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RESEARCH ARTICLE

Brood parasitism by the enigmatic and rare Pavonine Cuckoo in Amazonian Peru

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ABSTRACT

Brood parasitism is an uncommon and understudied strategy in Amazonian bird communities, within which only 5 species are known to be brood parasites. We present data on the brood-parasitic behavior of the Pavonine Cuckoo (*Dromococcyx pavoninus*) in 3 host species of small-bodied flycatchers in the Peruvian Amazon that construct hanging globular nests with side entrances. During the 7 yr of the study, we encountered 74 nests of these 3 hosts, but parasitism occurred only in 9 nests (12.2%) in 2 yr. Only 1 Pavonine Cuckoo egg was deposited in each host nest ($n = 7$), and eggs were markedly dissimilar in size and coloration between hosts and parasite. Incubation investment per day was slightly higher (4%) for 1 parasitized nest than for nonparasitized nests. Overall, 33% of parasitic eggs ($n = 6$) hatched; cuckoo nestlings apparently removed host eggs and killed host nestlings. The nestling period lasted 24 days, and the growth-rate constant based on nestling mass ($k = 0.23$) was slower for parasite nestlings than for their hosts ($k = 0.27$ and 0.31). Food provisioning rates were greater in 1 parasitized nest (2.1 ± 0.7 feedings hr^{-1} $nestling^{-1}$) than in nonparasitized nests (1.1 ± 0.4). Nestling cuckoos may further mimic the plumage of their host nestlings. Our results suggest that Pavonine Cuckoos negatively affect their hosts' breeding success and are engaged in a coevolutionary arms race with hosts that have defenses against parasitism.

Keywords: brood parasitism, *Dromococcyx pavoninus*, hosts, incubation behavior, nests, parental care, Pavonine Cuckoo

Parasitismo de cría por el enigmático y raro *Dromococcyx pavoninus* en la Amazonia peruana

RESUMEN

El parasitismo de cría es una estrategia reproductiva rara y poco estudiada en comunidades de aves amazónicas, en donde solo tres especies de Cucos se han reportado como parásitos de cría. En este trabajo presentamos información del comportamiento parasito de *Dromococcyx pavoninus* en tres hospederos en la Amazonia peruana. Los tres hospederos fueron pequeños atrapamoscas que construyen nidos globulares colgantes con entradas laterales. Durante los siete años de muestreo, encontramos 74 nidos de los tres hospederos, pero solo en nueve nidos (12.2%) se encontró evidencia de parasitismo. El tamaño de puesta fue de un huevo parasito por nido ($n = 7$), y los huevos presentaron un tamaño y coloración diferente a los de los hospederos. La inversión parental en incubación por día fue ligeramente más alta (4%) para un nido parasitado comparado con nidos no parasitados. En total 33% de los huevos del parásito ($n = 6$ huevos) eclosionaron y al parecer el polluelo del cuco removió los huevos del hospedero y en un nido mató al polluelo del hospedero. El periodo de polluelos fue de 24 días, y la constante de crecimiento basada en masa de los polluelos fue más lenta para *D pavoninus* ($k = 0.23$) que para los polluelos de dos hospederos ($k = 0.27$ y 0.31). La tasa de alimentación en nidos parasitados (2.1 ± 0.7 viajes/hora/polluelo) fue más alta que para nidos no parasitados (1.1 ± 0.4). Nuestros resultados sugieren que *D. pavoninus* afecta negativamente el éxito reproductivo de sus hospederos y está involucrado en una carrera armamentista co-evolutiva con sus hospederos, los cuales presentan defensas contra el parasitismo.

Palabras clave: cuidado parental, *Dromococcyx pavoninus*, hospederos, incubación, nidos, parasitismo de cría

INTRODUCTION

Obligate avian brood parasites are species that rely entirely on other host species for nest building, incubation, and nestling provisioning; about 1% of all birds exhibit this specialized behavior (Johnsgard 1997, Davies 2000). Avian brood parasitism is widespread and phylogenetically diverse, with ~90% of the obligate brood parasites occurring in the Old World and 10 obligate species occurring in the New World (Winfree 1999, Davies 2000).

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Brood parasites have been widely studied for centuries because they are excellent model systems for the study of coevolution and have negative impacts on many of their hosts (Davies 2000). Studies of the Common Cuckoo (*Cuculus canorus*) and the Brown-headed Cowbird (*Molothrus ater*), for example, have revealed many aspects of the arms race between hosts and parasites, including traits such as egg-color mimicry (Davies and Brooke 1989, Stoddard and Stevens 2011), host egg rejection (Peer and Sealy 2004, Abernathy and Peer 2014), egg-eviction behavior by parasites (Moskàt and Hauber 2010, Hargitai et al. 2012), and the existence of many species that seem to tolerate parasitic eggs and nestlings (Rothstein and Robinson 1998). Some brood parasites, especially the cowbirds (*Molothrus* spp.), also have contributed to the endangerment of many of their hosts and have changed the composition of entire bird communities (Robinson et al. 2013). Many brood parasites, however, remain very poorly known with respect to either host–parasite coevolution or their impacts on host populations (Johnsgard 1997).

Among the 5 families of birds that exhibit obligate brood parasitism, Cuculidae has the largest number of parasitic species (59; Payne 2005). Molecular evidence suggests that brood parasitism evolved independently in 3 cuckoo lineages: twice in the Old World cuckoos and once in New World lineages (Davies 2000, Sorenson and Payne 2005). In the New World, only 3 species of cuckoos in the sister genera *Tapera* and *Dromococcyx* have been reported as obligate parasites, and they belong to a well-supported subfamily of ground-cuckoos named Neomorphinae (Sorenson and Payne 2005, Remsen et al. 2015). Solitary and secretive, the 2 *Dromococcyx* species are frequently described as "heard far more often than seen" and are among the least-known cuckoo species in the world. Their breeding biology and parasitism behavior are poorly known, with only basic lists of known hosts and egg descriptions (Johnsgard 1997, Davies 2000, Payne 2005, Lowther 2013).

