



Review and Meta-analyses

Snake predators of bird eggs: a review and bibliography

Serpientes depredadoras de huevos de aves: una revisión y bibliografía

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ABSTRACT. Snakes are frequent predators of bird nests and therefore potentially have an important impact on bird population dynamics. However, while many species are known to consume nestlings and chicks, few species have been recorded consuming bird eggs. To effectively quantify the effects of bird egg predation by snakes on bird demographics, a key first step is to identify which snake species consume bird eggs. Unfortunately, detailed information on the dietary habits of most snakes is scarce and feeding records are poorly cataloged, making it difficult to ascertain which species do and do not eat bird eggs. We reviewed the literature and online community science reports to compile a global list of confirmed snake predators of bird eggs. In total, we gathered 471 feeding records of 123 snake taxa consuming the eggs of at least 210 bird species from 238 individual data sources. Geographical locations of records disproportionately represented well-sampled regions, and we infer that many snake species not included on our list also consume bird eggs. However, we found that oophagous snakes tend to be long (mean maximum length = 2057 mm) and mostly eat eggs that are small in diameter (mean egg diameter = 24 mm), suggesting that relative prey bulk is an important constraint of these interactions. Therefore, we expect that other snakes that eat birds are likely to mostly include congeneric and ecologically similar species to those reflected in our review. By knowing which snakes consume bird eggs, future research can consider species- and site-specific hypotheses when investigating the ecological effects of bird egg predation by snakes. Those results can also inform conservation practitioners on the causes and consequences of variation in nest success that may aid in decision-making when designing conservation management plans.

RESUMEN. Las serpientes son depredadores frecuentes de nidos de aves y consecuentemente tienen un impacto potencial importante sobre la dinámica poblacional de las aves. Sin embargo, a pesar que se sabe que muchas especies consumen pichones, se han registrado pocas especies consumiendo huevos de aves. Para cuantificar efectivamente los efectos de la depredación de huevos de aves por serpientes en la demografía de las aves, un primer paso clave es identificar cuales especies de serpientes consumen huevos de aves. Desafortunadamente, información detallada acerca de los hábitos alimenticios de la mayoría de las serpientes es escasa y los registros de alimentación están pobremente catalogados, haciendo difícil definir cuales especies comen y no comen huevos de aves. Revisamos la literatura y los reportes de la comunidad científica en línea para compilar una lista global de serpientes depredadoras de huevos de aves confirmadas. En total, obtuvimos 471 registros de alimentación de 123 taxones de serpientes que consumen huevos de, al menos, 210 especies de aves a partir de 238 fuentes de datos individuales. La ubicación geográfica de los registros representaron desproporcionadamente regiones bien muestreadas e inferimos que muchas de las especies de serpientes no incluidas en nuestra lista también consumen huevos de aves. Sin embargo, encontramos que las serpientes oofagas tienden a ser largas (longitud máxima promedio = 2057 mm) y comen mayormente huevos de diámetro pequeño (diámetro promedio del huevo = 24 mm), sugiriendo que el volumen relativo de la presa es una restricción importante de estas interacciones. Por lo tanto, esperamos que otras especies que comen aves, muy probablemente incluyen especies congénères o ecológicamente similares a las incluidas en nuestra revisión. Conociendo cuales especies consumen huevos de aves, los estudios futuros pueden considerar hipótesis específicas al sitio y a la especie al investigar los efectos ecológicos de la depredación de huevos de aves por serpientes. Esos resultados pueden también informar a conservacionistas sobre las causas y consecuencias de la variación en el éxito de los nidos, lo cual puede ayudar en la toma de decisiones durante el diseño de planes de manejo para conservación.

Key Words: *Bird eggs; diet; nest predation; predator-prey interactions; oophagy; snakes*

INTRODUCTION

Predatory attacks by snakes on nesting birds and their offspring have been well-documented globally (for example, in Africa: Lloyd 2004, mainland Asia: Khamcha et al. 2018, Australia: Fulton 2018, North America: DeGregorio et al. 2014, and the Neotropics: Menezes and Marini. 2017). However, while many species of snakes are known consumers of nestling birds, chicks, and brooding adults, few species are reported consuming bird eggs. Predation of eggs by snakes can reduce recruitment of birds and impact bird population dynamics (Lavers et al. 2010). In addition, by preying on eggs, snakes have the potential to influence bird life history patterns by forcing them to re-lay and brood successive clutches (DeGregorio et al. 2014). Given that

many species of birds provide important ecosystem services (Whelan et al. 2008, Whelan et al. 2015, Şekercioğlu et al. 2016), population fluctuations from reduced recruitment could potentially alter the functional integrity of a range of ecosystems (Mortensen et al. 2008, Gascon et al. 2015, Lowney and Thomson 2021). For example, extensive predation on birds and eggs by invasive brown tree snakes (*Boiga irregularis*) on the islands of Guam has fundamentally altered the local faunal community through extirpation of several species, ultimately causing trophic collapse (Wiles et al. 2003). Thus, by preying on bird eggs in large numbers, snakes have the potential to indirectly influence ecosystem functioning in many biological communities.

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Quantifying the extent to which snakes affect ecosystems by consuming bird eggs is hindered by numerous challenges. Several facets of these trophic interactions are unclear, including knowledge of which species of birds lay eggs that are at risk of snake predation, as well as the extent to which predation of bird eggs by snakes varies spatiotemporally (Weatherhead and Blouin-Demers 2004, Lahti 2009, Menezes and Marini 2017). Identification of which snakes consume bird eggs offers a critical first step in understanding these dynamics. Knowing which species of snakes consume eggs allows researchers to formulate predator-specific hypotheses across a range of habitats and environments (Reidy and Thompson 2012, Ibáñez-Álamo et al. 2015). Additionally, avian conservation practitioners can use that information to produce anti-predator strategies for bird conservation efforts. Unfortunately, information on snake feeding is poorly catalogued (Grundler 2020, Maritz et al. 2021b) making the compilation of a robust list of oophagous species challenging.

Snake diets are diverse, compositionally complex, and often difficult to adequately quantify (Greene 1997, Glaudas et al. 2017, Maritz and Maritz 2020). Unfortunately, the natural history data required to systematically describe snake diets are often lacking, particularly for taxa that occur in poorly-studied regions. For most species, we know very little about their feeding habits apart from generalized characterisations of their diets inferred from a limited quantity of published information (Maritz et al. 2021b). For many others, we lack even a basic understanding of their feeding habits. A recent global synthesis of snake feeding records by Grundler (2020) highlights the incomplete nature of our understanding of snake diets. Of the 3921 species of snakes distributed across the globe (Uetz et al. 2021), less than a third (1248 species) could be included in that dataset and the majority of those species were only represented by fewer than ten records. Due to this paucity of feeding records, our understanding of which types of prey are, or are not eaten by different species of snakes is limited. Consequently, many species of snakes not currently known to eat bird eggs may be oophagous.

