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Geographical variation and current knowledge on breeding traits of vultures in the neotropics

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Abstract

New World vultures (Cathartidae) have essential roles in ecosystem functioning, but are susceptible to increasing anthropogenic impacts. Knowledge of several breeding, behavioral, and distributional parameters of Neotropical vultures is poorly organized and have not been properly reviewed. Here, we made a comprehensive review of original breeding records from museums, literature, and citizen science (WikiAves) for each of the six species of vultures occurring in the Neotropical region. These data were used to review breeding patterns and geographical distribution, and identify information gaps. The 567 records of breeding from the Neotropics assembled are very biased, mostly for Black Vulture *Coragyps atratus* ($n = 319$) and Turkey Vulture *Cathartes aura* ($n = 166$), and unevenly distributed among regions and subspecies. The four other species still have a great lack of knowledge about their breeding in the wild (Lesser Yellow-headed Vulture *Cathartes burrovianus* ($n = 20$), Greater Yellow-headed Vulture *C. melambrotus* ($n = 2$), King Vulture *Sarcoramphus papa* ($n = 21$), and Andean Condor *Vultur gryphus* ($n = 30$)). We show for the first time that Neotropical Cathartidae have convergent breeding seasons among sympatric taxa, delay start of breeding with increasing latitude, and have an allometric relationship between adult size and egg size. Nevertheless, larger samples of breeding data, especially from some regions and taxa, such as the two "Yellow-headed Vulture" species, are still needed. We also show that breeding traits could be helpful for preventive management and conservation strategies involving both expanding and decreasing populations of vultures in the Neotropics.

Keywords Cathartidae · Knowledge gaps · Management · Nesting · New World vultures · Reproduction

Introduction

Vultures have important roles in ecosystem services, as bioindicators, and in traditional cultures. As scavengers, they remove decomposing organic matter, accelerating nutrient cycling processes and reducing the potential spread of pathogenic agents (Antas 2004; Donázar et al. 2012; McClure et al. 2018). Many of these birds are involved in mutualistic relationships with humans, obtaining their food primarily from human waste and/or livestock carcasses. Such behavior has been related to changes in species' abundance and distribution (Sick 1997; Buckley 1999), and may enable the maintenance of populations of threatened vultures (Gangoso et al. 2013). On the other hand, recent steep declines in many populations (Ogada et al. 2011) emphasize vultures' important role as indicator species, facilitating the detection of contaminants for example (Valladares et al. 2013; Alvarado Orellana et al. 2015). In South America, *Cathartes* vultures help to pinpoint leaking gas in pipelines (Márquez et al. 2005), due to their keen sense of smell (Houston 1988; Graves 1992; Sick 1997), and Black Vultures *Coragyps atratus* equipped with cameras were recently employed to track illegal dumps sites (USAID 2015). Also, in this continent's traditional cultures, species such as the Andean Condor *Vultur gryphus* had paramount roles (Rozzi 2004), but in more recent times most of their former symbolism was lost or changed (McGahan 1971;

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Jacome and Astore 2004). The so-called mystical tourism now represents a threat to these vultures, as it foments the illegal trade of their body parts for souvenirs and quasi-shamanic healing (Williams et al. 2011).

New World vultures (Cathartidae) are large birds (~ 1–12 kg; Dunning 2008), with small clutch sizes (1 to 3 eggs) and slow development (Arballo and Cravino 1999; Houston 2018). Thus, any change in their breeding might affect populations in the long term. Albeit as a group, Cathartidae are not particularly threatened in the present (McClure et al. 2018), the fast increase of anthropogenic impacts on most of their range is already promoting changes in their distribution and abundance (e.g., Butler 2003; Carrete et al. 2010). This situation could quickly worsen, as their specialized diet and small number of species can render New World vultures as a particularly vulnerable group of raptors (Campbell 2015). In this case, knowledge of several breeding and behavioral parameters is necessary to better design management plans (Lowney 1999; Novaes and Cintra 2015). In fact, the latest global assessment of raptors' status highly recommended research on life-history traits of New World vultures (McClure et al. 2018).

Of the seven species of Cathartidae, only the California Condor (*Gymnogyps californianus*) is restricted to the Nearctic region, while the others have their centers of distribution in the Neotropics (Houston 1988, 2018). In the Nearctic, the breeding biology of vultures is generally well known (e.g., Peterson 1961; Stewart 1974; Harrison 1975; Snyder and Hamber 1985; Coleman and Fraser 1989a, b; Rabenold 1986, 1987; Richardson 1989; Bridges 1998; Wheeler 2003; Houston et al. 2007; Johnsgard 2009; Igl and Peterson 2010; Burnett et al. 2013; Rollack et al. 2013). Yet, in the Neotropics, the knowledge seems much more limited, as many breeding reports are anecdotal, a typical situation for diurnal raptors of this region (Monsalvo et al. 2018). Also, most records of reproduction of the two larger Neotropical species, King Vulture *Sarcoramphus papa* and Andean Condor *V. gryphus*, are from captive birds (e.g., Miranda-Ribeiro 1918; Poulsen 1963; Klös 1984; Schlee 1994), with seemingly few field data (Ferguson-Lees and Christie, 2001).

Previous reviews on New World vultures (e.g., Ferguson-Lees and Christie 2001; Campbell 2015) do not provide some breeding data, such as egg measurements; do not validate frequencies of clutch sizes in a quantitative way; and also do not explicitly present information on museum egg sets, despite such data may be to some extent included in past literature analyzed by those authors (e.g., Belcher and Smooker 1934; Wolfe 1938). The amount of information that can be obtained solely from museum eggs (McNair 1987; Murphy 1989; Olsen and Marples 1993) reinforces the importance of this source on proper reviews about diurnal raptors' breeding. Yet, it is mandatory to validate the identification of museum specimens, preventing dissemination of cascading errors (Griffiths and Bates 2002; Monsalvo et al. 2018).

Thus, here we review breeding evidence from literature, museums, and a Brazilian citizen science website (WikiAves) for each of the six species, and respective subspecies, of New World vultures occurring in the Neotropical region. We assess the distribution of the records among the different taxa, analyze geographical distribution and variation in their breeding seasons and egg measurements, and validate clutch size frequencies for the different species. On this process, we present careful comparisons between information that we obtained and those present in other published reviews. We also indicate gaps of knowledge and evaluate the needs of further studies on the different taxa's breeding traits and distribution. Finally, we propose corrections for misidentified museum egg sets and briefly discuss potential management implications of breeding data.

Material and methods

We searched for original breeding records of the six species of Neotropical vultures in the literature, museums, and the WikiAves website, as described below.

Taxonomy and distribution maps

The taxonomy of Neotropical vultures is stable at the species level (but see Jaramillo 2003, for a proposal of a possible split in *Cathartes aura*), yet there are still some recent disagreements at the subspecies level (Ferguson-Lees and Christie 2001; Dickinson and Remsen-Jr. 2013; Clements et al. 2018). Since breeding traits might be useful in future taxonomic discussions or even conservation plans, we related each breeding report to the lowest taxonomic level possible, considering Wetmore's (1962, 1964) subspecies proposals—still the baseline for subspecific divisions today.

To enable proper assignment of each breeding report to the subspecies level, we drew each taxa distribution (Figs. 1, 2, 3, 4, 5, and 6) on top of BirdLife maps (2018). Subspecies' distributions were based on databases such as the Handbook of the Birds of the World (HBW; www.hbw.com), Global Raptor Information Network (GRIN; http://www.globalraptors.org/grin/indexAlt-ORIGINAL.asp), Birds of North America (BNA; https://birdsna.org), and WikiAves (WA; www.wikiaves.com); and also on Blake (1977), Weick and Brown (1980), Ferguson-Lees and Christie (2001), Restall et al. (2007), Dickinson and Remsen-Jr. (2013), and Clements et al. (2018).

All kinds of breeding evidence were used in distribution maps of breeding records for all regions and/or subspecies. However, poorly georeferenced records (i.e., those only at the country level, except for countries smaller than Bolivia—chosen as a "cutoff size" since it is an average-

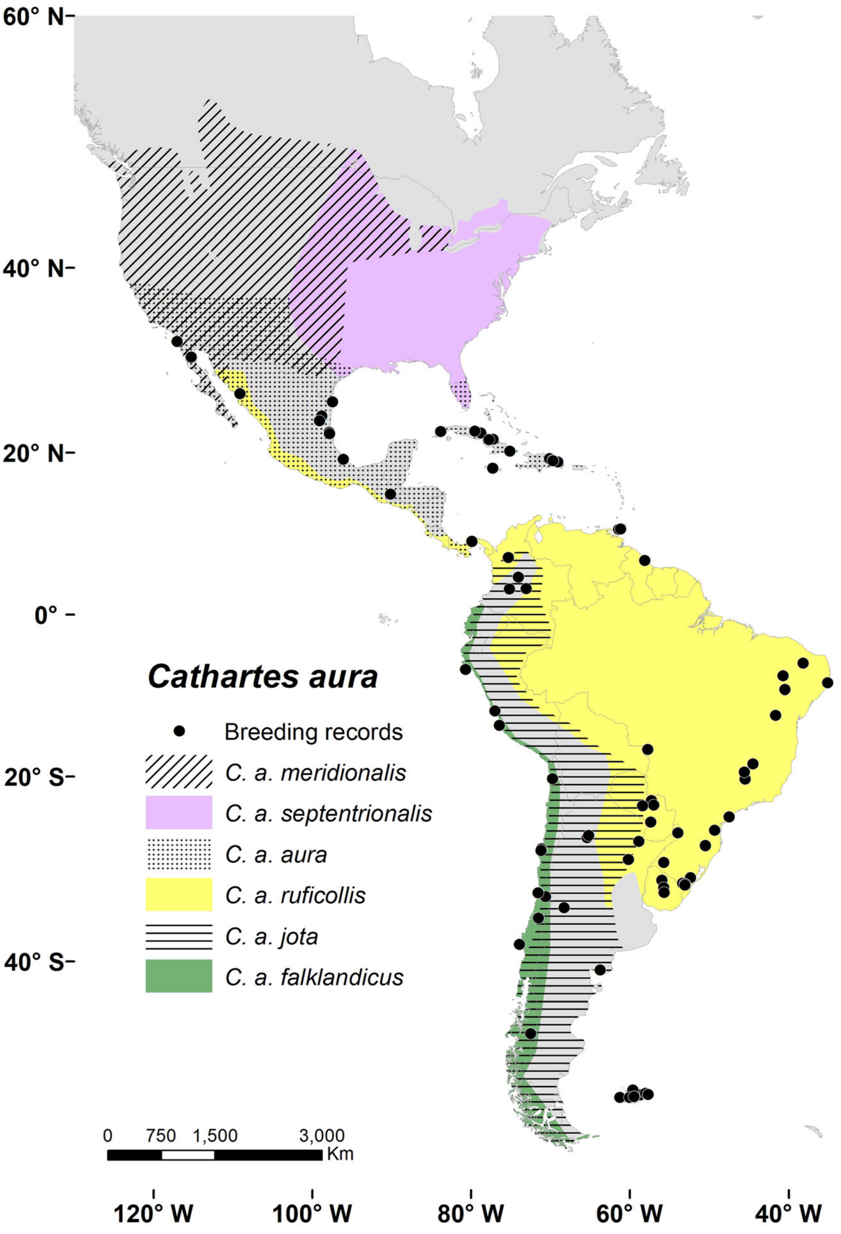


Fig. 1 Geographical distribution of original breeding records (dark circles) of Turkey Vulture *Cathartes aura* in the Neotropics, assigned to the subspecies level. Superimposing patterns refer to distributions with uncertain and/or conflicting limits, according to literature sources

sized country with an average location error of less than 500–600 km) were not plotted in the maps to avoid false inconsistencies with known distribution. A few breeding records fell outside current distribution, mostly as probable artifacts of inaccurate georeferencing, but relevant exceptions are discussed in the text.