Here, we report results of the first study of brood-parasitic behavior by the Pavonine Cuckoo (*Dromococcyx pavoninus*) in host species the Sepia-capped Flycatcher (*Leptopogon amaurocephalus*), Slaty-capped Flycatcher (*L. superciliaris*), and Ochre-bellied Flycatcher (*Mionectes oleagineus*) in the Amazonian lowlands (scientific names of hosts are used hereafter). We provide information on parasitic eggs, clutch size, incubation behavior, nestling development, parental care, and reproductive success and compare the information between parasitized and non-parasitized nests of 2 of the host species. We also use our observations to provide comparisons with Old World parasitic cuckoos. Elucidating aspects of the nesting biology of the Pavonine Cuckoo and its hosts may help us understand the ecology and evolution of this specialized behavior in the Neotropics, where only a few species have evolved as obligate brood parasites.

METHODS

Study Area

We conducted the study at 3 field stations situated in primary forest or old secondary forest, on the southeastern flank of the Andes and adjacent to Manu National Park, Peru. The first site was the Pantiacolla Lodge (12.642028°S, 71.239222°W; 412 m elevation) in Madre de Dios, Peru. The area comprises a mix of floodplain and terra firme forests, with dispersed bamboo patches (*Guadua* spp.) and an average canopy height of 27 m. The 2 other sites, ranging from lowland rainforest to montane cloud forest, were located in an undisturbed area adjacent to the Tono River (12.956222°S, 71.481639°W; 950–1,000 m elevation) and the Piñi Piñi River (12.8955°S, 71.403806°W; 550–1,200 m elevation) in Cusco, Peru.

Measurements and Nest Monitoring

We searched for nests during the 7 breeding seasons (August–December) of 2008 to 2014. We followed the protocol of Martin and Geupel (1993) for nest searching and monitoring, with some modifications. We measured nest and egg dimensions, and tarsus length and wing chord of nestlings, to the nearest 0.1 mm using a caliper. We weighed eggs, nestlings, and dry nest materials to the nearest 0.05 g using a digital pocket scale (Flipscale F2, Phoenix, Arizona, USA). Nestling provisioning behavior was recorded using a motion-sensor-triggered camera (PC85 Rapidfire Professional; Reconix, Holmen, Wisconsin, USA), which was placed ~70 cm from the nest and camouflaged with natural vegetation to avoid behavioral disturbance. The camera was programmed to take 1 photo min^{-1} and 10 photos in response to any movement on the nest. When we found a nest with eggs of a potential host species of the Pavonine Cuckoo, we determined the level of development of the eggs and checked the nest every other day to determine the presence of any parasitic egg.

We used thermal sensors to record incubation behavior in 3 nests of *Leptopogon amaurocephalus* (2 nonparasitized nests and 1 parasitized nest). One sensor was placed at the bottom of the nest, under the eggs, to record nest temperature; and another was attached to a branch close to the nest to record ambient temperature. Both sensors were connected to a U-12 HOBO data logger (Onset, Bourne, Massachusetts, USA) that was placed close to the nest and camouflaged; the data logger stored temperatures every 1 min. We used changes in temperature to estimate incubation behavior (Cooper and Mills 2005, David and Londoño 2013).

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Data Analysis

We compared egg dimensions between parasite and host species using a Kruskal-Wallis test because the variables were not normally distributed ($W = 0.959$, $P = 0.006$). When differences were significant, we used Tukey's HSD post hoc test. In addition, we assessed the brood-parasitic effect of Pavonine Cuckoos on the nesting behavior of *L. amaurocephalus* during incubation and nestling provisioning. We used a Mann-Whitney *U*-test to compare nest attentiveness, off-bout lengths, and off-bout numbers during incubation, because the Shapiro test indicated that these data were not normally distributed ($W = 0.906$, $P = 0.003$); we used *t*-tests to compare feeding trips during the nestling period, because the Shapiro test indicated a normal distribution ($W = 0.958$, $P = 0.181$). We calculated the nestling growth rate, following Ricklefs's (1967) equation, for the Pavonine Cuckoo and any host nestlings that successfully fledged. All statistical analyses were performed in R 3.1.1 (R Development Core Team 2015), and graphics were generated using the R package "ggplot2" 3.1.2 (Wickham 2009).

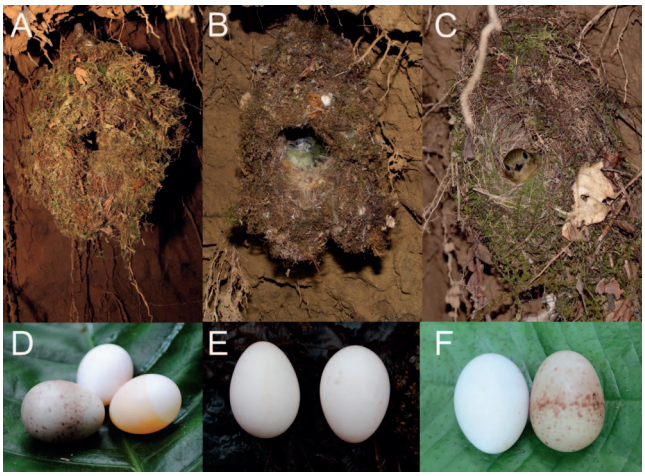


FIGURE 1. Nests and eggs of Pavonine Cuckoo hosts in lowland Amazonian forest in southeastern Peru. (**A**) *Leptopogon amaurocephalus* nest. (**B**) *L. superciliaris* nest. (**C**) *Mionectes oleagineus* nest. (**D**) *L. amaurocephalus* clutch with one parasitic egg. (**E**) *L. superciliaris* eggs. (**F**) *M. oleagineus* clutch with one parasitic egg. Photo credits: Santiago David (A, B), Justin Demianew (C, E), and Manuel A. Sanchez (D, F)

