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Running head: *Migration of the White-naped Xenopsaris*

Unmasking complex migration syndromes and seasonal plumage colouration of the White-naped *Xenopsaris albinucha*

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The White-naped *Xenopsaris albinucha* is an uncommon suboscine passerine with a disjunct distribution extending from Venezuela to the Southern Cone of South America. Considered to be sedentary over much of its range, the ornithological literature concerning this poorly-known species contains contradictory claims about potential migratory movements. Here we use citizen science and museum specimen data to investigate spatiotemporal variation in the distribution of the species. We found evidence for three disjunct breeding populations, of which one is resident, one is apparently partially migratory and one is fully migratory, with birds from the two latter populations coming into contact during the non-breeding season. Examining photographs from citizen science and museum specimens, we also found evidence for hitherto unsuspected seasonal variation in the species' plumage colouration. Our results suggest that the White-naped *Xenopsaris* has both resident and migratory populations and exhibits an eclipse plumage, a seemingly uncommon trait in passerines.

Keywords: allochrony, citizen science, eclipse plumage, partial migration, Tityridae

1 Research interest in austral and intra-tropical bird migration in South America has received
2 increased attention in recent decades, which has in turn helped to curtail the pervasive
3 assumption of residency in tropical birds (Chesser 1994, Alves 2007, Somenzari *et al.* 2018,
4 Jahn *et al.* 2020). Citizen science has proven to be an effective approach to understanding bird
5 migration at continental scales (Schubert *et al.* 2019, Lees *et al.* 2020) and has helped
6 ornithologists to discover migratory behaviour in species historically assumed to be resident
7 such as the Ash-throated Catiornis *Catiornis fuscus* (Lees 2016) and assess previously
8 suspected, but poorly understood migratory patterns such as those found in the Common Potoo
9 *Nyctibius griseus* (DeGroot *et al.* 2021). In addition, the use of citizen science data offers some
10 advantages over other forms of migration study, allowing the harvesting of potentially vast
11 amounts of data in space and time, which may unveil migratory patterns that might otherwise
12 remain hidden in smaller datasets. This is particularly the case in species which have both
13 sedentary and migratory individuals or populations, which may mask such movements (Lees
14 2016, Jahn *et al.* 2020).

15 A trait usually associated with birds' migratory behaviour is feather moult. For instance,
16 the presence of a prealternate moult—a second moult within the annual cycle—is more
17 common among migrants than residents, since migrants expose their feathers more during
18 migration and thus their feathers are more likely to wear and need to be replaced more
19 frequently (Howell 2010, Terrill *et al.* 2020). Birds that have an obligate prealternate moult
20 exhibit seasonal colour changes ('eclipse plumage'), while birds exhibiting a facultative
21 prealternate moult produce no appreciable change in appearance (Howell 2010). Because it was
22 formerly believed that most tropical birds were non-migratory, seasonal colour changes through
23 obligate prealternate moults were expected to be rare in these birds (Howell 2010). Now, given
24 that many Neotropical bird species have proven to be migratory (Chesser 1994, Jahn *et al.*
25 2020), we might expect that seasonal colour changes may be not so rare among them. Indeed,

26 very few Neotropical birds are known to exhibit eclipse plumage, including the Red-legged
27 Honeycreeper *Cyanerpes cyaneus*, the Blue-black Grassquit *Volatinia jacarina*, and some
28 *Sporophila* seedeaters and *Heliomaster* hummingbirds (Sick 1997, Howell 2010, Wolfe *et al.*
29 2021). However, because the presence of this trait is positively correlated with the number of
30 papers published per species (McQueen *et al.* 2019) and we lack basic natural history
31 knowledge for most Neotropical bird species (Lees *et al.* 2020), the prevalence of seasonal
32 plumage colours may be considerably underestimated in Neotropical birds.

33 Among the most poorly-known South American birds are the tityrids (Tityridae), whose
34 members have historically been scattered among the families Tyrannidae, Cotingidae and
35 Pipridae (Prum & Lanyon 1989, Ericson *et al.* 2006, Barber & Rice 2007). They are thought to
36 be mostly sedentary (Mobley 2004) and those few that show any signs of migration, such as
37 Crested Becard *Pachyramphus validus*, have poorly known movements (Chesser 1994, 1997,
38 Somenzari *et al.* 2018). One of its most enigmatic members is the White-naped Xenopsaris
39 *Xenopsaris albinucha* (hereafter Xenopsaris), a seemingly uncommon species believed to have
40 two disjunct populations—one in northern South America, extending from Venezuela to
41 Guyana (Fig. 1a), and a larger one from north-eastern Brazil to Argentina (Fig. 1b–d, Mobley
42 2004, Ridgely & Tudor 2009). Its migratory status is apparently unclear, illustrated by
43 contradictory information in the ornithological literature. The northern population is usually
44 considered to be resident (e.g., Hilty 2003, Restall 2007), but Ascanio *et al.* (2017) suggested
45 it may be migratory. On the other hand, the southern population is usually considered to be
46 migratory (Chesser 1997, 2005, Mobley 2004, Peña 2004), although some have also suggested
47 otherwise (e.g., Hayes 1994). A recent review of migratory birds in Brazil, which accounts for
48 most of its global range, did not classify the species as migratory (Somenzari *et al.* 2018). In
49 addition, it is reported that the species is resident in the Caatinga of north-eastern Brazil (Araujo
50 & Silva 2017), but although it is recorded year-round in this region, it appears to be more