For practical reasons, given that limits of subspecies ranges are still unclear and divergent among references, we adopted the same definition of Neotropical zone as Menezes and Marini (2017), excluding southernmost Florida and including all of Mexico. As we focused on the Neotropics, we did not compile any records from the Nearctic region, nor Nearctic subspecies of *Cathartes aura* (i.e., those with centers of distribution outside the Neotropical region).

Breeding parameters

Although we located several kinds of breeding evidence, only breeding seasons, nest sites, clutch sizes (or brood sizes, in cases without information on the number of eggs), and egg measurements were analyzed and briefly discussed. To estimate breeding seasonality, we focused on egg or nestling records with known dates, which was the same information used in seasonality estimates by Ferguson-Lees and Christie (2001). Egg or nestling records also can be referred as "viable nesting attempts," to describe large raptors' reproduction according to Steenhof et al. (2017) terminology. We opted to use only egg or nestling records given that the protracted period of

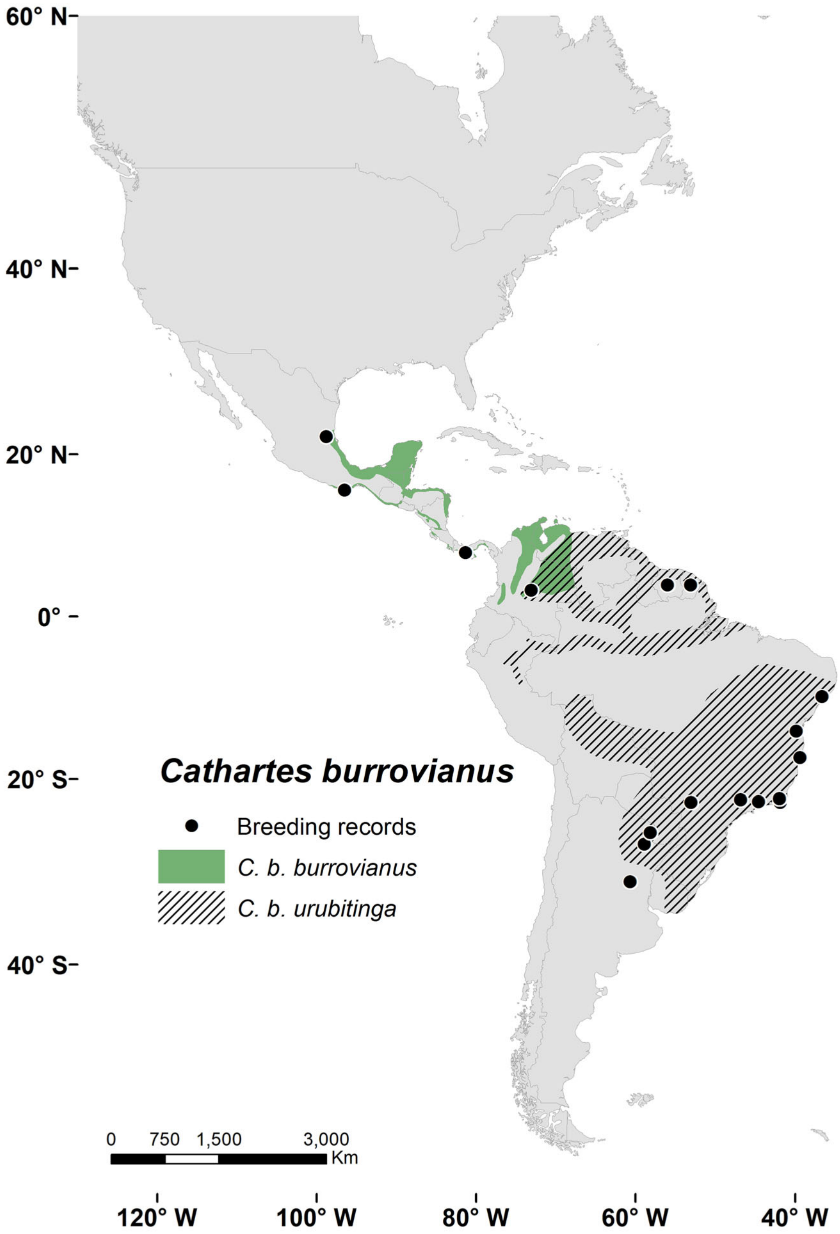


Fig. 2 Geographical distribution of original breeding records (dark circles) of Lesser Yellow-headed Vulture *Cathartes burrovianus*, assigned to the subspecies level. Superimposing patterns refer to distributions with uncertain and/or conflicting limits, according to literature sources

young birds' post-fledging dependency in this family (see Rabenold 1986; Houston 2018) might confound precise estimates of breeding seasonality in other cases. When egg and nestling dates were not known, backdating was used just in situations that allowed fairly accurate estimations—that is, when available information was detailed enough to obtain the former dates, considering what is known of the species' incubation and fledging periods. For instance, Wetmore (1965) does not provide some egg dates, but mentioned dates when he found recently fledged birds. These allowed an extrapolation that led to the months in which eggs were laid at those locations. Cases like these accounted for only around 3% ($n = 19$) of the total breeding records.

Literature search

We reviewed the literature to compile information on breeding data, dates, and locations. Until May 2017, we screened the GRIN database, searching for studies whose titles refer to reproductive aspects, mainly the bibliography contained in the topic "Breeding biology." As a search tool, we chose to use Google Scholar (http://scholar.google.com/), which we verified that is able to locate the same publications found with databases such as Searchable Ornithological Research Archive (SORA; http://elibrary.unm.edu/sora) and Scopus (Monsalvo et al. 2018).

The search terms were the current scientific names of these species, combined with nest, ninho, nido, nidificação,

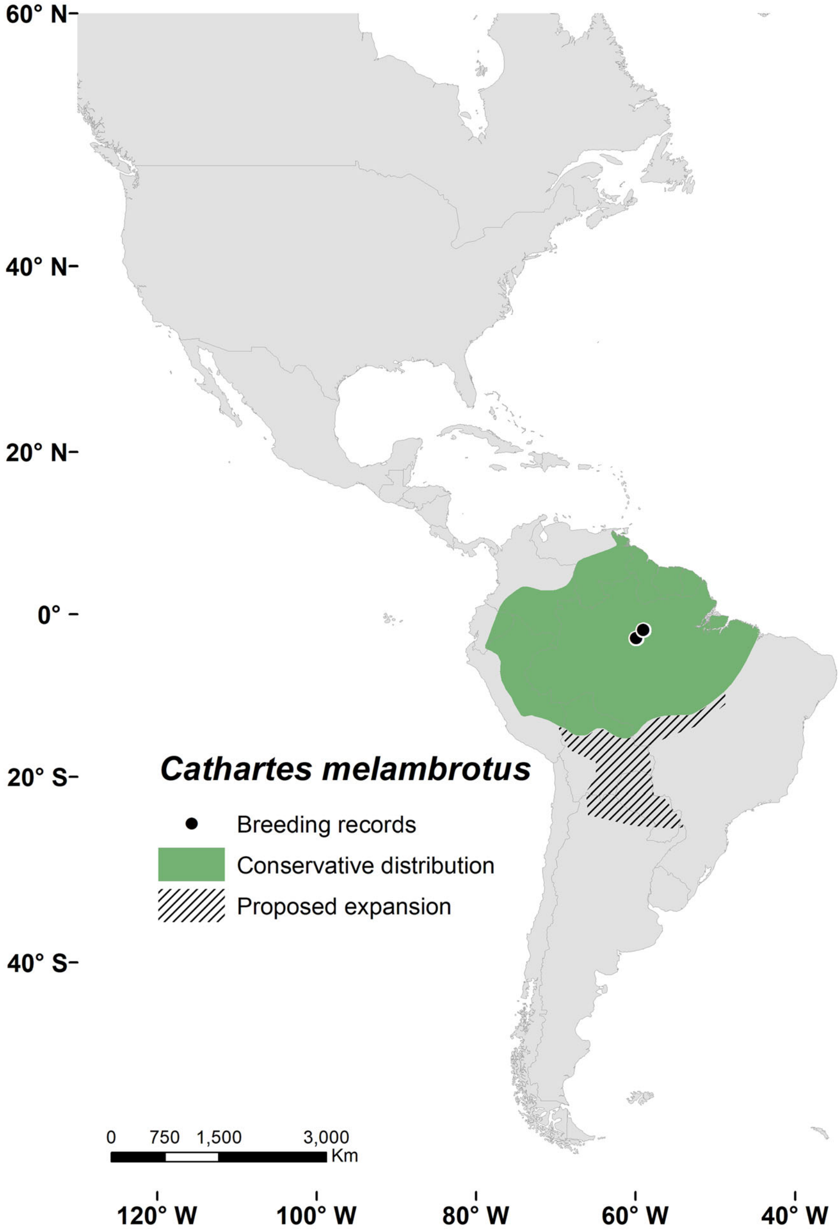


Fig. 3 Geographical distribution of original breeding records (dark circles) of Greater Yellow-headed Vulture *Cathartes melambrotus*. Further explanations on the main text

nidificación, reprodução, reproducción, breeding, and biologia reprodutiva. Terms like "nesting" and "biología reproductiva" were discarded due to great redundancy of results when using somewhat similar terms. We also reviewed citations contained in the publications. We considered all studies retrieved in these searches, from articles in any category of scientific journal, through monographs, conference abstracts, to technical reports, and unpublished manuscripts. Only a few studies could not be found or retrieved.

We also screened a bibliographical review of Brazilian birds (Oniki and Willis 2002), and books (Herklots 1961; Peterson 1961; Haverschmidt 1968; Harrison 1975; Hilty and Brown 1986; Sick 1997; Arballo and Cravino 1999; Ferguson-Lees and Christie 2001; Höfling and Camargo 2002; Belton 2003; Wheeler 2003; Antas 2004; De La Peña 2005; Márquez et al. 2005; Sigrist 2006; Gimenes et al. 2007; Gussoni and Guaraldo 2008; Novaes and Lima 2009). Breeding records on books were included in this review only if they clearly indicated in the text that it was an original data, or when it was a very relevant, detailed information that we could not retrieve elsewhere.

Still, many books contain secondary information without direct citation of the original source, preventing us from recovering it, and even determine the geographic region it refers to. Data without any locality information (i.e., not even assigned to a country), and also those that do not clearly discriminate which reproductive parameters were recorded, were discarded—but might have been used in "Discussion."