Despite the above limitations, published records of snakes consuming bird eggs have accumulated in the literature (Weatherhead and Blouin-Demers 2004, Ibáñez-Álamo et al. 2015). Over the past few decades, using camera monitoring systems, some snake species have been documented eating eggs for the first time (Cutler and Swann 1999, Pierce and Pobprasert 2007, Ribic et al. 2012, Khamcha et al. 2018). Moreover, novel feeding records published in natural history publications and online community science portals continue to confirm additional species as bird egg predators. However, because studies and platforms vary in their objectives, records are scattered in the literature and online. In some cases, reports may be difficult to access or are completely inaccessible to researchers or conservationists interested in using such data.

We compiled a comprehensive list of confirmed snake predators of bird eggs. We collated records of snakes consuming bird eggs from a range of sources of information and used the details within those reports to broadly summarize trends of bird egg predation by snakes globally. We also analysed several traits of the identified snake species and egg prey to test hypotheses regarding why those species consume bird eggs but many others do not. Specifically, we tested if the inclusion or exclusion of bird eggs in the diets of

snakes is associated with 1) differences in snake body size, 2) variation in snake habitat use, and 3) taxonomic relatedness between snake taxa. To contextualize which bird species are at risk, we also compared the size distribution of consumed bird eggs to that of a sample of bird eggs not reported in the diets of snakes. Lastly, we investigated the sizes of eggs consumed by snakes of varying body lengths.

METHODS

Data collection and inclusion criteria

Between August 2020 and July 2021, we searched for and collected data from reports of bird egg predation by snakes. Our main sources of data were formal publications (i.e., peer-reviewed journal articles and books) found on the online indexer Google Scholar, JSTOR, and SquamataBase (Grundler 2020) - an online natural history repository containing close to 11,000 records of predator-prey interactions across 1248 snake species. We also searched the literature cited within those publications to identify additional sources. Additionally, we collected data from unpublished academic theses and personal communications from researchers. Lastly, we collected data from community science records published on the online platform iNaturalist (<https://www.inaturalist.org>) and the social media network Facebook. Facebook records were obtained from the groups “Predation records - reptiles and amphibians (sub-Saharan Africa)” (published in Maritz and Maritz 2020), “Snakes of South Africa” (<https://www.facebook.com/groups/snakesofsouthafrica>), and “Wild snake predation records” (<https://www.facebook.com/groups/wild.snake.predation.records>).

We restricted our data collection to include records of snakes unambiguously eating bird eggs. We did not include reports with vague descriptions of snakes attacking nests unless eggs were directly specified as the prey rather than nestlings, chicks, or adult birds. Conservatively, we excluded records without clear evidence of snakes eating eggs. For a record of a snake species to be included it needed to meet these criteria: 1) snakes were observed eating, attempting to eat, or having eaten (shells in digestive tracts) eggs and 2) records were of snakes in the wild consuming eggs they found without human intervention. We included cases in which the eggs of captive or domesticated birds were consumed if those predatory attacks met the above criteria.

For each reported predation event, we identified the snake and bird species to the finest taxonomic level possible, and we noted the number of eggs involved. Geographic coordinates were noted from the original record or estimated using Google Maps. We updated snake species names to match their current taxonomic nomenclature as per Uetz et al. (2021). We provide a summary of these records detailing the taxonomic diversity of oophagous snake predators and their bird egg prey, as well as geographic biases in these trends.

Ecological traits of oophagous snakes and bird egg prey

Although the primary goal of this study was to compile a list of known snake predators of bird eggs, we were also interested in examining traits of those species that might explain why those snakes consume bird eggs but others do not. Differential prey use within a particular snake species is facilitated by several factors, chief among which include varying body size constraints (Arnold 1993, Greene 1997, Maritz and Alexander 2014) and variable

encounter rates of different prey (Alencar et al. 2013, Mori and Nagata 2016). Accordingly, we chose to examine and compare the body lengths and primary habitats of the snakes on our list to snakes not known to consume bird eggs. Snake body lengths correlate with their diet breadth as larger snakes can typically consume bulkier and heavier prey than smaller ones, and can therefore hunt a broader range of prey (Arnold 1993, Maritz et al. 2021c, Barends and Maritz 2022). Habitat use largely influences the probabilities at which snakes encounter different prey (for example, arboreal snakes are more likely to encounter arboreal prey; Harrington et al. 2018). Taken together, these traits are likely major limiting factors towards bird egg consumption by snakes.

Unfortunately, most accounts of snakes consuming bird eggs do not include linear measurements of the sizes of the individual snakes in question. To compensate for this, we instead used maximum body length data (i.e., length from snout to tail) of each species on our list (Electronic dataset 1) collected from Feldman et al. (2016). We also collected these data for all other species in the Feldman et al. (2016) dataset ($N = 3529$) for use in comparisons (Electronic dataset 2). Similarly, we gathered information on snake habitats to classify species as either aquatic, arboreal, fossorial, semi-arboreal, or terrestrial. We gathered these data for as many species as we could ($N = 2646$) from field guides and published datasets, including Pizzatto et al. (2007), Lawing et al. (2012), Feldman and Meiri (2014), Bars-Closel et al. (2017), Cyriac and Kodandaramaiah (2018), and Harrington et al. (2018).

We were similarly interested in examining traits of the consumed bird eggs that could provide insight into which bird eggs are at risk of predation by snakes. Because prey bulk (i.e., the cross sectional-diameter of prey) relative to snake size is an important consideration of dietary selectivity in snakes (Greene 1997) we chose to quantify the diameters of consumed eggs. Snakes typically ingest bird eggs length-wise (Gans 1952), and so the diameter of the eggs acts as the main dimensional constraint on ingestion. However, as before, most reports did not include measurements of the dimensions of the eggs consumed. We thus gathered information on average egg diameters for each of the bird species on our list (Electronic dataset 1). We gathered these data from resources detailing the reproductive traits of birds that breed in Australia (Garrett et al. 2015), Asia (Tsai et al. 2020), Britain and Europe (Harrison and Castell 2002, Storchová and Hořák 2018), Micronesia (Brandt 1962), North America (Baicich and Harrison 2005), South America (Mason 1985, Auer et al. 2007, Marques-Santos et al. 2015), and southern Africa (Tarboton 2011). For comparative purposes, we also gathered egg diameter data for a geographically and phylogenetically diverse sample of 2326 species of birds (~25% of all birds; Electronic dataset 2).

Statistical analyses

We analysed geographical trends of bird egg predation by snakes by comparing the numbers of 1) feeding records, 2) identified snake species and 3) identified bird egg prey species across major geographical regions. We demarcated regions as Africa, Asia, Australia, Central America, Europe, Micronesia, the Middle East, North America, and South America. We also examined the elevation (in metres above sea level) of each area where predation events were observed. We gathered elevation data where predation

events occurred ($N = 350$) at a resolution of 30 arc seconds from the Worldclim global elevation dataset (Fick and Hijmans 2017).

