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COMMENT

Antpittas and worm-feeders: a match made by evolution? Evidence for a possible commensal foraging relationship between antpittas (Grallariidae) and mammals

Grallariidae e mamíferos: evidências de uma possível relação de comensalismo

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Commensal foraging relationships between two groups of animals frequently involve one following another and capitalizing on the prey flushed by the movement of the other (Alcock, 1997; Weins, 1989). In broad terms, three of the best documented associations involving vertebrates are birds and mammals following ants (Elliot, 1950; Júnior and Zara, 2007; Martins, 2000; Rylands *et al.*, 1989; Willis and Oniki, 1978, 1992), birds following birds (Baker, 1980; Bennett and Smithson, 2001; Hino, 1998; Robbins, 1981), and birds following mammals (see below). Such relationships between birds and mammals have been reported from many regions of the globe (Wiens, 1989), and documented mammalian "beater" species include a wide array of taxonomic groups including elephants (Ruggiero and Eves, 1998), deer (Herring and Herring, 2007), coatis (Sick, 1984), peccaries, wolves (Silveira *et al.*, 1997), armadillos (Di Giacomo and Di Giacomo, 2006; Komar and Hanks, 2002), manatees (Scott and Powell, 1982), whales (Harrison, 1979; Obst and Hunt, 1990), dolphins (Evans, 1982; Monteiro-Filho, 1992), domestic cattle (Burger and Gochfield, 1982; Heatwole, 1965; Källander, 1993), and primates (Boinski and Scott, 1988; Heymann, 1992; Stott, 1947; Zang and Wang, 2000). Similarly, the types of birds involved in such bird-mammal feeding relationships cover a broad taxonomic spectrum, and include Accipitridae (Robinson, 1994), Laridae (Harrison, 1979), Procellariidae (Obst and Hunt, 1990), Ardaeidae (Rice, 1954), Trogonidae (Stott and Selsor, 1961), Bucerotidae (Chapin, 1939), Cuculidae (Siegel *et al.*, 1989; Smith, 1971), and several families of Passeriformes (Di Giacomo and Di Giacomo, 2006; Komar and Hanks, 2002; Levey, 1999; Stott, 1947). Unlike the well studied relationships between birds and ants in the lowland Neotropics (Willis, 1969; Willis and Oniki, 1978, 1992; Willson, 2004), little is known about the commensal foraging associations of Andean birds. Largely anecdotal accounts of many species of passerines associated with highland army ants (*Labidus* spp., Ecitoninae), however, are scattered throughout the literature (Dobbs and Martin, 1998; Hilty, 1974; Nieto-R. and Ramírez, 2006; Rios *et al.*, 2008; Vallely 2001), including several species of antpittas (Grallariidae) (Greeney and Gelis, 2005; Kofoed and Auer, 2004; Nieto-

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R. and Ramírez, 2006). Here, I present observations of Andean antpittas, which suggest that they may, at least on a facultative basis, partake in commensal foraging associations with mammals. This putative association, in turn, may help explain the success of recently implemented antpitta feeding stations which have reached wide-spread use in the tourist industry.

My observations of antpitta behavior were made during the course of field work throughout Ecuador over the past 12 years. I made most observations at Cabañas San Isidro and the adjacent Yanayacu Biological Station (00°36'S, 77°53'W) in the northeastern Andes, and at the Tapichalaca Biological Reserve (04º30'S, 79º10'W) in Ecuador's extreme southeastern Andes. I also include unpublished observations provided by several other field workers in Ecuador and Colombia.

Antpittas are among the most elusive of neotropical passerines, and their scarcity and retiring manner make them a daunting challenge for the student of birds. Predominantly, haunting montane forests, antpittas occur through the Neotropics and reach their peak diversity in the Andes of South America. Antpittas forage predominantly on (*Grallaria, Hylopezus, Myrmothera*), or near (*Grallaricula*), the ground (Krabbe and Schulenberg, 2003). In recent years, due to the prize that a sighting of these birds represents in the tourist industry, the practice of calling-in and feeding antpittas via the creation of "worm-feeders" has become wide-spread in Ecuador and Colombia (Woods *et al.*, 2011). This involves establishing a location where worms are regularly provided to antpittas and/or may be foraged for in enriched compost. At most localities where I have witnessed this phenomenon, antpittas are called in through whistles, calls, or other coaxing and, with time, are frequently tame enough to take food from human hands. That these largely terrestrial birds frequently forage on worms, often feeding them to their nestlings (Greeney *et al.*, 2008), comes as no surprise. What seems more surprising, however, is how readily they respond to the stimulus of human presence, vocalization, and movement at feeding stations. Many other wild birds are commonly brought in by feeding stations of various types. The common static feeders, however, are not accompanied by obvious (to birds) presence of humans. The following observations of behavior exhibited by Andean antpittas suggest a possible explanation.