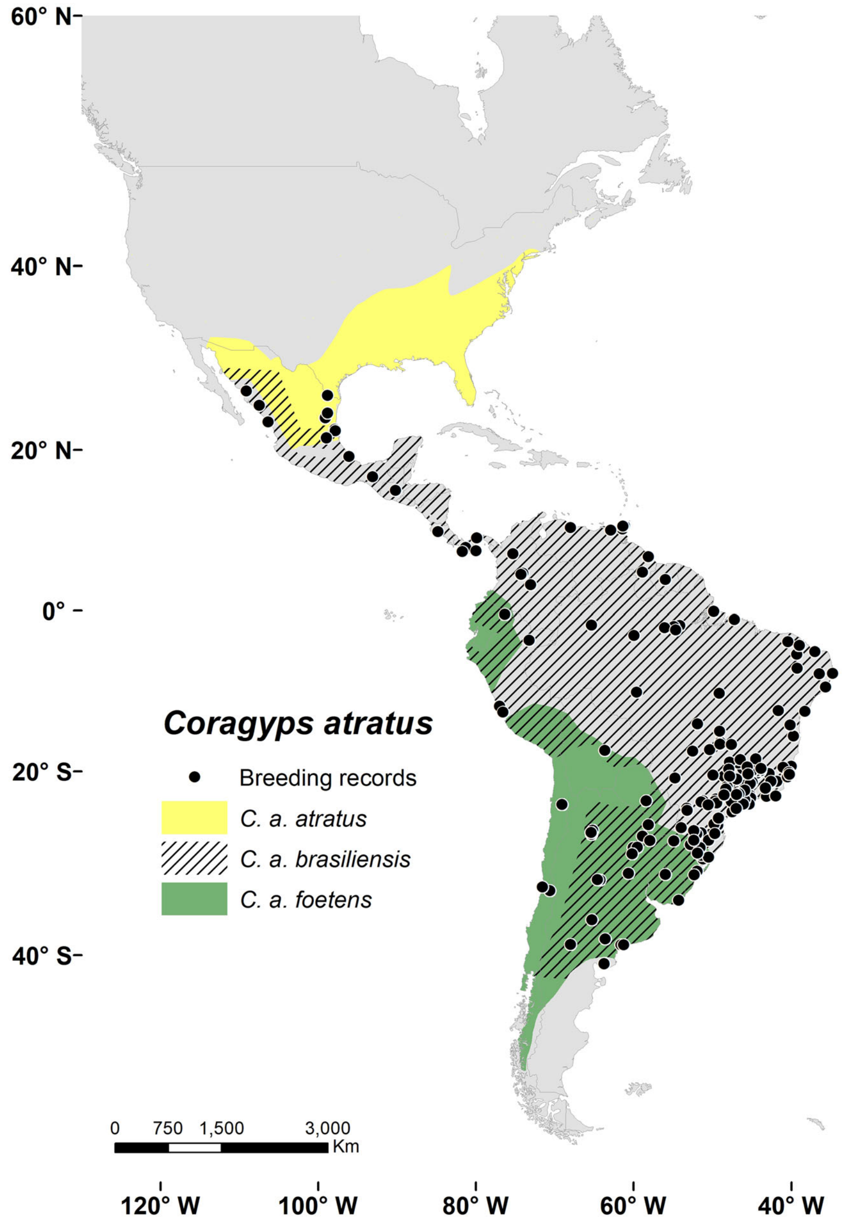


Fig. 4 Geographical distribution of original breeding records (dark circles) of Black Vulture *Coragyps atratus* in the Neotropics, assigned to the subspecies level. Superimposing patterns refer to distributions with uncertain and/or conflicting limits, according to literature sources

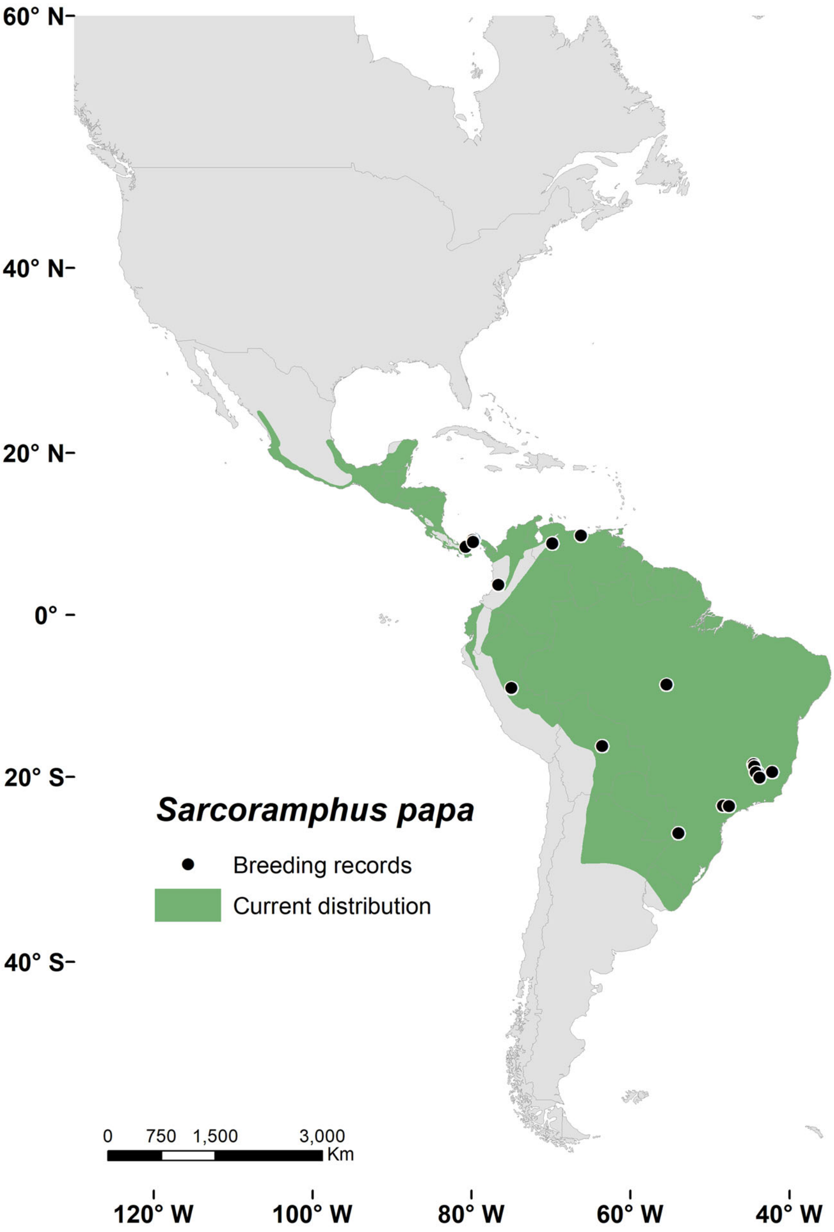
The recent comprehensive review on the biology of both New and Old World vultures by Campbell (2015) needs an update in some distribution maps, citations of breeding accounts, and breeding information of Cathartidae. To avoid perpetuating misinformation such as the ones in this book, we opted to exclude from our analysis all data provided in there that we could not retrieve elsewhere. Instead, we carefully compared that information with data that we obtained from other sources, pointing out every discrepancy.

In any case, when the same breeding record is present in more than one reference by a given author, we mention only the reference with more complete information. We also avoided potentially redundant information—that is, literature data from museum eggs that we had already analyzed (e.g., most egg data on Belcher and Smooker (1934); see Egg Measurements). Finally, besides literature reports, we included a few field observations (J.A.B.M.) and personal communications of unpublished breeding records.

Museum eggs

Eggs and labels were photographed in the following egg collections between 2014 and 2019: Western Foundation of Vertebrate Zoology (WFVZ, Camarillo, USA), the Delaware Museum of Natural History (DMNH, Wilmington, USA), American Museum of Natural History (AMNH, New York, USA), Natural History Museum—Smithsonian Institution (USNM, Washington, D.C.), the Natural History Museum (NHMUK, Tring, UK), National Museums of Scotland (NMS, Edinburgh, Scotland), the Zentralmagazin Naturwissenschaftlicher

Fig. 5 Geographical distribution of original breeding records (dark circles) of King Vulture *Sarcoramphus papa*



Sammlungen, Martin Luther University Halle-Wittenberg (MLUH, Halle (Saale), Germany), the Naturhistorisches Museum Wien (NMW, Vienna, Austria), the Museum d'Histoire Naturelle de Genève (MHNG, Geneva, Switzerland), the Naturhistorisches Museum Bern (NMBE, Bern, Switzerland), the Musée Zoologique de l'Université Louis Pasteur et de la Ville de Strasbourg (MZS, Strasbourg, France), the Muséum National d'Histoire Naturelle (MNHN, Paris, France), Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN, Buenos Aires, Argentina), Museu de La Plata (MLP, La Plata, Argentina), the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAVH, Villa de Leiva, Colombia), and in Brazil, MZUSP (São Paulo), MN (Rio de Janeiro), MPEG (Belém), and COMB (Brasília). We also visited the online egg collections of the FMNH (Chicago, USA), and the Arctos Collaborative Collection Management Solution (arctos.database.museum). Finally, we consulted the catalog of the Cris-Rivers Region Museum (CRRM, Oradea, Romania) (Béczy 1971).

Egg measurements

Eggs length and width were measured using digital photography (Bridge et al. 2007; Troscianko 2014) from photos taken at museums (or available online, as mentioned before). We used ImageJ, which allowed standardized measurements to the nearest 0.1 mm, enabling proper comparisons. Egg size was first used to compare species' eggs and hence validate

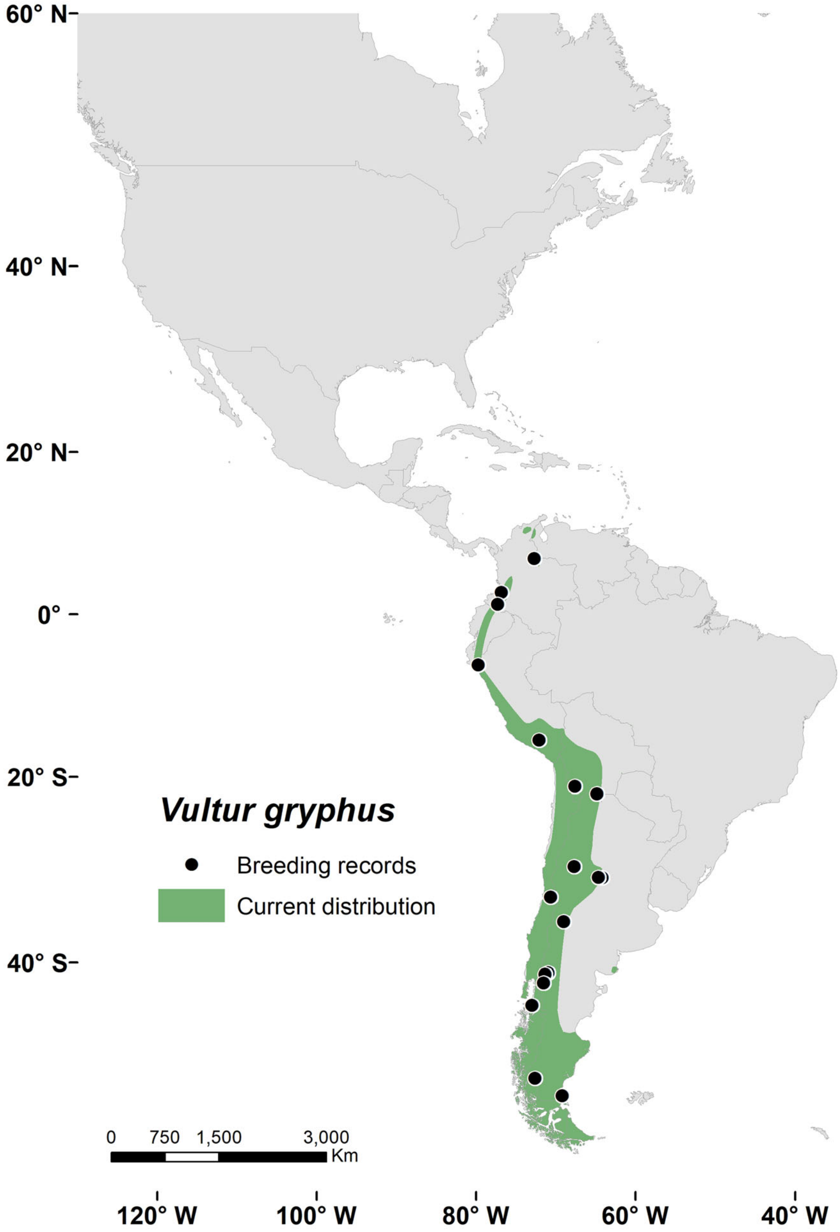


Fig. 6 Geographical distribution of original breeding records (dark circles) of Andean Condor *Vultur gryphus*

identification, using measurements from the literature and also considering the proportionality of egg size to female size (Winkler 2004). In this process, two eggs were discarded since its measurements and/or appearance are clearly distinct from Cathartidae eggs. These and other cases of misidentifications are presented and discussed in Suppl. 3, and also mentioned on species' Results sections when necessary.

For species with < 100 egg measurements from museums (that is, all but the Black Vulture), we also considered measurements from any original record found in the literature. When doing this, we carefully verified and excluded redundant information, like literature data on eggs from museums to which we had access (e.g., most egg data on Belcher and Smooker (1934)). We also discarded data that could not be soundly assigned to one subspecies of a polytypic species (e.g., when we could not determine the geographic origin of some records), and measurements that were (or could be) from wholly Nearctic subspecies.

