exploiting discriminating hosts produce begging calls mimicking host calls, thereby tricking the foster parents into accepting and feeding the parasite chick as one of their own, for example, bronze-cuckoos, *Chalcites* spp. (Anderson et al., 2009; Attisano et al., 2021; Langmore et al., 2008; Noh et al., 2021), and screaming cowbird, *Molothrus rufoaxillaris* (Lama et al., 2022; Ursino et al., 2018). By contrast, in brood parasitic *Vidua* finches, host parents do not discriminate the parasite (Schuetz, 2005), yet parasite nestlings mimic the begging behaviour of the host (Jamie et al., 2020). In these systems, mimicry might have resulted from nestling competition for parental provisioning rather than a coevolutionary arms race between the host and the parasite (Hauber & Kilner, 2007).

Whether begging calls of nestlings of different host races of a parasite match those of the specific hosts and if this variation represents host specialization remain unknown (Wang et al., 2020). The common cuckoo has host races with distinct eggs matching those of the specific hosts they parasitize (Gibbs et al., 2000; Stoddard & Stevens, 2010). However, nestlings of these host races do not match the begging calls of their hosts, thereby showing no host-race specialization of begging calls (Samaš et al., 2020). On the contrary, common cuckoo nestlings maximize parental provisioning by producing calls that are always exaggerated regardless of the host size or species (Kilner et al., 1999; Soler, 2017b). Similarly, the begging calls of the nestlings of great spotted cuckoo, a specialist parasite of Corvidae, do not match the begging calls of different hosts by which they are raised (magpie, *Pica pica*, carrion crow, *Corvus corone*, or jackdaw, *Corvus monedula*). However, they adjusted their call rate to maximize the provisioning rate from foster parents (Roldán et al., 2013).

Bronze-cuckoos and their hosts (family Maluridae and Acanthizidae) from Australasia and SE Asia are the best examples of an arms race at the nestling stage. In these systems, bronze-cuckoo nestlings evict the host eggs or young and monopolize the nest; however, some hosts discriminate and reject the parasite nestlings, thereby promoting selection for visual (Attisano et al., 2018; Langmore, et al., 2011; Noh et al., 2018) and vocal mimicry (Anderson et al., 2009; Attisano et al., 2021; Langmore et al., 2003, 2008; Noh et al., 2021) of the host nestlings by the parasite nestlings. In this group, we found examples of begging call mimicry by generalist and specialist brood parasites. The Horsfield's bronze-cuckoo *Chalcites basalis* is a generalist parasite that uses Maluridae as primary hosts and Acanthizidae as secondary ones (Payne, 2005). The cuckoo nestlings innately produce begging calls mimicking those of the primary host, the superb fairywren, *Malurus cyaneus*. However, if they find themselves in nests of a secondary host, the buff-rumped thornbill, *Acanthiza reguloides*, they can modify their calls to match those of the new host (Langmore et al., 2008). This process involves social shaping by the host parents with the cuckoo modifying call features that increase the likelihood of obtaining food from the host (Langmore et al., 2008). This plasticity in begging calls might reduce selection for host-race formation, which is supported by the lack of a phylogenetic structure of the Australian population of Horsfield's bronze-cuckoo (Joseph et al., 2002). By contrast, the little bronze-cuckoo, *Chalcites minutillus* is a specialist parasite that exploits several species of *Gerygone* hosts across its range (Noh et al., 2021; Payne, 2005). Recent evidence demonstrates that this species selection for mimicry of host nestlings has driven genetic and phenotypic divergence corresponding to host preference (Langmore et al., 2024). Consequently, nestling phenotypes of little bronze-cuckoo subspecies track divergent host nestling morphologies across their geographical range (Langmore et al., 2024). The nestlings of little bronze-cuckoo appear to be specialists, not only with regard to visual mimicry, but also in terms of vocal mimicry; they produce begging calls that match those of their main host, the large-billed gerygone, *Gerygone magnirostris*. However, unlike the Horsfield's bronze-cuckoo, their begging calls are not altered when raised by a secondary host, which suggests a fixed development of the calls (Noh et al., 2021).

The shining bronze-cuckoo has the widest distribution across the Australasian region from New Zealand to New Guinea (Payne, 2005). To date, no study has looked at the genetic relationships among subspecies; however, some cuckoo subspecies match the visual features of the nestlings of the main hosts across their geographical range: the fan-tailed gerygone, *Gerygone flavolateralis*, in New Caledonia, the grey warbler, *Gerygone igata*, in New Zealand and the yellow-rumped thornbill, *A. chrysorrhoa* in Australia (Attisano et al., 2023; Langmore et al., 2024). Compared with the hosts from Australia and New Zealand (Attisano et al., 2023), the host from New Caledonia rejects cuckoo nestlings (Attisano et al., 2023; Sato et al., 2015). The begging calls of shining bronze-cuckoo nestlings also match those of the two gerygone hosts in New Caledonia and New Zealand (Anderson et al., 2009; Attisano et al., 2021). However, it is unclear whether the call matching occurs only in relation to these two closely related gerygone hosts or is rather a general pattern resulting from selection for host specialisation of each cuckoo subspecies, similar to the selection for visual mimicry found across the range.

In this study, we investigated if nestlings of the three subspecies of shining bronze-cuckoo from Australia (*C. l. plagosus*), New Caledonia (*C. l. layardi*) and New Zealand (*C. l. lucidus*) present mimicry of begging calls of their respective hosts. We expect that the begging calls of each cuckoo subspecies of each cuckoo subspecies should match the local host more closely than the other hosts or cuckoo subspecies from other regions. Overall, the begging call structure should reflect coevolutionary interactions rather than the phylogeny of the cuckoo subspecies. Moreover, accurate matching of the host begging calls by cuckoo should increase the chances of recognition errors, thereby decreasing or eliminating rejection of the cuckoo nestlings by the host. Therefore, cuckoo nestlings likely match the begging calls of the non-rejecter hosts in Australia and New Zealand more closely than the rejecter host from New Caledonia. Finally, closely related hosts likely have higher similarity in their begging calls. Consequently, cuckoo subspecies parasitizing these hosts should have begging calls that are more similar to one another. Therefore, the begging calls of the two shining bronze-cuckoo subspecies exploiting gerygone hosts should be more similar to each other than to the begging calls of the subspecies exploiting the thornbill host.

METHODS

The begging calls of three shining bronze-cuckoo subspecies and their respective hosts from Australia, New Caledonia and New Zealand were recorded from July to January, which corresponds to the breeding season of hosts and cuckoos in the Australasian region (Attisano et al., 2023). The active nests at our field sites were regularly monitored at 2-day intervals, thereby recording the laying, hatching and fledging dates with a precision of 2 days. The timing was assessed as the average between two nest checks, thereby resulting in an uncertainty of ±1 day. Begging calls were recorded from 2005 to 2009 in an open eucalypt woodland in Australia (Campbell Park, 35°16′S, 149°10′E), from 2005 to 2007 in forest and scrub areas in New Zealand (Tawharanui Regional Park, North Island: 36°22′S, 174°50′E) and from 2015 to 2023 at three sites on the main island (Grande Terre) of New Caledonia in rainforest (Parc Provincial des Grandes Fougères, 21°39′S, 165°46′E), open forest, thickets (Farino and surrounding, 21°40′S, 165°46′E), open dry forest and savannah (Domaine de Deva, 21°36′S, 165°24′E). Field methods to monitor host nests and cuckoo breeding are described elsewhere (Anderson et al., 2013; Attisano et al., 2019; Medina & Langmore, 2019).

