

The breeding biology of *Grallaria* and *Grallaricula* antpittas

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ABSTRACT. *Grallaria* and *Grallaricula* antpittas are poorly known ground antbirds (Formicariidae), which reach their center of diversity in the tropical Andes region. Here we review published literature on the reproductive ecology of these two genera, summarizing and synthesizing the information. Nests have been described for 13 of the 31 species of *Grallaria* and four of the eight species of *Grallaricula*. For both genera, nests are open cups placed either against a strong support (e.g., tree trunks; *Grallaria*) or with multiple small supports (e.g., vine tangles; both genera). Nest lining is generally sparse, with nest cup composition ranging from humid material (e.g., moss) to primarily sticks and leaf material, depending on the species. *Grallaria* typically lay two bluish-green to turquoise eggs, sometimes with spotting, whereas *Grallaricula* lay 1–2 eggs with heavy markings and pale brown or buffy (rarely light green) background coloration. For the few species where information is available, both male and female parents are believed to participate in building, incubation, and nestling provisioning, with high incubation attentiveness (often >90%, especially later in incubation), and incubation periods of 17–21 d (*Grallaria*) and 15–20 d (*Grallaricula*). *Grallaria* nestlings are frequently fed earthworms (*Oligochaeta*) in addition to a variety of arthropods. Nestlings have pale skin (*Grallaria*) or dark skin (both genera), with pale or dark down (*Grallaria*) or red-brown down (*Grallaricula*). Nestlings in both genera usually have brilliant orange mouth linings and cloacas, and usually fledge 15–19 d post hatching. Rapid probing, where adults rapidly thrust their bills into the nest and lining, is commonly observed across species during incubation and nestling periods, but its function remains unknown. Overall, our knowledge of the breeding biology of antpittas has improved significantly in recent years. However, much remains to be learned for most species.

SINOPSIS. La biología reproductiva de aves de los géneros *Grallaria* y *Grallaricula*

Las aves de los géneros *Grallaria* y *Grallaricula* son especies de la familia Formicariidae cuales viven en el sotobosque. Estas son poco conocidas y llegan a su mayor diversidad en la región de los Andes Tropicales. Presentamos una revisión de la literatura sobre la ecología reproductiva de estos dos géneros, resumiendo y sintetizando la información disponible. Los nidos han sido descritos para los 13 de las 31 especies de *Grallaria* y para cuatro de las ocho especies de *Grallaricula*. Para los dos géneros, los nidos son tasas abiertas cuales se apoyan contra un objeto fuerte (ej., troncos de árboles; *Grallaria*) o cuales utilizan múltiples apoyos (ej., varios bejucos; los dos géneros). La capa interior es generalmente escasa, con la composición del nido consistiendo de materiales húmedos (ej., musgos) hasta principalmente compuesto por palitos y hojas, dependiendo de la especie. Las especies de *Grallaria* típicamente ponen dos huevos de color azul-verde o turquesa, algunas veces con puntos, mientras que las especies de *Grallaricula* ponen 1–2 huevos fuertemente pintadas con color de base pardo hacia pardo rojizo (rara vez siendo un verde claro). Para las pocas especies para la cual existe información, se cree que los dos padres macho y hembra participan en la construcción, incubación y aprovisionamiento de comida a los pichones, con un alto nivel de atención durante la incubación (muchas veces >90%, especialmente durante las últimas fases de la incubación), con periodos de incubación de 17–21 días (*Grallaria*) y de 15–20 días (*Grallaricula*). Los pichones de *Grallaria* son frecuentemente aprovisionados con lombrices (*Oligochaeta*) y así también con una variedad de artrópodos. Los pichones se caracterizan por tener una piel pálida (*Grallaria*) u oscura (los dos géneros), con plumón clara u oscuro (*Grallaria*) o rojizo-pardo (*Grallaricula*). Los pichones de los dos géneros típicamente tienen un gape y cloacas de color naranja brillante y típicamente vuelan del nido a los 15–19 días después de la eclosión del huevo. Una acción en la cual los adultos insertan rápidamente sus picos dentro del nido en la primera capa es comúnmente observada en las especies durante los periodos de incubación y cría de pichones, pero su función sigue siendo desconocida. En resumen, nuestro conocimiento sobre la biología reproductiva de estas especies ha mejorado significativamente en los últimos años. Sin embargo, mucho nos queda para aprender para la mayor parte de estas especies.

Key words: behavior, egg, nest, nest construction, nestling, nest site, seasonality

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Few groups of birds epitomize the Neotropics like antpittas and anthruses, collectively known as the ground-antbirds (Formicariidae; Sibley and Monroe 1990). With 51 species in five genera, antpittas are distributed throughout much of Central and South America. From sea level to altitudes over 4000 m, antpittas inhabit a variety of habitats, ranging from lowland rainforest and deciduous scrub-forest to high-elevation shrub-grassland. They reach their highest diversity in the humid mid-elevation forests of the northern and central Andes (Krabbe and Schulenberg 2003). Although their characteristic songs are often heard, antpittas are quintessentially elusive and rarely seen with more than fleeting glimpses. It is not surprising, therefore, that their habits are poorly known. Indeed, due to their secretive nature, the natural history of antpittas remains largely shrouded in mystery.

Describing the natural history of these unique birds is important beyond simple novelty or curiosity. Quantitative natural history information is critical to understanding broader patterns in nature and allowing the formation and testing of hypotheses of ecological or evolutionary significance. Understanding variation in behavioral characteristics associated with breeding, such as nest placement and nest architecture, for example, may elucidate either phylogenetic relationships among taxa (Zyskowski and Prum 1999) or selective pressures acting on breeding biology (Martin 1998). From a conservation perspective, human-related habitat destruction is particularly severe on the very Andean slopes where antpitta species richness reaches its peak. In fact, 19 species of antpittas are currently recognized at some level of conservation concern (Birdlife International 2004). Basic breeding data such as where, when, and the length of time the birds are engaged in breeding activities may allow biologists to predict the potential impacts of land use practices on populations of threatened species.

Not surprisingly, Alexander F. Skutch provided the first detailed account of antpitta breeding biology by observing a pair of Streak-chested Antpittas (*Hylopezus perspicillatus*) at their nest in Costa Rica (Skutch 1969). Subsequently, at a Pale-billed Antpitta (*Grallaria carrikeri*) nest in Peru, Wiedenfeld (1982) expanded on Skutch's work describing the behavior of adult antpittas at their nests, and reviewed antpitta breed-

ing information available at the time. Despite a handful of breeding-related notes published since Wiedenfeld's (1982) review, nests had been described for only six of 31 *Grallaria* species and only two of eight *Grallaricula* species prior to 2003 (Krabbe and Schulenberg 2003). Furthermore, a significant portion of these data were from captive birds (Bell and Bruning 1976) or of suspect validity (Krabbe and Schulenberg 2003, Martin and Greeney 2006, Greeney et al. 2006a). During recent years, however, a growing body of information has become available, greatly improving our understanding of antpitta breeding biology. New data have been published, ranging from descriptions of nests, eggs, and nestlings, to the documentation of incubation and nestling periods in the wild and the quantification of adult behavior during nest-building, egg-laying, incubation, and provisioning of nestlings. Here we provide a synthesis of the current state of knowledge, emphasizing work since Wiedenfeld's (1982) review, of the breeding biology of *Grallaria* and *Grallaricula* antpittas.

