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Bluffing in the forest: Neotropical *Neomorphus* ground-cuckoos and peccaries in a possible case of acoustic mimicry

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Acoustic communication is particularly important in environments such as dense tropical forests, where the dim light constrains the efficacy of visual signals. In these environments, complex species interactions could promote the evolution of acoustic signals and result in intriguing patterns of mimicry and convergence. In the Neotropical region, *Neomorphus* ground-cuckoos frequently associate with herds of collared peccaries and white-lipped peccaries. Bill clacking behavior in ground-cuckoos closely resembles the sound of teeth clacking in peccaries and these acoustic signals are used in agonistic and foraging contexts in both species. Here we demonstrate that the acoustic characteristics of bill clacking in ground-cuckoos are more similar to teeth clacking of peccaries than to bill clacking of the more closely related *Geococcyx* roadrunner. We propose that two hypotheses may explain the evolution of the clacking behavior in these taxa. First, because peccaries are known to successfully ward off attacks from large predators to defend their herds, mimicking their clacking can deceive predators, either by triggering clacking from nearby peccaries, or making it appear to the predators that peccaries are present when they are not. Second, ground-cuckoos and peccaries could mutually benefit from the use of similar signals to alert each other of the presence of predators. In this context, ground-cuckoos could serve as sentinels while peccaries could confer protection. We also discuss alternative explanations for this striking acoustic resemblance. Ground-cuckoos and peccaries provide an interesting opportunity to study how an ecological association could foster the evolution of acoustic mimicry.

The similarity of signals delivered by unrelated organisms fueled the idea of mimicry, in which certain organisms could profit from resembling others (Bates 1862). Mimicry systems usually involve three players: two signal senders (a mimic and a model), and a signal receiver. It occurs when the signal resemblance between the mimic and the model leads the receiver to change its reaction, which brings a selective advantage to the mimic (Dalziell et al. 2015). Mimicry may involve honest or dishonest visual, acoustic, chemical or tactile signals. Dishonest signals may be used by undefended organisms to escape predation by fooling predators into misidentifying them as a dangerous species. An example would be mimicking the appearance or sound of dangerous prey which is observed in nestling burrowing owls that emit calls similar to the sound caused by rattlesnakes when vibrating their rattle (Rowe et al. 1986), or when an amazonian bird nestling displays body movements and morphology that mimics a toxic caterpillar (Londoño et al. 2015). Dishonest calls may also be used to scare and steal food from other species (Flower 2011). In a discussion with FRA on the natural history and vocal behavior of Neotropical *Neomorphus* ground-cuckoos and peccaries, CB had an insight that the acoustic resemblance between the two taxa could represent an unreported and not yet realized example of acoustic mimicry. Thus, we propose here that this acoustic similarity – which was suggested in previous studies as Haffer 1977 and Sick 1997) – may be interpreted under the mimicry theory. Ground-cuckoos are Neotropical birds that have fascinated naturalists for decades for their elusiveness. The four species of the genus (*N. geoffroyi*, *N. radiolosus*, *N. rufipennis* and *N. pucheranni*, del Hoyo et al. 2017) are the closest relatives of the world famous *Geococcyx* greater-roadrunners (Sorenson and Payne 2005) from North and Central America. They share with roadrunners their body shape, terrestrial habitat, nest structures, omnivorous diet and the strategy of raising their young instead of being nest parasites. The sister genus *Geococcyx* differ by inhabiting dry open habitats, while *Neomorphus* ground-cuckos are found in both humid and dry forests and have more colorful plumage (Roth 1981, Sick 1997, del Hoyo et al. 2017).

