

A striking case of deceptive woodpecker colouration: the threatened Helmeted Woodpecker *Dryocopus galeatus* belongs in the genus *Celeus*

Martjan Lammertink^{1,2,3} · Cecilia Kopuchian^{4,5} · Hanja B. Brandl⁶ · Pablo L. Tubaro⁵ · Hans Winkler⁶

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Abstract The Helmeted Woodpecker *Dryocopus galeatus* is a threatened species of the Atlantic Forest in south-eastern South America. It has traditionally been placed in the genus *Dryocopus*, but it shows similarities in plumage and structure with woodpeckers in the genus *Celeus*. We sequenced mitochondrial and nuclear DNA that was sampled from live captured Helmeted Woodpeckers. We found that the Helmeted Woodpecker has a phylogenetic position embedded within the genus *Celeus*, and recommend its taxonomic treatment as *Celeus galeatus*. The Helmeted Woodpecker belongs to a clade within *Celeus* that includes

Kaempfer's Woodpecker *C. obrieni*, Rufous-headed Woodpecker *C. spectabilis*, and Cream-coloured Woodpecker *C. flavus*. It has the southernmost distribution range of the woodpeckers in this clade. The Helmeted Woodpecker is sympatric throughout its range with Lineated Woodpecker *Dryocopus lineatus* and Robust Woodpecker *Campephilus robustus* and these species from three different genera show a remarkable convergence in plumage colours and patterns. With the inclusion of Helmeted Woodpecker in *Celeus*, this genus has four out of 15 species on the International Union for Conservation of Nature (IUCN) red list, a higher proportion of red listed species than in the woodpecker family overall.

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✉ Martjan Lammertink
jml243@cornell.edu
Hans Winkler
hans-christoph.winkler@oeaw.ac.at

- ¹ CICyTTP-CONICET, Materi y España, 3105 Diamante, Entre Ríos, Argentina
- ² Proyecto Selva de Pino Paraná, Vélez Sarsfield y San Jurjo s/n, 3352 San Pedro, Misiones, Argentina
- ³ Cornell Lab of Ornithology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA
- ⁴ CECOAL (Centro de Ecología Aplicada del Litoral)-CONICET, Ruta Prov. 5, km 2.5, 3400 Corrientes, Argentina
- ⁵ División de Ornitología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina
- ⁶ Department of Integrative Biology and Evolution, Konrad Lorenz Institute for Ethology, Veterinary University Vienna, Savoyenstraße 1A, 1160 Vienna, Austria

Keywords Picidae · Molecular phylogeny · Atlantic Forest · Threatened bird · Plumage convergence · Mimicry

Zusammenfassung

Ein Fall verblüffend irreführender Spechtfärbung: der bedrohte Wellenohrspecht *Dryocopus galeatus* ist ein *Celeus*

Der Wellenohrspecht ist eine bedrohte Spechtart der atlantischen Wälder im Südosten Südamerikas. Er wurde traditionellerweise in das Genus *Dryocopus* eingeordnet, weist aber in Gefieder und Struktur Ähnlichkeiten zur Gattung *Celeus* auf. Wir sequenzierten mitochondriale und nukleare DNA aus Proben, die lebend gefangenen Individuen entnommen worden waren. Wir fanden heraus, dass der Wellenohrspecht phylogenetisch innerhalb der Gattung *Celeus* positioniert ist und empfehlen, ihn in dieses Genus zu klassifizieren. Dieser Specht gehört zu einer Stammlinie innerhalb von *Celeus*, die den Kaempferspecht *Celeus obrieni*, Zimtkopfspecht *C. spectabilis* und den Strohspecht

C. flavus enthält. Er stellt den südlichsten Vertreter dieser Gruppe dar. Sein Verbreitungsgebiet deckt sich mit jenen des Linienspechts *Dryocopus lineatus* und des Scharlachkopfspechts *Campephilus robustus* und diese drei Arten aus verschiedenen Genera weisen eine bemerkenswerte Konvergenz in Gefiederfärbung und -muster auf. Zusammen mit dem Wellenohrspecht beinhaltet die 15 Arten zählende Gattung *Celeus* vier auf der Roten Liste der IUCN stehende Arten, mehr als der Durchschnitt der Familie.