A total of 23 recordings were collected from 14 cuckoo nestlings aged between 3 and 14 days: 10 recordings from 8 *C. l. plagosus* from Australia (AU_parasite) and 13 recordings from 6 *C. l. layardii* from New Caledonia (NC_parasite). We could not record young cuckoo nestlings *C. l. lucidus* in New Zealand (NZ_parasite), but we included four recordings from one 19-day-old cuckoo nestling and three 20-day-old cuckoo fledglings (recorded on the fledging day). Shining bronze cuckoos young fledge around 20 days after hatching and remain close to the nest for at least 1—2 days while being fed by host parents (Gill, 1983; Attisano et al., 2023). Preliminary visual analysis of the spectrograms of the begging call recorded from these young cuckoos revealed close similarity in call structure among these cuckoos and with host nestlings aged 10—12 days (Supplementary material, Fig. S3). Two other studies found a strong similarity in call structure of young cuckoo fledging with younger host nestlings in New Zealand (Anderson et al., 2009; Ranjard et al., 2010). Therefore, if call mimicry of the host by NZ_parasite occurred, we expected to be able to detect it by comparing the begging calls of 19 - 20-day-old New Zealand cuckoos with younger host nestlings. A total of 32 recordings of host nestlings were collected from 23 nests, with each nest containing 1—3 host nestlings: 8 recordings from 7 nests of yellow-rumped thornbills containing chicks aged 3—12 days (AU_host), 18 recordings from 11 nests of fan-tailed gerygone containing chicks aged 3—11 days (NC_host) and 6 recordings from 6 nests of grey warbler containing chicks aged 8—12 days (NZ_host). In Australia, begging calls were recorded for 20 min using a Sony tie-clip miniature microphone (ECM T6) and a digital recorder (TASCAM DR-05). The microphone was clipped to vegetation approximately 20 cm from the nest entrance. In New Caledonia, nestlings were recorded using a digital recorder (Tascam DR-40) and a condenser microphone (Shure SM93), placed at the bottom of the nest 1—3 cm from the internal incubation chamber at multiple feeding events during 2—3 h of recording sessions. In New Zealand, nestling begging calls were recorded using a Sennheiser ME 66 microphone or a Panasonic RP-VC201 stereo tie-clip microphone, depending on nest accessibility, onto a Sony MZ-NH700 Hi-MD Minidisc. Young cuckoo fledglings were recorded using the Sennheiser ME66 directional microphone, while being fed by their host parents outside the nest. We measured only robust spectrogram-based features (see measurements below) from the recordings, therefore it is unlikely that the use of different recorders introduced biases or artefacts in the analyses.

Preliminary visual analysis of the spectrograms (settings: Hann window, 3 dB bandwidth 135 Hz, 90% overlap, hop size 51 samples, DFT 512 samples) showed that cuckoo and host nestlings aged 3—6 days produced short and high-pitched peeps, which then turned into calls with long duration and slow-frequency modulation at the age of 7—10 days and were finally fixed into calls with long duration, loud volume and fast-frequency modulations at the age of 11—14 days. Therefore, our recordings were divided into three age groups, each of 4-day duration: 3—6 days, 7—10 days and 11—14 days. The recordings of 19—20 day-old NZ_parasite in the 11—14 days group were included to allow comparison of this cuckoo subspecies with younger cuckoo and host nestlings in our data set. Audacity (version 3.6) was used to visually scan spectrograms and to determine when parents landed on the nest (marked by a loud thump followed by parental calls) causing a begging response from their nestlings and to export all the begging events in each recording into 30s-long separate audio files. All extracted recordings were normalized to 0 dB, and noise reduction was applied to eliminate background noise. A call was defined as a single uninterrupted trace on the spectrogram. For each recording session we selected the audio file with the best quality in which calls left a clear trace on the spectrogram and did not overlap with parental calls or other external sound sources. Ten consecutive calls were isolated from the selected audio files starting from the first begging in response to the parents' arrival (with the exception of one recording of a cuckoo nestling from New Caledonia in which only nine consecutive calls were isolated). If the nest contained multiple host nestlings with calls overlapping in time, then a single nestling (identifiable by calls with similar frequency, amplitude and timing) was isolated, and the loudest and clearly visible 10 consecutive calls in response to the parents' arrival were selected. The duration, lowest frequency, highest frequency, frequency bandwidth, centre frequency (frequency dividing the selection in two intervals of equal energy), 5% frequency (frequency at which the total energy of the call exceeds 5%), 95% frequency (frequency at which the total energy of the call exceeds 95%), peak frequency (frequency at which the highest amplitude occurs) and average call entropy (variation of sound intensity across time and frequency, with 0 being a call of constant frequency) from each call in the selected audio files was measured. Raven Pro 1.6.5 (Center for Conservation Bioacoustics, 2023) was used to produce spectrograms and measure call parameters.

Statistics

Linear discriminant analysis (LDA) and multinomial logistic regression (MLR) are commonly used as classification methods to predict the category of an element based on the characteristics of a training data set, thereby estimating the similarities among elements of groups. LDA assumes multivariate normality, whereas MLR can be used as a non-parametric alternative. Nevertheless, the reliability of LDA or MLR is dependent on the sample size and skewness of the outcome variable, with LDA being more reliable with low sample sizes and moderate violations of normality assumptions (Pohar et al., 2004; Jamie et al., 2020). We thus predicted begging call similarities among nestling species using both methods and obtained similar results. Therefore, we report LDA results in the main text and MLR results in the supplementary material (Tables S1—2). LDA was used to quantify the extent of begging call mimicry by each cuckoo subspecies of the respective local host using the function lda in R 4.4.1 (R Core Team, 2024). Following the method described by Jamie et al. (2020), all the measured calls from each chick, rather than their average, were used as the raw units for our analysis, and nine measured call parameters were included to maximize the discrimination power of the discriminant function. We aimed to investigate whether the begging calls of a cuckoo subspecies were more similar to the parasitized host than to non-hosts, thus shaped by coevolutionary interactions, or to the cuckoo subspecies from other regions, thus shaped by phylogenetic relatedness. Thus, the full data set was divided in accordance with the age group (3—6, 7—10 and 11—14), and two training subsets containing (1) the calls of the three host species and (2) the calls of the main host of the focal cuckoo subspecies plus the two non-focal cuckoo subspecies from the other regions were used. The two subsets were used to train LDA algorithms for each age group, and the subsets of the calls of the focal cuckoo subspecies (AU_parasite, NC_parasite or NZ_parasite) were used to predict the most likely classification of each call in accordance with the LDA classification function. Additionally, we verified if the begging calls of the two gerygone host species were more similar to each other, thus linked by phylogenetic relatedness, than to the Australian host and the three cuckoo subspecies. To do so, we used two training subsets that included all begging calls from nestlings of all ages combined without the focal gerygone and used the subsets of the focal gerygone calls (either NC_host or NZ_host) to predict the most likely classification according to the LDA function.