RESULTS

Nest Description and Sites

We found evidence of brood parasitism by the Pavonine Cuckoo in *L. amaurocephalus* ($n = 6$ nests), *L. superciliaris* ($n = 1$ nest), and *M. oleagineus* ($n = 2$ nests). Throughout the 7 yr of the study, we encountered a total of 74 nests of these 3 hosts species, but parasitism occurred in only 9 nests (12.2%) in 2 yr. In 2010, one of 7 nests (14.3%) of *L. superciliaris* was parasitized in the Tono station, but this nest was not further monitored. In 2013, the only nest of *L. amaurocephalus* that was found and monitored in the Piñi Piñi River station contained 1 Pavonine Cuckoo egg; this egg was depredated 5 days later. During 4 consecutive visits after it was located, however, we did not record any activity around the nest, so we consider it to have been abandoned before we found it. The remaining parasitized nests were found in Pantiacolla station in 2013. Among these, 5 of 13 nests (38.5%) of *L. amaurocephalus* and 2 of 7 nests (28.6%) of *M. oleagineus* were parasitized. Additionally, the fates of all parasitized nests monitored during our study were as follows: 5 (56%) were abandoned, 3 (33%) were depredated, and only 1 (11%) was successful. Compared with the 63 nonparasitized nests of these 3 hosts, 21 (34.4%) were abandoned (9 during egg-laying period), 27 (44.3%) were depredated, and only 15 (21.3%) were successful. The nests of all 3 hosts (*L. amaurocephalus*, *L. superciliaris*, and *M. oleagineus*) were globular, with side entrances hanging from roots under ravine banks along streams (Figure 1A–1C). On average, all nests were placed at 1.2 ± 0.9 m above water (minimum–maximum = 0.2–4.0 m; $n = 62$ nests), and the parasitized nests were located at 1.8 ± 0.6 m above water ($n = 9$ nests). We also monitored 117 nests of 11 other passerines species (e.g., *M. olivaceus*, *M. striaticollis*, *Myiobius barbatus*, *My. villosus*, *Onychorhynchus coronatus*, and *Rhynchocyclus fulvipectus*) with similar globular nest structures, but none of them were parasitized.

Clutch Size and Eggs

The host species deserted 4 of the parasitized nests found in the Pantiacolla station during 2013 (56%; 3 nests of *L. amaurocephalus* and 1 of *M. oleagineus*) and accepted a cuckoo egg at 3 nests (43%; 2 nests of *L. amaurocephalus* and 1 of *M. oleagineus*). All nests were parasitized after the clutch was completed, and only 1 cuckoo egg was deposited in each nest; 1 ($n = 4$ nests) or 2 host eggs ($n = 2$ nests) were removed, possibly by the adult cuckoo, and were found cracked under the nests. The clutch size of host species varied between 2 eggs ($n = 22$ nests) and 3 eggs ($n = 34$ nests). Host eggs were completely white and, on average, measured 18.9 ± 0.9 × 14.2 ± 0.6 mm ($n = 132$ eggs; Figure 1C–1E). By contrast, cuckoo eggs were white with brown spots and, on average, measured 19.9 ± 0.5 × 14.7 ± 0.4 mm ($n = 7$ eggs; Figure 1C–E). We observed differences in egg fresh mass among species (Kruskal-Wallis test, $\chi^2 = 19.18$, df = 3, $P < 0.001$; Figure 2A), where Pavonine Cuckoo eggs were 16.7% heavier than those of *L. amaurocephalus*, *L. superciliaris*, and *M. oleagineus* (Tukey's HSD; $P < 0.001$, $P = 0.020$, and $P < 0.001$, respectively); all the host species had similar egg masses (Tukey's HSD, $P = 0.998$). The Pavonine Cuckoo eggs, however, were very small compared to the adult mass

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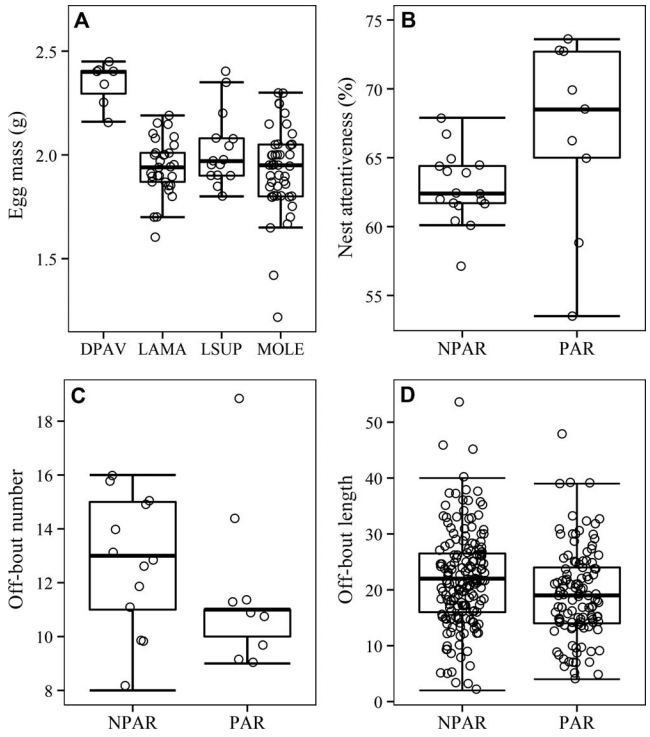


FIGURE 2. Comparative data on (**A**) egg mass of *Dromococcyx pavoninus* and 3 of its hosts; and daytime incubation behavior in parasitized and nonparasitized nests of *Leptopogon amaurocephalus*: (**B**) nest attentiveness, (**C**) off-bout number, and (**D**) off-bout length. Abbreviations: DPAV = *D. pavoninus*; LAMA = *L. amaurocephalus*; LSUP: *L. superciliaris*; MOLE: *Mionectes oleagineus*; PAR = parasitized; NPAR = nonparasitized.