Introduction

The Helmeted Woodpecker *Dryocopus galeatus* occurs in the Atlantic Forest in a relatively small range in southern Brazil, eastern Paraguay and northeastern Argentina. It is globally threatened, with International Union for Conservation of Nature (IUCN) vulnerable status, by deforestation and selective logging of its habitat (BirdLife International 2015). In plumage pattern it closely resembles two woodpecker species that are sympatric with it, the Lineated Woodpecker *Dryocopus lineatus* and the Robust Woodpecker *Campephilus robustus* (Chebez 1995). The Helmeted Woodpecker was first placed in the genus *Dryocopus* by Gray (1845). It has also been placed by early authors in the genera *Driopicus*, *Dryopicus*, *Ceophloeus* and *Campephilus* (Giebel 1877; Bertoni 1901), but it has been maintained in *Dryocopus* during recent decades (Peters 1948; Short 1982; Sibley and Monroe 1990; Winkler and Christie 2002; Gorman 2014). The Helmeted Woodpecker is a medium sized woodpecker with a body mass of ca. 128 g, and if it were a *Dryocopus*, it would be the smallest in that genus. The next smallest *Dryocopus* taxon is the Simeulue White-bellied Woodpecker *Dryocopus javensis parvus*, with a body mass of ca. 155 g (Lammertink 2007).

The Helmeted Woodpecker has several morphological characteristics that are reminiscent of woodpeckers in the genus *Celeus*, including size: body masses range from ca. 65 g in Waved Woodpecker *C. undatus* to ca. 153 g in Chestnut Woodpecker *C. elegans hellmayeri* (Winkler et al. 1995), a range that overlaps with the body mass of Helmeted Woodpecker. Several plumage patterns (cinnamon wing linings, barred face, long white upper tail coverts, expanded red malar area in male), long and erectable crest feathers, bill shape, and exposed nostrils of Helmeted Woodpecker are found in *Celeus* but not in *Dryocopus* (Short 1982). Nevertheless, the black upperparts, extensively red crest, and white-and-black barred underparts of the Helmeted Woodpecker are not found in *Celeus*, but are very similar to the plumage patterns of several New World

Dryocopus species. Based on the morphological similarities, Short (1982) considered the Helmeted Woodpecker to be an intermediate between the genera *Celeus* and *Dryocopus*. Whether or not *Celeus* and *Dryocopus* are sister groups remains without consensus in molecular phylogenies. Fuchs et al. (2007) and Fuchs et al. (2013) partly support this relationship; however, other molecular phylogenies indicate with more or less strong node support, and based on three to 12 loci, that *Celeus* is sister to the *Colaptes/Piculus* clade (Webb and Moore 2005; Benz et al. 2006; Fuchs et al. 2007; Moore et al. 2011; Fuchs et al. 2013; Winkler et al. 2014). Del Hoyo and Collar (2014) split the *Dryocopus* species of the New World as *Hylatomus*, but we follow Winkler et al. (2014) in maintaining these New World species in *Dryocopus*, along with Old World *Dryocopus* and with former *Mulleripicus* species of Asia that are sister to Old World *Dryocopus* (Fuchs et al. 2007, 2008, 2013; Winkler et al. 2014).

Whereas Short (1982) judged similarities in plumage of woodpecker genera and species to reflect phylogenetic affinity, for instance between the genera *Dinopium* and *Chrysocolaptes*, *Dryocopus* and *Campephilus*, and *Meiglyptes* and *Hemicircus*, or between the species Hairy Woodpecker *Leuconotopicus villosus* and Downy Woodpecker *Dryobates pubescens* (sensu Winkler et al. 2014), recent molecular phylogenies indicate that these similar taxa are not sister groups, but are in divergent branches of the woodpecker family (Weibel and Moore 2002a, b; Webb and Moore 2005; Benz et al. 2006; Fuchs et al. 2007, 2013; Winkler et al. 2014). At the same time, highly distinctive woodpecker taxa can form a single clade, as exemplified by the former *Mulleripicus* and Old World *Dryocopus*. Thus, to resolve the phylogenetic position of the Helmeted Woodpecker, an approach other than plumage similarity is required.