We evaluated the ecological traits of oophagous snakes by first analysing patterns of their body length distributions. We used a Kolmogorov-Smirnov test to compare the relative distribution of the maximum body lengths of oophagous snakes to all snakes included in Feldman et al. (2016). We then used a phylogenetic ANOVA to test for differences in average log-transformed maximum body lengths of snakes that do and do not consume bird eggs while accounting for the effects of phylogenetic autocorrelation caused by species relatedness. We performed this test with the "Geiger" package (Pennell et al. 2014) in R software v.4.1.1 (R Core Team 2021) using a pruned version of the phylogeny of squamate reptiles published by Tonini et al. (2016) ($N = 3503$ species) as the input phylogenetic tree. We similarly summarized oophagous snake habitat use and then compared body lengths (log10 transformed) by habitat use controlling for phylogeny via phylogenetic ANOVA.

We tested for the presence of a phylogenetic signal associated with bird egg consumption by snakes by calculating Blomberg's K (Blomberg et al. 2003). We considered a Blomberg's K value less than one to indicate that oophagy occurs randomly across our tree under Brownian motion evolution whereas K values greater than one suggest oophagy is more prevalent between closely related snake taxa (Blomberg et al. 2003). We performed this test using the "Phytools" package (Revell 2012) in R.

Similar to our analyses of snake body lengths, we performed the same comparative tests between consumed eggs and other eggs. We used a Kolmogorov-Smirnov test to compare the relative distributions of egg diameters of eggs eaten by snakes and all other eggs. We then looked for differences in average log-transformed diameters of consumed eggs and other eggs ($N = 2326$) via phylogenetic ANOVA. We used a pruned version of the phylogeny of extant birds published by Jetz et al. (2012) as the input tree for this test. Finally, we visually inspected the relationship between bird egg diameters and snake body lengths across all predation events by creating a Sankey plot depicting the flow between egg diameters (in mm) and snake length (in meters). For bird egg diameter size classes, we used bins of 10 mm, and for snake body length size classes we used bins of 1 m.

RESULTS

Records of bird egg predation by snakes

Our search produced a total of 471 records of confirmed predatory interactions between snakes and bird eggs across the globe (Table 1). Bird eggs were consumed by 123 different snake taxa (114 species and nine subspecies) belonging to 59 genera and seven families (Boidae, Colubridae, Elapidae, Psammophiidae, Pseudaspidae, Pythonidae, and Viperidae). Of these, Colubridae (70% of all 123 taxa) and Elapidae (13% of all 123 taxa) were most frequently reported (Fig. 1). The eggs of at least 210 species of birds across 159 genera, 71 families and 21 orders, including passerines and several non-passerine orders, were consumed. In 26 cases, bird eggs were only identified to genus, family, or order levels (seven cases, 14 cases, and five cases respectively). In 63 cases, bird eggs were not identified beyond the class level, or the exact identity of the species was ambiguously reported in the source material (for example, "the eggs of land birds").

Table 1. Recorded observations of avian oophagy by snakes.

Snake species	Snake common name	Bird species (no. recorded)	Bird common name	Geographic area	Source		
Boidae							
<i>Boa constrictor</i>	Boa constrictor	<i>Butorides striatus</i>	Striated Heron	Venezuela	Thomas (1984)		
		<i>Ciconia maguari</i>	Maguari Stork	Venezuela	Thomas (1984)		
		<i>Forpus passerinus</i>	Green-rumped Parrotlet	Venezuela	Menezes & Marini (2017)		
<i>Chilabothrus angulifer</i>	Cuban boa	<i>Phimosus infuscatus</i>	Bare-faced Ibis	Venezuela	Thomas (1984)		
		<i>Patagioenas leucocephala</i>	White-crowned Pigeon	Cuba	Godinez et al. (1987)		
<i>Chilabothrus chrysogaster</i>	Turk's Island boa	<i>Petrochelidon fulva</i>	Cave Swallow	Cuba	Mancina & Sosa (1997)		
		<i>Gallus gallus domesticus</i> † (2)	Domestic Chicken	West Indies	Schwartz & Henderson (1991)		
<i>Chilabothrus inornatus</i>	Puerto Rican boa	<i>Bubulcus ibis</i>	Cattle Egret	Puerto Rico	Wiley (2003)		
<i>Chilabothrus striatus</i>	Hispaniolan boa	<i>Gallus gallus domesticus</i> †	Domestic Chicken	Jamaica	Gosse (1851)		
		<i>Phasianus colchicus</i>	Ring-necked Pheasant	Dominican Republic	Ottenwalder (1980)		
<i>Epicrates assisi</i>	Striped rainbow boa	<i>Ploceus cucullatus</i>	Village Weaver	Dominican Republic	Wiley (2001)		
		<i>Psittacara chloropterus</i>	Hispaniolan Parakeet	Dominican Republic	Ottenwalder (1980)		
<i>Epicrates cenchria</i>	Rainbow boa	Unidentified	-	Brazil	Vitt & Vanglider (1983)		
		<i>Conopophaga peruviana</i>	Ash-throated Gnateater	Peru	Londoño pers comm.		
<i>Eunectes notaeus</i>	Yellow anaconda	<i>Tinamus tao</i>	Grey Tinamou	Brazil	Fiorillo (2019)		
		Unidentified	-	Brazil	Martins & Oliveira (1998)		
		<i>Aramus guarauna</i> (3)	Limpkin	Argentina; Brazil	Strüssmann & Szazima (1991); Waller et al. (2007); Miranda et al. (2017)		
		<i>Chauna torquata</i> (2)	Southern Screamer	Argentina	Waller et al. (2007); Miranda et al. (2017)		
Colubridae							
<i>Boiga cyanea</i>	Green cat snake	<i>Malacopteron cinereum</i>	Scaly-crowned Babbler	Thailand	Somsiri et al. (2019)		
		Unidentified	-	Thailand	Pierce & Pobprasert (2013)		
<i>Boiga cynodon</i>	Dog-toothed cat snake	Unidentified	-	South East Asia	Greene (1989)		
		<i>Gallus gallus domesticus</i> †	Domestic Chicken	Borneo	Pitman (1962b)		
<i>Boiga dendrophila</i>	Mangrove cat snake	Unknown "sea birds"	-	Borneo	Pitman (1962b)		
		<i>Anas platyrhynchos</i> †	Mallard	Guam	Savidge (1988)		
<i>Boiga irregularis</i>	Brown tree snake	<i>Columba livia</i>	Rock Pigeon	Guam	Savidge (1988)		
		<i>Coturnix coturnix</i> †	Common Quail	Guam	Savidge (1988)		
		<i>Francolinus francolinus</i>	Black Francolin	Guam	Vice et al. (2005)		
		<i>Gallus gallus</i>	Red Junglefowl	Guam	Savidge (1988)		
		<i>Melopsittacus undulatus</i> †	Budgerigar	Guam	Savidge (1988)		
		<i>Nymphicus hollandicus</i> †	Cockatiel	Guam	Savidge (1988)		
		<i>Passer montanus</i>	Eurasian Tree Sparrow	Guam	Savidge (1988)		
		<i>Serinus canarius</i> †	Island Canary	Guam	Savidge (1988)		
		<i>Streptopelia bitorquata</i> (2)	Sunda Collared Dove	Guam	Conry (1988); Savidge (1988)		
		<i>Taeniopygia guttata</i>	Sunda Zebra Finch	Guam	Savidge (1988)		
		Unidentified (4)	-	Australia; Guam	Savidge (1988); Greene (1989); Shine (1991)		
		<i>Boiga kraepelini</i>	Kelung cat snake	<i>Alcippe morrisonia</i>	Grey-cheeked Fulvetta	Taiwan	Chen et al. (2015)
				<i>Pitta nympha</i>	Fairy Pitta	Taiwan	Chen et al. (2015)
<i>Pomatorhinus musicus</i>	Taiwan Scimitar Babbler			Taiwan	Chen et al. (2015)		
<i>Pycnonotus sinensis</i>	Light-vented Bulbul			Taiwan	Chen et al. (2015)		
<i>Schoeniparus brunneus</i>	Dusky Fulvetta			Taiwan	Chen et al. (2015)		
<i>Boiga ochracea</i>	Tawny cat snake	Unidentified	-	East Asia	Greene (1989)		
		Unidentified	-	N/a	Greene (1989)		
<i>Boiga siamensis</i>	Gray cat snake	Unidentified	-	South East Asia	Greene (1989)		
<i>Borikenophis portoricensis</i>	Puerto Rican racer	<i>Zenaida aurita</i>	Zenaida Dove	Virgin Islands	Norton (1983)		
<i>Chironius grandisquamis</i>	Ecuador sipo	<i>Poliochroma exsul</i>	Chestnut-backed Antbird	Costa Rica	Visco & Sherry (2015)		
<i>Clelia clelia</i>	Black mussurana	<i>Myrmoborus leucophrys</i>	White-browed Antbird	Peru	Londoño pers comm.		
<i>Coluber constrictor constrictor</i>	Northern black racer	<i>Colinus virginianus</i> (2)	Northern Bobwhite	USA	Uhler et al. (1939); Staller et al. (2005)		
		<i>Haematopus palliatus</i>	American Oystercatcher	USA	Hackney et al. (2014)		
		<i>Passerina cyanea</i>	Indigo Bunting	USA	Stake et al. (2005)		
		<i>Spizella pusilla</i>	Field Sparrow	USA	Best (1974)		
		<i>Turdus migratorius</i> (2)	American Robin	USA	Fitch (1963b); Rodriguez-Robles & de Jesus-Escobar (1999)		
<i>Coluber constrictor flaviventris</i>	Yellowbelly racer	<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Degregorio et al. (2016)		
		<i>Agelaius phoeniceus</i>	Red-winged Blackbird	USA	Fitch (1963b)		
		<i>Cardinalis cardinalis</i>	Northern Cardinal	USA	Fitch (1963b)		
<i>Coluber constrictor foxii</i>	Blue racer	<i>Sialia sialis</i>	Eastern Bluebird	USA	Lennon (2013)		
<i>Conophis lineatus</i>	Road guarder	<i>Morococcyx erythropygus</i>	Lesser Ground-Cuckoo	Costa Rica	Scott (1983)		
<i>Dasypeltis atra</i>	Montane egg-eater	<i>Phyllastrephus cabanisi</i>	Cabanis's Greenbul	Kenya	Van de Loock & Bates (2016)		
		Unknown weaver	-	Uganda	Pitman (1974)		
<i>Dasypeltis inornata</i>	Southern brown egg-eater	<i>Gallus gallus domesticus</i> †	Domestic Chicken	South Africa	Maritz & Ping (2020)†		