For the Black Vulture, which had the largest number of measured museum eggs (> 100), reference values were obtained only from literature material that compiled greater amounts of egg measurements safely assigned to one or more known subspecies (e.g., Wetmore 1962). Only for this species' nominate subspecies (*Coragyps a. atratus*), we had to use some measurements ($n = 9$) of eggs from the USA (thus, Nearctic), given the great scarcity of Neotropical data for comparison purposes. Yet, as expected, such information was only used for the measurements' analysis, and Nearctic eggs were not incorporated anywhere else in this review's results. Also, eggs from captive birds were used for estimates of egg size just for the King Vulture and the Andean Condor, since there are scarce reports of eggs from the wild for these two species.

WikiAves records

The WikiAves website (www.wikiaves.com), a citizen science database, was searched for photographs of nests, eggs, nestlings, and their dates and localities until October 2018. Records with unclear identification were discarded. For the four less-known species (the two Yellow-headed and the King Vulture, and the Andean Condor), we also looked for photographs of any kind of breeding evidence, such as copulation records and dependent juveniles. When necessary, WikiAves individual records are cited on the main text by their reference numbers.

Results

We compiled a total of 567 original breeding records of Cathartidae in the Neotropics, excluding data from captive birds (see species accounts). Considering only records safely assigned to a species, the Black Vulture was the most frequent ($n = 319$; 56.3% of the records), followed by the Turkey Vulture ($n = 166$; 29.3%). Three of the remaining species accounted, individually, for no more than 5% of the records (Andean Condor, $n = 30$; King Vulture, $n = 21$; and Lesser Yellow-headed Vulture, $n = 20$). The Greater Yellow-headed Vulture is by far the least represented, with only two confirmed original breeding records.

Cathartes aura (Turkey Vulture)

Over 90% of the 772 clutches we located in museum collections were from the USA and Canada. Nearctic subspecies (and to a much lesser extent, Nearctic populations of *C. a. aura*) have abundant breeding information in the literature (e.g., Kirk and Mossman 1998; Campbell 2015) and will not be addressed here anymore.

Literature data for the nominate subspecies (*C. a. aura*) in the Neotropics is largely restricted to the Greater Antilles, while most of its 34 museum clutches are from Mexico (Table 1; Table S1). On the other hand, subspecies *C. a. ruficollis* has fairly more widespread information, coming from literature, museums, and WikiAves (Table S2)—but mostly small samples, from a few countries. *Cathartes a. falklandicus* is the least represented subspecies in the literature, but the most frequent in museums, with 55 clutches, while *C. a. jota* is poorly represented both in literature and in museums. Yet, over 11% of the breeding records from the Neotropical region could not have their subspecies safely confirmed based on distributional maps (Fig. 1). Six museum clutches in this situation belong to either *C. a. falklandicus* or *C. a. jota*.

Egg dates peak between March and April (late winter/early spring) for *C. a. aura* (Fig. 7). For *C. a. ruficollis*, Southern Hemisphere's dates suggest a breeding season beginning in winter and lasting until summer, while in the Northern Hemisphere nesting may start earlier, at late autumn. Egg dates of *C. a. jota* range from September to January, coinciding with *C. a. falklandicus*' dates, which peak in November. Thus, both latter subspecies can be considered mostly spring breeders. Breeding data that could not be safely assigned to one subspecies apparently agree with general regional patterns of seasonality.

Throughout its Neotropical range, the Turkey Vulture seems to be plastic in nest site choices, despite usually nesting at ground level (e.g., Miller 1947; Wetmore 1965). There are also reports of elevated nests at tree holes or clumps (e.g., Sick 1997; De La Peña 2005), and many nests in rocky outcrops (e.g., Fonseca 1923; Curti et al. 2014), even at cavities excavated on cliffs by psittacids (Masello and Quillfeldt 2012). Yet, we found no original reports of nesting in buildings or any man-made structures in the Neotropics. Neotropical clutch sizes (or brood sizes) were usually two ($n = 105$), more rarely one ($n = 43$), though can reach three eggs ($n = 2$). A museum egg set with six eggs (USNM 746) may consist of two or three distinct clutches put together.

Egg sizes in the Neotropics ($n = 47$) showed considerable variation, ranging from 63.3 × 45.8 mm to 79 × 50.3 mm (Fig. 8; Table 2). *Cathartes a. aura* and *C. a. ruficollis* had eggs close to both extremes of this egg-size range, while most *C. a. falklandicus*' eggs are fairly large. Egg measurements for *C. a. jota* were not obtained. There is no discernible pattern among egg measurements from different subspecies, except that eggs of *C. a. falklandicus* never figure among the smallest ones. Moreover, we did not find any visible distinction between egg sizes of this subspecies' disjunct populations (that is, Pacific coast's and Malvinas Islands').

Cathartes burrovianus (Lesser Yellow-headed Vulture)

Most literature data are anecdotal, including those from regions where the species is reported to breed but without further information (Hilty and Brown 1986; Chatellenaz 2005). Hartert and Venturi's (1909) and Wetmore's (1965) breeding records fell outside current distribution of the species (Fig. 2), but it is unclear whether they represent recent retractions of the range or merely information gaps on the BirdLife map. In museum collections, we located only five clutches originally

Table 1 Assessment of the geographical distribution of original breeding records of each of the six species, and respective subspecies, of New World vultures (Cathartidae) from the Neotropical region

Species	Subspecies	Breeding season	Nest site	Clutch or brood size	Egg descriptions	Other breeding reports	No. of museum egg sets	No. of breeding events on WikiAves	No. of personal observations (Brazil)
Cathartes aura									
	aura	Cuba	Cuba, Dominican Republic	Cuba, Dominican Republic, Mexico	Cuba, Dominican Republic, Mexico	Cuba	Mexico (26), Cuba (4), Jamaica (3), Guatemala (1)	0	NA
	ruficollis	Brazil, Trinidad and Tobago	Brazil, Panama, Uruguay	Brazil, Panama, Trinidad and Tobago	Brazil, Trinidad and Tobago, Uruguay	Argentina, Brazil	Brazil (7), Trinidad and Tobago (6), Paraguay (6), Uruguay (2), Guyana (1)	7* (Brazil)	0
	jota	Argentina	Argentina, Colombia	Colombia	-	-	Argentina (3), Colombia (1)	0	NA
	falklandicus	Chile	-	Islas Malvinas	Islas Malvinas	-	Islas Malvinas (32), Chile (18), Peru (4)	0	NA
	ssp. indet.	-	Argentina, Colombia	Argentina, Colombia	Argentina, Colombia	Argentina	Mexico (5), Chile (5), Peru (1), Paraguay (1), uncertain/unknown (2)	0	NA
C. burrovianus									
	burrovianus	-	-	Panama	-	-	Mexico (2)	0	NA
	urubitinga	Brazil	Argentina, Suriname, Trinidad and Tobago***	Argentina, Trinidad and Tobago***	Argentina, Suriname, Trinidad and Tobago***	Argentina	Argentina (1), Trinidad and Tobago (1***), French Guiana (1)	8** (Brazil)	0
	ssp. indet.	-	-	-	-	Colombia	-	0	NA
C. melambrotus									
	NA	-	-	-	-	Brazil	Paraguay (1)***	0	1
Coragyps atratus									
	atratus	-	-	-	-	-	Mexico (24)	0	NA
	brasiliensis	Argentina, Brazil, Trinidad and Tobago	Brazil, Colombia, Ecuador, Mexico, Panama, Peru, Suriname, Trinidad and Tobago	Brazil, Colombia, Ecuador, Mexico, Panama, Peru, Suriname, Trinidad and Tobago	Brazil, Colombia, Panama, Trinidad and Tobago	Brazil, Mexico	Brazil (40), Trinidad and Tobago (5), Venezuela (4), Mexico (3), Guatemala (1), Costa Rica (1), Colombia (1), Guyana (1), Peru (1)	92* (Brazil)	5
	foetens	-	-	-	-	-	Chile (18)	0	0
	ssp. indet.	Argentina, Brazil	Argentina, Uruguay	Argentina, Paraguay, Uruguay	Argentina, Paraguay	Argentina	Argentina (15), Mexico (12), Brazil (9), Paraguay (2), Colombia (1), Bolivia (1), Uruguay (1)	11* (Brazil)	0
Sarcoramphus papa									

Table 1 (continued)

Species	Subspecies	Breeding season	Nest site	Clutch or brood size	Egg descriptions	Other breeding reports	No. of museum egg sets	No. of breeding events on WikiAves	No. of personal observations (Brazil)
	NA	-	Brazil, Panama, Venezuela	Brazil, Panama, Venezuela	Brazil, Panama	Argentina, Colombia	Peru (1), Bolivia (1), "South America" (1), captivity (5)	5** (Brazil)	0
Vultur gryphus	NA	Argentina, Bolivia, Chile, Colombia, Ecuador	Argentina, Bolivia, Colombia	Argentina, Colombia	-	Argentina, Chile	Chile (4), Argentina (1), "Andes" (2), "South America" (1), unknown (1), captivity (14)	1** (Peru)	NA

Countries cited under breeding season, nest site, clutch or brood size, egg descriptions, and other breeding reports = refer to countries with literature breeding data on each of these subjects. *Nest records only (i.e., nests, eggs, and/or nestlings); **any kind of breeding record; ***species identification is discussed on the main text

and reliably identified as belonging to this species (Table 1; but see ahead). Among them, the northern subspecies (*C. b. burrovianus*) was the least represented, a situation also found in literature records. Two clutches (WFVZ—16222 and 16223) and also literature data (Belcher and Smooker 1934) come from Trinidad, an island not included in the species' range according to the BirdLife map. Due to this discrepancy, Trinidad's records were not included in the seasonality plot (Fig. 7).

Nominate subspecies (*C. b. burrovianus*) seem to start laying eggs in February, peaking in April (Fig. 7), being therefore mostly a spring nester, while breeding season of *C. b. urubitinga* seems more extended throughout its range. Nest site information was found only for *C. b. urubitinga* that might nest in cavities in large trees (Haverschmidt 1968), although ground nesting was reported more often (Belcher and Smooker 1934; Di Giácomo 2005; WA2267591).

Clutch size is always two ($n = 6$), given that single museum eggs were only obtained from the oviducts of collected female specimens (Hartert and Venturi 1909; WFVZ 168832) and a single nestling recorded in Brazil (WA52144) probably had a sibling. Egg sizes of Lesser Yellow-headed Vulture are the smallest among New World vultures (Fig. 12), often smaller than any other species' eggs, ranging from 57.1 × 45.6 to 72.3 × 47.2 mm, considering only soundly identified clutches (Fig. 9). Egg measurements from the nominate subspecies are usually smaller than most *C. b. urubitinga*'s eggs (Table 2).

The largest eggs labeled as Lesser Yellow-headed Vulture's in museums ("*Cathartes urubitinga*," WFVZ 16175), from Concepción, Paraguay, fit in the non-conservative geographic distribution of Greater Yellow-headed Vulture (Schlee 2000; Ferguson-Lees and Christie 2001; GRIN 2014; Houston et al. 2018—Fig. 3), and may belong to the latter (see below). Also, one possibly misidentified single egg (MPEG 126), labeled only as Brazil, is probably of Lesser Yellow-headed Vulture, based on its very small size (Fig. 9). Other cases of misidentified eggs involving this species are treated in Suppl. 3.