The recent molecular woodpecker phylogenies cited above have resulted in a generally congruent, well-resolved phylogenetic tree for the woodpecker family. Previous taxonomic riddles in the family such as the position of *Nesocittes*, *Hemicircus*, *Chrysophlegma*, *Picus*, *Micropternus* and *Sapheopipo* have been resolved. The phylogenetic position of the Helmeted Woodpecker, however, remains as one of the most vexing problems in woodpecker taxonomy (Benz and Robbins 2011; Moore et al. 2011). Clarifying the phylogenetic position of the Helmeted Woodpecker is all the more urgent because of its globally threatened status. A resolved phylogeny will aid in making correct inferences about its natural history and ecological requirements from comparisons with the biology of other, genuinely related Woodpecker species.

We present an analysis of the phylogenetic position of the Helmeted Woodpecker based on sequences from mitochondrial genes and a nuclear gene, using DNA

extracted from live captured individuals. We discuss the relationships of the Helmeted Woodpecker, its plumage convergence with two sympatric woodpecker species, and the implications for comparative research on this threatened woodpecker.

Methods

Sampled individuals

The following samples were taken from Helmeted Woodpecker individuals in Misiones Province, Argentina: (1) a blood sample from the brachial vein of an adult male mist-netted at the private reserve Centro de Investigaciones Antonia Ramos (CIAR) near Obera (24.44 S 55.12 W) on 11 October 2012, (2) breast feathers of an adult female mist-netted in Cruce Caballero Provincial Park (26.51 S 53.99 W) on 9 September 2013, (3 and 4) belly feathers with feather follicle lining from two sibling nestlings of ca. 16 days old that were being raised by the sampled adult female, on 22 October 2013. Locations 1 and 2–4 were 150 km apart. All samples were preserved in 96 % ethanol in ultra cold-freezers at -76°C . Remaining tissue is stored at Colección Nacional de Tejidos Ultracongelados, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina, under the voucher numbers provided in Table 1.

DNA extraction and sequencing

Two mitochondrial loci, NADH dehydrogenase subunit 2 (ND2) gene and the cytochrome C oxidase subunit (COI), as well as intron 7 of the nuclear gene β -fibrinogen (β -fibrinogen 7) were amplified by PCR and sequenced. The ND2 gene (1041 bp) was amplified with the primers L5216 and H6313 and thermocycle parameters described by Benz and Robbins (2011). A 746 bp fragment of the COI gene was amplified with the primers BIRDF1 and COIBirdR2 and the thermocycle parameters described by Kerr et al. (2009). For β -fibrinogen 7, a two-step nested PCR was performed to provide a sufficient amount of specific PCR product for further analysis. First, a fragment of approximately 1000 bp in length was amplified using the FIB-17L and FIB-17U primers of Pritchitko and Moore (1997) and the nuDNA thermocycle parameters of Benz and Robbins (2011). In the next step, the second internal primers FIB-BI7L2 and FIB-BI7U2 were run on a thermocycler to amplify a 877 bp fragment using the following touchdown program: 1 cycle of 95°C for 5 min; 6 cycles of 95°C for 45 s, 58 – 53°C , decreasing 1°C each cycle, and 72°C for 3.5 min; 24 cycles of 95°C for 45 s, 50°C for 45 s, and 72°C for 3.5 min; and 1 cycle of 72°C for 10 min.

Each PCR was carried out with an Eppendorf Thermocycler in a volume of 25 μl following reactive concentration of Kerr et al. (2009). The second PCR for β -fibrinogen 7 used the composition as described for the colony PCR in van Dongen et al. (2013), but with 1.25 units of polymerase and 0.1 μl of PCR product as template. Length and quality of the amplified β -fibrinogen 7 products were confirmed by running them on a 1.5 % agarose gel, and the amplified product of the sampled individual with the strongest band was subsequently cloned using a TOPO TA cloning kit (Invitrogen) following the manufacturer’s protocol. Sixteen transformed colonies were amplified via colony PCR as described in van Dongen et al. (2013). Successful amplification of the samples was again confirmed on a 1.5 % agarose gel before removing excess primers and dNTPs by digestion with exonuclease I and thermostable alkaline phosphatase (Thermo Scientific).