(5.05%), which is a common strategy in avian brood parasites. Overall, 25% of host eggs ($n = 32$ eggs) hatched in nonparasitized nests (including losses due to predators and abandonment), whereas only 1 egg (8%; $n = 12$ eggs) hatched in parasitized nests. The percentage of parasitic eggs that hatched was 33% ($n = 6$ eggs). If we consider only successful nests, 81% of host eggs ($n = 21$ eggs) hatched in nonparasitized nests, whereas none of the host eggs ($n = 1$ egg) hatched in parasitized nests. The remaining parasitized nests found in other stations were not monitored continuously, and we are not sure whether these were abandoned, depredated, or successful.

Incubation Behavior

We monitored incubation behavior in 3 nests of *L. amaurocephalus* for a total of 28 days (672 hr). Two of these nests were nonparasitized (432 hr of continuous monitoring), and 1 was parasitized (240 hr of continuous monitoring). Overall, incubation investment by adults varied significantly between the parasitized nest and the nonparasitized nests. On average, incubation attentiveness was 4% higher on the parasitized nest (66.8 ± 6.8%) than on the nonparasitized nests (62.8 ± 2.6%; Mann-Whitney *U*-test, $z = 121$, $P = 0.036$; Figure 2B). This result was supported when we compared off-bout length between the parasitized nest and the nonparasitized nests (Mann-Whitney *U*-test, $z = 90$, $P = 0.000$; Figure 2C); off-bout lengths were shorter in the parasitized nest (19.4 ± 8.1 min) than in the nonparasitized nests (22.9 ± 9.5 min). However, the off-bout number did not vary significantly between the parasitized nest (11.7 ± 3.1 trips day^{-1}) and the nonparasitized nests (12.5 ± 2.5 trips day^{-1}; Mann-Whitney *U*-test, $z = 9{,}610.5$, $P = 0.292$; Figure 2D). Clearly, more nests are needed before we can generalize this change in incubation length to brood parasitism.

Pavonine Cuckoo eggs hatched in only 2 parasitized nests. The first was an *L. amaurocephalus* nest with 2 host eggs and 1 parasitic egg; only the cuckoo egg hatched, whereas the 2 host eggs were ejected and found under the nest 4 days after hatching (the cuckoo nestling may have ejected these eggs). The second was an *M. oleagineus* nest with 2 host eggs and 1 parasitic egg; the cuckoo egg and 1 host egg hatched, and the other host egg was expelled 4 days later; the 2-day-old host nestling was found dead with evident injuries, presumably induced by the cuckoo nestling (Figure 3). Furthermore, during handling for measurements, the young, blind cuckoo nestling bit the researchers' fingers on several occasions, suggesting aggressive behavior toward other nestling on the nest (Figure 3). The cuckoo nestling was found dead on day 8 of development, without evident injuries or starvation signs.

Nestling Period

The Pavonine Cuckoo nestling period, obtained from a single successful nest of *L. amaurocephalus*, was 24 days; the nestling period of the hosts was usually 5 days shorter (19.1 ± 1.4 days, $n = 8$ nests). The cuckoo nestling also developed more slowly after hatching than host nestlings (Figures 4 and 5); the calculated specific growth rate (k) of the Pavonine Cuckoo (0.23), based on the mass of 1 nestling, was lower than the means (± SD) of 0.27 ± 0.02 for *L. amaurocephalus* ($n = 5$ nestlings) and 0.31 ± 0.05 for *M. oleagineus* ($n = 6$ nestlings) (Figure 4A). On the last day in the nest, the cuckoo nestling weighed 32.85 g, with a relative mass of 70.8% in relation to Pavonine Cuckoo adult mass (~46.4 g; Dunning 2008) (Figure 6A). Compared to the hosts, the cuckoo nestling was 246% larger than adult *L. amaurocephalus* (13.3 g; $n = 38$ individuals) and 284% larger than adult *M. oleagineus* (11.5 g; $n = 71$ individuals). Growth rates (k) for the cuckoo nestling based on tarsus and wing lengths were 0.16 and 0.17, respectively. Growth rates of tarsus and wing in nestlings of the 2 hosts were faster than that of the cuckoo nestling (tarsus: 0.20–0.23; wing: 0.20–0.21; Figure 4B, 4C). When the cuckoo nestling fledged, its wings were 42.3% shorter than those of adult Pavonine Cuckoos (134.1 ± 4.05 mm; $n = 18$ individuals; Payne 2005), whereas the