Cathartes melambrotus (Greater Yellow-headed Vulture)

The breeding biology of the Greater Yellow-headed Vulture is largely unknown, since we found only a few anecdotal references of its breeding (Table 1). In addition, no eggs originally ascribed to this species were found in museums and no photos were published at the WikiAves website. The species breeds near Manaus, state of Amazonas, Brazil (Cintra and Naka 2012), and an adult bird regurgitating to a juvenile was photographed on 27 October 2015, near Presidente Figueiredo, in that same Brazilian state (J.S.B.F. Souza, pers. comm.). We propose that the largest eggs identified as Lesser

Yellow-headed Vulture (WFVZ 16175), from Paraguay, may instead belong to Greater Yellow-headed Vulture. Together, their fairly large measurements (75.3 × 49.1 and 75.9 × 48.5 mm; Fig. 9), the date the eggs were collected (15 September 1933), and the clutch size match the other scarce breeding evidence for *C. melambrotus*. According to this set's data slip, the nest site was on the ground, "between prickly thickness."

Coragyps atratus (Black Vulture)

Around 84% of the 588 clutches we located in museum collections were from the USA. Populations from the Nearctic also have abundant breeding information in the literature (e.g., Buckley 1999; Campbell 2015) and will not be addressed here anymore. Northern Hemisphere's breeding records are mostly museum clutches from Mexico, of the nominate subspecies (*C. a. atratus*) but many also of *C. a. brasiliensis* (Table 1). Albeit often anecdotal, South American data on the latter subspecies cover a vast array of localities (Fig. 4). Yet, 59 breeding records from this continent could not be safely assigned to the subspecies level. Conversely, the only records for *C. a. foetens* are museum clutches from Chile. The southernmost breeding report for the species, from Argentina (De Lucca 2016), may represent a recent, modest range expansion.

In Mexico, Black Vulture's nesting season is restricted to the first half of the year (Fig. 7); hence, northernmost Neotropical populations are mostly spring breeders. Yet, further south in Central America, egg dates range from October to February (autumn to winter), albeit one clutch from Guatemala (NHMUK—1884-9-2-19-19a) dates from May. Eggs of South American *C. a. brasiliensis* were found every month of the year, but numbers peak during the austral winter, while the majority of *C. a. foetens*' clutches are from September to November. Clutches of indeterminate subspecies from South America are mostly from austral winter to spring.

The Black Vulture is very plastic in nest site choices. Ground nesting seems common throughout the Neotropics, frequently among roots at bases of trees (e.g., Magnusson and Lima 1983; Rios 2014). Seemingly atypical nest sites are dunes at beaches (Belenguer and Zalba 1997) and termite mounds (WA2915). A few populations may prefer elevated nests

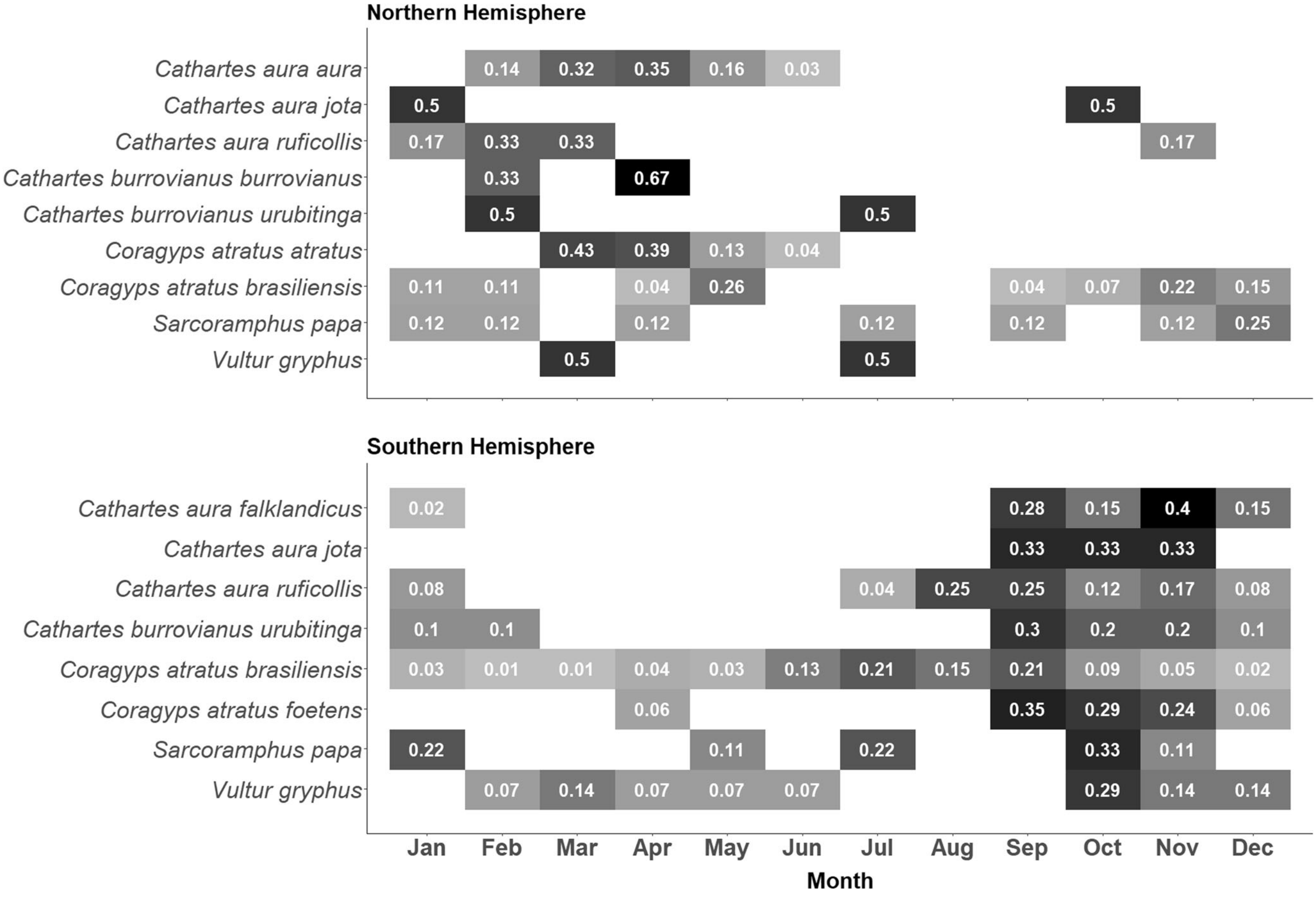


Fig. 7 Relative frequencies, per month of the year, of breeding records pertaining to Cathartidae taxa, in the Neotropical region. Top, Northern Hemisphere's records; at bottom, Southern Hemisphere's records

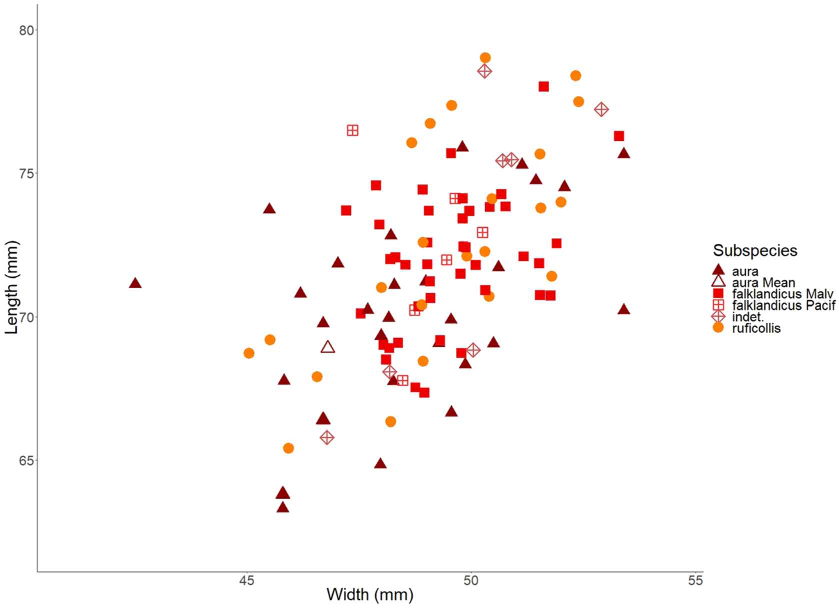


Fig. 8 Egg measurements (length, width, mm) of Turkey Vulture *Cathartes aura*, assigned to subspecies level when possible. Mean = refers to a mean value provided by a literature source, based on a certain amount of eggs; Malv = record coming from the Malvinas Islands' population; Pacif = records from the Pacific coast's populations; indet = indeterminate subspecies. Further explanations on the main text

(e.g., tree cavities up to 6 m high; Di Giácomo 2005), and the species may use abandoned cavity nests like those of larger psittacids (Guedes et al. 2000), even at cliffs (De Lucca 2016). The habit of nesting in buildings seems common in South America, where the Black Vulture uses skyscrapers in big cities as nest sites (Hill and Scherer-Neto 1991; Maurício et al. 2013; J.A.B.M. pers. obs.). For instance, at least 27% of the reports from the WikiAves database (Table S2) involve nesting at the top of buildings or in other man-made structures.

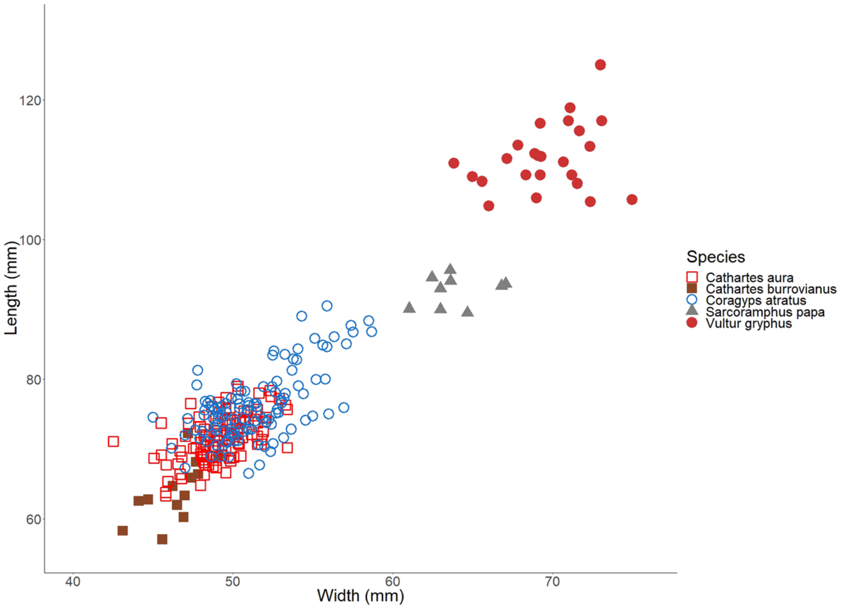
The modal clutch or brood size in the Neotropics is two ($n = 220$), with only 64 single eggs (or chicks), two clutches of three eggs, and three clutches of four eggs. The noteworthy three independent reports of four-egg clutches (one cited by von Ihering (1900), one pictured in Gussoni and Guaraldo (2008) and one from WikiAves (WA17212)) deserve further analysis. Measurements of Neotropical eggs ($n = 106$, all from museum collections) ranged from 67.7 × 51.7 to 89.1 × 54.3 mm (Fig. 10; Table 2). Three clutches originally assigned to Black Vultures have exceptionally small or large eggs and are discussed in Suppl. 3. The three subspecies had some eggs among the smallest measurements for the species, but most of the largest eggs belong to *C. a. brasiliensis*, and/or come from southern Brazil (and thus, may also belong to *C. a. foetens*; Fig. 4). Yet, the number of clutches that could not be assigned

Table 2 Egg measurements obtained for the three polytypic species of New World vultures (Cathartidae) from the Neotropical region, assigned to subspecies level

			Length (mm)			Width (mm)		
	Subspecies	*n*	Mean	Min	Max	Mean	Min	Max
Cathartes aura								
	aura	30	70.2	63.3	75.9	48.5	42.5	53.4
	ruficollis	23	72.6	65.4	79.0	49.4	45.0	52.4
	jota	0	-	-	-	-	-	-
	falklandicus	47	72.0	67.3	78.0	49.4	47.2	53.3
C. burrovianus								
	burrovianus	3	61.4	57.1	64.7	45.3	44.1	46.2
	urubitinga	9	65.1	58.3	72.3	47.0	43.1	49.1
Coragyps atratus								
	atratus	9	76.9	72.8	84.0	5.18	4.88	5.44
	brasiliensis	65	75.4	67.7	88.4	50.9	46.2	58.5
	foetens	6	75.2	71.6	79.4	49.7	45.0	55.0

n = number of individual eggs. Mean values given by literature sources were not included here

Fig. 12 Egg measurements (length, width, mm) of soundly identified records of five Cathartidae species



to a particular subspecies impaired a consistent analysis of size variation among subspecies.