Though allied with obligate followers of army ants (i.e., some species of Thamnophilidae; *sensu* Remsen *et al.*, 2011), antpittas are thought to only opportunistically join mixed-species foraging assemblages at ant swarms. Relatively few species have been reported foraging at ant swarms (Greeney and Gelis, 2005; Kofoed and Auer, 2004; Nieto-R. and Ramírez, 2006). These records, along with my own observations and those kindly provided by Eliot T. Miller, however, suggest that most species of antpittas will opportunistically follow montane ant swarms. Between Miller and myself we have recorded Chestnut-crowned Antpitta (n = 2), White-bellied Antpitta (n = 2), Chestnut-naped Antpitta (n = 5), and Jocotoco Antpitta (n = 4) in attendance at army ant swarms. I have also observed several species of *Grallaricula* antpittas associating with ants, including Slate-crowned Antpitta (*G. nana*; n = 6) and Ochre-breasted Antpitta (*G. flavirostris*; n = 2). The frequency of these observations, especially given the difficulty with which antpittas are observed in the wild, suggests that antpittas may associate with ant swarms more frequently than is reported in the literature, and that the behavior is wide-spread within the family.

Perhaps, surprisingly, other than in situations as described above, I have had my best looks at antpittas while crashing through dense understory vegetation in search of their nests. I first noticed "following behavior" in a Chestnut-crowned Antpitta while I was moving noisily through *Chusquea* bamboo at Yanayacu in 2001. During a brief pause, I noticed a single adult perched several meters away on a low branch. Apart from an occasional flicking of its wings, it appeared unperturbed by my presence. After moving another 20 m, I paused again. Within moments an adult antpitta appeared and observed me as before. This continued for more than 30 min., covering perhaps 100 m of dense bamboo. I was not followed after emerging from the bamboo. In subsequent years I have had similar experiences with Chestnut-naped Antpitta (n = 1), White-bellied Antpitta (n = 1), Rufous Antpitta (n = 2), Watkins's Antitta (*G. watkinsi*; n = 4), Jocotoco Antpitta (n = 6), and twice more with Chestnut-crowned Antpitta. To the best of my knowledge, in all cases, I was not near their nest at the time. Given the natural ability of antpittas to remain hidden, in concert with my own focus on making a hole through the vegetation, it seems likely that I have been followed through the undergrowth more often than I am aware. Jose Maria Loaiza B. related a similar experience whereby he has been followed by Scaled Antpitta (*G. guatimalensis*) and Ochre-breasted Antpitta. He observed both species coming to forage at leaf litter he had disturbed, following him for some distance to repeatedly capture prey from the areas of overturned soil and leaves. Though this is the only other report of such behavior in antpittas that I am aware of, it seems likely that it may often go unnoticed or unreported. In addition to my observations above, I have had similar experiences of being followed by two *Grallaricula* antpittas, Slate-crowned (n = 4) and Peruvian (*G. peruviana*; n = 2). In addition to these observations under natural conditions, during the construction of trails near Yanayacu, I frequently witness Chestnut-crowned, White-bellied, and Giant Antpittas spending long periods of time foraging in the recently disturbed earth, often only a few meters from those working on the trail.

Most species of antpittas occur sympatrically with a range of large mammals. Other than large cats, montane mammalian predators (which might pose a threat if followed) are generally small (e.g., Mustellidae) and would not likely be profitable "beaters." Large herbivores, however, are diverse, and include agoutis, pacas, deer, tapirs, and bears (Eisenberg *et al.*, 1999; Jarrín-V., 2001; Tirira, 1999), of which the latter two often create considerable noise and physical disturbance to their surroundings (pers. obs.). Thus, the attraction of antpittas to large, noisy mammals may not be maladaptive. In fact, given their potential phylogenetic predisposition to following army ant swarms, along with their apparent curiosity and occasional boldness around humans, I suggest that a natural foraging technique of antpittas is to follow in the wake of large mammals and capitalize on prey items exposed by their foraging. In my experience, bears are particularly destructive as they tear apart bromeliads and logs, but most other montane herbivores also forage by pawing through and disrupting leaf litter (Emmons and Feer, 1997; Jarrín-V., 2001). Given this possibly natural means of foraging by antpittas, I suggest that they have an innate propensity to be attracted to human activity and are thus easily trained to respond to non-subtle cues (i.e. vocalizations, movements of tourist groups) indicating sources of food provided by humans. While the effects of worm feeders on antpitta biology are unstudied, it seems that perhaps feeding stations may mesh more naturally with antpitta natural history than is at first obvious. Thus, despite the fear of some that worm-feeder tourism may have negative impact on the many species of threatened antpittas (BirdLife International, 2009), this seems unlikely to me. While the foraging behavior and prey selection of the smaller, less terrestrial *Grallaricula* diverges from that of *Grallaria* antpittas, I suggest they may adopt a similar foraging strategy. Their apparent scarcity at feeding stations is likely a reflection of a difference in prey choice, and their relatively reduced experience with worms as food.

Commensal foraging relationships involving birds as "follower" species are common and wide-spread geographically and taxonomically (see introduction). Reports of birds following humans, potentially for the same reasons, however, are few (e.g., Skutch, 1969); though some species are known to follow gorillas (Ruggiero and Eves, 1998). The array of taxonomic associations found to date, however, suggest that many species may, at least opportunistically, follow any organism which is flushing prey within its natural habitat. The dearth of information on the natural history of antpittas in general is a reflection of their shy and elusive habits (Greeney *et al.*, 2008), and I suggest that the association between antpittas and large mammals has not been previously documented only due to the difficulty of observing both antpittas and large Andean mammals. Though this presents a challenge, it is likely that any student of neotropical biology will be highly rewarded by studying and documenting this potential interaction.

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