51 common during the region's rainy season, and becomes rarer during the dry season (R.D.L.
52 pers. obs.), suggesting that there may be some seasonal movement. Adding to the migration
53 puzzle, *Xenopsaris* seems to exhibit some seasonal variation in plumage colours. Individuals
54 that remain in the Caatinga during the dry season and migrant individuals recorded in the
55 Pantanal of south-western Brazil often exhibit a mix of black and brown feathers on the crown
56 (V.Q. Piacentini pers. comm., R.D.L. pers. obs.), unlike breeding individuals that exhibit a
57 black crown. Although its moult strategy is undescribed, its closest relatives—the becardas
58 (genus *Pachyramphus*; Barber & Rice 2007)—exhibit a complex alternate moult strategy
59 (Johnson & Wolfe 2018), which reinforces the hypothesis of seasonal plumage colours in the
60 species. Birds exhibiting this strategy go through three moults in their first cycle and two moults
61 in all subsequent cycles (Johnson & Wolfe 2018), which means that adults can alternate
62 between a more conspicuous, breeding plumage and a non-breeding plumage. Here, we use
63 vouchered records from citizen science databases and museum specimen data to investigate the
64 spatiotemporal distribution of *Xenopsaris* and its putative seasonal colour changes.

65 **METHODS**

66 **Data collection**

67 We obtained photographic, video and audio records from WikiAves (www.wikiaves.com.br),
68 eBird (www.ebird.org) and xeno-canto (www.xeno-canto.org) and museum specimen data
69 archived online (only records with locality and date retrieved from www.gbif.org,
70 www.vertnet.org and www.sibbr.gov.br) up to 31 December 2020. Geographical coordinates
71 were taken from the original sources or, if not listed, from ornithological gazetteers (Paynter
72 1982, 1989, 1992, 1995, Paynter & Traylor 1991). We checked all records and discarded those
73 misidentified and duplicate records of the same bird (e.g., the same photograph in different
74 databases or several photographs of the same bird taken by different observers). Finally, all

75 evidence of breeding (occupied nests and first cycle juveniles), when present, and plumage
76 colours (see below) were coded for each record in our dataset.

77 **Analyses of spatiotemporal distribution**

78 To visualize seasonal variation in *Xenopsaris* distribution, we generated distribution maps for
79 discrete periods throughout the year and plotted ordinal dates (day number: 1–366) of each
80 record against its corresponding latitude and longitude. We also categorised the records in
81 equal-length ‘peak seasons’ (following the rationale of Lees & Martin 2015, Lees 2016; see
82 also Areta & Juhant 2019) to test whether there is a significant shift of the centre of the species’
83 range between such seasons. The peak breeding season was determined as the middle four
84 months within the duration of all records with evidence of breeding, the peak non-breeding
85 season was determined as the opposite four months on the calendar, and the remaining 4 months
86 were coded as the migration period. We expected to find a significant shift of the centre of the
87 species’ range between the peak breeding and peak non-breeding seasons if it is migratory
88 (Chesser 1994), then we compared mean latitudes and longitudes of *Xenopsaris* during the peak
89 breeding and peak non-breeding seasons using Welch’s *t*-tests. This categorisation into ‘peak
90 seasons’ was used only for the abovementioned statistical analysis and all conclusions were
91 made based on the entire dataset without predefined life-cycle periods (see Areta & Juhant
92 2019).

93 To test the assumption of migration of *Xenopsaris* in the Caatinga—where it is recorded
94 year-round, but where partial migration is suspected in the dry season—we plotted the number
95 of records per month to visualize whether there is seasonality in the monthly number of records.
96 To control for any possible bias in seasonal variation in observer effort, we compared these
97 totals with those of another bird from a family with no regular migrants, the Stripe-backed
98 Antbird *Myrmorchilus strigilatus* (Zimmer & Isler 2003). It has two disjunct populations that

99 are sympatric with both migratory populations of *Xenopsaris* in their breeding grounds—one
100 in the Caatinga of northeastern Brazil (*Myrmorchilus strigilatus strigilatus*), which is sympatric
101 with the north-eastern population of *Xenopsaris*, and another from Bolivia to Argentina (*M. s.*
102 *suspicax*), which is sympatric with the southern population of *Xenopsaris*. We used its two
103 disjunct populations to control separately for seasonal variation in observer effort in these two
104 regions. For this, we constructed contingency tables with the monthly number of records of the
105 two species and performed Pearson’s chi-square tests to test the null hypothesis that there is no
106 difference in the seasonality of these records.

107 Finally, given that *Xenopsaris* occurs mainly in habitats with pronounced seasonality,
108 we overlaid the distribution maps onto maps with data on precipitation and temperature (means
109 from 1970–2000) extracted from WorldClim (Fick & Hijmans 2017) with 2.5 arc-minutes
110 resolution to explore the possible influences of environmental variables on the observed
111 seasonal variation.