Despite being mostly famous for their elusive behavior, some of the most striking aspects of *Neomorphus* ground-cuckoos' biology relates to their foraging strategies. Besides performing roadrunner-like fast sprints to capture small invertebrates, they take advantage of army-ant-swarm raids along with other army-ant-following birds preying on insects and other small animals trying to escape (Lopez-Lanus et al. 1999). They also follow monkeys and feed on defecated fruits and seeds (Siegel et al. 1989), and are known to track herds of collared peccaries *Pecari tajacu* (Lopez-Lanus et al. 1999) and white-lipped peccaries *Tayassu pecari* (Haffer 1977). Herds of peccaries are known to bulldoze the forest floor, rooting through soil, clearing and stirring the forest floor detritus (Keuroghlian and Eaton 2009), making leaf litter invertebrates and vertebrates more exposed for predation by the ground-cuckoos. In portuguese, this association with peccaries is historically known by locals and, for this reason, ground-cuckoo local common names are jacu-porco ('pig-cuckoo') or jacu-queixada ('white-lipped peccary-cuckoo'; Haffer 1977, Sick 1997, Lopez-Lanus et al. 1999). Peccary distributions overlap with the entire range of ground-cuckoo species (Gongora et al. 2011, Keuroghlian et al. 2013, del Hoyo et al. 2017), and besides their extensive sympatry, the most intriguing aspect of their interactions is that ground-cuckoos not only associate with, but also sound like peccaries: the repertoire of all species of ground-cuckoos include bill clackings (del Hoyo et al. 2017), which sound strikingly similar to peccary teeth clacking (Haffer 1977, Sick 1997; Fig. 1). Teeth clacking consist of a series of powerful 'pops' or 'clacks' generated by rapid movements of the mandible, which peccaries use as a defense signal against predators, when alarmed, and during interspecific agonistic interactions (Byers and Bekoff 1981, Sowls 1984). We evaluated this acoustic similarity between ground-cuckoos and peccaries and identified predominant patterns of vocal variation across taxa using a principal component analyses (PCA). The PCA was performed on the correlation matrix of measurement of clacking signals of the greater-roadrunner, white-lipped peccary, collared peccary and ground-cuckoos, and produced four components that explained 40.67, 21.21, 12.28 and 11.53% of the variation in clacking elements (Fig. 1, Supplementary material Appendix 1 Table A1). Vocal PC1, which largely reflected clacking complexity, increased with the number of clacks in a vocal bout and decreased with spectral parameters (peak and center frequency, entropy). Clacking PC1 was generally higher for roadrunners and lower for ground-cuckoos and peccaries (Fig. 1). In other words, clackings of the greater-roadrunner differ from the clackings produced by the other species for being composed of multiple bill clackings instead of solo teeth clackings (peccaries) and solo bill clackings (ground-cuckoos) and by having lower entropy, peak and center frequencies. Ground-cuckoos use bill clacking while foraging and in agonistic interactions with other birds over ant-swarms (Lopez-Lanus et al. 1999), communicating with their young (Karubian et al. 2007), and during contact with humans (VQP unpubl., G. Thom pers. comm.). Given this scenario, why do such distantly related organisms produce so similar sounds?