Generalized linear models (GLM) with gamma distribution were used to analyse differences in call duration, lower frequency, higher frequency, frequency bandwidth, peak frequency and average entropy between each cuckoo subspecies and their respective host. The 5%, 95% and centre frequency were excluded from GLM analysis because our aim was to detect the most significant differences in the higher order and more informative call parameters between hosts and parasites. The average values of the focal call parameter for each individual were used as outcome variable, and the species, age and their interaction were used as response variables. An interaction comparing the New Zealand host and parasite was not included as our data included only one age group (11–14 days) for the New Zealand parasite. The models were validated by checking for the normality of model residuals and model fit. The function Anova from the package car was used to extract ANOVA tables for each GLM model.

Finally, the call rate (in calls/s) was compared among species and age groups. The call rate was log transformed to achieve a normal distribution, and linear regression (function lm in R) was used to test the relationship of call rate with call duration. Then, two-way ANOVA (function aov in R) was performed with call rate as outcome variable and species, age group and their interaction as response variables. The two-way ANOVA indicated the significant effect of species (check Results). Therefore, a Tukey post hoc test (function TukeyHSD in R) was used to identify significant differences in pairwise comparisons between species (Supplementary Material Table S4).

Ethical Note

The recordings were collected by placing a microphone outside the nest while parents were away during their foraging bouts, and the nestlings were not manipulated. The microphone was installed in less than 1 min; therefore, the disturbance of the breeding was kept at a minimum. None of the monitored breeding attempts failed as a result of the recording procedure. The research in New Caledonia was conducted under permit numbers 2476-2015, 2372-2017, 3469-2018, 2720-2019, 1679-2023 and 5818-2023 issued by Province Sud (New Caledonia), and ethical approval was not required. Research in New Zealand was conducted with approval by the Massey University Animal Ethics Committee. The research in Australia was conducted with approval by Environment ACT (licence numbers LT2005164, LT2006229, LT2007266 and LT2009378) and the Australian National University Animal Experimentation Ethics Committee (permit numbers F.BTZ.00.06, F.BTZ.61.03 and F.BTZ.39.09).

RESULTS

The discriminant function classified the begging calls of each cuckoo subspecies in all age groups as being more similar to the parasitized host than to the hosts from other regions, thereby showing that the cuckoo calls closely matched the host across the whole nestling period (Table 1; Fig. 1). The spectrograms of the begging calls showed a resemblance of the call structure between each cuckoo subspecies and the respective parasitized hosts, thereby supporting the high similarity scores of the discriminant analysis (Supplementary material, Figs. S1–3). The begging calls of each cuckoo subspecies were often classified as being more similar to the phylogenetically unrelated main host than to the begging calls of cuckoo subspecies from other regions, but the discrimination function returned relatively high similarity scores of begging calls from the two cuckoo subspecies from New Caledonia and New Zealand (Table 2).

Table 1
Predicted similarity of begging calls in accordance with the linear discriminant function for each of the cuckoo–host pairs from each region

	AU_host	NC_host	NZ_host
Age 3–6 days			
AU_parasite	**47**	23	–
NC_parasite	27	**72**	–
Age 7–10 days			
AU_parasite	**13**	0	7
NC_parasite	0	**54**	6
Age 11–14 days			
AU_parasite	**10**	0	0
NC_parasite	0	**20**	10
NZ_parasite	4	5	**31**

Values in boldface indicate the natural cuckoo–host pair occurring in each region. AU: Australia; NC: New Caledonia; NZ: New Zealand. NZ_parasite cuckoos from New Zealand are 19–20 days old.

The frequency and entropy of the calls explained the main differences between cuckoos and hosts from Australia and New Caledonia, whereas only differences in the entropy of the calls were observed in New Zealand (Table 3, Fig. 2). In addition, age-related differences in call duration were found in Australia and New Caledonia, with the cuckoo–host pair from New Caledonia showing pronounced differences in the high frequency and entropy of the calls, whereas the cuckoo–host pair from New Zealand showed no major age-related differences (Table 3). Overall, the cuckoo–host pair from New Caledonia had the largest difference between species and age classes, whereas the cuckoo–host pair from New Zealand was the most similar compared with that from the other two regions (Table 3; Fig. 2).

Across all ages, the begging calls of the host from New Caledonia ($N = 180$) had high similarity scores with the respective brood parasite (64%), relatively high similarity to the closely related host from New Zealand (34%) and low similarity to the New Zealand cuckoo subspecies (2%; Supplementary material, Table S3). On the contrary, the calls of the host from New Zealand ($N = 60$) were mostly similar to the calls of the closely related host from New Caledonia (95%) than to the respective brood parasite (5%), and they showed no similarity to the cuckoo subspecies from New Caledonia (Supplementary material, Table S3). The hosts from New Caledonia and New Zealand showed no similarity to the Australian host and cuckoo subspecies (Supplementary material, Table S3). A visual inspection of the spectrograms showed high similarity to the begging calls of gerygone chicks from New Caledonia and New Zealand (Supplementary material, Figs. S2–3), thereby supporting the prediction scores of the discriminant function and a similarity of begging calls caused by phylogenetic relatedness of these two host species.

Call rate was related to call duration, with longer calls leading to a slower rate (linear model; $F_{1,63} = 14.52$, $P < 0.001$), but it did not depend on nestling age (ANOVA; $F_{2,50} = 2.089$, $P = 0.134$). Species had an effect on call rate (ANOVA, $F_{5,50} = 3.841$, $P = 0.005$). However, a post-hoc comparison revealed that this effect was not due to the differences within a natural cuckoo–host pair from the same region, but rather due to differences between AU_host and nestlings from other regions (AU_host versus NC_parasite, $P = 0.008$; AU_host versus NZ_parasite, $P = 0.048$; AU_host versus NZ_host, $P = 0.014$; Supplementary material, Fig. S4; Table S4).