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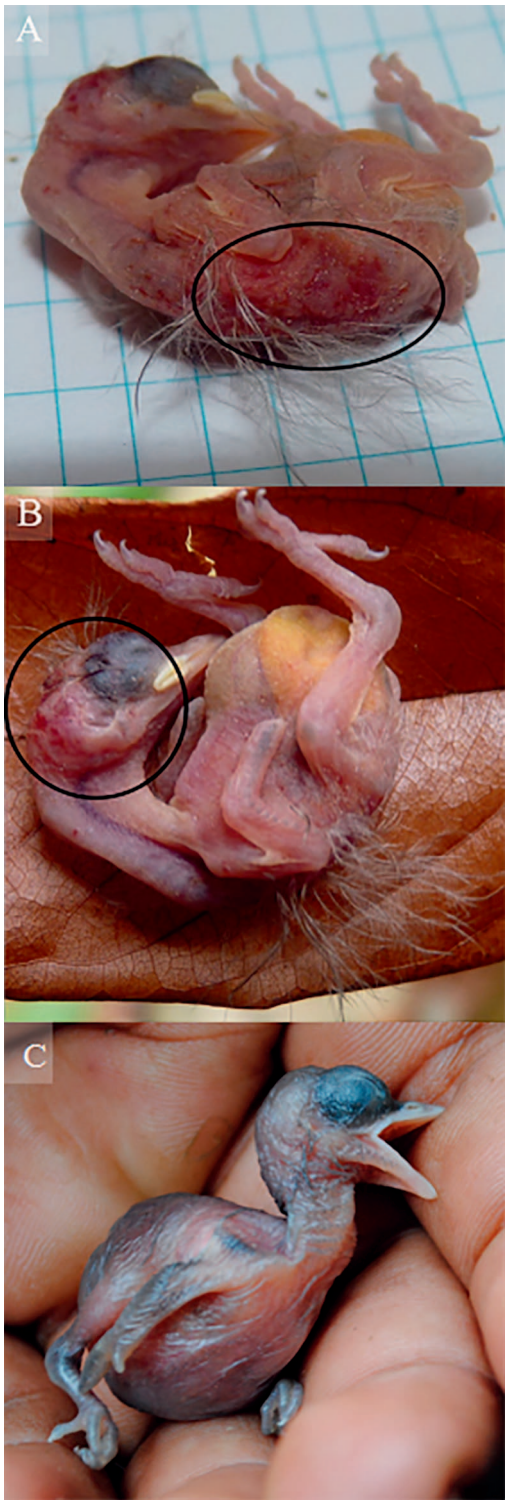


FIGURE 3. Evidence of aggressive behavior (attacks) toward a host nestling by a nestling Pavonine Cuckoo. (**A**) Back blood trauma on host nestling. (**B**) Blood trauma on skull of host nestling. (**C**) Cuckoo nestling attacks the hand of a researcher during measurements.

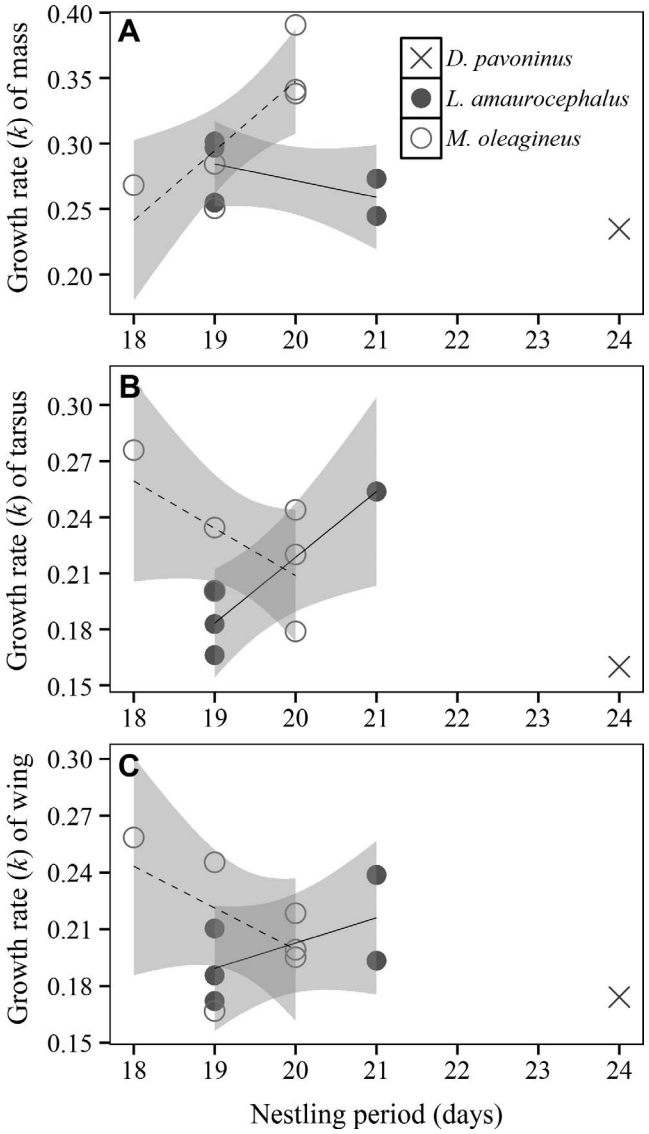


FIGURE 4. Relationship between growth rate—(**A**) mass, (**B**) tarsus length, and (**C**) wing chord—and nestling period in *Dromococcyx pavoninus* and 2 of its hosts, *Leptopogon amaurocephalus* and *Mionectes oleagineus*, obtained from 12 nests monitored in the buffer zone of Manu National Park, Peru, 2008–2014. Each point represents a nestling.

wings of host nestlings were 33.7–29.1% shorter than those of adults (60.5± 3.4 mm; $n = 71$ individuals) (Figure 6B). Similarly, the tarsus was 26.5% shorter in the cuckoo fledgling than in adults (27.35 ± 1.2 mm; $n = 18$ individuals; Payne 2005); and in *M. oleagineus*, the tarsus was 7.8% shorter in fledglings than in adults (15.1 ± 0.8 mm; $n = 71$ individuals); but tarsus length was similar between fledgling and adult *L. amaurocephalus* (15.2 ± 0.7 mm; $n = 38$ individuals) (Figure 6C).