METHODS

We searched the published literature to acquire, to the best of our knowledge, all relevant reference material from which to synthesize information on the breeding biology of two genera of antpittas, *Grallaria* and *Grallaricula* (hereafter referred to as antpittas). We considered only direct evidence of breeding (e.g., active nests and fledglings) rather than indirect evidence (e.g., breeding condition and singing), except where published accounts of secondary material conflict with other sources (e.g., J. Bull in Wiedenfeld 1982, Schäfer 2002).

We were able to find published sources of such data for the following species: Great Antpitta (*Grallaria excelsa*), Giant Antpitta (*G. gigantea*), Variegated Antpitta (*G. varia*), Scaled Antpitta (*G. guatemalensis*), Moustached Antpitta (*G. alleni*), Plain-backed Antpitta (*G. haplonota*), Tawny Antpitta (*G. quitensis*), Rufous-faced Antpitta (*G. erythrotis*), White-bellied Antpitta (*G. hypoleuca*), Pale-billed Antpitta (*G. carrikeri*), Jocotoco Antpitta (*G. ridgelyi*), Chestnut-crowned Antpitta (*G. ruficapilla*), Watkins's Antpitta (*G. watkinsi*), Rufous Antpitta (*G. rufula*), Hooded Antpitta (*Grallaricula cucullata*), Ochre-breasted Antpitta (*G. flavirostris*),

Peruvian Antpitta (*G. peruviana*), Rusty-breasted Antpitta (*G. ferrugineipectus*), and Slate-crowned Antpitta (*G. nana*). Additionally, we include observations of Stripe-headed Antpittas (*Grallaria andicolus*; J. Fjelds , unpubl. data) in Peru, and of Chestnut-naped Antpittas (*G. nuchalis*; J. Jui a, J. Harris, and H. Greeney, unpubl. data) in Ecuador. We have omitted commonly cited data concerning *Grallaria guatemalensis* from Trinidad (Belcher and Smooker 1936) because the authors did not actually confirm that the nest belonged to this species. We also do not include data on nest architecture for Rufous-faced Antpitta (Bell and Bruning 1976) because the nest was constructed in captivity. For brevity, throughout the article, we use only the species name in our discussions.

RESULTS

Nests. Antpitta nests are invariably open cups, most commonly less than 3 m above ground (Table 1, but with some notable exceptions; Holley et al. 2001, Kofoed and Auer 2004, Martin and Dobbs 2004, Greeney et al. 2008). Previous descriptions of domed structures or ground nesting were found to be incorrect (Sch fer 2002, Greeney et al. 2006a). Materials used in the outer layers of nests vary between and within species (Tables 1 and 2), but linings are uniformly sparse and composed of fine materials such as rootlets, dry grass, mammal hairs, or fungal rhizomorphs. In general, for both genera, nest materials tend to reflect the microhabitats where nests are built, for example, a high percentage of bamboo-derived materials in the nests of *ruficapilla* (Martin and Greeney 2006) and *nana* (Greeney and Sornoza 2005, Greeney and Miller 2008), both inhabitants of *Chusquea* bamboo thickets.

For *quitensis* (Greeney and Martin 2005) and *andicolus* (Fjelds , pers. comm.), tightly clustered new and old nests suggest high site fidelity (Greeney and Martin 2005). Similar clustering of new and old nests has also been found for *peruviana* (Greeney, unpubl. data) and suggested for *flavirostris* (Holley et al. 2001).

Grallaria. The nests of *Grallaria* appear to fall into two general categories with respect to nest placement (Table 1). Some species use sites with multiple small supports, such as small branches, vine tangles, and bamboo stems,

whereas other species use well-supported sites against tree trunks, fallen logs, or broken stumps. For *guatemalensis*, the species with the largest number of nest descriptions over the broadest geographic distribution, both types of nest placement have been described, with most nests in well-supported sites against vertical trunks and on top of fallen trees (Edwards and Lea 1955, Miller 1963, Rowley 1966, Dobbs et al. 2001, 2003).

The types of materials used to construct nests generally follow a similar dichotomous pattern (Table 1). *Grallaria* nests appear to fall into one of two categories, those built mainly of moss and those consisting mostly of dead or drier material such as sticks and leaves. For four Ecuadorian nests of *alleni*, however, two were moss-free, one contained little moss, and was well decorated with moss (Freile and Renjifo 2003, Greeney, unpubl. data). Additionally, two nests in Colombia were described as being made predominantly of moss (Londo n et al. 2004). Similarly, closely related *guatemalensis* shows some variation in the amount of moss used in construction, especially between different geographic locations (Dobbs et al. 2001 and references therein). Mud has reportedly been used in nest construction by both *quitensis* and *watkinsi*, but the degree to which it is used within and among species is unclear.

Nests are basically round cups, often described by previous authors as shallow (Donahue 1985, Quintela 1987, Protomastro 2000, Kofoed and Auer 2004). Compared to *Grallaricula* nests, however, they are relatively deep (i.e., more than half as deep as wide; Table 1). In one case, *rufula* adults were not visible above the rim of the nest when incubating (Greeney and Gelis 2005a).

Grallaricula. Unlike the *Grallaria* antpittas, the nests of *Grallaricula* are typically in rather poorly supported locations such as thin saplings, vine tangles, small branches, or thin bamboo shoots. Such sites have proved to be precarious, even resulting in the loss of a nestling from the nest of *peruviana* in Ecuador (Greeney et al. 2004b).

Grallaricula nests are relatively shallow cups (Table 2). As for *Grallaria* nests, *Grallaricula* nests seem to fall into two categories based on materials used, perhaps largely dictated by preferred nesting microhabitats. *Grallaricula nana* uses mostly or entirely dead, dry material,

Table 1. Characteristics of the nests of 13 species of *Grallaria* antpittas.