112 **Analysis of seasonality in plumage colouration**

113 To test the assumption of seasonal colour changes in *Xenopsaris*, we classified the colouration
114 of its most variable parts (underparts and crown) in all photographic records in our dataset that
115 had enough quality. In addition, we examined nine specimens at the Museu de Zoologia da
116 Universidade de São Paulo (MZUSP) and others through high quality photographs. Crown
117 colouration was assigned to one of four categories (entirely black, black with brown feathers,
118 mostly brown or scalloped) and underparts to one of two categories (white or yellow). Finally,
119 we used the data on plumage colouration to visualize whether there are any spatiotemporal
120 patterns related to sex and age. Juveniles, which have a have a scalloped appearance (Teixeira
121 *et al.* 1989, Ridgely & Tudor 2009), were expected not to migrate and their records would
122 therefore be restricted to the breeding grounds, while adult males and females, which are

123 distinguished mainly by crown colouration (Mobley 2004, Ridgely & Tudor 2009), were
124 expected to be found across the entire range of the species.

125 **RESULTS**

126 Our search recovered 924 records of *Xenopsaris* from WikiAves (879 photographs and 45
127 sound recordings), 533 lists with media from eBird, 37 sound recordings from xeno-canto and
128 69 museum specimens archived online. Once duplicate and misidentified records were
129 removed, the final database contained 943 independent records (Supporting Online Information
130 Table S1). These range from 1897 to 2020, but the overwhelming majority are between 2009–
131 2020 (Fig. S1),

132 Our analysis uncovered both resident and migratory populations of *Xenopsaris* (Figs.
133 1–3). The disjunct population in northern South America was present in the same 717,629 km²
134 region year-round, while south of the Equator, ‘populations’ that extend patchily from north-
135 eastern Brazil to Argentina showed marked seasonal variation in extent (Fig. 2). From
136 December to March, most records of these populations were clustered in two disjunct areas—
137 one in north-eastern Brazil and another in the Southern Cone of South America, from Paraguay
138 to northern Argentina (Fig. S3). From April to November, the area occupied by these
139 populations expanded towards central Brazil until it formed a single continuous distribution
140 (Figs. 2 and S3). During this period, some individuals remain within the Caatinga of north-
141 eastern Brazil (Figs. 1b and S3), while the southern part of the range is almost totally abandoned
142 (largely between May and August, see Fig. 2a). However, although the Caatinga region was
143 occupied year-round, the monthly number of records in this region showed a decrease between
144 April and November, suggesting that a portion of this population undertakes migratory
145 movements away from the region during the dry season (Fig. 1b). The control species, Stripe-
146 backed Antbird, showed no seasonal variation in the monthly number of records in both areas

147 of its disjunct distribution (Fig. S5), and the null hypothesis that there is no difference between
148 the seasonality observed in the records of *Xenopsaris* and those of the control species was
149 rejected both for the north-eastern ($X^2 = 55.4$, $df = 11$, $P < 0.0001$) and southern ($X^2 = 262.6$, df
150 $= 11$, $P < 0.0001$) population, thus suggesting that the observed pattern of seasonality in records
151 of *Xenopsaris* is probably not due to differences in observer effort.

152 All breeding records within our dataset clustered in three disjunct areas: (1) one in
153 northern South America, from northern Venezuela to Guyana; (2) one in the Caatinga of north-
154 eastern Brazil; and (3) one in the Southern Cone of South America, from Argentina to southern
155 Brazil (Fig. S2). The breeding records from northern South America fall between 1 August–8
156 September, while the breeding records from north-eastern Brazil and southern South America
157 fall between 26 December–30 May and 19 November–2 March, respectively (Fig. S2).
158 Removing the records of first cycle juveniles and considering only those of occupied nests, the
159 periods narrow to 8 September (only one record in Guyana), 26 December–4 April (nine records
160 from north-eastern Brazil) and 19 November (only one record in Rio Grande do Sul, Brazil).
161 To delimit the life-cycle periods for the following analysis, we used these breeding periods
162 retrieved from our dataset combined with periods previously reported in the literature for
163 Venezuela (June–September; Cruz & Andrews 1989), north-eastern Brazil (one record in May;
164 Teixeira *et al.* 1989) and Argentina (October–January; Di Giacomo & Leiberman 2000, Peña
165 2004). Because the population in northern South America showed no sign of migration and its
166 breeding season is asynchronous in relation to that of the populations south of the Equator (Fig.
167 S2), the peak breeding season was determined based only on the migratory populations to fall
168 between December and March (i.e., the middle four months within the duration of all breeding
169 records). Accordingly, the peak non-breeding season was determined to fall between June and
170 September, and the remaining four months (April, May, October and November) were coded
171 as the migration period (Fig. 3).