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<i>Dasypeltis medici</i>	East African egg-eater	<i>Phyllastrephus flavostriatus</i>	Yellow-streaked Greenbul	Mozambique	Macdonald & Dean (1978)
<i>Dasypeltis Scabra</i>	Common egg-eater	<i>Anthus cinnamomeus</i>	African Pipit	South Africa	Bates & Little (2013)
		<i>Cercotrichas coryphaeus</i>	Karoo Scrub Robin	South Africa	Lloyd et al. (2009)
		<i>Columba guinea</i> (2)	Speckled Pigeon	South Africa	Dyer (1996)
		<i>Coturnix coturnix</i>	Common Quail	South Africa	Bates & Little (2013)
		<i>Crithagra flaviventris</i>	Yellow Canary	South Africa	Hockey et al. (2005)
		<i>Euplectes ardens</i>	Red-collared Widowbird	South Africa	Pryke & Lawes (2004)
		<i>Euplectes orix</i>	Southern Red Bishop	South Africa	Kok et al. (1977)
		<i>Gallus gallus domesticus</i> [†] (3)	Domestic Chicken	South Africa; Uganda	Loveridge (1936); Pitman (1958b); Maritz & Maritz (2020)
		<i>Haematopus moquini</i> (2)	African Oystercatcher	South Africa	Bates & Little (2013); Maritz & Maritz (2020)
		<i>Lagonosticta nitidula</i>	Brown Firefinch	South Africa	Hockey et al. (2005)
		<i>Lanius collaris</i>	Southern Fiscal	South Africa	Bruderer (1991)
		<i>Larus dominicanus</i>	Kelp Gull	South Africa	Dyer (1996)
		<i>Larus hartlaubii</i>	Hartlaub's Gull	South Africa	Underhill et al. (2009)
		<i>Macronyx capensis</i>	Cape Longclaw	South Africa	Bates & Little (2013)
		<i>Malcorus pectoralis</i>	Rufous-eared Warbler	South Africa	Hockey et al. (2005)
		<i>Melaenornis infuscatus</i>	Chat Flycatcher	South Africa	Lloyd (2004)
		<i>Merops</i> sp.	-	South Africa	Fry (1984)
		<i>Passer melanurus</i>	Cape Sparrow	South Africa	Underhill et al. (2009)
		<i>Pavo cristatus</i> [†] (3)	Indian Peafowl	South Africa; Zimbabwe	Olivier (2020) [†] Schick (2019) [†]
		<i>Phalacrocorax capensis</i>	Cape Cormorant	South Africa	Dyer (1996)
		<i>Phalacrocorax coronatus</i>	Crowned Cormorant	South Africa	Underhill et al. (2009)
		<i>Philetairus socius</i>	Sociable Weaver	South Africa	Hockey et al. (2005)
		<i>Ploceus castanops</i>	Northern Brown-throated Weaver	Uganda	Pitman (1958b)
		<i>Ploceus cucullatus</i>	Village Weaver	Uganda	Pitman (1958b)
		<i>Ploceus nigerimus</i>	Viellot's Black Weaver	Uganda	Pitman (1958b)
		<i>Ploceus</i> sp.	-	Sudan	Pitman (1962a)
		<i>Poicephalus rueppellii</i>	Rüppell's Parrot	Namibia	Selman (1998)
		<i>Prinia flavicans</i>	Black-chested Prinia	South Africa	Jacobsen (1989)
		<i>Prinia maculosa</i> (2)	Karoo Prinia	South Africa	Rowan & Brueckhusen (1962); Nalwanga et al. (2004)
		<i>Pseudonigrita arnaudi</i>	Grey-capped Social Weaver	Kenya	Cheng et al. (2019)
		<i>Pterocles namaqua</i>	Namaqua Sandgrouse	South Africa	Lloyd et al. (2001)
		<i>Pycnonotus capensis</i> (2)	Cape Bulbul	South Africa	Kruger (2004); Hockey et al. (2005)
		<i>Quelea quelea lathami</i>	Red-billed Quelea	South Africa	Pienaar (1969)
		<i>Sarothrura boehmi</i>	Streaky-breasted Flufftail	Zambia	Jamie (2016)
		<i>Scleroptila africana</i>	Grey-winged Francolin	South Africa	Little & Crowe (1993)
		<i>Spermestes cucullatus</i>	Bronze Mannikin	Kenya	Loveridge (1945)
		<i>Sporaeoginthus subflavus</i>	Orange-breasted Waxbill	South Africa	Colahan (1982)
		<i>Sterna bergii</i>	Greater Crested Tern	South Africa	Underhill et al. (2009)
		<i>Streptopelia senegalensis</i>	Laughing Dove	South Africa	Rowan (1983)
		<i>Threskiornis aethiopicus</i>	African Sacred Ibis	South Africa	Underhill et al. (2009)
		Unknown weaver	-	South Africa	Barbour & Loveridge (1928)
		<i>Vanellus lugubris</i>	Senegal Lapwing	South Africa	Ward (1989)
		Unidentified (3)	-	DRC; Mozambique; South Africa	Schmidt et al. 1923; Loveridge (1953); De Waal (1977)
<i>Dendrelaphis tristis</i>	Daudin's bronzeback snake	<i>Copsychus fulvicatus</i>	Indian Robin	Sri-Lanka	Pitman (1962b)
<i>Dendrophidion percarinatum</i>	South American forest racer	<i>Poliochrania exsul</i>	Chestnut-backed Antbird	Costa Rica	Visco & Sherry (2015)
<i>Dispholidus typus</i>	Boomslang	<i>Philetairus socius</i>	Sociable Weaver	South Africa	Greuel (2020)
		<i>Poicephalus rueppellii</i>	Rüppell's Parrot	Namibia	Selman et al. (2000)
		<i>Prinia maculosa</i>	Karoo Prinia	South Africa	Nalwanga et al. (2004)
		<i>Rhinopomastus cyanomelas</i>	Common Scimitarbill	Zimbabwe	Pitman (1962a)
		<i>Serinus canicollis</i>	Cape Canary	South Africa	Pitman (1962a)
		<i>Spermestes cucullatus</i>	Bronze Mannikin	Kenya	Loveridge (1945)
		Unknown weaver	-	South Africa	Pitman (1958a)
		Unidentified (3)	-	South Africa; Sudan; Tanzania	Barbour & Loveridge (1928); Smith et al. (2019); Maritz & Maritz (2020)
<i>Drymarchon corais</i>	Western indigo snake	<i>Gallus gallus domesticus</i> [†]	Domestic Chicken	Brazil	Bernarde & Abe (2006)
		Unknown phasianid (3)	-	Brazil	da Costa-Prudente et al. (2014)
		Unidentified (2)	-	Brazil	Bernarde & Abe (2006); Menezes & Marini (2017)
<i>Drymarchon couperi</i>	Eastern indigo snake	<i>Gallus gallus domesticus</i> [†] (2)	Domestic Chicken	USA	Stevenson et al. (2010); Campbell & Smith (2018) [†]
<i>Drymarchon melanurus</i>	Blacktail cribo	<i>Ortalis vetula mcalli</i>	Plain Chachalaca	USA	Marion & Fleetwood (1978)
<i>Dryocalamus</i> sp.		<i>Malacopteron cinereum</i>	Scaly-crowned Babbler	Thailand	Somsiri et al. (2019)