Species ^a	N	Primary materials	Height (m) [N]	Substrate	Outer			Inner		Reference(s)
					diameter (cm) [N]	height (cm) [N]	diameter (cm) [N]	depth (cm) [N]		
<i>Grallaria exelsa</i>	3	moss, dead leaves	6.9 [3]	trunk or thick fork	37.5 [2]	22.5 [2]	13 [2]	7.5 [2]	Koefed and Auer 2004	
<i>Grallaria varia</i>	6	dead leaves	1.8 [5]	stump or trunk	20 ^b [1]	?	11.5 [2]	4.3 [2]	Erard 1982, Quintela 1987, Protomastro 2000	
<i>Grallaria guatemalensis</i>	9 ^c	dead leaves, sticks, moss ^d	0.9 [7]	small branches or trunk	18.5 [8]	14.3 [8]	9.9 [7]	5.1 [8]	Edwards and Lea 1955, Miller 1963, Rowley 1966, Dobbs et al. 2001, 2003	
<i>Grallaria alleni</i>	5	dead leaves, sticks, moss ^e	1.3 [4]	small branches or stem clusters	19.7 [3]	17.6 [3]	10.8 [3]	5.4 [3]	Freile and Renjifo 2003, Londoño et al. 2004	
<i>Grallaria haplonota</i>	1	dead leaves, sticks	1.6 [1]	small vines	24 [1]	16 [1]	10.5 [1]	8.5 [1]	Greeney et al. 2006a	
<i>Grallaria quitensis</i>	5	moss, mud	1.2 [4]	small branches or forks	20 [3]	14 [3]	10.6 [3]	6.8 [3]	Greeney and Martin 2005	
<i>Grallaria hypoleuca</i>	1	sticks, rootlets	1.3 [1]	thick tree fork	14.2 [1]	?	10.7 [1]	6.4 [1]	Price 2003	
<i>Grallaria andicola</i>	3	moss, leaves	3 [3]	small branches	?	?	?	?	J. Fjeldså pers. comm.	
<i>Grallaria nuchalis</i>	1	leaves, sticks	3 [1]	small branches	18.5 [1]	17 [1]	14 [1]	10 [1]	Juina et al. in review	
<i>Grallaria carrikeri</i>	1	leaves, sticks	3 [1]	horizontal trunk	19.5 [1]	?	13 [1]	5 [1]	Wiedenfeld 1982	
<i>Grallaria ruficapilla</i>	1	sticks, dead leaves	2 [1]	small braches	27 [1]	18.5 [1]	11.5 [1]	7 [1]	Martin and Greeney 2006	
<i>Grallaria watkinsi</i>	2	sticks, leaves, mud	3.6 [2]	small branches	21.8 [2]	8.3 [2]	10.7 [2]	5 [2]	Martin and Dobbs 2004, Greeney et al. 2008	
<i>Grallaria rufula</i>	2	moss	1.4 [2]	stump or trunk	20 [1]	12 [1]	9.5 [2]	5.75 [2]	Whitney 1992, Greeney and Gelis 2005a	

^a*Erythrolis* was excluded because the only described nest was from captivity (Bell and Bruning 1976).

^bIt is unclear from Quintela's (1987) description if this refers to inner or outer diameter.

^cThe account in Belcher and Smooker (1936) was not included as the nest was not confirmed to be of this species.

^dIn all cases, moss seems to be a relatively small component.

^eA few nests had considerable amounts of moss, others little.

Table 2. Characteristics of the nests of four species of *Grallaricula* antpittas.

Species	N	Primary materials	Height (m) [N]	Substrate	Outer		Inner		Reference(s)
					diameter (cm) [N]	height (cm) [N]	diameter (cm) [N]	depth (cm) [N]	
<i>Grallaricula flavirostris</i>	4	moss	2.4 [4]	small branches	9.7 [4]	5.5 [1]	?	4.6 [1]	Holley et al. 2001, Maillard and Vogel 2003
<i>Grallaricula peruviana</i>	2	moss	1.6 [2]	small branches	13.5 [1]	6 [1]	8.5 [1]	4.5 [1]	Greeney et al. 2004a, b,
<i>Grallaricula ferrugineipectus</i>	3	twigs, leaf rachises	0.8 [3]	small branches	14.7 [3]	4.7 [3]	5.7 [3]	2.6 [3]	Schwartz 1957
<i>Grallaricula nana</i>	3	twigs, dead leaves	1.9 [5] ^a	small branches	10.8 [3]	5.9 [3]	6.8 [3]	2.6 [3]	Greeney and Somoza 2005, Greeney and Miller 2008

^aIncluding two inactive nests.

predominantly of bamboo origin, seemingly providing effective camouflage in their preferred *Chusquea* bamboo microhabitat (Greeney and Sornoza 2005, Greeney and Miller 2008). In contrast, *flavirostris* (Holley et al. 2001, Maillard and Vogel 2003), and *ferrugineipectus* (Schwartz 1957) use more humid materials.

Nest building. Nest building behavior is perhaps the least studied aspect of antpitta breeding biology. In *excelsa* (Kofoed and Auer 2004) and *peruviana* (H. Greeney, unpubl. data), males and females build nests together. In addition, for most other species of antpittas where data are available, both sexes add material to the nest during incubation. These observations suggest that both sexes also participate during the construction phase, but there are few data for the period prior to egg laying.

Seasonality. The degree to which breeding is seasonal for antpittas is unclear. A fledgling *ridgelyi* observed at the end of the dry season in southern Ecuador suggests breeding during the dry season (Greeney and Gelis 2005b), whereas a fledgling *gigantea* observed at the end of the wet season in northwestern Ecuador suggests breeding during the wetter months (Greeney and Nunnery 2006). Nest records for *nana* (southern and northeastern Ecuador; Greeney and Sornoza 2005, Greeney and Miller 2008), *nuchalis* (southeastern and western Ecuador; Fjeldså and Krabbe 1990, Juiña et al., unpubl. data), and *ruficapilla* (northeastern Ecuador; Martin and Greeney 2006) suggest breeding during drier periods. However, in central Ecuador, *ruficapilla* appear to breed exclusively during the wetter months (M. Juiña, pers. comm.). *Grallaria quitensis* apparently breeds exclusively during the drier months in northeastern Ecuador (Greeney and Martin 2005, H. Greeney, unpubl. data). *Grallaria excelsa* (Kofoed and Auer 2004) and *watkinsi* have only been reported breeding during wetter months (Martin and Dobbs 2004, Greeney et al. 2008), and *guatemalensis* seems to prefer wetter periods throughout its range (Edwards and Lea 1955, Miller 1963, Rowley 1966, Dobbs et al. 2001, 2003). The single nest of a *hypoleuca* was reported during the wet season in northeastern Ecuador (Price 2003). *Grallaria alleni* have been reported breeding in both dry and wet months west of the Andes in Colombia and Ecuador (Freile and Renjifo 2003, Londoño et al. 2004, Greeney and Gelis 2006). Similarly, in northeastern Ecuador,

peruviana has been found nesting twice, once in mid-dry season and once during the wetter period (Greeney et al. 2004a,b). A nest of *rufula* in northeastern Ecuador was found during the wetter months, but one in southeastern Ecuador was during the drier months. In Bolivia and Costa Rica, *flavirostris* reportedly breeds during the wetter months (Holley et al. 2001, Maillard and Vogel 2003), whereas nests have been found during both wet and dry seasons in eastern Ecuador (Greeney and Gelis, unpubl. data) and a fledgling was reported in the early dry season in western Ecuador (Solano-Ugalde et al. 2007).