172 We found a significant shift in the centre of the species' range during the peak non-
173 breeding season compared to the peak breeding season. The mean latitudes of *Xenopsaris*
174 records during the breeding (15.32°S, $n = 359$) and non-breeding (9.20°S, $n = 245$) periods
175 were significantly different ($t = -7.8$, $df = 607.2$, $P < 0.0001$). On the other hand, mean
176 longitudes during the peak breeding (48.12°W) and peak non-breeding (48.32°W) seasons were
177 not significantly different ($t = -0.43$, $df = 604.2$, $P = 0.66$). Removing the northern resident
178 population from this analysis did not change these results. Mean latitudes during the peak
179 breeding (16.54°S, $n = 338$) and peak non-breeding (10.43°S, $n = 239$) periods remained
180 significantly different ($t = -8.58$, $df = 549.5$, $P < 0.0001$) while mean longitudes (peak breeding
181 = 47.13°W, peak non-breeding = 47.12°W) remained not significantly different ($t = -0.10$, $df =$
182 571.6, $P = 0.99$).

183 Overlaying the distribution maps onto maps with data on precipitation and temperature,
184 we found that the species abandons the southern part of its range during the region's coldest,
185 driest period (Figs. 3, S3 and S4). Between May and August, when the average monthly
186 temperature and precipitation reach their lowest values (mean 13 °C and 40 mm), the southern
187 population largely vacates its breeding grounds (Figs. 2, S3 and S4). The north-eastern
188 population seems to undertake migratory movements during the region's driest period (June–
189 October), when the average monthly precipitation reaches 9 mm (Figs. 1b and S4). Temperature
190 does not seem to affect this population because unlike the Southern Cone of South America,
191 where there is a great annual variation in temperature (range of average monthly temperature =
192 13–26 °C; Fig. 1c), north-eastern Brazil experiences little seasonal variation in temperature
193 (23–26 °C; Fig. 1b).

194 Finally, examining museum specimens ($n = 10$) and photographic records with enough
195 quality to classify plumage colours ($n = 804$), we found that there is variation in the plumage
196 colouration of *Xenopsaris* over the annual cycle, suggesting that the species may have an eclipse

197 plumage. From October to April, most birds exhibited an entirely black crown, whereas from
198 May to September most birds exhibited either a black crown with brown feathers or a
199 predominantly brown crown (Fig. 4). This seasonal change in crown colouration makes both
200 sexes look alike and thus precluded sexes from being distinguished in our dataset. Records of
201 scalloped-crowned birds (i.e., juveniles) were concentrated between December and May (Fig.
202 4) and restricted to the three disjunct breeding areas (Fig. S2), thus confirming the assumption
203 that first cycle juveniles do not migrate. Underpart colouration showed less pronounced
204 seasonal variation, with yellow-bellied birds being more common between April and September
205 (Fig. S6). In addition, most birds with an entirely black crown exhibited white underparts
206 (98.5%) while birds with brown crown usually exhibited yellow underparts (68.4%). Based on
207 our photographic dataset and following the terminology of Johnson & Wolfe (2018), first cycle
208 juveniles have scalloped appearance and usually white underparts (Fig. 4b); first cycle
209 formative birds seem to lose the scalloped appearance, acquire yellowish underparts and replace
210 pointed rectrices with more rounded ones (Fig. 4c); and first cycle alternate birds seem to
211 acquire black feathers on the crown and become whiter on their underparts (Fig. 4d). Over the
212 successive cycles, birds seem to replace their browner remiges and rectrices with darker ones
213 until they acquire their definitive cycle basic/alternate plumage (Fig. 4e–g).

214 **DISCUSSION**

215 Our results suggest that *Xenopsaris* has both resident and migratory populations. The disjunct
216 population of northern South America is apparently resident, while the populations ranging
217 from Argentina to north-eastern Brazil undertake different kinds of migratory movements.
218 More specifically, the southern population is an austral migrant that breeds in southern South
219 America and seems to winter mainly in central Brazil, while the north-eastern population seems
220 to be a partial intra-tropical migrant that breeds in the Caatinga of north-eastern Brazil and
221 migrates south-westward during the dry season (although their destination remains unknown).

222 However, there remains a possibility that it is only the southern population that is migratory
223 and moves north until it overlaps with the distribution of a resident population in north-eastern
224 Brazil. We consider this unlikely because the decrease in the number of records within the
225 Caatinga is congruent with both the region's rainfall and food resources seasonality (Fig. 1b;
226 see below), which suggests that a portion of the north-eastern population does undertake
227 migratory movements during the dry season. In addition, a control species did not show such a
228 variation in the monthly number of records (Fig. S5), suggesting that this pattern is probably
229 not biased by a seasonal variation in observer effort, and based on the field experience of one
230 of us (R.D.L.), *Xenopsaris* indeed appears to become rarer in some specific locations in the
231 Caatinga during the dry season. Therefore, our analyses suggest that both the southern and
232 north-eastern populations migrate, in opposite directions, and then overlap during the non-
233 breeding season (Fig. 3). Further study with tracking technologies, such as geolocators, is
234 needed to determine the destination of these populations and where they come into contact
235 during the non-breeding season.