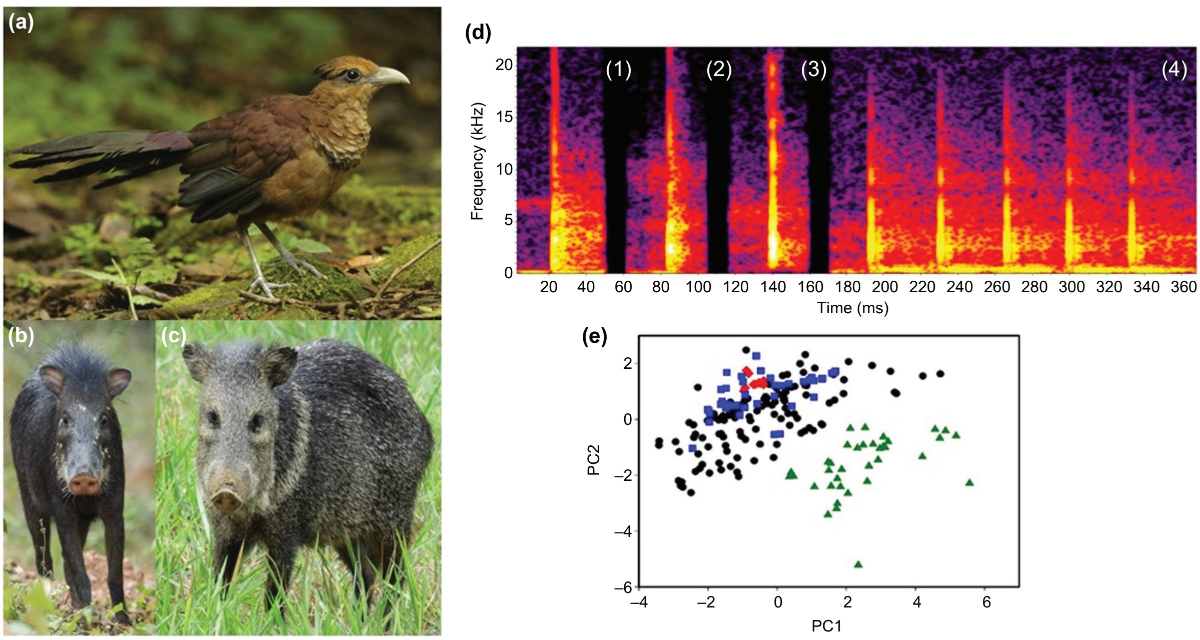

Figure 1. (a) Rufous-vented ground-cuckoo *Neomorphus geoffroyi*. (b) White-lipped peccary *Tayassu pecari*. (c) Collared peccary *Pecari tajacu*. (d) Sonogram displaying tooth or bill clackings of: (1) white-lipped peccary, (2) collared peccary, (3) banded-ground-cuckoo *Neomorphus radiolosus*, and (4) greater-roadrunner *Geococcyx californianus*. (e) Scatter plot of the first (PC1) and second (PC2) components of a principal component analysis following a spectrographic analysis of tooth or bill clackings of white-lipped peccary (black circles), collared peccary (red diamonds), ground-cuckoos (blue squares) and greater-roadrunner (green triangles). The clacking elements, measured in Raven 1.4 (Charif et al. 2010) were center frequency, high frequency, low frequency, average entropy, aggregate entropy, length of clackings and number of clackings. Signals were digitized at a sample rate of 44.1 kHz and 24 bit depth in WAVE format. Spectrograms were made with a 256-point (11.6 ms) Hann window (3 dB bandwidth = 248 Hz), with 87.9% overlap, and a 1024-point DFT, yielding time and frequency measurement precision of 0.70 ms and 43 Hz. Sources of samples, including geographical locality, are provided in Supplementary material Appendix 1 Table A1. See acknowledgments for photo credits.

Although ground-cuckoo and peccary acoustic communication behavior are poorly known, it is possible to formulate two hypotheses based on the similarity of their acoustic signals. First, it is possible that ground-cuckoos (mimic) emit a dishonest signal resembling peccary (model) tooth clacks. Here, the communication would occur either between cuckoos and taxa other than peccaries, or between cuckoos and peccaries. When receivers are taxa other than peccaries, ground-cuckoos would deceive predators by sounding like teeth clacking peccaries during alarm displays, as peccary herds not only sound threatening, but may be sufficiently aggressive to kill a jaguar (Scognamillo et al. 2003). Under such a hypothesis, alarm displays could not only deter predators common to both ground-cuckoos and peccaries, but could be effective against mesopredators (e.g. raccoons/coatis, mustelids, canids, small felids) that threaten ground-cuckoos, but not peccaries. Peccaries' main predators are large felids and humans (Kiltie and Terborgh 1983). This acoustic resemblance may also grant protection to nesting birds and to their eggs and nestlings against predators. Indeed, there are records of predation of adult ground-cuckoos during egg incubation (Roth 1981), and although their predators are not known, carnivorous mammals are likely candidates. Ground-cuckoos build their nests approximately at 2.5–5 m high (Roth 1981, Sieving 1992) and thus are accessible to felids. In addition, explosive bill clacking similar to those produced by peccaries is used by ground-cuckoos during alarm displays (Haffer 1977), including encounters with humans. Nestlings begin to clack their bills by the 15th day after hatching (Karubian et al. 2007), and therefore, predator avoidance may already function in the nest. Alternatively, peccaries could act as both model and receiver. In this case, cuckoos could deliver bill clacks deceptively to fool and alarm peccaries herds to stimulate their movimentation and, consequently, to augment rates of prey exposure.