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<i>Elachistodon westermanni</i>	Indian Egg-eater	<i>Columba livia</i>	Rock Pigeon	India	Visvanthan (2015)
		<i>Passer domesticus</i>	House Sparrow	India	Dandge (2008)
		<i>Ploceus philippinus</i>	Baya Weaver	India	Dandge & Tiple (2016)
		Unidentified	-	India	Dandge (2008)
<i>Elaphe anomala</i>	Korean rat snake	<i>Paradoxornis heudei</i>	Reed Parrotbill	China	Chen et al. (2020)
<i>Elaphe carinata</i>	Taiwanese rat Snake	<i>Accipiter soloensis</i>	Chinese Sparrowhawk	China	Ma et al. (2016)
		<i>Aegithalos glaucogularis</i>	Silver-throated Bushtit	China	Li et al. (2012)
		<i>Chrysolophus pictus</i>	Golden Pheasant	China	Wang et al. (2014)
		<i>Nipponia nippon</i> (2)	Crested Ibis	China	Yu et al. (2006); Yu et al. (2015)
		<i>Pomatorhinus musicus</i>	Taiwan Scimitar Babbler	China; Taiwan	Chen et al. (2015)
<i>Elaphe climacophora</i>	Japanese rat snake	Unidentified	-	Japan	Mori & Nagata (2016)
<i>Elaphe quadrivirgata</i>	Japanese four-lined rat snake	Unknown "land birds"	-	Japan	Hasegawa & Moriguchi (1989)
		Unknown "sea birds"	-	Japan	Hasegawa & Moriguchi (1989)
<i>Elaphe quatuorlineata</i>	Four-lined snake	<i>Dendrocopos major</i>	Great Spotted Woodpecker	Italy	Cattaneo (1979)
		<i>Parus major</i>	Great Tit	Italy	Sorace et al. (2000)
		<i>Passer domesticus</i>	House Sparrow	Italy	Cattaneo (1979)
		<i>Phasianus colchicus</i> (2)	Ring-necked Pheasant	Greece; Italy	Cattaneo (1979); Cattaneo & Grano (2013)
		Unidentified (2)	-	Italy	Fillipi et al. (2005)
<i>Elaphe schrenkii</i>	Amur ratsnake	Unidentified	-	China	Schultz (1988)
<i>Elaphe taeniura</i>	Beauty snake	<i>Accipiter soloensis</i>	Chinese Sparrowhawk	China	Ma et al. (2016)
		<i>Aegithalos concinnus</i>	Black-throated Bushtit	China	Li et al. (2012)
		<i>Collocalia</i> sp.	-	Borneo	Pitman (1962b)
		<i>Emberiza jankowskii</i>	Jankowski's Bunting	China	Jiang et al. (2008)
<i>Elaphe taeniura friesi</i>	Taiwanese beauty snake	<i>Pitta nympha</i>	Fairy Pitta	Taiwan	Chen et al. (2015)
<i>Hemorrhhois hippocrepis</i>	Horseshoe whip snake	<i>Pterocles orientalis</i>	Black-bellied Sandgrouse	Morocco	Znari et al. (2008)
<i>Heterodon nasicus</i>	Western hognose snake	<i>Chondestes grammacus</i>	Lark Sparrow	USA	Langford & Janovy (2011)
<i>Lampropeltis alterna</i>	Grey-banded kingsnake	<i>Callipepla squamata</i>	Scaled Quail	USA	Vermilya & Acuna (2004)
<i>Lampropeltis californiae</i>	California kingsnake	<i>Aimophila ruficeps</i>	Rufous-crowned Sparrow	USA	Morrison & Bolger (2002)
		<i>Callipepla californica</i> (3)	California Quail	Mexico; USA	Klauber (1931); Compton (1933); Wisemen et al. (2019)
		<i>Vireo bellii</i>	Bell's Vireo	USA	Pembererton & Carriger (1916)
		<i>Zenaida macroura</i>	Mourning Dove	USA	Hollingsworth (2016)
<i>Lampropeltis calligaster</i>	Prairie kingsnake	<i>Colinus virginianus</i> (2)	Northern Bobwhite	USA	Fitch (1978); Fitch (1998)
		<i>Coturnix coturnix</i>	Common Quail	USA	Klimstra (1959)
		<i>Passerina cyanea</i>	Indigo Bunting	USA	Thompson III et al. (1999)
		<i>Spizella pusilla</i>	Field Sparrow	USA	Thompson III et al. (1999)
<i>Lampropeltis getula</i>	Common kingsnake	<i>Colinus virginianus</i>	Northern Bobwhite	USA	Staller et al. (2005)
		<i>Molothrus ater</i>	Brown-headed Cowbird	USA	Cavitt (2000)
		<i>Spiza americana</i>	Dickcissel	USA	Cavitt (2000)
		Unknown passerine	-	USA	Cavitt (2000)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
<i>Lampropeltis holbrooki</i>	Speckled kingsnake	<i>Passerina cyanea</i>	Indigo Bunting	USA	Stake et al. (2005)
		<i>Spizella pusilla</i>	Field Sparrow	USA	Stake et al. (2005)
		<i>Sturnella magna</i>	Eastern Meadowlark	USA	Landoll & Husak (2011)
<i>Lampropeltis triangulum</i>	Eastern milksnake	<i>Melospiza melodia</i>	Song Sparrow	USA	Brown (1979b)
		<i>Spizella pusilla</i>	Field Sparrow	USA	Bent & Austin Jr (1968)
<i>Lampropeltis zonata</i>	California mountain kingsnake	<i>Oreortyx pictus</i>	Mountain Quail	USA	Wentz (1953)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
<i>Leptophis ahaetulla</i>	Giant parrot snake	Unidentified	-	Argentina	Lopez et al. (2003)
<i>Leptophis mexicanus</i>	Mexican parrot snake	Unidentified	-	Mexico	Henderson (1982)
<i>Lycodon davisonii</i>	Blanford's bridle snake	<i>Alophoixus pallidus</i>	Puff-throated Bulbul	Thailand	Khamcha & Gale (2020)
		<i>Cyornis sumatrensis</i>	Indochinese Blue Flycatcher	Thailand	Khamcha & Gale (2020)
		<i>Kittacincla malabarica</i>	White-rumped Shama	Thailand	Khamcha & Gale (2020)
		<i>Malacocincla abbotti</i>	Abbott's Babbler	Thailand	Khamcha & Gale (2020)
		<i>Malacopteron cinereum</i>	Scaly-crowned Babbler	Thailand	Khamcha & Gale (2020)
		<i>Pycnonotus finlaysoni</i>	Stripe-throated Bulbul	Thailand	Khamcha & Gale (2020)
<i>Lycodon semicarinatus</i>	Ryukyu odd-tooth snake	<i>Otus elegans</i>	Ryukyu Scops Owl	Japan	Toyama et al. (2015)
<i>Masticophis bilineatus</i>	Sonoran whipsnake	<i>Zenaida asiatica</i>	White-winged Dove	Mexico	Gatica-Colima (2015)
<i>Masticophis flagellum</i>	Coachwhip	<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Stake & Cimprich (2003)
<i>Oligodon formosanus</i>	Formosa kukri snake	<i>Pomatorhinus musicus</i>	Taiwan Scimitar Babbler	Taiwan	Chen et al. (2015)
<i>Ophedryx aestivus</i>	Rough greensnake	<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Nelson et al. (2006)
<i>Oxyrhopus petola</i>	Forest flame snake	<i>Conopophaga ardesiaca</i>	Slaty Gnatcatcher	Peru	Londoño pers comm.
		<i>Hafferia fortis</i>	Sooty Antbird	Peru	Cerón-Cardona & Londoño (2017)
		Unidentified (2)	-	Brazil	Cunha & Nascimento (1983); Gaiarsa et al. (2013)
<i>Pantherophis alleghaniensis</i>	Eastern rat snake	<i>Gallus gallus domesticus</i> † (4)	Domestic Chicken	USA	Brown & Mitchell (2005); Folsom 2018; Jokay 2020; Rice 2020