236 The actual drivers of *Xenopsaris* migration remains to be further explored, but as is often
237 the case for other South American migrant passerines (Chesser 2005, Jahn *et al.* 2010, 2020),
238 fluctuations in temperature and precipitation, linked to food availability, seem most likely. Both
239 temperature and precipitation rate vary widely in the Southern Cone of South America and both
240 may affect the movements of the migratory southern population (Fig. 3). On the other hand,
241 only precipitation rate varies widely in the Caatinga of north-eastern Brazil. In this region, the
242 largest extent of the seasonally dry tropical forest biome (Fig. 1, Pennington *et al.* 2009),
243 pronounced rainfall seasonality (Nimer 1972, Andrade 2017) strongly influences arthropod
244 abundance (Vasconcellos *et al.* 2010, França *et al.* 2020) and acts as a cue to set the timing and
245 intensity of bird breeding and moulting (Cavalcanti *et al.* 2016, Araujo *et al.* 2017). The
246 observed decrease in the number of records of *Xenopsaris* in the Caatinga between April and

247 November is congruent with both the rainfall seasonality (Fig. 1b) and the seasonality in the
248 abundance of arthropods in the region (Vasconcellos *et al.* 2010, França *et al.* 2020), suggesting
249 that part of the Caatinga population undertakes migratory movements during the dry season,
250 after breeding (December–May), when food becomes scarce; yet some individuals remain year-
251 round there (Figs. 1 and S3). Both the southern and north-eastern population seem to migrate
252 to central Brazil, a region also characterized by pronounced rainfall seasonality and which is in
253 the dry season when the birds arrive there (Fig. 1d). However, most phytophysiognomies of
254 this region do not shed their mature leaves during the dry season and harbour some arthropod
255 abundance throughout the year (Pinheiro *et al.* 2002, Silva *et al.* 2010), unlike the vegetation
256 of the Caatinga, that loses almost completely its leaves during the dry season, thus affecting
257 more dramatically arthropod abundance (Vasconcellos *et al.* 2010).

258 Several bird species are known to migrate to the Caatinga from breeding grounds in
259 southern South America (e.g., Ruiz-Esparza *et al.* 2011, Pereira & Azevedo-Júnior 2013, Bravo
260 *et al.* 2017), but there are few proven cases of species that do the contrary—breed in the
261 Caatinga and migrate out of it (e.g., Lees 2016). *Xenopsaris* adds another example to this poorly
262 studied pattern, which likely includes several other species whose migratory patterns remain to
263 be properly studied, such as the Dark-billed Cuckoo *Coccyzus melacoryphus*, White-winged
264 Becard *Pachyramphus polychopterus* and Variegated Flycatcher *Empidonomus varius* (R.D.L.
265 pers. obs.).

266 Maps depicting the total geographic distribution of *Xenopsaris* usually infer that there
267 are two disjunct populations; one in the northern corner of South America, from Venezuela to
268 Guyana, and a larger one from north-eastern Brazil to Argentina (Moblely 2004, Ridgely &
269 Tudor 2009). Our analyses, however, revealed that there are three disjunct breeding
270 populations, of which one is certainly fully migratory, one is probably partially migratory and
271 one is likely resident. Birds from the two migratory populations come into contact during the

272 non-breeding season whereas the third population is resident and breeds asynchronously in
273 relation to the others (Fig. S2). Two subspecies of *Xenopsaris* are currently recognized—the
274 nominate form was described from Argentina while *X. a. minor* was described from Venezuela
275 based only on its smaller size (Hellmayr 1927, Traylor 1979)—corresponding to the southern
276 and northern populations, respectively. Although their diagnosis is quite superficial, the fact
277 that they show distinct migratory behaviours, asynchronous breeding seasons and are isolated
278 by geographic distance suggests that there may be no gene flow between them. As demonstrated
279 for other Neotropical passerines, changes in migratory behaviour within a lineage can drive
280 allochronic speciation (Turbek *et al.* 2018, Uy *et al.* 2018, Gómez-Bahamón *et al.* 2020), and
281 with the resolution of the migratory status of this species, it now becomes an attractive model
282 to further explore the differentiation between migratory and sedentary populations in a partially
283 migratory species, as well as to study determinants of partial bird migration (e.g., Jahn *et al.*
284 2010).

285 Finally, our results suggest that *Xenopsaris* has distinct breeding and non-breeding
286 plumage. There is a period of the annual cycle when most birds exhibit an entirely black crown
287 (October–April) whereas for the remainder of the year most birds exhibit either a brown crown
288 or a black crown with brown feathers (May–September; Fig. 4a). Birds can undergo seasonal
289 colour changes through various ways, including feather moult, feather abrasion, colour fading,
290 and application of cosmetics (Butcher & Rohwer 1989, Delhey *et al.* 2007, Tökölyi *et al.* 2008,
291 McQueen *et al.* 2019). We assume that *Xenopsaris* exhibits a complex alternate strategy like
292 its closest relatives (Barber & Rice 2007, Johnson & Wolfe 2018) and thus undergoes seasonal
293 colour changes by moulting, but further investigation both on its moult strategy and on the
294 cause of its seasonal colour changes are warranted.