We obtained food-provisioning rates from 3 nests of *L. amaurocephalus*, 2 of them nonparasitized and 1 parasit-

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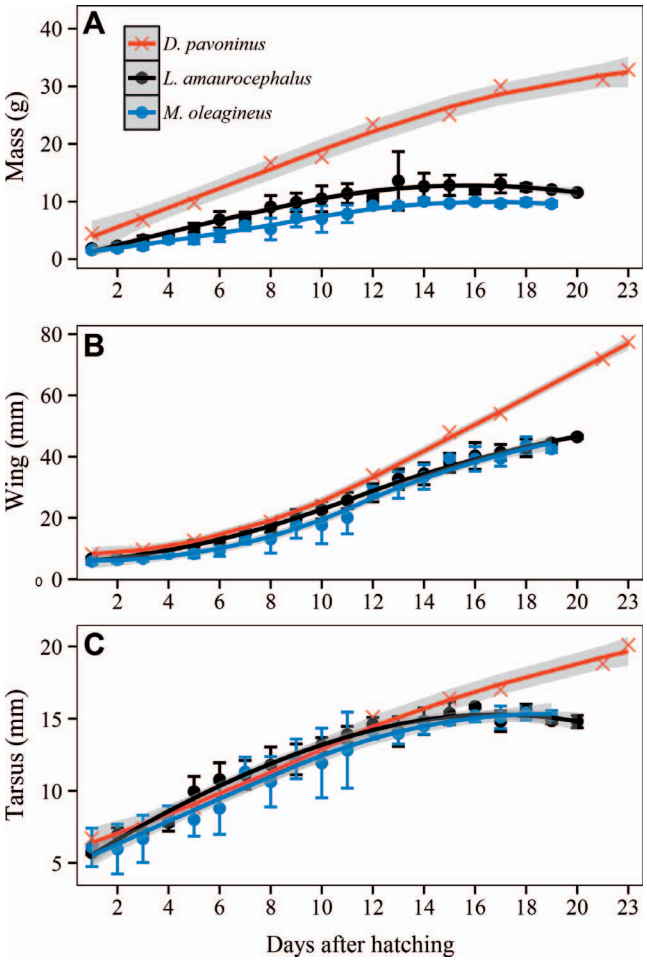


FIGURE 5. Growth curves for (**A**) mass, (**B**) tarsus length, and (**C**) wing chord throughout the nestling period in *Dromococcyx pavoninus* and 2 of its hosts, *Leptopogon amaurocephalus* and *Mionectes oleagineus*, obtained from 16 nests monitored in the buffer zone of Manu National Park, Peru, 2008–2014. Data points and error bars are estimated means and standard deviations, respectively.

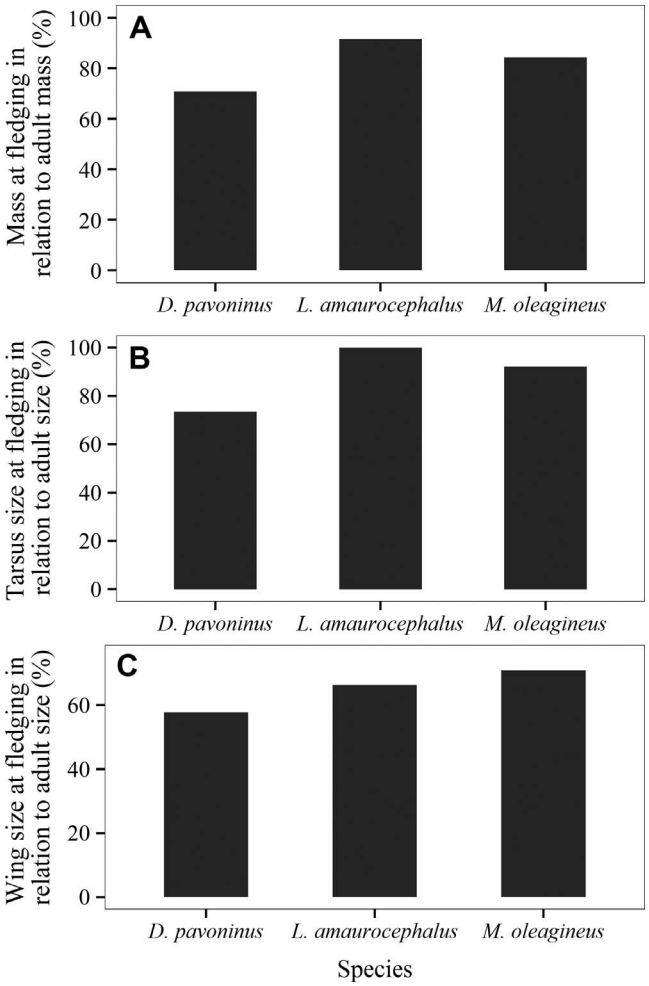


FIGURE 6. Development of (**A**) mass, (**B**) tarsus length, and (**C**) wing chord at fledging as percentages of adult length in *Dromococcyx pavoninus* and 2 of its hosts, *Leptopogon amaurocephalus* and *Mionectes oleagineus*.

ized. The rate in the parasitized nest (2.1 ± 0.7 feedings hr^{-1} $nestling^{-1}$) was greater than that in the nonparasitized nests (1.1 ± 0.4 feedings hr^{-1} $nestling^{-1}$), and this difference was significant (*t*-test, $t = -5.19$, $P < 0.001$; Figure 7). The burden of rearing a cuckoo nestling, therefore, appears to be about twice as great for *L. amaurocephalus* compared to rearing its own young.