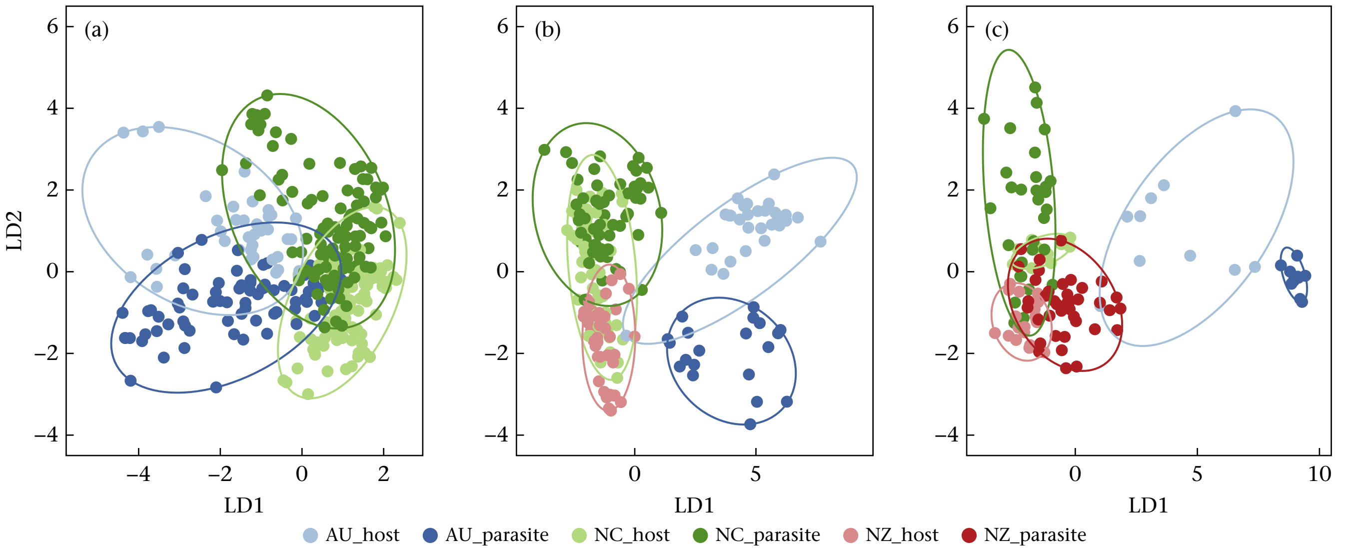

Figure 1. Linear discriminant biplots for begging calls of chicks aged (a) 3–6 days, (b) 7–10 days and (c) 11–14 days. Shining bronze-cuckoos from New Zealand aged 19–20 days are included in the day 11–14 group. Labels indicate the region. AU: Australia; NC: New Caledonia; NZ: New Zealand. Ellipses indicate hulls surrounding all nestlings within each species, with smaller distances indicating higher similarities between groups.

DISCUSSION

The begging calls of nestlings of each shining bronze cuckoo subspecies match closely those of their respective hosts. However, none of the begging calls of cuckoo subspecies is a perfect match of the host, and the species-specific differences in the frequency and entropy of the begging calls might allow the host to discriminate the parasite nestling. Such differences are more pronounced in the cuckoo–host pair from New Caledonia, indicating a less accurate matching of the host in the cuckoo subspecies from New Caledonia compared with the other subspecies. This might explain why the host from New Caledonia rejects the cuckoo nestlings, whereas the hosts from Australia and New Zealand do not. As expected, the begging calls of the two gerygone hosts from New Caledonia and New Zealand are more similar to each other than to the thornbill host from Australia because of phylogenetic relatedness. Similarly, the begging calls of the two cuckoo subspecies from New Caledonia and New Zealand are more similar to each other than to the cuckoo subspecies from Australia, thereby indicating convergence in begging call features caused by parasitism of two closely related hosts. Overall, the results support our hypothesis that the structure of the begging calls of each shining bronze-cuckoo subspecies is mainly shaped by coevolutionary interactions with their hosts rather than phylogeny.

Table 2
Predicted similarity of begging calls in accordance with the linear discriminant function for each of the three cuckoo subspecies compared with the local main host and the other cuckoo subspecies from other regions

	Main host	AU_parasite	NC_parasite	NZ_parasite
Age 3–6 days				
AU_parasite	**52**	–	18	–
NC_parasite	**62**	37	–	–
Age 7–10 days				
AU_parasite	**20**	–	0	–
NC_parasite	**55**	5	–	–
Age 11–14 days				
AU_parasite	**10**	–	0	0
NC_parasite	**15**	0	–	15
NZ_parasite	8	0	**32**	–

Values in boldface indicate the pair combination with the highest predicted similarity. AU: Australia; NC: New Caledonia; NZ: New Zealand. NZ_parasite cuckoos from New Zealand are 19–20 days old.

Discrimination of parasite nestlings by the host is a major factor driving the selection for matching of the host begging calls by the parasite (Jamie & Kilner, 2017). However, some factors may contribute to the similarity in the structure of begging calls between parasites and hosts. For example, phylogenetic relationships might constrain variation in begging call features, thereby resulting in a similar call structure in parasites and hosts, or the similarity could result from random matching between the parasite and the host (Grim, 2005). However, the shining bronze-cuckoo and its hosts are not closely related, thus it is highly unlikely that the call matching is ancestral. Moreover, the pattern of similarity is not random as the nestlings of the three shining bronze-cuckoo subspecies closely match the nestlings of the respective host visually and acoustically (Attisano et al., 2023). Parallel evolution caused by shared ecological factors might also result in the matching of begging call features, for example, nest predation might influence the frequency and amplitude of the calls (Briskie et al., 1999) and lead to a partial similarity of the begging calls between the parasite and the host (Grim, 2005). However, the three hosts live in highly different habitats, and they are exposed to different main predators: birds in New Caledonia (Attisano et al., 2020); reptiles, birds and mammals in Australia (Guppy et al., 2017) and introduced mammals in New Zealand (Remeš et al., 2012). Thus, selection by nest predators does not explain the matching of multiple call features of the hosts by the three shining bronze-cuckoo subspecies across their range. Therefore, call matching of the host by the shining bronze-cuckoo subspecies is likely explained by mimicry resulting from coevolutionary interactions driven by host discrimination (Dalziell & Welbergen, 2016; Jamie & Kilner, 2017), which is consistent with the highly accurate visual mimicry of host nestlings by the three cuckoo subspecies.

This finding is exemplified by the cuckoo–host pair from New Caledonia. The fan-tailed gerygone host removes 90% of the parasite nestlings within 24 h from hatching using visual features and hatching order to discriminate parasite nestling (Attisano et al., 2018, 2021). A closely related rejector host from Australia, the

Table 3
Results of the generalized linear models for the comparison of begging call features in cuckoo–host pairs from Australia, New Caledonia and New Zealand

	Species			Age			Species:Age		
	χ^2	*df*	*P*	χ^2	*df*	*P*	χ^2	*df*	*P*
C .l. plagosus vs *A. chrysorroa* (Australia)									
Duration	0.259	1	0.611	12.362	2	**0.002**	3.157	2	0.206
Lowest frequency	10.350	1	**0.001**	1.949	2	0.377	0.893	2	0.640
Highest frequency	8.954	1	**0.003**	1.477	2	0.478	0.070	2	0.965
Frequency bandwidth	1.618	1	0.203	1.115	2	0.573	0.324	2	0.850
Peak frequency	6.721	1	**0.010**	1.480	2	0.477	0.915	2	0.633
Average entropy	2.019	1	0.155	3.846	2	0.146	2.563	2	0.278
C. l. layardi vs *G. flavolateralis* (New Caledonia)									
Duration	0.056	1	0.813	13.084	2	**0.001**	0.098	2	0.952
Lowest frequency	13.623	1	**<0.001**	5.717	2	0.057	0.146	2	0.930
Highest frequency	0.803	1	0.370	6.582	2	**0.037**	1.358	2	0.507
Frequency bandwidth	13.496	1	**<0.001**	1.530	2	0.465	2.972	2	0.226
Peak frequency	1.563	1	0.211	3.937	2	0.140	0.492	2	0.782
Average entropy	29.139	1	**<0.001**	15.747	2	**<0.001**	1.896	2	0.387
C. l. lucidus vs *G. igata* (New Zealand)									
Duration	<0.001	1	0.991	1.235	1	0.266	–	–	–
Lowest frequency	1.292	1	0.256	1.912	1	0.167	–	–	–
Highest frequency	1.216	1	0.270	1.183	1	0.277	–	–	–
Frequency bandwidth	3.139	1	0.076	0.132	1	0.716	–	–	–
Peak frequency	0.010	1	0.919	1.222	1	0.269	–	–	–
Average entropy	9.969	1	**0.002**	0.748	1	0.387	–	–	–

Values in boldface indicates significant differences ($\alpha < 0.05$).

large-billed gerygone *G. magnirostris*, is able to discriminate about 69% of the nestlings of the little bronze-cuckoo via visual features (Noh et al., 2018) and acoustic differences in begging calls (Noh et al., 2021). The variation in rejection rates between the two gerygone hosts can be explained by the accuracy of visual and auditory matching of the host by the parasite. The New Caledonian shining bronze-cuckoo is indeed a less accurate match of its host compared to the Australian little bronze-cuckoo (Noh et al., 2018, 2021; Sato et al., 2010). This would explain the high rejection rates of the parasite and absence of recognition errors in the fan-tailed gerygone (Attisano et al., 2018, 2021) compared to the lower rejection rates of the large-billed gerygone and the fact that this host sometimes reject its own nestlings by mistake (Noh et al., 2018, 2021; Sato et al., 2010). The results of this study suggest that, apart from the visual features of the nestlings, the fan-tailed gerygone might use acoustic differences in the structure of the begging calls to discriminate parasite nestling. This process has led to selection for mimicry of the host begging call by the New Caledonian shining bronze-cuckoo to escape host discrimination.