Sequencing reactions for COI and ND2 fragments and the cloned β -fibrinogen 7 PCR products were performed with the respective PCR primers. For ND2, two internal primers were additionally used for sequencing: H5776 (Klicka et al. 2000) and L5758 (Sorenson et al. 1999). Big Dye chemistry (Applied Biosystems) was used for all the sequencing reactions and the products were sequenced on an ABI PRISM 3130 \times 1 automated sequencer (Applied Biosystems).

Phylogenetic analysis

Alignments were produced with MUSCLE version 3.8 (Edgar 2004) and optimized manually. The reading frames of all mitochondrial sequences proved to be intact, as expected for functional genes. We obtained sequences from one, two or three fragments per sample. There were no discrepancies between overlapping sections. Both maximum-likelihood and Bayesian methods were used to infer phylogenetic relationships. We conducted a Bayesian analysis on the combined mitochondrial ND2 gene and the nuclear β -fibrinogen 7 with MrBayes 3.2 (Ronquist et al. 2012). For this analysis, the data set was partitioned by genes, with the GTR+I+G model specified for each partition. All analyses were run for 2,000,000 generations with four Markov chains and uniform priors under default heating values sampling every 100 generations. The first 200,000 generations were discarded as burn-in. Checking with Tracer 1.5 (Rambaut and Drummond 2009) showed that stationarity of likelihoods was achieved before that point. The hierarchical likelihood ratio test implemented in ModelTest 2.1.4 (Posada and Crandall 1998; Darriba et al. 2012) confirmed the GTR+I+G model as suitable for the ND2– β -fibrinogen 7 data set.

Single gene trees were computed with a maximum-likelihood method, which includes an approximate

Table 1 Specimens of woodpecker species used in this study

Taxon	Voucher	Geographic origin	Accession number		
			β -Fibrinogen	ND2	COI
<i>Dryocopus galeatus</i>	MACN-Or-ct6954	Misiones, Argentina		KT216670	KT216665
<i>D. galeatus</i>	MACN-Or-cp290	Misiones, Argentina	KT216671	KT216669	KT216666
<i>D. galeatus</i>	MACN-Or-cp291	Misiones, Argentina			KT216667
<i>D. galeatus</i>	MACN-Or-cp289	Misiones, Argentina			KT216668
<i>D. pileatus</i>	WSU 8615; KUNHM 6629	Kentucky, USA; Kansas, USA	U67902	DQ479187	NC_008546
<i>D. lineatus</i>	NRM 967106	Paraguay	DQ352394	DQ361291	AY940779
<i>D. martius</i>	MNHN C30	France	DQ188114	DQ188166	GU571371
<i>Mulleripicus funebris</i>	USNM B3804	Philippines	DQ479215	DQ479195	AY940784
<i>Celeus castaneus</i>	UNAM 99-162; USNMC052-10	Mexico	JF433136	JF433273	JQ174335
<i>C. grammicus</i>	LSUMNS 6892; LGEMA-9650	Loreto, Peru; Brazil	JF433140	JF433271	JN801548
<i>C. undatus</i>	KUNHM 5829; USNMF034-11	Guyana	JF433142	JF433266	JQ174346
<i>C. flavus</i>	KUNHM 5840	Guyana	JF433145	JF433279	AY940775
<i>C. obrieni</i>	Cob1399	Maranhão, Brazil	KC858931	KC858944	
<i>C. spectabilis</i>	LSUMNS 10664	Ucayalí, Peru	JF433138	JF433280	
<i>C. elegans</i>	KUNHM 5764	Guyana	JF433129	JF433261	JQ174338
<i>C. flavescens</i>	KUNHM 304	Paraguay	DQ479228	DQ479174	
<i>C. lugubris</i>	USNM 5899; MACN-Or-ct 1876	Corrientes, Argentina	JF433133	JF433255	FJ027328
<i>C. loricatus</i>	LSUMNS 28510	Colon, Panama	JF433144	JF433262	
<i>C. torquatus</i>	LSUMNS 9422; LGEMA-9727	Pando, Bolivia; Brazil	JF433135	JF433264	JN801549
<i>Colaptes auratus</i>	KUNHM 2534	USA	U67897	DQ479176	AY942868
<i>Colaptes melanochloros</i>	NRM 947052; WUD:95-3.2	Paraguay	DQ352390	DQ361298	FR686475
<i>Colaptes punctigula</i>	KUNHM 963; WUD:95-15.1	Peru	DQ479204	DQ479178	FR686479
<i>Colaptes rubiginosus</i>	KUNHM 3926; FMNH:343228	Guyana	DQ479221	DQ479182	FR686489
<i>Piculus chrysochloros</i>	NRM 966938; FMNH 334419	Paraguay	DQ352392	DQ361309	AY927183
<i>Campephilus melanoleucos</i>	NRM 966949	Paraguay	KC813199	GU566534	AY940777