A second hypothesis involves evolution of acoustic mimetism or acoustic convergence as mutual communication of danger (Marler 2004). Here, vocal communication would be honest and restricted between peccaries and cuckoos. For example, ground-cuckoos could function as sentinels to peccaries, emitting alarm calls to alert the peccaries of the presence of danger. In this case, peccaries would benefit from the sentinel behavior of ground-cuckoos to be less vigilant and increase their time and energy foraging (Baigrie et al. 2014), while ground-cuckoos would benefit by avoiding predation based on the alarmed peccary herd. However, it is possible that peccaries are not the only players getting more food. Cuckoos could also increase their food intake in these situations, as the more time peccaries invest foraging and bulldozing through the forest, the more resources become available to them. Therefore, these two hypotheses lay out evolutionary scenarios in which acoustic mimicry originates through routes involving either simpler or more complex effects of decreased predation risks and increased food intake on the vocal communication of cuckoos and peccaries.

Mimicry is not the only possible explanation for similar acoustic signals, as this may be caused by convergent evolution due to habitat similarity, phylogenetic inertia, as a by-product of selection for other traits or simply by chance (Dalziell et al. 2015). The acoustic mimicry hypothesis could be tested through experiments in the field and by employing comparative analyses. For example, phylogenies, divergence time estimates and ancestral state reconstruction would allow inference of how and when peccary and peccary-like sounds evolved in the entire ungulate and cuckoo radiation, respectively. Such inferences would be interesting to test if bill clacking evolved after teeth clacking, which is the most likely scenario under our first hypothesis. Species-level phylogenetic studies of ground-cuckoos and allies (Sorenson and Payne 2005) and peccaries and allies (Gongora and Moran 2005) are already available, but future studies including the tempo of evolution for both groups will pave the way to such historical inferences.

However, preliminary evidence provide some support to the mimicry hypothesis. The closest relative of ground-cuckoos, the roadrunners, exhibit bill clackings that are similar in structure to the ones of ground-cuckoos, except that their sound consists of multiple bill clackings. Notwithstanding, ground-cuckoos bill clacks and peccaries' tooth clacks are more similar to one another acoustically than either of them is to roadrunners (Fig. 1). Furthermore, an assessment of other members of the cuckoo family in public avian sound archives (xeno-canto and Macaulay Library at Cornell Univ.) indicates that the production of sounds resembling peccaries (i.e. solo bill clackings) is unique to Neotropical ground-cuckoos and hence likely originated in their common ancestor.

We suggest that the association of ground-cuckoos with herds of peccaries, the extensive sympatry among these species, and their acoustic similarity provide anecdotal evidence in support of the acoustic mimicry hypothesis. Neotropical forests are rich in species diversity and full of ecological interactions and evolutionary processes. Mimicry is one of the possible explanations for the ground-cuckoo/peccary acoustic resemblance, and the rarity and elusive behavior of both ground-cuckoos and peccaries make this a challenging but potentially rewarding research opportunity in ecology and evolution.

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Supplementary material (Appendix JAV-01266 at <www.avianbiology.org/appendix/jav-01266>). Appendix 1.