The grey warbler and yellow-rumped thornbill hosts do not have nestling discrimination ability as they have not been observed rejecting shining bronze-cuckoo nestlings either by ejection from the nest or by nest abandonment (Medina & Langmore, 2016; Thorogood et al., 2017). The matching of the host begging calls by the shining bronze-cuckoo nestlings in these systems might result from parasite tuning into the offspring–parent communication system of the host to manipulate parental provisioning (Davies, 2011). In this case, nestling discrimination by the host might not be a necessary condition to select for begging call mimicry (Grim, 2005), and the matching could result from the parasite nestling producing calls that maximize the chances of obtaining food from the host parents (Langmore et al., 2008). Other brood parasites signal their hunger state to the host parents with exaggerated begging traits such as a fast call rate (Kilner et al., 1999; Roldán et al., 2013; Tuero et al., 2016) or postural components of the begging display (Jamie et al., 2020), which induce host parents to increase feeding rate, thereby providing an adequate amount of food to the demanding parasite chick (Soler, 2017b). The postural components of the begging display were not quantified in this study, but we did not find evidence of exaggerated traits such as a faster call rate in any of the shining bronze-cuckoo subspecies as they all matched the begging rate of individual host chicks across the range. The grey warbler and yellow-rumped thornbill hosts might have a preference for chicks begging at the 'right' rate, that is the rate of a single host chick, rather than an exaggerated one mimicking a whole brood (Davies et al., 1998). This phenomenon could depend on a limit to the amount of food that the small hosts of the shining bronze-cuckoo can provide as they all have relatively small brood sizes of one to three chicks and therefore might not be able to increase their provisioning rate in response to exaggerated begging displays of the cuckoo.

Each of the three cuckoo subspecies visually matches their respective host in each region (Attisano et al., 2023). Therefore, the matching of the host begging calls supports a scenario of selection for multimodal mimicry of the hosts by the shining bronze-cuckoo. The shining bronze-cuckoo from Australia matches visual and acoustic features of its host and the visual mimicry is the most accurate among the three cuckoo subspecies (Attisano et al., 2023; this study). In New Zealand, phylogenetic comparative analysis shows that the local shining bronze-cuckoo subspecies matches the begging calls of the grey warbler host more closely than any other New Zealand passerine species (Anderson et al., 2009; McLean & Waas, 1987; Ranjard et al., 2010), and in this study we found that the acoustic mimicry of the host is the most accurate among the three cuckoo subspecies. Although only the fan-tailed gerygone host from New Caledonia currently discriminates the cuckoo nestling, the evidence suggests that the grey warbler from New Zealand and the yellow-rumped thornbill from Australia might have been able to discriminate parasite nestlings at least at some point in the past, most likely in the early stages of the coevolutionary arms race with the shining bronze-cuckoo. Nowadays these hosts might no longer accurately discriminate the parasite due to the refined level of mimicry achieved by the shining bronze-cuckoo nestlings. The presence of moderately effective anti-parasitic defences at the nest-building and egg stages in both these hosts (Anderson et al., 2013; Medina & Langmore, 2016), might further relax selection for improved defences at later stages of the arms race (Britton et al., 2007) and as a consequence the nestling discrimination behaviour

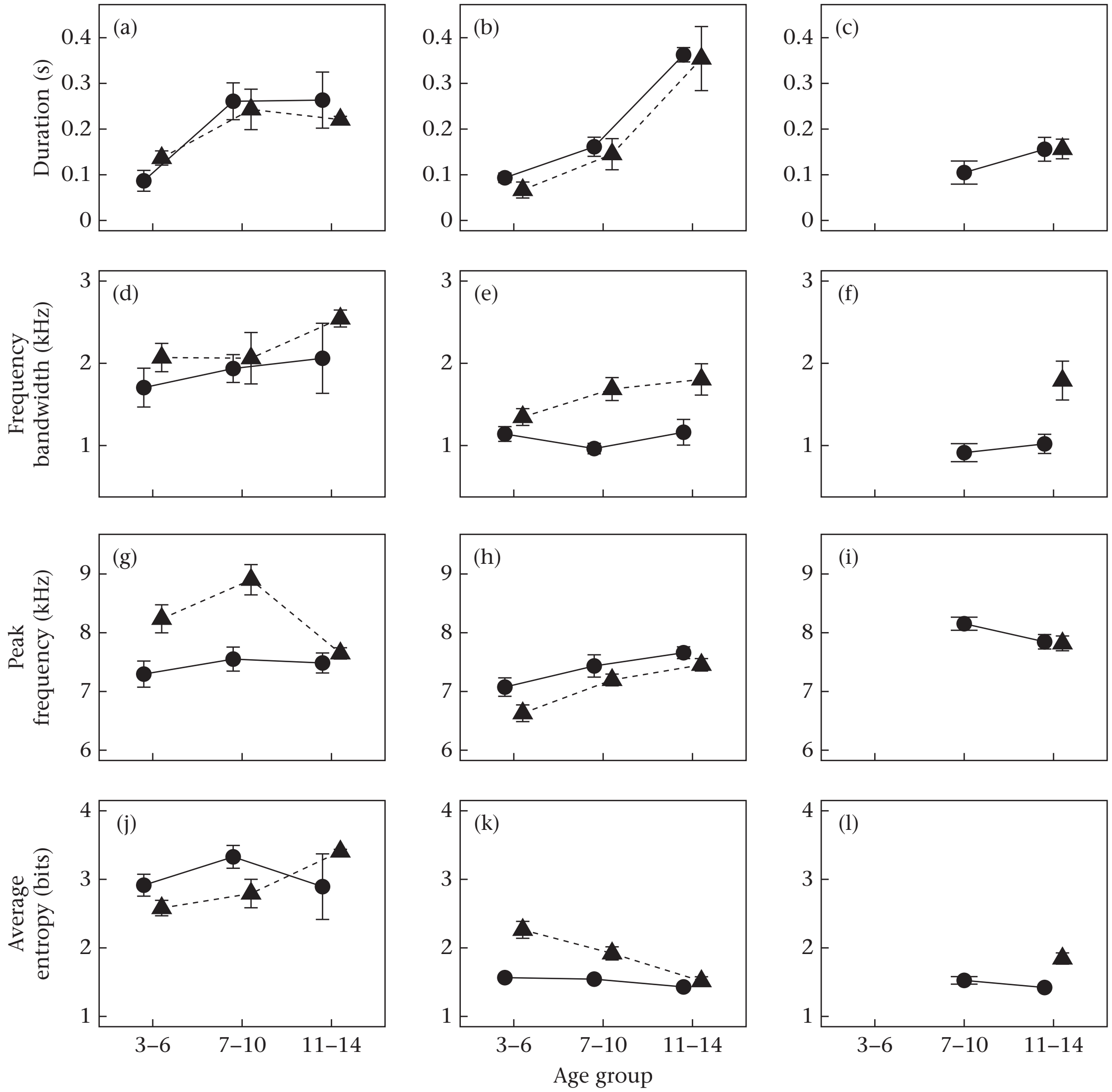

Figure 2. Duration, frequency bandwidth, peak frequency and average entropy of begging calls of cuckoo (triangles) and host (circles) pairs from (a, d, g, j) Australia, (b, e, h, k) New Caledonia and (c, f, i, l) New Zealand. Error bars represent 95% confidence intervals.

has been lost or reached frequencies too low to be detected during field monitoring.