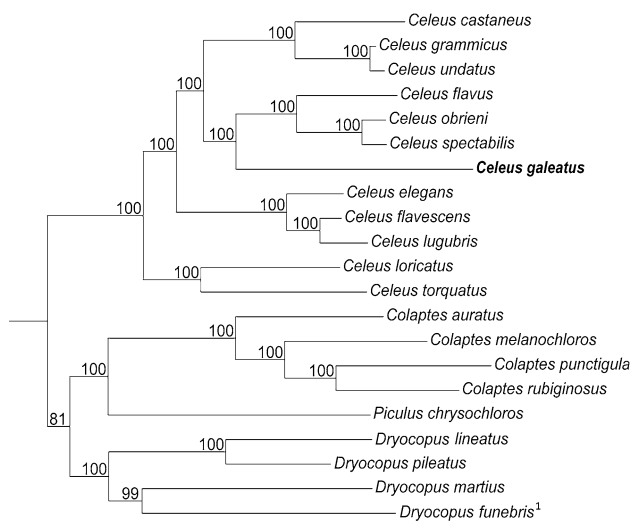
likelihood ratio test with a nonparametric correction described in detail in Anisimova et al. (2011). Program PhyML-aBayes, a version of PhyML (Guindon et al. 2010), was used to compute the trees under a GTR-model, free rates and the BEST search option. In all cases, *Campephilus melanoleucos* served as outgroup. Similar to the findings of Benz and Robbins (2011), our support values for nodes in the single-gene trees were relatively low.

Results

A Bayesian analysis of the combined nuclear β -fibrinogen 7 gene and the mitochondrial ND2 gene yielded a phylogenetic tree with strong node support (Fig. 1) that shows the Helmeted Woodpecker to be embedded within the genus *Celeus*. According to this tree, the Helmeted Woodpecker is sister to a clade of three *Celeus* species: Cream-coloured Woodpecker *C. flavus* of the Amazon basin and the northern Atlantic Forest, Rufous-headed

Woodpecker *C. spectabilis* of the western Amazon and Kaempfer's Woodpecker *C. obrieni* of the Cerrado in northeastern Brazil. The last two are sister species and are rare bamboo-foraging specialists. The only *Celeus* species that is sympatric with the Helmeted Woodpecker is the Blond-crested Woodpecker *C. flavescens*, from which it is well separated phylogenetically (Fig. 1) as well as ecologically (as discussed below).

In maximum-likelihood analysis of individual gene trees (Figs. S1–S3), β -fibrinogen 7 showed generally low resolution near the terminal nodes, but supported the grouping of *galeatus* with *obrieni* and *spectabilis*. In the ND2 tree, *galeatus* was associated with the *obrieni-spectabilis-flavus* and *castaneus-undatus-grammicus* clades, with the lower nodes not resolved. With respect to ND2 genetic distances, its closest relatives are *obrieni*, *spectabilis*, and *flavus*, in that order. The COI tree was the least complete, because sequences are available for only a few *Celeus* species. Particularly, those species that had been established as close relatives in the foregoing analyses (*obrieni* and



¹Formerly *Mulleripicus funebris*, following Winkler et al. (2014)

Fig. 1 Bayesian analysis on the combined mitochondrial ND2 gene and the nuclear β -fibrinogen gene, intron 7. Estimated Bayesian posterior probability is given with each node. *Campephilus melanoleucos* formed the outgroup

spectabilis) were missing. There was support for the sister group relationship between the representatives of main clades in *Celeus*, that is, *flavus* and *grammicus*; otherwise, the intragenetic relationships were poorly resolved. Importantly, however, in all the individual gene trees, the Helmeted Woodpecker was positioned within the *Celeus* clade.