It is strongly suspected that *gigantea* shows elevational movements on the east slope of Ecuador, with birds moving down in elevation during the drier period from September to December (M. Lysinger, pers. comm.). However, this does not seem to be the case in western Ecuador (J. Freile, pers. comm.). During other periods of the year, we have never observed adults directly or heard vocalizations at lower elevations (2000–2300 m). From September to December, however, multiple adults are easily encountered. Concurrently with apparent movements to lower elevations, we have noted the almost complete lack of vocalizations by this species (H. Greeney, pers. obs.). The lack of singing during the period when adults are present at lower elevations suggests seasonal breeding at higher elevations that coincides with the wet season (February–June).

In summary, we lack sufficient data for any one species, certainly across their geographic range, to fully assess the seasonality of antpitta breeding. Certainly, seasonality would be expected to vary geographically, even within species, because the degree of seasonality varies greatly among tropical locations. Most likely, species in strongly seasonal habitats breed more seasonally than those in regions where antpittas may take advantage less extreme changes, perhaps breeding opportunistically year round.

Eggs, laying, clutch size, and water loss.

For both genera, eggs are generally short-subelliptical (Palmer 1962) and rounder than most passerine eggs we have observed. Egg coloration, however, varies between genera (Tables 3 and 4). Laying time has been documented for three species of *Grallaria* (Table 3), and all lay eggs in the late afternoon (Dobbs et al. 2003, Greeney et al. 2006a, Greeney and

Harms 2008). For *Grallaricula*, laying time has been documented at one nest of *peruviana*, with its single egg laid in the morning (Greeney 2006). As suggested by Dobbs et al. (2003), late afternoon laying by *Grallaria* may reflect their terrestrial habits. Most passerines lay early in the morning (Skutch 1952, Davis 1955, H. Greeney, R. Dobbs, P. Martin, and R. Gelis, pers. obs.), possibly an adaptation to avoid additional flight costs of carrying a fully formed egg while foraging during the day. Terrestrial birds presumably experience relatively little cost in carrying an egg, and may thus be freed from this constraint. Although other suboscines (e.g., tyrant flycatchers and manakins) also tend to lay later in the day than oscines (e.g., mid-day; Skutch 1952), suggesting a possible phylogenetic constraint for *Grallaria*, late afternoon laying by *Grallaria* nevertheless appears to be somewhat unique among passerines.

The rate at which eggs lose mass during incubation may be used as a surrogate for estimating water loss during this period (Ar and Rahn 1980). Other than reports of water loss for *ruficapilla*, *guatemalensis*, and *peruviana* (Tables 3 and 4), each from a single clutch (Dobbs et al. 2003, Greeney 2006, Martin and Greeney 2006), we know nothing about water loss from antpitta eggs.

Grallaria. All *Grallaria* eggs described have a turquoise to blue-green ground color (Table 3). Other descriptions of egg coloration were found to be in error (see Krabbe and Schulenburg 2003, Martin and Greeney 2006). Eggs are largely unmarked, contrasting with other genera of Grallariinae (Wetmore 1972, Tostain 1986, Tostain and Dujardin 1988). Price (2003) described evenly distributed red-brown markings on the eggs in a single clutch of *hypoleuca* eggs. Observations of multiple clutches of *quitensis* reveal intraspecific variation, with eggs varying from unmarked to fairly strongly marked with red-brown flecking and blotching (Greeney and Martin 2005).

Clutches in *Grallaria* almost always consist of two eggs across all species examined to date (Table 3). One single-egg clutch has been reported for *rufula*, and this may have been an incomplete clutch, a clutch where one egg was lost to predation, or a true one-egg clutch (Whitney 1992). Clutch sizes of two have been reported for other antpitta genera (Wiedenfeld 1982, Tostain and Dujardin 1988, Robinson et al.

Table 3. Eggs, clutch sizes, and the laying and incubation periods of 13 species of *Gnallaria* antpittas.

Species	Egg markings?	Mean clutch size [N]	Laying interval (days)	Time of day laying	Incubation period ^a (days) [N]	% diurnal incubation [N]	% daily loss of original egg mass [N]	Reference(s)
<i>Gnallaria excelsa</i>	no	2 [1]	?	?	?	99 [1]	?	Koefed and Auer 2004
<i>Gnallaria varia</i>	no	1.7 [3]	?	?	17 [1]	?	?	Euler 1900, Ihering 1900, Énard 1982, Protomastro 2000
<i>Gnallaria guatimalensis</i>	no	2 [6]	2	13:00–18:00	19 [1]	87–96 [1]	0.85 [2]	Edwards and Lea 1955, Rowley 1966, Dobbs et al. 2001, 2003
<i>Gnallaria alleni</i>	no	2 [4]	?	?	?	62–88 [1]	?	Freile and Renjifo 2003, Londoño et al. 2004, Greeney and Gelis 2006
<i>Gnallaria haplonota</i>	no	2 [1]	2	15:30–17:45	?	83.6 [1]	?	Schönwetter 1979, Greeney et al. 2006a
<i>Gnallaria quitensis</i>	variable	2 [5]	2	after 16:00	21.5 [1]	72–97 [2]	?	Greeney and Martin 2005, Greeney and Harms 2008
<i>Gnallaria erythrotis</i>	no	2[6] ^b	?	?	15[1] ^c	?	?	Bell and Bruning 1976
<i>Gnallaria andicola</i>	no	2 [1]	?	?	?	?	?	J. Fjeldså, pers. comm.
<i>Gnallaria hypoleuca</i>	yes ^d	2[1]	?	?	?	88[1]	?	Schönwetter 1979, Price 2003
<i>Gnallaria nuchalis</i>	no	?	?	?	?	?	?	Schönwetter 1979
<i>Gnallaria ruficapilla</i>	no	2 [2]	?	?	?	?	0.67 [2]	Martin and Greeney 2006, H. Greeney, unpubl. data
<i>Gnallaria watkinsi</i>	no	2 [1]	?	?	?	?	?	Martin and Dobbs 2004
<i>Gnallaria rufula</i>	no	1.5 [2]	?	?	?	?	?	Whitney 1992, Greeney and Gelis 2005a

^aMeasured from clutch completion to hatching of first egg.

^bSix clutches laid by the same bird in captivity.

^cFrom a nest in captivity, this figure is widely cited, but it is not clear from the reference how correct it is.

^dIt is unclear from the description, but markings may have been stains from the nest (Price 2003), Schönwetter (1979) does not mention markings.

Table 4. Eggs, clutch sizes, and the laying and incubation periods of five species of *Grallaricula* antpittas.