In conclusion, we found support for our hypothesis that the structure of the begging calls of each shining bronze-cuckoo subspecies is shaped primarily by coevolutionary interactions, and that the calls of each subspecies has been altered to match those of the specific host in their area of distribution. The selection for a refined multimodal mimicry of the host via visual and acoustic signals has promoted phenotypic differentiation of the parasite nestlings across the distribution range with the formation of geographically and genetically separated host races (Gill, 1998; Noske, 2019), which are adapted to exploit the specif local host.

Author Contributions

Alfredo Attisano: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Michael G. Anderson**: Writing – review & editing, Investigation, Funding acquisition, Data curation. **Naomi E. Langmore**: Writing – review & editing, Investigation, Funding acquisition, Data curation. **Roman Gula**: Writing – review & editing, Funding acquisition. **Jörn Theuerkauf**: Writing – review & editing, Funding acquisition, Conceptualization.

Data Availability

Data, R code and additional analyses are available as supplementary material.

Declaration of Interest

The authors declare that they have no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2025.123083.

References

Anderson, M. G., Gill, B. J., Briskie, J. V., Brunton, D. H., & Hauber, M. E. (2013). Latitudinal differences in the breeding phenology of Grey Warblers covary with the prevalence of parasitism by Shining Bronze-Cuckoos. *Emu - Austral Ornithology, 113*(2), 187–191. https://doi.org/10.1071/MU12086

Anderson, M. G., Ross, H. A., Brunton, D. H., & Hauber, M. E. (2009). Begging call matching between a specialist brood parasite and its host: A comparative approach to detect coevolution. *Biological Journal of the Linnean Society, 98*(1), 208–216. https://doi.org/10.1111/j.1095-8312.2009.01256.x

Attisano, A., Gill, B. J., Anderson, M. G., Gula, R., Langmore, N. E., Okahisa, Y., Sato, N. J., Tanaka, K. D., Thorogood, R., Ueda, K., & Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. *Journal of Animal Ecology, 92*(1), 30–43. https://doi.org/10.1111/1365-2656.13849

Attisano, A., Groß, L. B., Sato, N. J., Okahisa, Y., Tanaka, K. D., Gula, R., Ueda, K., & Theuerkauf, J. (2020). Impact of brood parasitism and predation on nest survival of the fan-tailed gerygone in New Caledonia. *Journal of Avian Biology, 51*(7), Article e02476. https://doi.org/10.1111/jav.02476

Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. *Scientific Reports, 8*(1). https://doi.org/10.1038/s41598-018-28710-5

Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. *Current Zoology, 67*(6), 653–663. https://doi.org/10.1093/cz/zoab066

Attisano, A., Thiel, F., Sato, N., Okahisa, Y., Bolopo, D., Tanaka, K. D., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2019). Breeding biology of the fan-tailed gerygone *flavolateralis* in relation to parasitism by the shining bronze-cuckoo *Chalcites lucidus*. *Journal of Ornithology, 160*(1), 91–103. https://doi.org/10.1007/s10336-018-1592-6

Briskie, J. V., Martin, P. R., & Martin, T. E. (1999). Nest predation and the evolution of nestling begging calls. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1434), 2153–2159. https://doi.org/10.1098/rspb.1999.0902

Britton, N. F., Planqué, R., & Franks, N. R. (2007). Evolution of defence portfolios in exploiter–victim systems. *Bulletin of Mathematical Biology, 69*(3), 957–988. https://doi.org/10.1007/s11538-006-9178-5

Center for Conservation Bioacoustics. (2023). *Raven Pro: Interactive sound analysis software*. The Cornell Lab of Ornithology Version 1.6.5. http://ravensoundsoftware.com/.

Dalziell, A. H., & Welbergen, J. A. (2016). Mimicry for all modalities. *Ecology Letters, 19*(6), 609–619. https://doi.org/10.1111/ele.12602

Davies, N. B. (2011). Cuckoo adaptations: Trickery and tuning. *Journal of Zoology, 284*(1), 1–14. https://doi.org/10.1111/j.1469-7998.2011.00810.x

Davies, N. B., Kilner, R. M., & Noble, D. G. (1998). Nestling cuckoos, *Cuculus canorus*, exploit hosts with begging calls that mimic a brood. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 265*(1397), 673–678. https://doi.org/10.1098/rspb.1998.0346

Dawkins, R., & Krebs, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London. Series B. Biological Sciences, 205*(1161), 489–511. https://doi.org/10.1098/rspb.1979.0081

De Mársico, M. C., Ursino, C. A., Scardamaglia, R. C., & Reboreda, J. C. (2019). Coevolutionary arms race between a specialist brood parasite, the Screaming Cowbird, and its host, the Grayish Baywing. *Journal of Ornithology, 160*(4), 1221–1233. https://doi.org/10.1007/s10336-019-01697-0

Gibbs, H. L., Sorenson, M. D., Marchetti, K., Brooke, M. de L., Davies, N. B., & Nakamura, H. (2000). Genetic evidence for female host- specific races of the common cuckoo. *Nature, 407*(6801), 183–186. https://doi.org/10.1038/35025058

Gill, B. (1983). Brood-parasitism by the Shining Cuckoo Chrysococcyz lucidus at Kaikoura, New Zealand. *Ibis, 125*(1), 40–55. https://doi.org/10.1111/j.1474-919X.1983.tb03082.x

Gill, B. J. (1998). Behavior and ecology of the shining cuckoo Chrysococcyx lucidus. In Parasitic birds and their hosts. *Studies in Coevolution (Rothstein SI, Robinson SK.* Oxford University Press.

Gloag, R., & Kacelnik, A. (2013). Host manipulation via begging call structure in the brood-parasitic shiny cowbird. *Animal Behaviour, 86*(1), 101–109. https://doi.org/10.1016/j.anbehav.2013.04.018

Grim, T. (2005). Mimicry vs. similarity: Which resemblances between brood parasites and their hosts are mimetic and which are not? *Biological Journal of the Linnean Society, 84*(1), 69–78. https://doi.org/10.1111/j.1095-8312.2005.00414.x

Grim, T. (2017). Host defence against brood parasite nestlings: Theoretical expectations and empirical evidence. In , *Soler M. Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 539–556). Springer International Publishing.