295 Eclipse plumage is a very uncommon trait in passerines, even less common in South
296 American ones, and it is predicted that, across passerines, this trait is more common in

297 migratory species and in species living in highly seasonal environments (Howell 2010,
298 McQueen *et al.* 2019), which is particularly the case with *Xenopsaris*. Because conspicuous
299 colours may be simultaneously advantageous for mate attraction and disadvantageous if they
300 increase detectability to predators, birds that undergo postbreeding colour change can have the
301 best of both worlds—being conspicuous when they need to be, during the breeding season, and
302 less conspicuous during the non-breeding season, then decreasing predation risk (McQueen *et*
303 *al.* 2019). *Xenopsaris* undergoes seasonal colour changes in its shiniest part, the crown, which
304 may offer some survival advantage during its migration. It remains to be further explored
305 whether seasonal colour changes in *Xenopsaris* occur in both sexes or only in males. Males and
306 females are often easy to tell apart in museum specimens (Fig. S7), but the species' sexual
307 dimorphism may not be as evident in photos of the birds in the wild, especially considering that
308 the seasonal change in crown colouration makes both sexes look alike.

309 **CONCLUSION**

310 The assumption of residency of the White-naped *Xenopsaris*, as well as the inference
311 that the species had a continuous, though patchily distributed, population south of the Equator
312 (Mobley 2004), are likely due to the paucity of records of the species in the traditional sources
313 such as museum collections and the literature. Citizen science data helped us to mitigate these
314 sampling gaps associated with small sample sizes and allowed to unveil the species' migratory
315 patterns and to reveal that the species has actually three instead of two disjunct populations. In
316 addition to their importance for the study of bird migration (Lees 2016, Schubert *et al.* 2019,
317 DeGroot *et al.* 2021), our results also highlight the potential value of citizen science data to
318 study patterns of seasonal variation in plumage colouration. Because the presence of eclipse
319 plumage in passerines is positively correlated with the number of papers published per species,
320 the prevalence of this trait may be underestimated in less-studied birds (McQueen *et al.* 2019),

321 and thus citizen science databases can offer a valuable, easy-to-access source of data to help
322 reducing such knowledge gaps.

323

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329 DATA AVAILABILITY STATEMENT