Sarcoramphus papa (King Vulture)

Despite several detailed breeding reports in the literature from captive birds (Miranda-Ribeiro 1918; Cuneo 1968; Bohrer 1979; Antas and Silveira 1980; Schlee 1994; Márquez et al. 2005), data from the wild are scattered and mostly anecdotal. Only eight eggs are deposited in the museums we accessed, most of these laid in captivity (Table 1). Yet, two eggs from wild birds come from countries with no breeding records on literature, Peru and Bolivia. More detailed data come from only three countries: Panama (Lundy 1957; Wetmore 1965; Smith 1970), Venezuela (Ramo and Busto 1988; Schlee 1995), and Brazil (Carvalho-Filho et al. 2004; Petri et al. 2013; WA2423099; WA2392238), but each of these referring to one or two nests only. The only thoroughly monitored nest is the one by Carvalho-Filho et al. (2004).

Across the species' distribution, eggs are found from July to February (Fig. 7), and in an equatorial region (Colón, Panama—Smith 1970), nests with eggs were found in both extremes of this seasonal range. The only exception to this breeding period is a breeding condition male collected in the Cauca Valley—outside current distribution of the species (Fig. 5)—by the end of April (Hilty and Brown 1986). Nevertheless, most egg dates came from localities close to the equator. Farther south,

Fig. 9 Egg measurements (length, width, mm) of eggs originally assigned to Lesser Yellow-headed Vulture *Cathartes burrovianus*, with proposed corrections on some identifications. Mean = refers to a mean value provided by a literature source, based on a certain amount of eggs; Yellow-headed Trinidad = records from Trinidad, probably referring to *C. burrovianus urubitinga*. Further explanations on the main text and in Suppl. 3

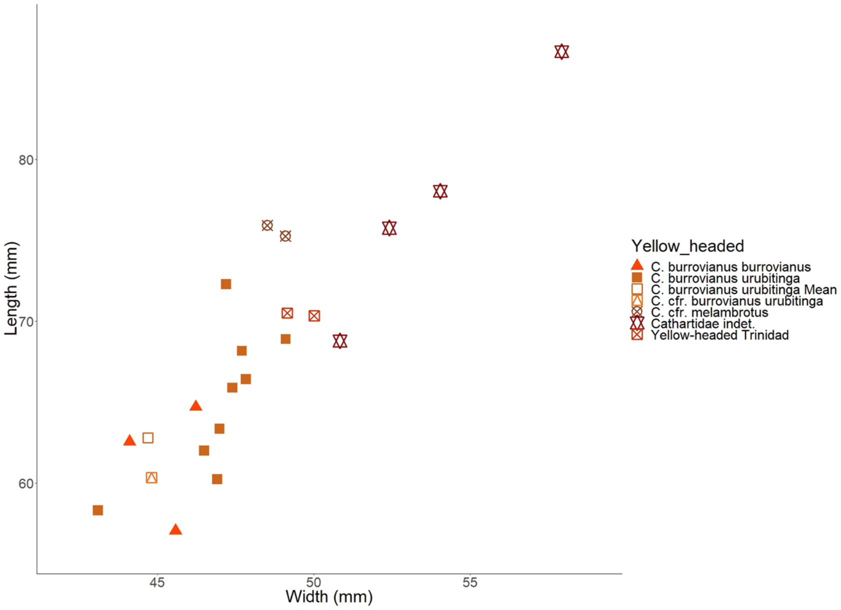
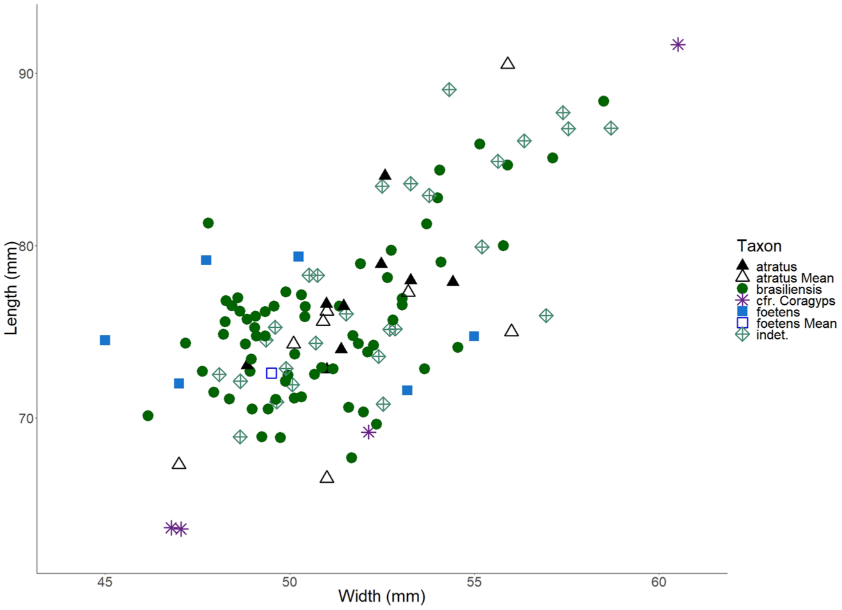


Fig. 10 Egg measurements (length, width, mm) of Black Vulture *Coragyps atratus*, assigned to subspecies level when possible. Mean = refers to a mean value provided by a literature source, based on a certain amount of eggs; cfr. *Coragyps* = eggs with uncertain identification; indet = indeterminate subspecies. Further explanations on the main text and in Suppl. 3



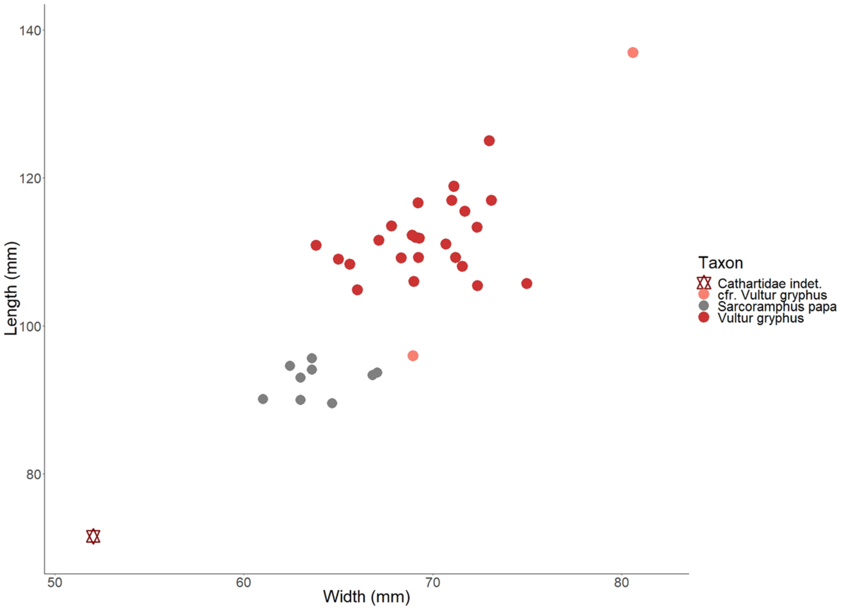
eggs were only found in the second half of the year (Fig. 7), from austral winter to spring, albeit nestlings could be found until May (WA2588159).

The King Vulture has variable nest site choice. Although some nests were at ground level (Smith 1970; Schlee 1995), the species may also nest up to ~10 m high in small caves (Silva and Regalado 1998), holes in trees (Ramo and Busto 1988) or even man-made structures (Petri et al. 2013)—and one even higher nest (apparently dozens of meters aboveground, on a cliff) was reported (Carvalho-Filho et al. 2004). Clutch size was always one. Contrary to all previous species, all eggs are white and unmarked like condors', albeit smaller (Figs. 11 and 12). One rather small, marked egg was certainly misidentified (Suppl. 3). Measurements of 10 eggs from museums and the literature showed very little variation, and almost all eggs were equal or larger than 90 × 63 mm (Fig. 11).

Vultur gryphus (Andean Condor)

The only vulture in the Neotropics currently with some conservation concern ("Near Threatened," IUCN 2020), the Andean Condor already has captive breeding programs (Liebermann et al. 1993; Capdevielle 2004) and studies (Poulsen 1963; Coimbra-Filho 1968; Whitson and Whitson

Fig. 11 Egg measurements (length, width, mm) of eggs originally assigned to King Vulture *Sarcoramphus papa* and Andean Condor *Vultur gryphus*, with proposed corrections on some identifications. Further explanations on the main text and in Suppl. 3



1969; Gailey and Bolwig 1973; Klös 1973; Bruning 1984; Klös 1984; Samour et al. 1984). Accordingly, of the 21 egg sets deposited in the museums we accessed, two-thirds were of captive birds (Table 1).

This species' biology was recently reviewed by Lambertucci (2007); thus, we will emphasize reports from wild nests not included there. Besides breeding records from Chile and especially Argentina (Fig. 6), countries already mentioned in that review, there are both older and recent reports of nesting in Colombia (e.g., McGahan 1971; Sáenz-Jiménez et al. 2016) and Bolivia (Martínez et al. 2010). It is also noteworthy a historical record of a nest on the Atlantic coast of Santa Cruz, Argentina (Adams 1907). The only record from the WikiAves database (WA642304; an adult male feeding a juvenile one) comes from Peru.

Cliffs and slopes seem to be its preferred nesting locations, and the nest site may be either a cave or a ledge (e.g., McGahan 1971; Lambertucci and Mastrantuoni 2008; Sáenz-Jiménez et al. 2016). Sometimes nests are fairly close to water (e.g., Adams 1907), and ground nesting may also occur (Lambertucci and Speziale 2009). Yet, detailed descriptions of nesting from the wild still come from only a few breeding pairs (e.g., Lambertucci and Mastrantuoni 2008), including one whose nesting was monitored in consecutive years (Heredia and Piedrabuena 2010; Gargiulo 2012).

Some studies managed to investigate further aspects like breeding rates and patterns (Wallace and Temple 1988; Herrmann et al. 2010), including an analysis of latitudinal variation in egg-laying date (Sáenz-Jiménez et al. 2016). We retrieved nesting records not reviewed in that analysis, and results suggest that northern Andes populations lay eggs earlier in the year (Fig. 7), and southern ones mostly in the second half of the year. We found no sound evidence of clutch sizes larger than one egg, with the only supposed two-egg clutch (NHMUK 1972.11.53) coming from captivity. Measurements of eggs ranged from 105 × 66 to 125 × 73 mm (Fig. 11), plus two eggs with outlying measurements discussed in Suppl. 3.

Discussion

As for most other species of the Neotropical region (Heming et al. 2013; Xiao et al. 2017), especially diurnal raptors (Monsalvo et al. 2018), breeding biology knowledge of vultures in the Neotropics is mostly based on rather small samples and/or scattered and anecdotal records, unevenly distributed among species, subspecies, and regions. Some literature data do not include any locality information, nor discriminate which reproductive parameters were included in breeding seasons' information provided in their text (e.g., Antas 2004; Dodge et al. 2014).

Geographical variation and distribution of breeding data among the different taxa

Egg-laying of the Turkey Vulture seems to vary with latitude, as suggested by Ferguson-Lees and Christie (2001). However, those authors' affirmations of a nesting season beginning in December in Cuba, and earlier in Costa Rica, are inconsistent with what we found for the subspecies *Cathartes a. aura*. All of its egg dates are from the first half of the year (Fig. 7), corresponding to the pattern found by Denis et al. (2013) with Cuban museum eggs of this subspecies. Thus, we recommend breeding research to focus on Central American countries (especially other than Mexico), to clarify this point.