Guppy, M., Guppy, S., Marchant, R., Priddel, D., Carlile, N., & Fullagar, P. (2017). Nest predation of woodland birds in south-east Australia: Importance of unexpected predators. *Emu - Austral Ornithology, 117*(1), 92–96. https://doi.org/10.1080/01584197.2016.1258997

Hauber, M. E., & Kilner, R. M. (2007). Coevolution, communication, and host chick mimicry in parasitic finches: Who mimics whom? *Behavioral Ecology and Sociobiology, 61*(4), 497–503. https://doi.org/10.1007/s00265-006-0291-0

Jamie, G. A., Belleghem, S. M. V., Hogan, B. G., Hamama, S., Moya, C., Troscianko, J., Stoddard, M. C., Kilner, R. M., & Spottiswoode, C. N. (2020). Multimodal mimicry of hosts in a radiation of parasitic finches. *Evolution, 74*(11), 2526–2538. https://doi.org/10.1111/evo.14057

Jamie, G. A., & Kilner, R. M. (2017). Begging call mimicry by brood parasite nestlings: Adaptation, manipulation and development. In M. Soler (Ed.), *Avian Brood Parasitism: Behaviour, ecology, evolution and coevolution* (pp. 517–538). Springer International Publishing. https://doi.org/10.1007/978-3-319-73138-4_28.

Joseph, L., Wilke, T., & Alpers, D. (2002). Reconciling genetic expectations from host specificity with historical population dynamics in an avian brood parasite, Horsfield's Bronze-Cuckoo *Chalcites basalis* of Australia. *Molecular Ecology, 11*(4), 829–837. https://doi.org/10.1046/j.1365-294X.2002.01481.x

Kilner, R. M. (2002). The evolution of complex begging displays. In *The evolution of begging: Competition, cooperation and communication (Wright J and Leonard ML (pp. 87–106). Kluwer Academic Publishing*.

Kilner, R. M., Noble, D. G., & Davies, N. B. (1999). Signals of need in parent–offspring communication and their exploitation by the common cuckoo. *Nature, 397*(6721), 667–672. https://doi.org/10.1038/17746

Lama, F., Ursino, C. A., Reboreda, J. C., & De Mársico, M. C. (2022). Acoustic discrimination by hosts favours vocal trickery in fledglings of the brood-parasitic screaming cowbird. *Behavioral Ecology and Sociobiology, 76*(5), 71. https://doi.org/10.1007/s00265-022-03175-9

Langmore, N. E., Grealy, A., Noh, H.-J., Medina, I., Skeels, A., Grant, J., Murray, K. D., Kilner, R. M., & Holleley, C. E. (2024). Coevolution with hosts underpins speciation in brood-parasitic cuckoos. *Science, 384*(6699), 1030–1036. https://doi.org/10.1126/science.adj3210

Langmore, N. E., Hunt, S., & Kilner, R. M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature, 422*(6928), 157–160. https://doi.org/10.1038/nature01460

Langmore, N. E., Maurer, G., Adcock, G. J., & Kilner, R. M. (2008). Socially aquired host-specific mimicry and the evolution of host races in Horsfield's bronze cuckoo *Chalcites basalis*. *Evolution, 62*(7), 1689–1699. https://doi.org/10.1111/j.1558-5646.2008.00405.x

Langmore, N. E., Stevens, M., Maurer, G., Heinsohn, R., Hall, M. L., Peters, A., & Kilner, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society B: Biological Sciences, 278*(1717), 2455–2463. https://doi.org/10.1098/rspb.2010.2391

McLean, I. G., & Waas, J. R. (1987). Do cuckoo chicks mimic the begging calls of their hosts? *Animal Behaviour, 35*(6), 1896–1898. https://doi.org/10.1016/S0003-3472(87)80083-0

Medina, I., Kilner, R. M., & Langmore, N. E. (2020). From micro- to macroevolution: Brood parasitism as a driver of phenotypic diversity in birds. *Current Zoology, 66*(5), 515–526. https://doi.org/10.1093/cz/zoaa033

Medina, I., & Langmore, N. E. (2016). Batten down the thatches: Front-line defences in an apparently defenceless cuckoo host. *Animal Behaviour, 112*, 195–201. https://doi.org/10.1016/j.anbehav.2015.12.006

Medina, I., & Langmore, N. E. (2019). Nest illumination and the evolution of egg rejection in hosts of brood parasites. *Auk, 136*(1), 1–6. https://doi.org/10.1093/auk/uky002

Noh, H. J., Gloag, R., & Langmore, N. E. (2018). True recognition of nestlings by hosts selects for mimetic cuckoo chicks. *Proceedings of the Royal Society B: Biological Sciences, 285*(1880), Article 20180726. https://doi.org/10.1098/rspb.2018.0726

Noh, H. J., Gloag, R., Leitão, A. V., & Langmore, N. E. (2021). Imperfect mimicry of host begging calls by a brood parasitic cuckoo: A cue for nestling rejection by hosts? *Current Zoology, 67*(6), 665–674. https://doi.org/10.1093/cz/zoab056

Noske, R. (2019). New Zealand shining bronze-cuckoo *Chalcites lucidus* are regular visitors to Southeast Queensland. *Sunbird, 48*, 149–158.

Payne, R. B. (2005). *The Cuckoos*. Oxford: OUP.

Pohar, M., Blas, M., & Turk, S. (2004). Comparison of logistic regression and linear discriminant analysis: A simulation study. *Metodološki Zvezki, 1*(1), 143–161.

R Core Team. (2024). *R a language and environment for statistical computing*. R Foundation for Statistical Computing, Version 4.4.1. https://www.R-project.org

Ranjard, L., Anderson, M. G., Rayner, M. J., Payne, R. B., McLean, I., Briskie, J. V., Ross, H. A., Brunton, D. H., Woolley, S. M. N., & Hauber, M. E. (2010). Bioacoustic distances between the begging calls of brood parasites and their host species: A comparison of metrics and techniques. *Behavioral Ecology and Sociobiology, 64*(11), 1915–1926. https://doi.org/10.1007/s00265-010-1065-2

Remeš, V., Matysioková, B., & Cockburn, A. (2012). Nest predation in New Zealand songbirds: Exotic predators, introduced prey and long-term changes in predation risk. *Biological Conservation, 148*(1), 54–60. https://doi.org/10.1016/j.biocon.2012.01.063

Roldán, M., Soler, M., Márquez, R., & Soler, J. J. (2013). The vocal begging display of Great Spotted Cuckoo *Clamator glandarius* nestlings in nests of its two main host species: Genetic differences or developmental plasticity? *Ibis, 155*(4), 867–876. https://doi.org/10.1111/ibi.12088

Samaš, P., Žabková, K., Petrusková, T., Procházka, P., Požgayová, M., & Honza, M. (2020). Nestlings of the common cuckoo do not mimic begging calls of two closely related Acrocephalus hosts. *Animal Behaviour, 161*, 89–94. https://doi.org/10.1016/j.anbehav.2020.01.005

Sato, N. J., Tanaka, K. D., Okahisa, Y., Yamamichi, M., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2015). Nestling polymorphism in a cuckoo-host system. *Current Biology, 25*(24), R1164–R1165. https://doi.org/10.1016/j.cub.2015.11.028

Sato, N. J., Tokue, K., Noske, R. A., Mikami, O. K., & Ueda, K. (2010). Evicting cuckoo nestlings from the nest: A new anti-parasitism behaviour. *Biology Letters, 6*(1), 67–69. https://doi.org/10.1098/rsbl.2009.0540

Schuetz, J. G. (2005). Reduced growth but not survival of chicks with altered gape patterns: Implications for the evolution of nestling similarity in a parasitic finch. *Animal Behaviour, 70*(4), 839–848. https://doi.org/10.1016/j.anbehav.2005.01.007

Soler, M. (2017a). *Avian brood parasitism: Behaviour, ecology, evolution and coevolution*. Springer International Publishing.