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<i>Pantherophis emoryi</i>	Great Plains rat snake	<i>Picoides borealis</i>	Red-cockaded Woodpecker	USA	Delaney et al. (2008)
		<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Degregorio et al. (2016)
		<i>Bartramia longicauda</i>	Upland Sandpiper	USA	Cavitt (2000)
		<i>Setophaga chrysoparia</i> (2)	Golden-cheeked Warbler	USA	Stake (2001); Stake et al. (2004)
<i>Pantherophis guttatus</i>	Eastern corn snake	<i>Colinus virginianus</i>	Northern Bobwhite	USA	Staller et al. (2005)
		<i>Setophaga chrysoparia</i>	Golden-cheeked Warbler	USA	Stake et al. (2005)
		<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Stake et al. (2005); Degregorio et al. (2016)
<i>Pantherophis obsoletus</i>	Western rat snake	Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
		<i>Aix sponsa</i> (2)	Wood Duck	USA	Leopold (1966); Hansen & Frederickson (1990)
		<i>Anas platyrhynchos</i> [‡]	Mallard	USA	Ormand (2019) [†]
		<i>Aphelocoma coerulescens</i>	Florida Scrub-Jay	USA	Carter et al. (2007)
		<i>Bonasa umbellus</i>	Ruffed Grouse	USA	Brown (1979a)
		<i>Branta canadensis maxima</i>	Canada Goose	USA	Aldrich & Endicott (1984)
		<i>Colinus virginianus</i> (2)	Northern Bobwhite	USA	Uhler et al. (1939); Staller et al. (2005)
		<i>Coturnix coturnix</i>	Common quail	USA	Conant (1938)
		<i>Dendrocygna autumnalis</i>	Black-bellied Whistling-Duck	USA	Schramer (2019) [†]
		<i>Egretta caerulea</i>	Little Blue Heron	USA	Taylor & Michael (1971)
		<i>Gallus gallus domesticus</i> [‡] (10)	Domestic Chicken	USA	Brown (1979a); Stickle et al. (1980); Smith (2017) [‡] ; Brown & Smith (2017) [‡] ; Allison & Smith (2018) [‡] ; Shellabarger (2019) [‡] ; Ormand (2019) [‡] ; Calhoun (2020) [‡] ; Wilkerson (2020) [‡] ; Hayes & Rice (2020) [‡]
		<i>Hirundo rustica</i>	Barn Swallow	USA	Carter (1970)
		<i>Passer domesticus</i>	House Sparrow	USA	Wishard & Cavataio (2020)
		<i>Passerina cyanea</i> (2)	Indigo Bunting	USA	Thompson III et al. (1999); Stake et al. (2005)
		<i>Setophaga chrysoparia</i> (2)	Golden-cheeked Warbler	USA	Stake et al. (2004); Stake et al. (2005)
		<i>Sialia sialis</i>	Eastern Bluebird	USA	Brown (1979a)
		<i>Spizella pusilla</i> (2)	Field Sparrow	USA	Thompson III et al. (1999); Stake et al. (2005)
		<i>Thryothorus ludovicianus</i>	Carolina Wren	USA	Brown (1979a)
		<i>Turdus</i> sp.	-	USA	Britto (2020) [†]
		Unknown duck	-	USA	Stickle et al. (1980)
		<i>Vireo atricapilla</i>	Black-capped Vireo	USA	Stake et al. (2005)
<i>Zenaidura macroura</i>	Mourning Dove	USA	Fitch (1963a)		
Unidentified (3)	-	USA	Fitch (1963a); Stickle et al. (1980); Rodriguez-Robles & de Jesus-Escobar (1999)		
<i>Pantherophis spiloides</i>	Midland rat snake	<i>Bubulcus ibis</i>	Cattle Egret	USA	Dusi & Dusi (1968)
		<i>Egretta caerulea</i>	Little Blue Heron	USA	Dusi & Dusi (1968)
<i>Pantherophis vulpimus</i>	Eastern fox snake	<i>Anas clypeata</i>	Northern Shoveler	USA	Wheeler (1984)
		<i>Anas discors</i>	Blue-winged Teal	USA	Andrews (1952)
		<i>Anas discors</i>	Blue-winged Teal	USA	Wheeler (1984)
		<i>Anas platyrhynchos</i>	Mallard	USA	Andrews (1952)
		<i>Coturnix coturnix</i>	Common Quail	USA	Conant (1938)
		<i>Gallus gallus domesticus</i> [‡] (2)	Domestic Chicken	USA	Conant (1938); Jadin & Orlofske (2020)
		<i>Melospiza melodia</i>	Song Sparrow	USA	Langlois (1964)
		<i>Mergus merganser</i>	Common Merganser	Canada	Wilson (1985)
		<i>Phasianus colchicus</i> (3)	Ring-necked Pheasant	Canada; USA	Stokes (1952); Langlois (1964); Vogt (1981)
		<i>Spiza americana</i>	Dickcissel		Klug et al. (2010)
		Unknown duck	-	Canada	Rivard (1976)
		Unidentified	-	USA	Rodriguez-Robles & de Jesus-Escobar (1999)
		<i>Philodryas patagoniensis</i>	Patagonia green racer	<i>Xanthopsar flavus</i>	Saffron-cowled Blackbird
<i>Streptopelia capicola</i>	Ring-necked Dove			Zimbabwe	Pitman (1962b)
<i>Philothammus hoplogaster</i>	Green water snake	<i>Aramides cajanea</i>	Gray-cowled Wood-Rail	Panama	Robinson & Robinson (2001)
<i>Phrynonax poecilonotus</i>	Puffing snake	<i>Crotophaga major</i>	Greater Ani	Panama	Riehl & Jara (2009)
		<i>Hafferia fortis</i>	Sooty Antbird	Peru	Cerón-Cardona & Londoño (2017)
		<i>Hylophylax naevioides</i>	Spotted Antbird	Panama	Robinson et al. (2005)
		<i>Penelope jacquacu</i>	Spix's Guan	Peru	Dixon & Soini (1986)
		<i>Penelope</i> sp.	-	Brazil	Martins & Oliveira (1998)
		<i>Poliocramia exsul</i> (2)	Chestnut-backed Antbird	Costa Rica; Panama	Robinson et al. (2005); Visco & Sherry (2015)