330 All data used in this article are available in the Supplementary Online Material.

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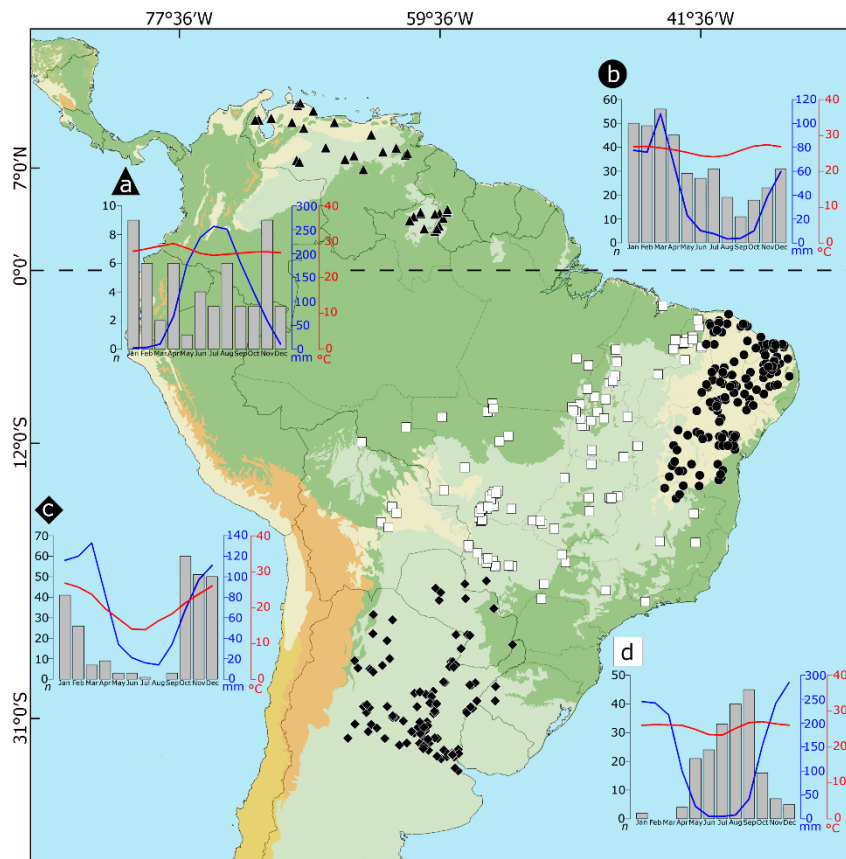
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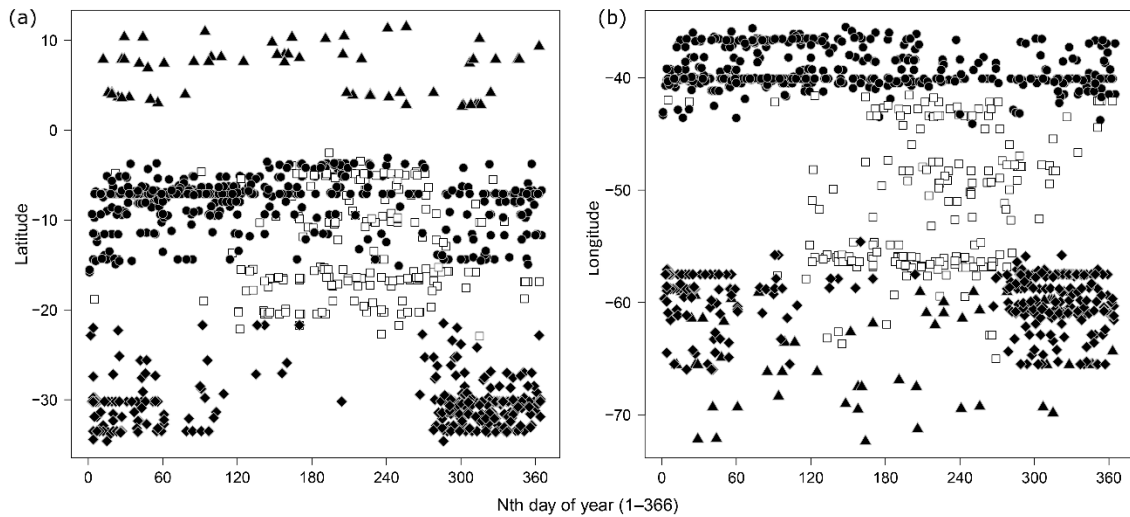
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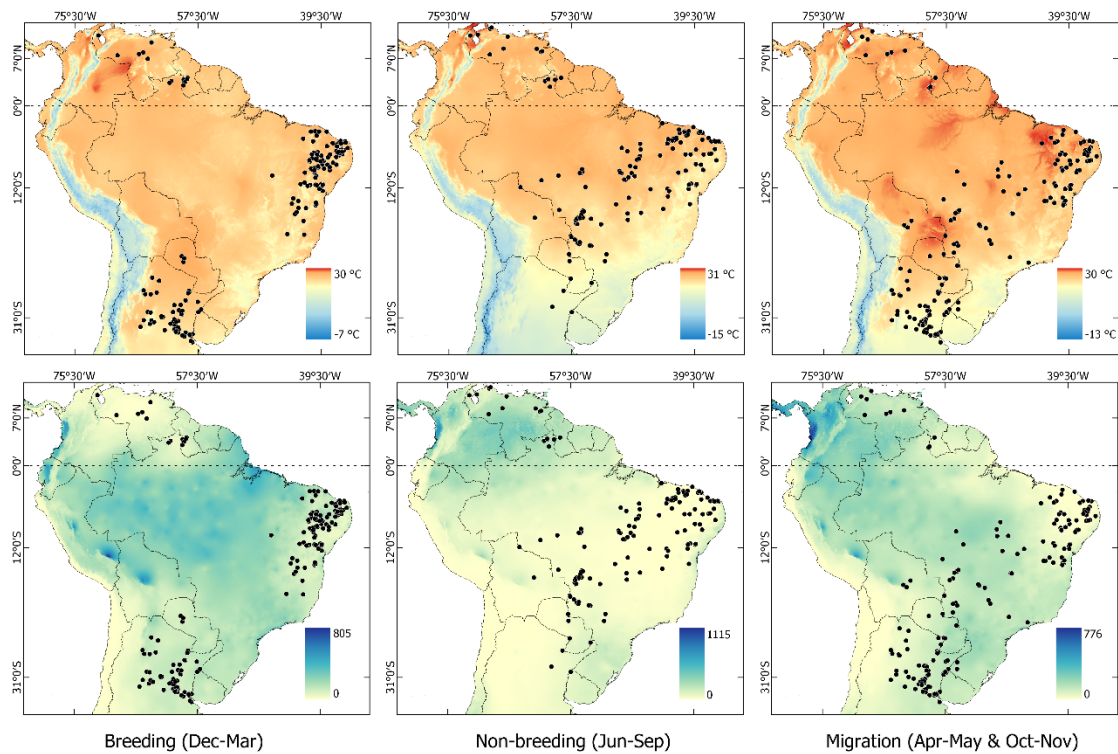
464 **Figure 1.** Geographic distribution of *Xenopsaris* categorised into four regions: northern (a,
 465 black triangles), north-eastern (b, black circles), southern (c, black diamonds) and central (d,
 466 white squares). The map includes all records in our dataset, but the histograms include only
 467 photographic records, because sound recordings are skewed towards the breeding period and
 468 museum specimens are concentrated in months where several specimens were collected
 469 together. Histograms show the number of photographic records per month in each region
 470 against variation in average monthly rainfall and temperature (blue and red lines, respectively).
 471 Environmental data showed in histograms were taken from a central locality within each of the
 472 four regions (means from 1970–2000 extracted from WorldClim). The scale on the left side of
 473 each histogram shows the number of records while the scales on the right side show the average
 474 monthly rainfall (mm) and temperature (°C). Scales on different graphs are different. The main
 475 biomes where *Xenopsaris* occurs are in light yellow (seasonally dry forests), light green

476 (savannas and grasslands) and dark green (rainforests). The Caatinga, mentioned throughout
477 the text, is the light-yellow area in north-eastern Brazil.