Only one cuckoo nestling completed the nestling period. On day 2 of development, the nestling was highly aggressive, opening its bill and pecking us when we took it out of its nest for measurements. The nestling was completely naked, with dark skin, closed eyes, and white commissures, and the bill was dark gray at the base and had a white tip (Figure 8A). On day 4, the gray pinfeathers began to emerge on the back and head; the eyes were partially open, surrounded by light gray ocular skin. On day 6, the bill was completely black; bright yellow pinfeathers began to emerge on flanks, throat, wings, and tail; and it expelled a brown liquid stool when handled. On day 9, its eyes were fully open; pinfeathers had emerged throughout the body; orange feathers began to emerge on secondaries, wing coverts, breast, and belly; and the flanks were bright yellow. On day 11, black feathers with a yellow sheen had unsheathed on its back, head, shoulder, and tail. Unsheathed feathers were yellow on the chest and belly, gray-yellow on the throat, and buffy with black margins on the wings. On day 16, the feathers on the throat and chest of the nestling were grayer, its naked orbital skin was very conspicuous, and it had an indistinct pale superciliary. On day 22, the nestling kept its crest conspicuously erected. On day 24, the nestling was very active and expelled a brown liquid stool with an abnormally strong smell. By the next day, the nestling was found outside the nest, ~2 m away. Its plumage coloration resembled that of its host, *L.*

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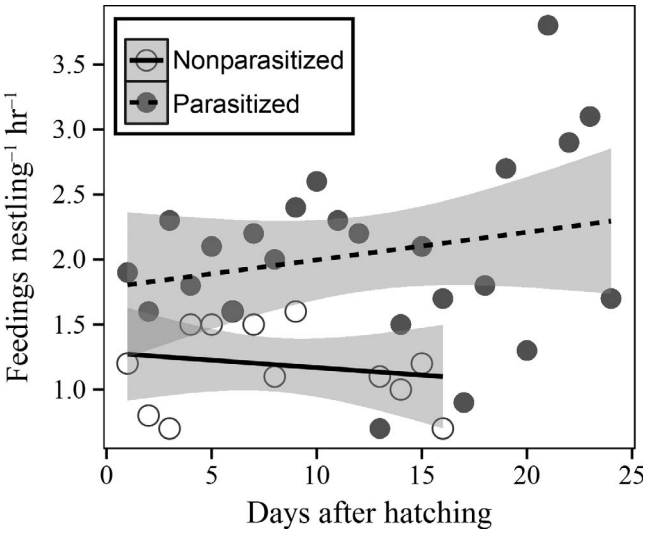


FIGURE 7. Comparison of feeding rate between parasitized and nonparasitized nests of *Leptopogon amaurocephalus*, monitored during a complete nestling period.

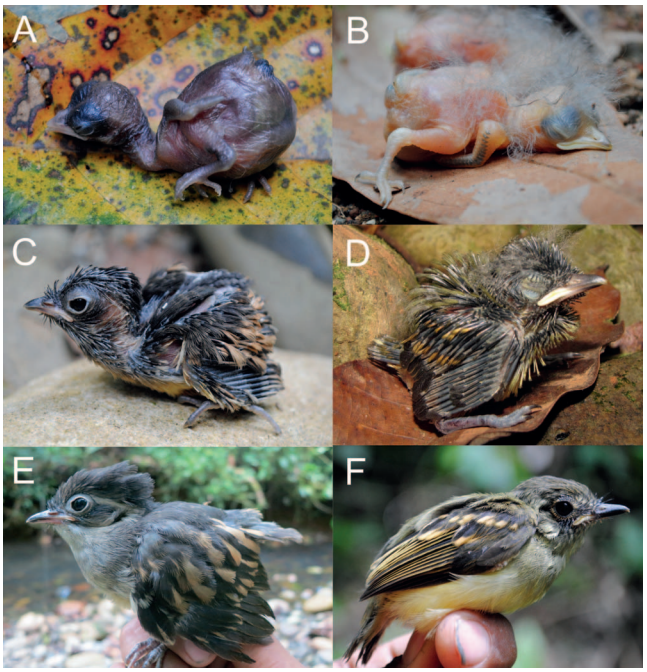


FIGURE 8. Photographic comparison of the morphological development of *Dromococcyx pavoninus* and *Leptopogon amaurocephalus* nestlings throughout the nestling period. (**A**) *D. pavoninus* nestling at day 2. (**B**) *L. amaurocephalus* nestling at day 2. (**C**) *D. pavoninus* nestling at day 11. (**D**) *L. amaurocephalus* nestling at day 10. (**E**) *D. pavoninus* nestling at day 22. (**F**) *L. amaurocephalus* nestling at day 18. Photo credit: Manuel A. Sanchez-Martínez

amauraocephalus, and we want to call attention to this. Although, at hatching, the skin color differed substantially between the host (pink) and the parasitic cuckoo (black), when nestling feathers started to emerge, plumage coloration on the belly, throat, and wing bars were alike (Figure 8).

DISCUSSION

The Pavonine Cuckoo was first reported as parasitic 65 yr ago, but little information on its natural history has been published since then (Lowther 2013). The present study begins to fill this gap in the natural history of this Neotropical parasitic cuckoo. Only 4 species have previously been reported as hosts of the Pavonine Cuckoo, and 3 of them are small flycatchers that build closed globular nests with side entrances (Payne 2005, Lowther 2013). Here, we report an additional 3 hosts of Pavonine Cuckoo that also follow this pattern—small birds with globular nests, which were the only species parasitized among 143 passerine species whose nests we monitored in the area during 7 yr (G. A. Londoño personal observation). We did not observe how the Pavonine Cuckoo lays its eggs in these small nests; in Australia, cuckoos in the genus *Chrysococcyx*, which also parasitize small, dome-shaped hosts, squeeze their shoulders into the entrance to lay directly in the nest (Brooker et al. 1988).

The female Pavonine Cuckoo synchronized its laying with that of its host, such that laying always occurred after the host had begun laying. This behavior may indicate that female cuckoos monitor host nests before parasitizing them; hosts that are parasitized before they have begun laying often abandon their nests (Davies 2000). The laying period is also when the nest is most likely to be neglected by the host (Mermoz 1996) and therefore easier to parasitize undetected. This egg-laying synchronization between parasite and hosts has also been observed between the Common Cuckoo and its host the Great Reed Warbler (*Acrocephalus arundinaceus*), in which 94.4% of the eggs were laid in host nests during the 4 days of host laying (Moskàt et al. 2006).