Discussion

A well-supported tree (Fig. 1), constructed with a nuclear intron and a mitochondrial gene, as well as congruent individual gene trees show that the Helmeted Woodpecker is embedded within the genus *Celeus*, and we thus recommend its taxonomic treatment as *Celeus galeatus*. Our finding based on molecular sequences that the Helmeted Woodpecker belongs in the genus *Celeus* is congruent with the similarities in plumage and exposed nostrils between this species and *Celeus* woodpeckers, as first pointed out by Short (1982). Another similarity is that in *Celeus* and Helmeted Woodpecker, there is little to no differentiation between sexes at the nestling stage (Winkler et al. 1995; Lammertink and Klavins 2012; M. Lammertink unpublished data), whereas in *Dryocopus*, including the former *Mulleripicus*, nestlings can readily be sexed (Winkler et al. 1995). Several behaviours of Helmeted Woodpeckers are unlike those in any *Dryocopus*, including being active at crepuscular hours and roosting in natural decay cavities (Cockle 2010; Lammertink et al. 2012). There is no information available yet to assess whether such

behaviours are found in other *Celeus* woodpeckers. Mention has been made of the voice of Helmeted Woodpeckers being reminiscent of *Celeus* (Collar et al. 1992; Brooks et al. 1993), though both the Blond-crested Woodpecker *Celeus flavescens* and the Lineated Woodpecker *Dryocopus lineatus* have calls in their vocal repertoires that are rather similar to the long call of the Helmeted Woodpecker (M. Lammertink pers. obs.). The *tududu* contact call of Helmeted Woodpecker does not appear to have an equivalent in any *Celeus* or *Dryocopus* species.

Helmeted Woodpecker forms a clade with Cream-coloured Woodpecker *C. flavus*, Rufous-headed Woodpecker *C. spectabilis* and Kaempfer's woodpecker *C. obrieni* (Fig. 1), three taxa that occur over a wide range of continental South America, from the Amazon basin to the Cerrado and northern Atlantic Forest in northeast Brazil. The Helmeted Woodpecker is the sister taxon of the other three species in this clade and occurs south of the ranges of the other three. Two of the species in the clade, Rufous-headed Woodpecker *C. spectabilis* and Kaempfer's woodpecker *C. obrieni* are bamboo specialists that do nearly all (*obrieni*) or a substantial part (*spectabilis*) of their foraging on ants that live inside stems of bamboo of the genus *Guadua* (Kratter 1998; Leite et al. 2013; de Sousa Azevedo et al. 2013). The Helmeted Woodpecker mostly forages on wood substrates but has also been recorded to forage on ants in *Guadua trinitii* and *Merostachys multiramea* bamboo (Santos 2008; Lammertink et al. 2012). The Cream-coloured Woodpecker *C. flavus* however primarily forages on nests of arboreal ants (Winkler et al. 1995).

The only *Celeus* that occurs sympatrically with the Helmeted Woodpecker is the Blond-crested Woodpecker, which is part of another clade in *Celeus* of species of open woodlands, secondary forests, plantations and parks, including the Chestnut woodpecker *Celeus elegans* and the Pale-crested Woodpecker *Celeus lugubris* (Fig. 1). The Ochre-backed Woodpecker *Celeus ochraceus* of open Cerrado woodlands is also part of this clade (Benz and Robbins 2011). In Misiones province, Argentina, at sites where the Helmeted Woodpecker reaches its highest densities in tall, well preserved forests, the Blond-crested Woodpecker is rare, and vice versa, at sites where the Blond-crested Woodpecker is common, in opened-up forests, the Helmeted Woodpecker is rare or absent (Bodrati and Cockle 2006). If the Helmeted Woodpecker were a *Dryocopus*, it would be the only *Dryocopus* to occur sympatrically throughout its range with another *Dryocopus* woodpecker, that is, the Lineated Woodpecker. It is, on the other hand, not uncommon for two or more *Celeus* to occur sympatrically, with up to four and five *Celeus* species having been recorded at sites in the Amazon basin (Terborgh et al. 1984; Zimmer et al. 1997; Zimmer and Hilty 1997; HW pers. obs.).