Species	Mean clutch size [N]	Laying interval (days)	Time of laying	Incubation period ^a (days) [N]	% diurnal incubation [N]	% daily loss of original egg mass [N]	Reference(s)
<i>Grallaricula cucullata</i>	1 ^b	?	?	?	?	?	Schönwetter 1979
<i>Grallaricula flavirostris</i>	1.8 [4]	?	?	17–21 ^c	23 ^d	?	Holley et al. 2001, Maillard and Vogel 2003
<i>Grallaricula peruviana</i>	1 [1]	n/a	05:30 – 09:00	20 [1]	78 [1]	0.9 [1]	Greeney et al. 2004a, Greeney 2006
<i>Grallaricula ferrugineipectus</i>	2 [3]	?	?	16–17 [1] ^c	93 ^d	?	Schwartz 1957
<i>Grallaricula nana</i>	1 [3]	n/a	?	?	65 [1]	?	Greeney and Sornoza 2005, Greeney and Miller 2008

^aMeasured from clutch completion to hatching of first egg.

^bOnly one egg was described, but it is not known if this represents a complete clutch.

^cEstimated.

^dData are based on the percentage of arrivals where an adult was present at nests during incubation.

2000, Greeney et al. 2005), with the exception of *Grallaricula* (see below).

Grallaricula. Described eggs for *Grallaricula* are fairly consistent between nests, species, and geographic areas. All are described as having a background of pale brown or buffy with fairly heavy markings of black, brown, and white. The only exception are the eggs of *ferrugineipectus* (Schwartz 1957), described as having a light green ground color. Unlike *Grallaria*, *Grallaricula* antpittas appear to have more variable clutch sizes, seeming to vary little within species, but ranging from 1 to 2 between species (Table 4). Sample sizes are small, however, and more data are needed to assess the relative frequencies of one- and two-egg clutches across species.

Incubation. In general, antpittas show high levels of nest attendance during incubation, often covering the eggs for over 90% of the day (Tables 3 and 4). A high degree of nest attendance is possible because both adults incubate the eggs. Generally, high levels of attendance are not reached until later in the incubation period, and most species show limited attendance during (and just after) egg laying. Often, low levels of attendance are seen for several days after completion of the clutch (Dobbs et al. 2001, Greeney 2006, Greeney et al. 2006a, Greeney and Harms 2008). For *quitensis* (Greeney and Harms 2008), *alleni* (Londoño et al. 2004), and *peruviana* (Greeney 2006), studies suggest that eggs are left unattended for the longest periods during early morning. Interactions between adult *Grallaria* at nests are usually minimal, with switches occurring with little temporal overlap of the two adults. Sometimes adults gently peck each others' cheeks or pass material from one to the other (e.g., *quitensis*; Greeney and Martin 2005), but switches are usually unceremonious (e.g., *hypoleuca*; Price 2003). At the few *Grallaricula* nests that have been studied, adults usually do not switch places at the nest. Instead, one adult leaves just prior to the other's arrival (Greeney and Sornoza 2005, Greeney 2006). Although the relative role of the sexes is unknown for most species, in sexually dimorphic *peruviana* at least, the female spends the night on the nest, but the male performs 58% of daytime incubation duties (Greeney 2006). In all species, it appears that both sexes participate in incubation, inferred by the observation of two adults exchanging places at nests during the incubation period.

Grallaria. Incubation periods are not known for most *Grallaria* antpittas. *Grallaria erythrotis* in captivity incubated for 15 d (Bell and Bruning 1976), whereas most other species appear to incubate for 17–20 d (Table 3). The longest reported incubation period for the genus is 21.5 d for *quitensis*, perhaps due to cooler temperatures at its high-altitude nesting site. Greeney and Harms (2008) even report the successful hatching of a clutch after weathering an ice storm. Periods of attendance are generally long, with the mean duration of incubation bouts ranging from 0.9–1.1 h for *quitensis* (Greeney and Martin 2005, Greeney and Harms 2008), 0.9–1.7 h for *alleni* (Londoño et al. 2004), 1.9 h for *guatemalensis* (Dobbs et al. 2003), and 2.2 h for *haplonota* (Greeney et al. 2006a). *Grallaria excelsa* had mean on bouts of 1.5 h at one nest in Venezuela (Kofoed and Auer 2004), and *hypoleuca* had mean bouts of 1.3 h at one nest in eastern Ecuador (Price 2003). Additionally, Erard (1982) recorded incubation bouts lasting 1–2.5 h for *varia*.

In *quitensis*, the most thoroughly studied *Grallaria*, daily coverage of the eggs gradually increased from less than 40% on the day after clutch completion to 97% later in incubation, with a mean of 86% coverage after the onset of regular incubation rhythms (Greeney and Harms 2008). Otherwise, *Grallaria* show a range of daily coverage from 62% to 99% (Table 3).

Grallaricula. For *Grallaricula*, reported estimates of incubation periods range from 15 to 20 d (Table 4). The longest confirmed incubation period is that of *peruviana* where the single egg hatched after 20 d at one nest in eastern Ecuador (Greeney 2006). At one nest of *peruviana*, the mean duration of incubation bouts was 0.6 h, with daily percent coverage of just 50% post laying, and increasing to over 90% near hatching (Greeney 2006). For the only other species with published information, *nana*, the mean duration of incubation bouts was 0.9 h (Greeney and Sornoza 2005).

Nestlings. One striking feature of antpitta nestlings is their seemingly underdeveloped stage at fledging. In all species that we have observed, nestlings leave the nest in juvenal plumage that looks little like that of adults. They are unable to fly and at one nest of *alleni*, the single nestling leaped to the ground below the nest and immediately ran and stumbled into a protected spot under a root mass cavity in

the leaf litter (H. Greeney, unpubl. data). We suggest that fledglings spend the first week or so in such situations, waiting for the attention of adults. Described fledging events are few, but for *alleni* (Greeney and Gelis 2006) and *watkinsi* (Greeney et al. 2008), fledging appears to be fairly unceremonious, with nestlings hopping downward from the rim, seemingly in response to adult vocalizations below the nest. Almost nothing, however, is known of the postfledging period. Dobbs et al. (2003) noted a musky smell associated with nestling *guatemalensis*, but we have not noticed such a smell at the nests of other species, and the meaning of this remains unclear.

Grallaria. The nestling period for most species of *Grallaria* remains unknown, with estimates ranging from 15–19 d (Table 5). *Grallaria* nestlings appear to fall into two distinguishable types and colors. Nestlings of some species are pale or pink-skinned with whitish or grayish down, whereas others are dark-skinned and have dark down (Table 5). One similarity reported for all species with described nestlings, however, is the bright orange to red-orange mouth linings and cloacas. In dark-skinned species, these areas contrast with the surrounding skin, but are also obvious in the paler-skinned species. We know little about growth rates and feather development, but, for *guatemalensis* in southern Ecuador, eyes opened at 6–8 d and primary pin feathers broke their sheaths at around 9–10 d (nestling period 17–19 d; Dobbs et al. 2001).