Dates from *C. a. ruficollis*, however, agree with former reports from both Northern (Belcher and Smooker 1934) and Southern Hemispheres (Antas 2004)—the seemingly longer season we found for the latter may be reflecting a larger and more widespread sample (Fig. 1; Fig. 7; Table S1). For the two remaining subspecies (*Cathartes a. jota* and *C. a. falklandicus*, often synonymized—Kirk and Mossman 1998), breeding record dates overlap, and are very consistent with literature reports from their range (Ferguson-Lees and Christie 2001; Dodge et al. 2014; Campbell 2015).

Even though adult *Cathartes a. falklandicus*' body measurements are said to have a bimodal distribution between Pacific coast's (smaller sizes) and Malvinas Islands' (larger sizes) populations (Wetmore 1964), we did not verify any size differences between eggs from those regions (Fig. 8). Besides, there is still a need to elucidate *C. a. jota*'s egg measurements. In any case, egg sizes from the Neotropics never reached the larger ones (i.e., over 80 mm in length; Kirk and Mossman 1998) from Nearctic Turkey Vultures. This might relate to the larger sizes attained by adults of wholly Nearctic subspecies (Wetmore 1964; Ferguson-Lees and Christie 2001), therefore agreeing with Bergman's body mass rule, as stated by Campbell (2015). Overall, our analysis does not seem to support Jaramillo's (2003) proposal of a split in *Cathartes aura*, even though this would require elucidation of other aspects of its biology as well, such as migratory behavior (Olmos et al. 2006; Zilio et al. 2014).

Egg dates from the nominate species of Lesser Yellow-headed Vulture, *C. b. burrovianus*, appear to be slightly earlier in the year than stated by Ferguson-Lees and Christie (2001) (Fig. 7). Yet, our findings are consistent with those authors' suggestion of a poorly demarcated, and probably more protracted breeding season for the subspecies *Cathartes b. urubitinga*, even at smaller portions of its range (Di Giácomo 2005). For instance, WikiAves' copulation records from Brazil (Table S2) concentrate on the second half of the year, the same temporal pattern found with egg dates from Trinidad, in the opposite Hemisphere. Also, eggs from other equatorial regions were collected in February and July.

Despite limited sample sizes, egg measurements seem to further support subspecies division for the Lesser Yellow-headed Vulture, as eggs from the nominate subspecies' range apparently are slightly smaller than most *C. b. urubitinga*'s eggs (Fig. 9; Table 2), agreeing with alleged differences on adult birds' sizes (Wetmore 1964). Yet, the hypothesis of monotypy for this species, with only clinal variation in adult size (Ferguson-Lees and Christie 2001), still could not be ruled out. In any case, field research on Lesser Yellow-headed Vulture's breeding aspects is still greatly needed.

For the Black Vulture, we also found some latitudinal variation in the breeding season (Ferguson-Lees and Christie 2001). Yet, some aspects still need investigation. For instance, Belcher and Smooker (1934) stated that in Trinidad nests were found from November to February, but two of the seven museum clutches from there (collected by Smooker himself; WFVZ—16123 and 16127) date from May. Furthermore, albeit *Coragyps a. brasiliensis*' egg dates are very extended in both Hemispheres (Fig. 7), we cannot discard shorter nesting seasons at smaller portions of this subspecies' vast range. In Central America, we demonstrated that Black Vulture's breeding occurs mostly in autumn and winter (like suggested by other reviews—Ferguson-Lees and Christie 2001; Campbell 2015), but Mexican populations nest on spring. Farther south, data on *C. a. foetens* indicate that its breeding season is also largely restricted to austral spring (Fig. 7), agreeing with other authors (Ferguson-Lees and Christie 2001; De La Peña 2005). Yet, further research on its reproduction is still necessary.

We found no clear support for Wetmore's (1962) assumption that egg-size differences between Black Vulture's subspecies would be very evident, closely matching alleged adult size variation between these taxa (Fig. 10; Table 2). Actually, many eggs of the subspecies *C. a. brasiliensis* figured among the largest ones, contrasting with that author's supposition that they should be the smallest. It is possible that Wetmore's statements were biased by small samples, as sometimes in the past very few eggs were used as representative measurements for a subspecies (e.g., Wolfe 1938). Moreover, at least in southeastern Brazil, *C. a. brasiliensis* may show extensive intra-population body mass variation (Spina 2019), what in turn could reflect on significant egg-size variation (see ahead). On the other hand, the samples that we used were also somewhat restrained by unclear subspecies identification in many cases. Likewise, future research should better clarify the occurrence of adult size variation within and between subspecies, by obtaining larger samples of measurements and weights from throughout Black Vulture's range.

There is also a necessity of new field data for the King Vulture, as Ferguson-Lees and Christie (2001) previously noted. Breeding information is greatly needed especially farther away from the equator, to investigate if there are any regional patterns in egg-laying dates outside equatorial regions (where no pattern was noted). Also, new data could help to definitely discard doubtful literature reports of two- or even three-egg clutches for this species (Euler 1900; Bohrer 1979; Sick 1997) that persist on recent literature (Ferguson-Lees and Christie 2001; Sigrist 2006; Campbell 2015), but for which we found no reliable evidence.

We also found no indication of clutch sizes larger than one egg for the Andean Condor, at least in the wild, as formerly noted by Adams (1907). In addition, our findings further support a significant breeding range retraction in eastern Argentina (Donázar et al. 2012). Nevertheless, the Andean Condor still has poor knowledge from the field (Lambertucci 2007), and this scarcity of basic data weakens geographical analyses of breeding traits. Sáenz-Jiménez et al. (2016) investigated variation in egg-laying date across the species' range, concluding that northern Andes populations lay in the first half of the year, and southern ones in the second. Such latitudinal variation was partly supported by our findings (Fig. 7), and also some local reports on breeding seasonality (Ríos-Uzeda and Wallace 2007; Herrmann et al. 2010). Nevertheless, more data are still required, especially from the northern populations of this condor (Fig. 6).

Information gaps and inconsistencies on the "Yellow-headed" vultures

Firstly, field research in Trinidad is greatly needed, to confirm which "Yellow-headed" species occur there. Despite BirdLife maps including part of the island on the range of *Cathartes melambrotus* (Fig. 3), all data (not only breeding reports) we found from Trinidad refer instead to *C. burrovianus*. For instance, even though museum eggs assigned to the latter species were collected years before Greater Yellow-headed Vulture recognition (Wetmore 1964), their sizes, consistent with literature data (Hellebrekers 1942; Di Giácomo 2005—Fig. 9), suggest they may indeed belong to the Lesser Yellow-headed Vulture. Thus, egg measurements seem to support the fact that this species, and not Greater Yellow-headed Vulture, is present in Trinidad, contrary to BirdLife maps.

In fact, Belcher and Smooker (1934) confirmed the presence of Lesser Yellow-headed Vulture in Trinidad in the 1930s. Still, Ffrench (1991) states that there is "no satisfactory record (of the Lesser Yellow-headed Vulture)" from that island, while recently Campbell (2015) argues that records of this species on Trinidad may instead refer to *C. aura ruficollis* that have a yellowish-white nape. Nonetheless, we point out to the fact that Belcher and Smooker (1934) relied their identification on proper field-marks (see Ferguson-Lees and Christie 2001; Erize et al. 2006; van Perlo 2009) that clearly distinguish Lesser Yellow-headed Vulture from all other *Cathartes* species.

We also raise doubts on Campbell's (2015) affirmation that "numerous accounts describe the nesting feature and habits"—including nest sites, clutch sizes' frequencies, and egg descriptions—of the Greater Yellow-headed Vulture. On his text, such information is not assigned to any particular reference. Later on, the author cites just three references allegedly referring to this species, from which two refer to studies made on Central and North America, well outside that species' range. The third reference cited by Campbell is a former version of Hilty and Brown's (1986) book on the birds of Colombia. Even though we did not have access to that older version (authored by Hilty alone, on the 1970s), the more recent book does not include any kind of breeding data of the Greater Yellow-headed Vulture, despite presenting records of breeding for all other Cathartidae that occur on Colombia.

Elsewhere in literature, we also did not retrieve any other citation referring to Greater Yellow-headed Vulture's breeding (Table 1). The only records came from Cintra and Naka (2012), and the very scant information presented by Ferguson-Lees and Christie (2001)—that copulation was reported in August in French Guiana, and the species is stated to nest in large tree cavities, laying two eggs. In fact, this almost complete absence of reproductive information is hardly surprising, as this is a mainly Amazonian species (Fig. 3), and the Amazon is one of the world's most deficient regions on bird breeding data (Xiao et al. 2017). Such a pattern was also found with other Neotropical raptors and, despite logistical constraints to conduct field research in the Amazon, may also be an artifact of researchers' unawareness of the lack of data for several species (Monsalvo et al. 2018).

In any case, misidentifications involving Lesser and Greater Yellow-headed Vultures (Borrero 1982) may have further prevented knowledge of the breeding biology of the latter. These mistakes are most likely related to the fact that the original description of Greater Yellow-headed Vulture (Wetmore 1964) relies largely on probably inadequate characters—that may change with birds' behavior, age, and with plumage's wearing out (F. Pallinger, pers. comm., J.A.B.M. pers. obs.), as demonstrated for the Turkey Vulture (Hatch 1970; Wheeler 2003). It is likely that many reports and even voucher specimens of both "Yellow-headed" species remain misidentified until proper genetic analyses tell them apart (Lee and Prys-Jones 2008), such as the case reported by Griffiths and Bates (2002). It is even possible that some fairly large measurements or body masses assigned to adult Lesser Yellow-headed Vultures on the literature (Weick and Brown 1980; Ferguson-Lees and Christie 2001) derive from similar misidentifications or outdated classifications, and refer in fact to Greater Yellow-headed Vulture specimens.

The two largest eggs identified as Lesser Yellow-headed Vulture (WFVZ 16175; Fig. 9) seem to belong to Greater Yellow-headed Vulture. Albeit its measurements fall within both Turkey Vulture and Black Vulture egg-size ranges, if we regard the collector (A. Schulze) as a skilled identifier of birds, these mistakes seem unlikely. Both Yellow-headed species were not split at the year of the collection (1933) and so distinguishing them was impossible. This set may be the first properly described eggs of the Greater Yellow-headed Vulture, and also the southernmost breeding record of the species. This may be evidence that its range stretches far south than in conservative distribution estimations (Weick and Brown 1980; Houston et al. 2018—Fig. 3), what was already suggested from a few field sightings (Schlee 2000; Ferguson-Lees and Christie 2001; GRIN 2014). Yet, the distribution would be nothing like the one depicted by Campbell (2015) that shows the species occurring throughout eastern and southern Brazil, in clear disagreement with all references we located on this species' range, and also with our personal field and museum experiences.

Two other egg sets that we considered misidentified (Suppl. 3) were originally assigned to the Lesser Yellow-headed Vulture, but its measurements are even larger than those of WFVZ 16175 (Fig. 9), putting them also on the size ranges of fairly larger species such as the Turkey and Black Vultures. Such mistakes are not rare, as historical specimens sometimes were misidentified, overseen, or wrongly assigned to a locality in the past (Olson 2008; Boessenkool et al. 2010; Knox and Piertney 2012). These situations seem fairly common with diurnal raptors (Monsalvo et al. 2018). Nonetheless, the present study further supports the relevance of museum vouchers, both as important means to verify misidentifications (Griffiths and Bates 2002) and, more importantly, as providers of breeding data that could not be obtained from literature sources (Monsalvo et al. 2018). Such was the case of museum sets that were the only breeding records we obtained for some countries and/or subspecies (Table 1).