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		<i>Tinamus major</i>	Great Tinamou	Panama	Robinson & Robinson (2001)
		Unknown seedeater	-	Guyana	Beebe (1946)
		Unidentified (2)	-	Chile; Panama	Sexton & Heatwole (1965); Menezes & Marini (2017)
<i>Phrynonax polylepis</i>	Northeastern puffing snake	<i>Ortalis guttata</i>	Speckled Chachalaca	Peru	Angulo & Chavez (2017)
		<i>Penelope jacquacu</i> (2)	Spix's Guan	Peru	Dixon & Soini (1986)
		<i>Sporophila</i> sp.	-	Guyana	Beebe (1946)
<i>Phrynonax shropshirei</i>	Shropshire's puffing snake	Unidentified	-	Ecuador	Cisneros-Heredia (2005)
<i>Pituophis catenifer</i>	Gopher snake	<i>Anas acuta</i>	Northern Pintail	USA	Rodriguez-Robles (2002)
		<i>Anas platyrhynchos</i>	Mallard	USA	Rodriguez-Robles (2002)
		<i>Aythya americana</i>	Redhead	USA	Rodriguez-Robles (2002)
		<i>Callipepla californica</i>	California Quail	USA	Rodriguez-Robles (2002)
		<i>Callipepla gambelii</i>	Gambel's Quail	USA	Rodriguez-Robles (2002)
		<i>Colinus virginianus</i>	Northern Bobwhite	USA	Cavitt (2000)
		<i>Coturnix coturnix</i>	Common Quail	USA	Rodriguez-Robles (2002)
		<i>Eremophila alpestris</i>	Horned Lark	USA	Rodriguez-Robles (2002)
		<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	USA	Rodriguez-Robles (2002)
		<i>Lanius ludovicianus</i>	Loggerhead Shrike	USA	Hathcock (2013)
		<i>Melanerpes formicivorus</i>	Acorn Woodpecker	USA	Rodriguez-Robles (2002)
		<i>Numenius americanus</i>	Long-billed Curlew	USA	Rodriguez-Robles (2002)
		<i>Numida meleagris</i>	Helmeted Guineafowl	USA	Rodriguez-Robles (2002)
		<i>Otus flammeolus</i>	Flammulated Owl	USA	Rodriguez-Robles (2002)
		<i>Pheucticus melanocephalus</i>	Black-headed Grosbeak	USA	Pemberton & Carriger (1916)
		<i>Quiscalus quiscula</i>	Common Grackle	USA	Rodriguez-Robles (2002)
		<i>Recurvirostra americana</i>	American Avocet	USA	Rodriguez-Robles (2002)
		<i>Sialia currucoides</i>	Mountain Bluebird	USA	Rodriguez-Robles (2002)
		<i>Sialia mexicana</i>	Western Bluebird	USA	Rodriguez-Robles (2002)
		<i>Spiza americana</i>	Dickcissel	USA	Rodriguez-Robles (2002)
		<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow	USA	Rodriguez-Robles (2002)
		<i>Sturnella</i> sp.	-	USA	Rodriguez-Robles (2002)
		<i>Troglodytes aedon</i>	House Wren	USA	Rodriguez-Robles (2002)
		<i>Turdus migratorius</i>	American Robin	USA	Rodriguez-Robles (2002)
		Unknown duck	-	USA	Rodriguez-Robles (2002)
		Unknown passerine	-	USA	Rodriguez-Robles (2002)
		<i>Zenaida macroura</i>	Mourning Dove	USA	Rodriguez-Robles (2002)
		Unidentified	-	USA	Rodriguez-Robles (2002)
<i>Pituophis catenifer affinis</i>	Sonoran gopher snake	<i>Coccyzus americanus</i>	Yellow-billed Cuckoo	USA	Root et al. (2015)
<i>Pituophis catenifer deserticola</i>	Great Basin gopher snake	<i>Centrocercus urophasianus</i>	Greater Sage-Grouse	USA	Lockyer et al. (2013)
<i>Pituophis catenifer sayi</i>	Bullsnake	<i>Anas platyrhynchos</i>	Mallard	USA	USFW & Smith (2018) [†]
		<i>Aythya americana</i>	Redhead	USA	Imler (1945)
		<i>Cistothorus palustris</i>	Marsh Wren	USA	Imler (1945)
		<i>Colinus virginianus</i>	Northern Bobwhite	USA	Brown (1979a)
		<i>Fulica americana</i>	American Coot	USA	Imler (1945)
		<i>Mareca strepera</i>	Gadwall	USA	Imler (1945)
		<i>Meleagris gallopavo</i>	Wild Turkey	USA	Guthrie (1932)
		<i>Phasianus colchicus</i>	Ring-necked Pheasant	USA	Imler (1945)
		<i>Recurvirostra americana</i> (2)	American Avocet	USA	Imler (1945)
		<i>Stelgidopteryx ruficollis</i>	Southern Rough-winged Swallow	USA	Best (1977)
		<i>Sturnella magna</i>	Eastern Meadowlark	USA	Imler (1945)
		<i>Turdus merula</i>	Eurasian Blackbird	USA	Imler (1945)
		Unknown duck	-	USA	Imler (1945)
		Unidentified (2)	-	USA	Diller & Wallace (1996); Iverson & Akres (2001)
<i>Pituophis melanoleucus lodingi</i>	Black pine snake	<i>Colinus virginianus</i>	Northern Bobwhite	USA	Rudolph et al. (2002)
<i>Pituophis melanoleucus melanoleucus</i>	Northern pine snake	<i>Aix sponsa</i>	Wood Duck	USA	Wheeler (1984)
<i>Platyceps rhodorachis</i>	Common cliff racer	<i>Colinus virginianus</i>	Northern Bobwhite	USA	Brown (1979a)
<i>Pseudalsophis dorsalis</i>	Central Galapagos racer	<i>Argya caudata</i>	Common Babbler	Iran	Moosavi et al. (2011)
		<i>Zenaida galapagoensis</i>	Galapagos Dove	Ecuador	Ortiz-Catedral et al. (2019)
		Unidentified	-	Ecuador	Ortiz-Catedral et al. (2019)
<i>Pseudalsophis occidentalis</i>	Western Galapagos racer	Unidentified	-	Ecuador	Ortiz-Catedral et al. (2019)
<i>Ptyas dhumnades</i>	Big-eyed rat snake	<i>Accipter soloensis</i>	Chinese Sparrowhawk	China	Ma et al. (2016)
		<i>Aegithalos concinnus</i>	Black-throated Bushtit	China	Li et al. (2012)
<i>Ptyas mucosus</i>	Oriental rat snake	<i>Hypsipetes ganeesa</i>	Square-tailed Bulbul	India	Balakrishnan (2010)
		<i>Pitta nympha</i>	Fairy Pitta	Taiwan	Chen et al. (2015)
<i>Rhachidelus brazili</i>	Brazilian bird snake	Unidentified (2)	-	Brazil	Franca et al. (2008); Gaiarsa et al. (2013)
<i>Spalerosophis diadema</i>	Diadem snake	<i>Podoces panderi</i>	Turkestan Ground Jay	Uzbekistan	Burnside et al. (2020)
<i>Spilotes pullatus</i>	Tropical chicken snake	<i>Crotophaga major</i>	Greater Ani	Panama	Riehl & Jara (2009)
		<i>Turdus rufiventris</i>	Rufous-bellied Thrush	Brazil	Cochran (2013)
		<i>Turdus</i> sp.	-	Brazil	Marques & Sazima (2004)
		Unidentified (2)	-	Brazil	Martins & Oliveira (1998); Menezes & Marini (2017)