Helmeted Woodpecker is one of three woodpecker species in the Atlantic Forest of similar appearance; that is, woodpeckers with black upperparts, black tails, black-and-white barred underparts, and prominent red crests in both sexes (Fig. 2). They are the three largest woodpecker species in the woodpecker assemblage of eight species in tall Atlantic Forest, although the other two are substantially heavier than the Helmeted Woodpecker, with the Lineated Woodpecker weighing ca. 210 g and the Robust Woodpecker ca. 270 g. The three species belong to divergent clades in the woodpecker family (Benz et al. 2006; Fuchs et al. 2007). Plumage convergence in sympatric species of divergent lineages is a frequent phenomenon in woodpeckers, with striking examples including the convergence between sympatric *Dinopium* and *Chrysocolaptes*, between *Dryocopus* and *Campephilus*, and *Dendrocopos* and *Leiopicus* (Cody 1969; Winkler et al. 1994; Prum 2014; *Leiopicus* sensu Winkler et al. 2014). There have been several explanations proposed for plumage convergence in woodpeckers from divergent lineages (Winkler et al. 1994), including interspecific territoriality (Cody 1969; 1973), which is not supported by field observations. Prum and Samuelson (2012) proposed that the mechanism for plumage convergence is interspecific social dominance mimicry (see also Diamond 1994; Rainey and Grether 2007), in which a subordinate species evolves to mimic and deceive a dominant species into misidentifying the mimic as an individual of the dominant species, and into overestimating its size and the costs of aggression. The body mass ratios of 78 % between Lineated and Robust Woodpecker, and 61 % between Helmeted and Lineated Woodpecker, are above the average ratio of 56–58 % between presumed mimics and models in birds, although the ratio ranges from

18 to 90 % (Prum 2014). Nearly all examples of plumage convergence in woodpeckers of divergent lineages involve species pairs, and the Robust-Lineated-Helmeted Woodpecker complex is the clearest example of a convergent trio of species in woodpeckers. In other bird families, complexes of multiple species of presumed mimics occur, with a complex of six similar species of six different genera of tyrant flycatchers (Tyrannidae) as an outstanding example (Prum 2014).

With the inclusion of the Helmeted Woodpecker in *Celeus*, four out of 15 *Celeus* species are on the IUCN red list of globally threatened birds (BirdLife International 2015). Helmeted Woodpecker (vulnerable), Kaempfer's Woodpecker (endangered), and Atlantic Black-breasted Woodpecker *C. tinnunculus* (vulnerable) are threatened by clearance and modification of specialised habitats: tall mature Atlantic Forest in the cases of Helmeted Woodpecker and Atlantic Black-breasted Woodpecker, and breaks of *Guadua paniculata* bamboo in Cerrado woodlands in the case of the Kaempfer's Woodpecker. In addition, the Ringed Woodpecker *C. torquatus* has near-threatened status. It occurs in a wider range of primary and disturbed habitats than the other three, but is under pressure from deforestation in the northern Amazon basin. Across the woodpecker family, 42 out of 254 species (17 %) are Red Listed, so the proportion of Red Listed species in *Celeus* (27 %) is relatively high. The IUCN (2015) Red List is based on a taxonomic reassessment of the non-passeriformes by del Hoyo and Collar (2014), which led to many taxonomic changes across the Picidae based on consistent criteria for voice and plumage characters. Consequently, the high proportion of Red Listed species in *Celeus* cannot be attributed to a different taxonomic treatment of *Celeus*



Fig. 2 The Atlantic Forest woodpecker species involved in possible tri-fold interspecific social dominance mimicry. From left to right: Helmeted Woodpecker *Celeus galeatus*, Lineated Woodpecker

Dryocopus lineatus, Robust woodpecker *Campephilus robustus*. Photos by M. Lammertink taken in Parque Provincial Cruce Caballero, Misiones, Argentina

versus other Picids. Our finding that the Helmeted Woodpecker belongs in the genus *Celeus* allows for comparative research and the development of common conservation strategies for the threatened congeners.

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