General patterns and gaps in knowledge on Cathartidae breeding biology

Our analysis showed apparent convergence between breeding seasons of sympatric Neotropical Cathartidae taxa. Two cases should be considered. First, we found a great overlap in breeding seasons of largely sympatric northern Neotropical taxa in Mexico. Nominate subspecies from both Turkey, Lesser Yellow-headed, and Black Vultures mostly lay eggs during the first months of the year (late winter and spring; Fig. 7). Also, we showed a second similar convergence occurring farther south, with taxa from temperate regions of South America. The two southernmost Turkey Vulture's subspecies (*C. a. jota* and *C. a. falklandicus*) nest at the same time of the year, and their breeding seasons overlap with that of the partly sympatric Black Vulture subspecies, *C. a. foetens* (Fig. 7). Also, in all these cases above, the taxa involved exhibit fairly short breeding seasons.

Both duration and convergence in breeding seasons were hardly assessed with Neotropical raptors (Monsalvo 2018).

Yet, these are well-known paradigms in avian life-history theory (Marchant 1960; Newton 2010). Cases of overlapping nesting seasons are most probably driven by extrinsic, environmental, and/or ecological factors of a region (Partridge and Harvey 1988), rather than being just a possible phylogenetic "signature" of the group (Tieleman et al. 2004). Whichever these extrinsic drivers are, this convergence may relate to increased seasonality on these ranges, and breeding seasons might coincide with peaks of food availability, a pattern already noted in raptors (e.g., Olsen and Marples 1993). These vultures' populations start breeding with the onset of spring, like Nearctic populations of these same species (Kirk and Mossman 1998; Buckley 1999), and other large raptors from temperate and/or seasonal regions elsewhere in the world (Newton 2010).

Conversely, in the equatorial region, we found a different pattern with evidence of a lengthy and barely traceable breeding season for the Lesser Yellow-headed Vulture (like previously suggested by Ferguson-Lees and Christie (2001)). The same pattern occurs with the King Vulture, whose egg dates can be seven months apart in one same locality. In contrast, earlier local studies at lower latitudes argued for discernible and fairly shorter breeding seasons for other Cathartidae, such as Turkey and Black Vultures (Belcher and Smooker 1934; McHargue 1977). A trend of longer breeding seasons towards the equator is another long-held notion in bird life-history (MacArthur 1964; Newton 2010). But, there is a lack of strong evidence of it from several avian clades, like diurnal raptors (Whitacre 2012; Monsalvo 2018).

Thus, more breeding data are still necessary for all New World vultures in equatorial regions. In many references, "seasonality" information presented consists of no more than anecdotal information on nesting dates from scattered reports (e.g., McHargue 1977, 1981; Ferguson-Lees and Christie 2001; Campbell 2015). Even our comprehensive analysis still struggled with paucity of data from many areas. In fact, scarcity of basic field data on Southern Hemisphere birds is an enduring problem, being repeatedly stressed by many studies (Baker 1938; Partridge and Harvey 1988; Olsen and Marples 1993; Newton 2010), and affecting most Neotropical taxa (Bierregaard 1995; Heming et al. 2013; Monsalvo et al. 2018).

When it comes to geographical distribution of the data, we emphasize the relevance of citizen science databases like WikiAves. It provided breeding records both for poorly known species and for more common ones (Table S2), and some of these records came from countries without breeding information from other sources (Table 1). We are not aware of similar databases in other Neotropical countries that provide such an amount of reliable digital records, allowing researchers to verify possible misidentifications by checking phenotypic traits. Initiatives like this website are indeed proving to be an effective complementary measure to attenuate information gaps on diurnal raptors (Monsalvo et al. 2018) and other birds (Heming et al. 2013; Marini and Heming 2017).

For some species, we demonstrated a latitudinal trend on nesting dates, with the onset of breeding seasons increasing with latitude. This is the first time that this trend is documented for northern Neotropical Black Vultures by using a higher amount of reproductive data. Formerly, it was only suggested by isolated literature information (Ferguson-Lees and Christie 2001). Latitudinal clines in egg-laying dates are already known for Nearctic populations of both Black (Buckley 1999) and Turkey Vultures (Kirk and Mossman 1998). A comparable clinal variation was also suggested for the Andean Condor in South America (Sáenz-Jiménez et al. 2016; this study). Such a cline may also occur on other diurnal raptors from the Andes (Monsalvo 2018) or other Neotropical regions (Santana and Temple 1988). This subject surely requires further investigation, as it supports the long-held notion of latitudinal clines in laying dates (Baker 1938).

Nest site information presented on literature reviews generally agrees with our findings (e.g., Ferguson-Lees and Christie 2001; Campbell 2015), except that we found a few infrequent nest sites not reported on the former (e.g., psittacid nests, termite mounds). We also verified that clutch size information given on literature reviews (e.g., Ferguson-Lees and Christie 2001; Campbell 2015) mostly reflects the frequencies that we found. Exceptions are the case of King Vulture and Andean Condor, and maybe of the Greater Yellow-headed Vulture, like mentioned before. Many larger-than-usual clutch sizes at museums might result of distinct clutches put together and/or of cases of second clutches (especially for captive birds; see ahead). Yet, the records of four-egg clutches from wild Black Vultures might result from two females laying in the same nest. This behavior was suggested for the Turkey Vulture in the Nearctic (Kirk and Mossman 1998)—and may be facilitated in Black Vulture, as it may show "loosely social" nesting habits (Ferguson-Lees and Christie 2001).

Patterns of egg measurements and appearance, and also clutch sizes, found on this review clearly agree with Cathartidae phylogeny of Johnson et al. (2016). We could note the occurrence of two primary clades: one with the condors and the King Vulture (larger adult size, and clutch of one large, all-white egg), and the other with the remaining four smaller species (usually clutches of two marked eggs). We also demonstrated apparent allometry between female sizes and egg measurements (Winkler 2004) at the species level. Patterns of egg sizes (Fig. 12) follow body masses' differences for the six species (Dunning 2008). It is possible that some atypical egg measurements from captivity specimens result of these females' particular body conditions. In fact, for other diurnal raptors, it is still unclear if egg measurements from captivity correspond to those of eggs laid by free-ranging individuals (Cabot Nieves et al. 2013). At lower taxonomic levels, however, results were different. This study could neither corroborate nor discard alleged size differences between subspecies' egg sizes (von Ihering 1900; Wetmore 1962). In fact, we are still validating the occurrence of this, and other possible undetected patterns, in an ongoing meta-analysis (author's unpub. data).

Implications and suggestions for management actions

Vultures' nests can be highly susceptible to anthropogenic disturbances (Lambertucci and Speziale 2009), and nest site limitation seems to be a common issue faced by vultures worldwide (Buckley 1999; Mullié et al. 2017). Evidence of this was the central role attributed to the decrease of adequate nest sites in past declines of Black Vulture population in North America (Buckley 1999; Wheeler 2003), as well as populations of other vultures in urban areas elsewhere (Mullié et al. 2017). The lack of records of Turkey Vulture nesting in man-made structures in the Neotropical region deserves further examination. The species is traditionally considered to be very tolerant to anthropogenic impacts (Schlee 2000), and in the Nearctic, is reported to nest in structures like deserted buildings (Houston et al. 2007) and even abandoned vehicles (Igl and Peterson 2010). This growing availability of such novel nesting sites is apparently leading to range expansion and increasing population trends of the Turkey Vulture in North America (Avery 2004).

Yet, the only Neotropical populations of Turkey Vulture reported to nest in buildings are those from Islas Malvinas (Falkland Islands), as cited by Campbell (2015). It is noteworthy that Turkey Vulture is the only species of Cathartidae that occurs on those islands. Elsewhere in the Neotropics, buildings are a common nest site choice among Black Vultures (Maurício et al. 2013; Leal 2016; Ferreira and Lopes 2017), as also shown on WikiAves nesting records. This behavior might be facilitating the increase on this species' numbers in South American big cities (Hill and Scherer-Neto 1991; J.A.B.M., pers. obs.), and may be playing a role in its apparent widespread range expansion (Sick 1997). Growing numbers of Black Vultures might represent a threat to less common Cathartidae, preventing their access to food sources (Carrete et al. 2010). In fact, Black Vultures can displace Turkey Vultures from some human-developed areas (Novaes and Cintra 2015). Thus, we suggest that interspecific competition for nest sites with Black Vultures may be impairing Turkey Vultures' capacity to nest in man-made structures in the Neotropics, and therefore to cope with the increasing anthropogenic impacts on the region. This subject certainly requires further studies.

The Black Vulture is an expanding "winner" species that may be acting as a biotic homogenizing factor, and management actions may be necessary to minimize its impacts (Nascimento 2003; Carrete et al. 2009, 2010). Moreover, in cases of mitigation of human-vulture conflicts, we suggest that measures focusing on reducing nest sites availability to this species might be very effective. Besides, we consider egg removal, if used alone, a highly questionable management strategy to control Black Vulture's populations in localities such as airport surroundings (Monteiro-Neto and Sanaiotti 2007). As the species is known to produce a second clutch if the first is lost (Hill and Scherer-Neto 1991; Buckley 1999; Di Giácomo 2005), a behavior also documented for other New World vultures (Kirk and Mossman 1998), egg removal can be counter-productive. In fact, in the case of the California Condor, egg removal—and therefore, "encouragement" of second clutches—was used as a mean to increase its population growth (Snyder and Hamber 1985). So, it should be viewed as an effective measure whenever there is a need to boost (instead of halt) productivity of New World vultures' populations.

The occurrence of replacement-clutching is also well known in captive King Vultures (Cuneo 1968; Antas and Silveira 1980; Schlee 1994), a species with a decreasing population trend (IUCN 2020). Yet, it is not clear whether this trait occurs in the wild, and further studies should verify the existence of this ability. The need for this and other breeding data of this species is particularly important, as the King Vulture is frequently considered to be very sensitive to habitat alteration (Hilty and Brown 1986; Blendinger et al. 2004; Thiollay 2007; De Labra et al. 2013). However, there is also evidence suggesting that the species may take advantage of some human activities (Olmos et al. 2006). The nest record in a man-made structure (Petri et al. 2013) shows that King Vultures might be able to use artificial breeding sites. Artificial nest sites mimicking real ones could be a useful strategy to bolster raptors' populations (Liébana et al. 2013), and it was suggested that such man-made nests may even help improve ecosystem services provided by these birds (Murúa et al. 2004).

Factors affecting the nesting stage seem to play a significant role in New World vultures' demography (Buckley 1999), as adults and their nests become highly susceptible to a number of threats (Coleman and Fraser 1989b; Wheeler 2003). As shown by the conservation cases of both California and Andean Condors, we reinforce that proper vulture management actions must focus on breeding traits (Lambertucci 2007; Lambertucci et al. 2014), and specifically at the nesting stage (Snyder and Hamber 1985), to be both cost-effective and successful.

Conclusion

Overall, breeding biology knowledge of the six vultures in the Neotropical region is unevenly distributed among species, subspecies, and regions, as for most other species of the Neotropics. Information gaps sometimes are not restricted to breeding biology, as we verified many inconsistencies on accounts of geographical distribution, and maybe about adult birds' measurements and body mass. Even though the two most common species, Turkey Vulture and Black Vulture, have a fairly good amount of breeding data from the Neotropical region, this information is poorly organized. Both still have scant knowledge on some of their subspecies, and most breeding reports are anecdotal. Thus, there is still a need for further studies about the reproductive traits of their populations. Two other species, the Lesser Yellow-headed Vulture and the King Vulture, have very limited information about their breeding biology and should be viewed as research priorities. Another research priority is the Greater Yellow-headed Vulture, a species with a trend of population decline (IUCN 2020), that present information gaps in several aspects of its biology and distribution. The Andean Condor still lack comprehensive data from wild nests, despite many ongoing captive breeding initiatives. Overall, these non-charismatic species, which provide important ecosystem services, still need more field research on their breeding biology that could enable proper preventive management and conservation strategies.

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Authors' Contributions JABM and MÂM idealized the study, all authors collected data, JABM wrote the original draft, and all authors revised and edited the manuscript.

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Data Availability Data is available upon request to the authors.

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