Grallaricula. Although the nestlings of *Grallaricula* are described for only three species, they contrast with those of *Grallaria* in two major ways. First, all known *Grallaricula* nestlings are naked and dark-skinned at hatching. Secondly, at least for *peruviana* (Greeney et al. 2004b), *nana* (Greeney and Miller 2008), and *flavivirostris* (H. Greeney and R. Gelis, unpubl. data), nestlings develop red-brown down similar to that of *Grallaria* nestlings. Like *Grallaria* nestlings, however, most *Grallaricula* nestlings have strongly contrasting orange mouth linings and cloacas. Surprisingly, however, the recently described nestling of *nana* from northeastern Ecuador has a pale-yellow gape with a white mouth lining (Greeney and Miller 2008). This trait is also seen in nestlings of this species in southeastern Ecuador (B. Harris, pers. comm.). Until the nestlings of additional *Grallaricula* are described, the significance of this deviation from

Table 5. Nestling characteristics and parental care in 11 species of *Grallaria* anpittas.

Species	Young nestling skin color	Nestling down color	Nestling period	Nestling food ^a	Feeding visits per nestling/h (no. of young, age) ^b	% brooding (age of young) ^b	Reference(s)
<i>excelsa</i>	?	?	?	Oligochaeta, Arthropoda	0.2 (1, mid)	12 (mid)	Koefed and Auer 2004
<i>varia</i>	black	black	?	?	?	?	Érard 1982, Quintela 1987, Protomastro 2000
<i>guatemalensis</i>	black	black	17–19	Oligochaeta, Lepidoptera, Coleoptera, ^c	0.5–1.3 (2, young)	79–83 (young)	Miller 1963, Dobbs et al. 2001, 2003
<i>alleni</i>	dark gray-pinkish	black	15–17	Diplopoda Oligochaeta, Tettigoniidae, Anura	1.1–1.5 (2, mid) 1.1 (2, old) 1.7–2.5 (2, mid-old)	23–34 (mid) 12 (old) 2 (mid to old)	Freile and Renjifo 2003, Londoño et al. 2004, Greeney and Gelis 2006, H. Greeney unpubl.
<i>quitensis</i>	pink	gray	?	?	?	?	Greeney unpubl.
<i>erythrotis</i>	dark	dark	?	?	?	?	Bell and Bruning 1976
<i>hypoleuca</i>	?	gray	?	?	?	?	Price 2003
<i>nuchalis</i>	dark	dark	?	Oligochaeta, Arthropoda	0.9 (2, young) 1.9 (2, young)	9 (young) 0 (mid)	Juñá et al. in review
<i>carrikeri</i>	?	?	?	Oligochaeta	1 (2, young)	60 (young)	Wiedenfeld 1982
<i>ruficapilla</i>	pink	gray	18	?	?	?	Martin and Greeney 2006, H. Greeney unpubl.
<i>watkinsi</i>	pink	gray-black	?	Arthropoda, Oligochaeta	1.2 (2, mid)	76 (mid)	Martin and Dobbs 2004, Greeney et al. 2008
					1.3 (2, old)	22 (old)	

^aGiven in relative order of abundance in reports.^bNestlings within two days of pin feathers breaking their sheaths were considered “mid” aged, otherwise they were considered “young” or “old.”^cBeetle adults and larvae described in Dobbs et al. (2001, 2003) were incorrectly identified as Carabidae, but are instead Scarabaeidae.

Table 6. Nestling characteristics and parental care in four species of *Grallaricula* antpittas.

Species	Young nestling skin color	Nestling period	Nestling food ^a	Feeding visits per nestling/h (no. of young, age) ^b	% brooding (age of young) ^b	Reference(s)
<i>flavirostris</i>	?	14–16 ^c	?	?	?	Holley et al. 2001
<i>peruviana</i>	dark	?	?	?	?	Greeney et al. 2004b
<i>ferruginepectus</i>	dark	14–16 ^c	Arthropoda	?	?	Schwartz 1957
<i>nana</i>	?	?	Arthropoda, Lepidoptera, Oligochaeta	5.4 (1, old)	3.4 (old)	Greeney and Miller 2008

^aGiven in relative order of abundance in reports.

^bNestlings within 2 d of pin feathers breaking their sheaths were considered “mid” aged, otherwise they were considered “young” or “old.”

^cEstimated.

other species remains unknown. The nestling periods of *Grallaricula* spp. are similar, but slightly shorter than those of *Grallaria* (Table 6).

Parental care. As far as is known for antpittas, both sexes care for nestlings. This aspect of antpitta breeding, however, is less studied than incubation.

Grallaria. For species of *Grallaria* with published information, adults apparently deliver multiple prey items per nest visit. Most species are reported to feed a variety of invertebrate prey, especially earthworms (Oligochaeta), but identification is difficult because prey items are delivered in such large quantities (Table 5). Earthworms are often mentioned as nestling food, but their relative importance in the diet of nestlings is largely unknown. *Grallaria watkinsi* delivered earthworms on only 15% of trips to the nest (Greeney et al. 2008) and *alleni* delivered earthworms on 22% of trips (Greeney and Gelis 2006). At *carrikeri* (Wiedenfeld 1982), *guatemalensis* (Dobbs et al. 2001), and *nuchalis* (Juiña et al. in review) nests, adults brought earthworms on 37%, 42%, and 47% of deliveries, respectively. *Grallaria guatemalensis* in southern Ecuador fed nestlings a potentially toxic millipede, but how commonly this occurs is unknown (Dobbs et al. 2003). During this same study, Dobbs et al. (2003) reported that a brooding adult regurgitated food for nestlings, but this is the only reported instance of regurgitation by antpittas. To our knowledge, the single report of a frog being fed to nestling *alleni* (Greeney and Gelis 2006) is the only instance of vertebrates in nestling diets. Feeding and brooding rates vary

greatly among species, as well as within species depending on the age of the nestlings (Table 5). Because sample sizes are small, however, the factors affecting this variation are unknown, and may vary based on time of day or weather (Dobbs et al. 2003).

Nestling *Grallaria* typically produce fecal sacs only in the presence of adults, usually accompanied by an obvious and vigorous shaking of the entire body and rump as they turn around in the nest. This invariably draws the attention of adults to their bright orange cloaca, allowing adults to retrieve the fecal sac. Nestling *alleni*, however, were observed to begin defecating in the absence of adults just prior to fledging (Greeney and Gelis 2006). Too few data are available to fully assess the rate at which adults consume or carry away fecal sacs, and how this relates to nestling age. *Grallaria watkinsi* adults ate 92% of fecal sacs from older nestlings (Greeney et al. 2008), whereas adult *guatemalensis* consumed 94% of fecal sacs at the nest for nestlings of a variety of ages (Dobbs et al. 2003). In contrast, *alleni* adults consumed only 39% of fecal sacs at the nest, carrying the rest away (Greeney and Gelis 2006).