Soler, M. (2017b). Begging behaviour, food delivery and food acquisition in nests with brood parasitic nestlings. In , *Soler M. Avian brood parasitism: Behaviour, ecology, evolution and coevolution* (pp. 493–516). Springer International Publishing.

Stoddard, M. C., & Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proceedings of the Royal Society B: Biological Sciences, 277*(1686), 1387–1393. https://doi.org/10.1098/rspb.2009.2018

Thorogood, R., Kilner, R. M., & Rasmussen, J. L. (2017). Grey Gerygone hosts are not egg rejecters, but Shining Bronze-Cuckoos lay cryptic eggs. *Auk, 134*(2), 340–349. https://doi.org/10.1642/AUK-16-128.1

Tuero, D. T., Gloag, R., & Reboreda, J. C. (2016). Nest environment modulates begging behavior of a generalist brood parasite. *Behavioral Ecology, 27*(1), 204–210. https://doi.org/10.1093/beheco/arv140

Ursino, C. A., Gloag, R., Reboreda, J. C., & De Mársico, M. C. (2018). Host provisioning behavior favors mimetic begging calls in a brood-parasitic cowbird. *Behavioral Ecology, 29*(2), 328–332. https://doi.org/10.1093/beheco/arx167

Wang, J., Li, Q., & Yang, C. (2020). Coevolution of acoustical communication between obligate avian brood parasites and their hosts. *Avian Research, 11*(1), 43. https://doi.org/10.1186/s40657-020-00229-2

1. Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Kuehn, R., Gula, R., Ueda, K., & Theuerkauf, J. (2018). Visual discrimination of polymorphic nestlings in a cuckoo-host system. Scientific Reports, 8: 1–10. https://doi.org/10.1038/s41598-018-28710-5 [IF$_{2018}$: 4.011; Q1; MNSW: 140 points]

1.1. Sato, N.J.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

Nozomu Sato

1.2. Tanaka, K.D.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej oraz poprawieniu manuskryptu.

Podpis

1.3. Okahisa, Y.

Oświadczam, że mój wkład w powyższy artykuł polegał na zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

Yuji Okahisa

1.4. Kuehn, R.

Oświadczam, że mój wkład w powyższy artykuł polegał na uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

1.5. Gula, R.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

1.6. Ueda, K.

Oświadczam, że mój wkład w powyższy artykuł polegał na uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

Keisuke Ueda

1.7. Theuerkauf, J.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

2. Attisano, A., Hlebowicz, K., Gula, R., & Theuerkauf, J. (2021). Threat recognition and response in an avian brood-parasite host from New Caledonia. Current Zoology, 67: 255–262. https://doi.org/10.1093/cz/zoaa061 [IF$_{2021}$: 2.734; Q1; MNSW: 100 points]

2.1. Hlebowicz, K.

Oświadczam, że mój wkład w powyższy artykuł polegał na zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

Hlebowicz Kasper

2.2. Gula, R.

Oświadczam, że mój wkład w powyższy artykuł polegał uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

2.3. Theuerkauf, J.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

3. Attisano, A., Sato, N. J., Tanaka, K. D., Okahisa, Y., Ueda, K., Gula, R., & Theuerkauf, J. (2021). Discrimination and ejection of eggs and nestlings by the fan-tailed gerygone from New Caledonia. Current Zoology, 67: 653–663. https://doi.org/10.1093/cz/zoab066 [IF$_{2021}$: 2.734; Q1; MNSW: 100 points]

3.1. Sato, N.J.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania, zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

Nozomu Sato

3.2. Tanaka, K.D.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

3.3. Okahisa, Y.

Oświadczam, że mój wkład w powyższy artykuł polegał na zebraniu danych w terenie oraz poprawieniu manuskryptu.

Podpis

Yuji Okahisa

3.4. Ueda, K.

Oświadczam, że mój wkład w powyższy artykuł polegał na uzyskaniu finansowania, oraz poprawieniu manuskryptu.

Podpis

Keisuke Ueda

3.5. Gula, R.

Oświadczam, że mój wkład w powyższy artykuł polegał na uzyskaniu finansowania, oraz poprawieniu manuskryptu.

Podpis

3.6. Theuerkauf, J.

Oświadczam, że mój wkład w powyższy artykuł polegał na sformułowaniu głównej hipotezy badawczej, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

4. Attisano, A., Gill, B.J., Anderson, M.G., Gula, R., Langmore, N.E., Okahisa, Y., Sato, N.J., Tanaka, K., Thorogood, R., Ueda, K., Theuerkauf, J. (2023). Polymorphism at the nestling stage and host-specific mimicry in an Australasian cuckoo-host arms race. Journal of Animal Ecology 93: 30-43, https://doi.org/10.1111/1365-2656.13849 [IF$_{2023}$: 3.5; Q1; MNSW: 140 points]

4.1. Gill, B.J.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Nowej Zelandii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

B.J. Gill

4.2. Anderson, M.G.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Nowej Zelandii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

M. Anderson

4.3. Gula, R.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania na badania w Nowej Kaledonii oraz poprawieniu manuskryptu.

Podpis

4.4. Langmore, N.E.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Australii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

Naomi Langmore

4.5. Okahisa, Y.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na zebraniu danych w Nowej Kaledonii oraz poprawieniu manuskryptu.

Podpis

Yuji Okahisa

4.6. Sato, N.J.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Nowej Kaledoniii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

Nozomu Sato

4.7. Tanaka, K.D.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Nowej Kaledoniii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

4.8. Thorogood, R.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej i zebraniu danych do badań w Nowej Zelandii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

Rose Thorogood

4.9. Ueda, K.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania do badań w Nowej Kaledoniii oraz poprawieniu manuskryptu.

Podpis

Keisuke Ueda

4.10. Theuerkauf, J.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na sformułowaniu hipotezy głównej do badań w Nowej Kaledoniii, uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

5. Attisano, A., Anderson M.G., Langmore N.E., Gula, R., Theuerkauf J. (2025). Begging call mimicry and formation of host-specific lineages in the shining bronze-cuckoo *Chalcites lucidus*. Animal Behaviour 221:123083, https://doi.org/10.1016/j.anbehav.2025.123083 [IF$_{2025}$: 2.3; Q1; MNSW: 140 points]

5.1. Anderson, M.G.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania, zebraniu danych do badań w Nowej Zelandii, oraz poprawieniu manuskryptu.

Podpis

M.Anderson

5.2. Langmore, N.E.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania, zebraniu danych do badań w Australii, oraz poprawieniu manuskryptu.

Podpis

Naomi Langmore

5.3. Gula, R.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis

5.4. Theuerkauf, J.

Oświadczam, że mój wkład w powyższy artykuł artykułu polegał na uzyskaniu finansowania oraz poprawieniu manuskryptu.

Podpis