Egg mass differed between the Pavonine Cuckoo and its hosts, the host eggs being 16.7% lighter than the cuckoo eggs. As is typical of cuckoos, the Pavonine Cuckoo's eggs were much smaller than those of nonparasitic species of similar body mass. The adult Pavonine Cuckoo is almost 3× heavier than its adult hosts, yet its eggs are just 1.2× heavier than the hosts' eggs. Furthermore, egg coloration was markedly dissimilar between parasite and hosts (Figure 1D–1F), which may reflect the darker conditions inside the domed nests, which would make it more difficult for the host to detect differences in egg coloration. This mismatch between host–parasite egg size and coloration, however, may have caused the high abandonment rate (60%) of parasitized nests of *L. amaurocephalus* after the cuckoo laid its egg in the nest. Both egg size and coloration

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are important parameters in the ability of a host to recognize foreign eggs (Davies 2000, Marchetti 2000, Krüger and Davies 2004, Payne 2005, Stoddard and Stevens 2010), and egg acceptance by the host is more likely when the parasite's eggs match the coloration of its preferred host (Davies 2000, Mark 2013). Given that parasitized nests appear not to fledge host young, the selection for rejecting Pavonine Cuckoo eggs or abandoning the nest should be strong. On the other hand, the extremely low incidence and erratic presence (in only 2 of 7 yr) may make it difficult for stronger rejection of parasitic eggs to evolve, given the possible costs of mistaken identity (Rothstein and Robinson 1998). Some desertion events may be attributable to disturbance caused by researchers or to other factors besides parasitism, given the moderate desertion rate in nonparasitized nests (~34%).

At hatching, the nestling was naked and similar to most brood-parasitic cuckoo nestlings. Payne (2005) suggested that this lack of natal down might be an adaptation of nestlings to be more sensitive to the touch of host eggs, which they evict. We suspect that nestling parasites expelled host eggs in 2 nests, because we found host eggs cracked under these nests. Only one of the parasitized nests in our study produced a parasite fledgling. That nestling left the nest when it was 70.8% of adult body weight, which is low compared to other brood-parasitic cuckoos (>80% of adult weight; Payne 2005); however, it was completely covered by feathers and was actively moving when we found it outside of the nest. It is possible that disturbance of the nest during nestling measurements caused the nestling to fledge prematurely (Payne 2005). The Pavonine Cuckoo's nestling period (24 days) was longer than those of other small brood-parasitic cuckoos (18–20 days; Payne 2005), including the closely related Striped Cuckoo (*Tapera naevia*, 18 days; Payne 2005). It was also 5 days longer than the nestling period of *L. amaurocephalus* (19 days), which represents an extra cost to the host that can decrease the capacity of the foster parents to invest in the next reproductive attempt (Hoover and Reetz 2006). The expulsion of feces when handled may represent an antipredator adaptation as it does in the Great Spotted Cuckoo (Canestrari et al. 2014).

We found that the Pavonine Cuckoo negatively affects its host's breeding success in 2 ways. The first is when the female cuckoo removes a host egg from the nest, reducing the effective clutch size of the host. Removal of host eggs has been proposed as a strategy of parasites to improve the incubation efficiency of their eggs (Rothstein 1990, Lerkelund et al. 1993). Second, cuckoo nestlings appeared to directly remove the rest of the host eggs and to kill the host nestlings. We obtained evidence of these behaviors, which have been interpreted as a tactic to ensure that all parental care of the foster parents is delivered to the cuckoo nestling (Payne 2005). Otherwise, the shorter developmental time of the host might lead to abandonment of the nest before the parasitic young fledged.

Another cost of brood parasitism for the host was increased parental investment in parasite nestlings and eggs. We observed higher nest attentiveness and higher nestling provisioning rates in parasitized nests than in nonparasitized nests. This higher parental investment has also been observed in Yellow Warblers (*Setophaga petechia*) parasitized by Brown-headed Cowbirds (*Molothrus ater*), in which parasitized nests had significantly higher nest attentiveness than nonparasitized nests (Tewksbury et al. 2002). Similarly, higher provisioning rates have been reported for nests with parasite nestlings than for nests without parasites of the same species (Dearborn et al. 1998, Hoover and Reetz 2006). Thus, the presence of a cuckoo nestling in nests of *L. amaurocephalus* might represent a higher cost to host adults, but more data are needed to understand whether this increase in parental investment reduces future reproductive success by decreasing adult survival, decreasing energy available for investment in subsequent broods, or increasing the time until the next reproductive attempt (Dearborn et al. 1998, Tewksbury et al. 2002, Hoover and Reetz 2006).

One of the most remarkable results reported here is that brood parasitism was so infrequent in our study sites in southeastern Peru. Only 3 host species were ever found with brood-parasitic eggs in their nests, and those were in only 2 yr of the study. Tropical bird communities seem to be remarkably resistant to brood parasitism. Even where the Shiny Cowbird is present in South America, it is largely restricted to open, human-dominated habitats. The 60% abandonment rate we found suggests that the 3 host species have some defenses against even this low level of brood parasitism. The Pavonine Cuckoo's possible mimicry of a host's nestling plumage further suggests that hosts may have evolved nestling recognition and are engaged in a coevolutionary arms race with this parasite. Perhaps the only way the Pavonine Cuckoo can succeed is by exploiting naive hosts for 1–2 yr and then moving on. In Cocha Cashu, *Dromococcyx* spp. were never found in more than 1 yr defending the same territories (S. K. Robinson and J. Terborgh personal observation). Taken together, these results suggest that lowland tropical-forest bird communities may be extremely resistant to brood parasitism.

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Author contributions: M.A.S.-M., G.A.L., and S.D. conceived the study, degigned the methods, and analyzed the data. M.A.S.-M. conducted the research and collected the data. M.A.S.-M., G.A.L., S.D., and S.K.R. wrote the paper. G.A.L. and S.K.R. contributed substantial materials, resources, and/or funding.

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