478

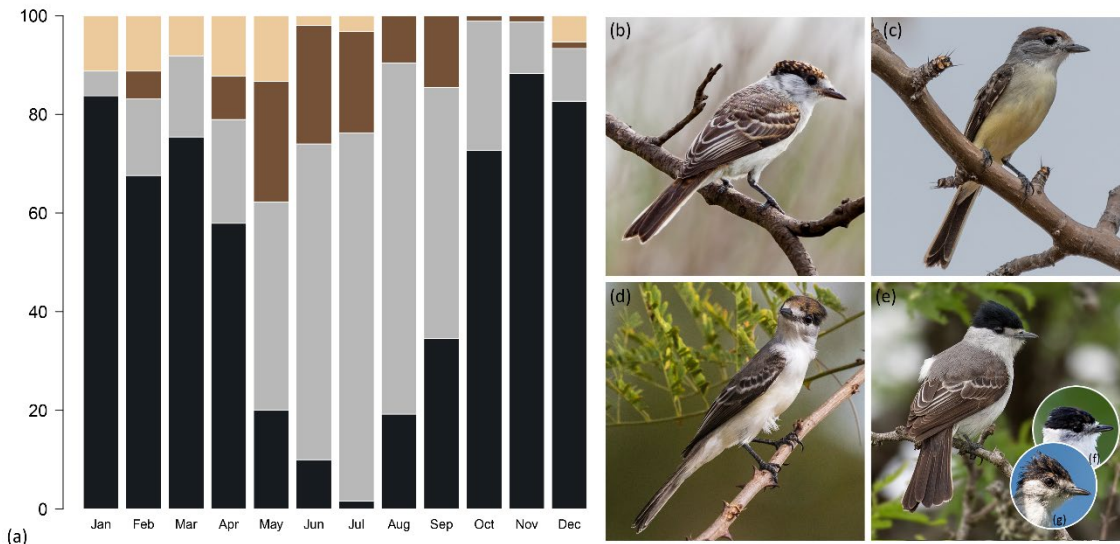
479 **Figure 2.** Spatiotemporal variation of *Xenopsaris* across the annual cycle illustrated by the day
 480 number of each record plotted against its latitude (a) and longitude (b). **(a)** Records north of
 481 0°N involve the geographically isolated northern population, which was recorded year-round,
 482 while records south of 0°N depict the migratory populations, which undertake different kinds
 483 of migration (see the main text). Between April and September (~100–260th days) there are
 484 almost no records south of 30°S, indicating that southern birds migrate northward and then
 485 overlap spatially and temporally with birds from the Caatinga. **(b)** The migratory population
 486 that winter in central Brazil (~50°W) stays there mainly between May and November (~150–
 487 310th days). Symbols follow those in Figure 1.



488

489 **Figure 3.** Fluctuations in temperature and precipitation seem to be linked to the migration of
 490 *Xenopsaris*, as suggested by the overlap of these environmental variables and the species'
 491 spatiotemporal variation. The northern population is recorded year-round, while the southern
 492 population migrates during the coldest, driest period of its breeding grounds and the north-
 493 eastern population seems to migrate during the region's driest period. The above maps show
 494 the species' spatiotemporal variation against seasonal variation in average temperature (°C)
 495 while the bottom maps show the species' spatiotemporal variation against seasonal variation in
 496 precipitation rate (mm). The layers of environmental variables are means from 1970–2000
 497 extracted from WorldClim (Fick & Hijmans 2017) for the months of February (breeding),
 498 August (non-breeding), and October (migration). For monthly maps, see Figures S3 and S4.

499



500 **Figure 4.** (a) Variation (%) in *Xenopsaris* crown colouration over the annual cycle (only
 501 photographic records with enough quality and checked museum specimens were included, $n =$
 502 776). Most birds exhibit an entirely black crown (black bars) between October and April,
 503 whereas for the remainder of the year most birds exhibit a black crown with brown feathers
 504 (grey bars) or a brown crown (brown bars). Juveniles, that have a scalloped crown (yellow
 505 bars), are almost restricted to the breeding period. Note that brown-crowned birds (brown bars)
 506 succeed scalloped-crowned birds (yellow bars), illustrating the moult period of first cycle
 507 juvenile to first cycle formative plumage. The few scalloped-crowned birds recorded in June
 508 and July had an intermediate appearance. The northern resident population is not included
 509 because it breeds asynchronously relative to the other populations and had too few photographic
 510 records ($n = 28$). Examples of *Xenopsaris* plumages: first cycle juvenile (b), first cycle
 511 formative (c), possibly first cycle alternate (d), adult male breeding plumage (e) and possibly
 512 the non-breeding plumage (f, g). Photos by Hector Bottai (b), Eugênio Oliveira (c, g), Chico
 513 Rasta (d), Alexandre Gualhanone (e) and Henrique Coelho (f).