As with most passerines, brooding of nestlings by antpittas decreases with nestling age (Table 5). Late in the nestling period, adults usually brood nestlings only during inclement weather (i.e., *watkinsi*; Greeney et al. 2008). For example, *guatemalensis* adults at a nest in Ecuador brooded very young nestlings for 83% of the observation period, whereas adults at a second nest brooded 10–12-d-old nestlings for only 23%

of the day (Dobbs et al. 2003). At these nests, adults brooded during bouts with mean durations of 30 and 18 min, respectively. At a nest of *watkinsi*, breeding in hot, deciduous forests of southwestern Ecuador, adults spent most of the day shading, rather than brooding, nestlings (Greeney et al. 2008). At this same nest, adults spent up to 7% of the day at the nest together, something not observed in other species. For most species, it appears that an adult spends the night at the nest until young fledge.

Grallaricula. There is little to report on parental care in this genus (Table 6). Greeney and Miller (2008) studied *nana* in northeastern Ecuador and found that a single nestling was fed by both adults who, in contrast to *Grallaria*, delivered single prey items. This species also showed relatively high feeding rates compared to *Grallaria*, perhaps reflecting the delivery of single prey items.

The single nestling produced 1.2 fecal sacs per hour, except on the day before fledging, when fecal sac production dropped to 0.5/h. All fecal sacs were carried from the nest by adults. The nestling was brooded for less than 5% of the observation period, mostly during heavy rain. Observations of *peruviana* and *flavirostris* suggest that these generalizations may hold true for other *Grallaricula* as well (H. Greeney and R. Gelis, unpubl. data).

Additional adult behaviors at nests. Antpittas engage in a wide range of behaviors while incubating and brooding. For example, *peruviana* occasionally forages from the nest while incubating, making short sallies from the rim to capture prey (Greeney 2006). Video evidence also revealed that *peruviana* occasionally brings food to the nest during incubation. On the few occasions this was witnessed, the adult usually ate the prey themselves, but a female once brought a prey item that was fed to the incubating male (Greeney 2006). This appears to be the only reference to courtship feeding for either genus of antpitta. Other behaviors, such as the characteristic rocking motion of adults while settling on eggs or nestlings, have recently been observed with the aid of video cameras (Dobbs et al. 2001). Antpittas frequently preen themselves and, occasionally, their nestlings while at the nest.

Behavior when approaching the nest is generally similar among antpitta species. Adult

peruviana (Greeney et al. 2004b, Greeney 2006) and *flavirostris* (Holley et al. 2001, Maillard and Vogel 2003) reportedly skulk low and approach from below, and this seems generally true for all species we have observed.

Sleeping and vigilance. Among most species of antpittas, adults frequently close their eyes, apparently sleeping for short periods, while incubating or brooding. Periods of nonvigilant activities at the nest, such as preening, probing, and vocalizing, have not been described for most species. For the few species where it has been reported, *Grallaria* appears to be slightly less vigilant than *Grallaricula*. *Grallaria haplonota* adults spent 4.4% of their time at the nest in nonvigilant activities (Greeney et al. 2006a). Similarly, *quitensis* adults spent 3.9% of their time in activities that probably reduced their level of vigilance (Greeney and Harms 2008). In contrast, *peruviana* spent only 2.8% of its time nonvigilant (Greeney 2006), whereas *nana* adults were engaged in other activities 2.4% of their time at the nest (Greeney and Sornoza 2005). Although these differences may seem small, given an approximate mean of 190 h of daylight incubation time for most antpittas, a 1% change in time budget would result in almost two additional hours of nonvigilant activity at the nest.

Vocalizations. Most antpittas studied to date vocalize at the nest, particularly, during incubation, with *Grallaricula* antpittas apparently less vocal than *Grallaria*. *Grallaria* vocalizations at the nest vary from the muted trills of *guatemalensis* (Dobbs et al. 2003) and *excelsa* (Koefed and Auer 2004; although they did not confirm that it was the adult that was vocalizing) to the extremely vocal *haplonota* that has been recorded singing up to 52 times/h while incubating (Greeney et al. 2006a). Similarly, *quitensis* adults may vocalize up to 35 times/h, with a mean of 4.5 songs/h across the entire incubation period at one nest (Greeney and Martin 2005, Greeney and Harms 2008). Adults at one *quitensis* nest sang at rates up to 17 songs/min, with bouts of singing lasting as long as 4.2 min (Greeney and Harms 2008). During the nestling period, both male and female *watkinsi* sang at rates of 5.8 songs/h (Greeney et al. 2008), but *alleni*, with similar-aged nestlings, did not appear to vocalize at the nest (Greeney and Gelis 2006).

Rapid probing. All antpittas that we have observed have engaged in a behavior termed “rapid probing” or “tremble thrusting” (Haftorn 1994, Greeney 2004). The maneuver is apparently performed by both sexes and involves the rapid thrusting of the bill into and out of the nest lining in a sewing machine-like fashion. First described in antpittas at *guatemalensis* nests (Dobbs et al. 2001), the behavior seems fairly uniform in performance across all antpittas observed to date, except that the notably more erratic movements of *alleni* probes differ from the smoother movements of others (Greeney and Gelis 2006). Interestingly, although common among other birds as well (Haftorn 1994, Greeney et al. 2006b), this behavior was not observed (although observations were limited) at two nests of Thrush-like Antpittas (*Myrmothera campanisoma*; Greeney et al. 2005, Greeney, unpubl. data).

Rapid probing occurs during both incubation and nestling stages, and its function remains unclear (Deeming 2002, Greeney et al. 2006b). Several hypotheses have been proposed, including shaking debris from the nest (Haftorn 1994), turning the eggs (Hartshorne 1962), nest construction or improvement (Greeney et al. 2006b, Greeney and Merino 2007), and parasite removal (Haftorn 1994, Dobbs et al. 2003). At nests of *nana* (Greeney and Sornoza 2005) and *haplonota* (Greeney et al. 2006a), rapid probing apparently causes rolling of the egg, but its high frequency suggests that egg-turning is not its primary function.

The use of this behavior across antpitta species and by other species of birds suggests that it may be an important, relatively unexplored aspect of nesting biology. *Grallaricula peruviana* (Greeney 2006) and *Grallaria quitensis* (Greeney and Harms 2008) rapid probe up to 7.5 and 8.3 times/h, respectively. During incubation, *haplonota* rapid probed up to 38 times during any given bout of movement at the nest, and included at least one such movement during 87% of its nonvigilant activity bouts at the nest (Greeney et al. 2006a). *Grallaricula nana* rapid probed during 48% of all movement bouts during incubation, for a mean of 1.2 rapid probes per bout (Greeney and Sornoza 2005). *Grallaria quitensis* rapid probed at a rate of 3.1 times/h (Greeney and Harms 2008). Rapid probing by Slate-crowned Antpittas was not observed at a nest with older nestlings, but adults spent little

time at the nest except to feed young (Greeney and Miller 2008). Our observations suggest that rapid probing may serve a variety of functions and that further investigation of its function, evolution, and maintenance may prove valuable in understanding other aspects of breeding biology, such as variation in nest structure and ectoparasite loads.

Nest maintenance. During incubation, most species of antpittas continue to add material to the nest, usually adding to the lining. *Grallaria quitensis* brought lining material to the nest during 28% of nest visits throughout incubation (Greeney and Harms 2008). In addition, while sitting at the nest during all phases of nesting, most species spend some time arranging or shifting material around the nest. Little material, however, seems to be added once eggs hatch.

Nest predators. Little is known about predators of antpitta nests. Dobbs et al. (2001) reported that nestling *guatemalensis* were eaten by a Tayra (*Eira barbara*; Mustelidae). On several occasions, they also observed Mountain coatis (*Nasua olivacea*; Procyonidae) pass close to nests, with the adults remaining motionless and undetected. Greeney and Gelis (2005a) reported the predation of a *rufula* nest with eggs by a Turquoise Jay (*Cyanolyca turcosa*). Apart from these, however, no information is available.

In general, the response of antpittas to potential predators is to remain motionless and flush from nests only when discovery seems eminent. Several species, including *varia* (Érard 1982, Donahue 1985, Protomastro 2000), *guatemalensis* (Dobbs et al. 2003), and *peruviana* (H. Greeney, unpubl. data), reportedly exhibit a characteristic behavior when approached at the nest. Adults slowly raise their bill to about a 70° angle, exposing the vertically streaked throat pattern toward the observer. This disruptive coloration makes them difficult to detect by human observers. At a nest of *watkinsi*, however, this behavior was not observed, and adults looked directly at the approaching observer (Martin and Dobbs 2004). Similarly, at a nest of *rufula*, a species where adults lack the vertically streaked throat pattern, we did not observe this behavior (H. Greeney and R. Gelis, unpubl. data).

Adults typically flush quickly and silently from nests. At a Scaled Antpitta nest, however, Dobbs et al. (2003) noted a wing fluttering distraction display. Our observations at many

subsequent nests suggest that distraction displays may be infrequent. Flush distance reported for most *Grallaria* is less than 2 m. For *Grallaricula*, our observations suggest that flush distance is generally closer to 8–10 m (Greeney, unpubl. data). Reasons for this difference remain unclear, but may reflect differences in nest predator assemblages.

DISCUSSION

All *Grallaria* antpitta nests reported to date are bulky open cups, but nest material, and possibly nest location, vary among species and may, in some cases, reflect phylogenetic relationships. For example, *ruficapilla*, *watkinsi*, and *nuchalis* are all closely related (Krabbe et al. 1999) and all use primarily sticks and leaves to build somewhat messy nests located relatively high above the ground among small branches. Most other *Grallaria* species, in contrast, tend to build tight nests composed primarily of moss and other herbaceous material, usually located relatively low, and on or against a trunk or main fork of a tree. There is little documented variation in the appearance of *Grallaria* eggs (only slight variation in spotting), but there appears to be some interspecific variation in the coloration of nestling skin and down (e.g., *ruficapilla* and *watkinsi*, again, show similarities that are consistent with a close phylogenetic relationship). Within *Grallaricula*, there also appears to be a dichotomous division between species building mossy nests versus dry-material nests, but little quantifiable difference in nest placement. *Grallaricula* eggs and nestlings appear to be fairly uniform, with the notable exception of the pale mouth lining of *nana* (Greeney and Miller 2008). Interestingly, it appears that deviations from the standard dark skin and dark down of *Grallaria* nestlings, as well as this difference in *nana*, all represent species that nest in more exposed habitats (e.g., bamboo and paramo). The adaptive significance of this is unknown, but may be related to light intensity or solar radiation levels. With sample sizes so small, however, much remains to be learned about the degree to which these characteristics vary among species and geographic races.

Despite recent work, the breeding biology and natural history of antpittas remains poorly known. Although descriptions of nests, eggs, and nestlings provide a broader sampling of antpitta breeding biology and morphology, we

still lack this basic information for most species and know almost nothing about possible variation in these characters within species. Nests remain undescribed in the literature for 29 of 51 (57%) antpitta species (*Pittasoma*, *Grallaria*, *Hylopezus*, *Myrmothera*, and *Grallaricula* combined). Further, sample sizes of greater than or equal to three nests are available for only eight of the 20 species (40%) for which the nest has been described. Thus, acquiring larger sample sizes of breeding data for species where few nests have been described is of utmost importance. Increased sample sizes of nest records within species will also facilitate a better understanding of breeding seasonality and its relationship with wet and dry seasons, which vary geographically. For most species, there are currently too few nest records within particular geographic regions to permit meaningful analysis of breeding seasonality and climate data.

The use of video cameras to document and quantify the behavior of adults at nests represents one of the most significant advances in recent work. However, the respective roles of each adult remain unknown for most species, in part because they are not sexually dimorphic and thus not distinguishable (with the exception of the sexually dichromatic *peruviana*). For most species, color-banding (or other marking techniques) will be needed to identify males and females recorded on video tapes. More generally, banding will be important for generating empirical data on site fidelity, annual survival, and longevity. Nevertheless, video work to date has revealed a number of important findings. For example, species of both genera, in particular many *Grallaria*, provision their nestlings with large numbers of earthworms.

The difficult task of locating nests has hindered our ability to study the breeding biology of antpittas. Although both species inhabit high elevations and relatively open habitats, and thus likely differ from most antpittas in numerous aspects of their breeding ecology and behavior, *quitensis* (Greeney and Martin 2005, Greeney and Harms 2008) and *andicolus* (J. Fjeldså, pers. comm.) offer rare opportunities for researchers to attain large datasets and thereby greatly improve our knowledge of antpitta territorial behavior, site fidelity, dispersal, survival, and reproductive success at both the individual and population levels. Such baseline data would provide an unparalleled basis for comparison

for previous and future studies of *Grallaria* species. Continued habitat alteration and forest fragmentation is a major conservation concern in the high Andes (e.g., *Polylepis* forest; FjeldsÅ 2002, Kessler 2002). Understanding the effects of degradation and fragmentation of *Polylepis* forests on the reproductive ecology of species such as *quitensis* and *andicolus* would provide valuable information that (1) is directly applicable to the conservation and management of *Polylepis* birds, and (2) provides a reference point for the conservation and management of vulnerable, but poorly known antpitta species in other habitats (e.g., upper tropical and subtropical forest at lower elevations).

Additionally, the Andean slopes and foothills, where most antpittas live, are under considerable threat through human alterations, and less than 5% of montane habitat in the northern Andes remains intact (Hendersen et al. 1991). While many species of antpittas may have evolved under conditions of natural habitat patchiness (e.g., created by frequent landslides in steep Andean terrain), historical natural disturbances generally created a mosaic of early successional growth, bamboo (e.g., *Chusquea*), and primary forest, as opposed to patches of forest in a landscape dominated by grazing and agricultural uses. As fragmentation has a well-recognized impact on predator assemblages and nesting success (e.g., Tewksbury et al. 2006), data on all aspects of antpitta breeding are desperately needed.

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