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<i>Spilotes sulphureus</i>	Yellow-bellied chicken snake	<i>Campylopterus largipennis</i>	Grey-breasted Sabrewing	Peru	Londoño pers comm.
		<i>Chlorothraupis carmioli</i>	Carmioli's Tanager	Peru	Londoño pers comm.
		<i>Conopophaga peruviana</i>	Ash-throated Gnateater	Peru	Londoño pers comm.
		<i>Cryptopipo holochlora</i>	Green Manakin	Peru	Londoño pers comm.
		<i>Crypturellus bartletti</i>	Bartlett's Tinamou	Peru	Londoño pers comm.
		<i>Crypturellus variegatus</i>	Variiegated Tinamou	Peru	Londoño pers comm.
		<i>Dysithammus mentalis</i>	Plain Antvireo	Peru	Londoño pers comm.
		<i>Geotrygon montana</i>	Ruddy Quail-Dove	Peru	Londoño pers comm.
		<i>Glyphorynchus spirurus</i>	Wedge-billed Woodcreeper	Peru	Londoño pers comm.
		<i>Hylophylax naevius</i>	Spot-backed Antbird	Peru	Londoño pers comm.
		<i>Lepidothrix coronata</i>	Blue-crowned Manakin	Peru	Londoño pers comm.
		<i>Myrmoborus myotherinus</i>	Black-faced Antbird	Peru	Londoño pers comm.
		<i>Myrmothera campanisona</i>	Thrush-like Antpitta	Peru	Londoño pers comm.
		<i>Saltator maximus</i>	Buff-throated Saltator	Peru	Londoño pers comm.
		<i>Sclerurus mexicanus</i>	Tawny-throated Leaf-tosser	Peru	Londoño pers comm.
		<i>Tangara schrankii</i>	Green-and-gold Tanager	Peru	Londoño pers comm.
		<i>Tinamus major</i>	Great Tinamou	Peru	Londoño pers comm.
		Unknown passerine	-	Brazil	Londoño pers comm.
		<i>Willisornis poecilinotus</i>	Common Scale-backed Antbird	Peru	Londoño pers comm.
			Unidentified	-	Peru
<i>Telescopus dhara</i>	Arabian tiger snake	Unknown passerine	-	Jordan	Amr & Disi (1998)
<i>Thamnophis hammondi</i>	Two-striped garter snake	<i>Spizella atrogularis</i>	Black-chinned Sparrow	USA	Pemberton & Carriger (1916)
<i>Thamnophis sirtalis</i>	Common garter snake	<i>Dolichonyx oryzivorus</i>	Bobolink	USA	Gabrielson (1922)
		<i>Spiza americana</i>	Dickcissel	USA	Olson & Warner (2001)
		<i>Spizella pusilla</i>	Field Sparrow	USA	Olson & Warner (2001)
<i>Toxicodryas blandingii</i>	Blandings tree snake	Unidentified (2)	-	Uganda	Cansdale (1961); Pitman (1974)
<i>Zamenis longissimus</i>	Aesculapean snake	<i>Muscicapa striata</i>	Spotted Flycatcher	Poland	Najbar (2007)
		Unidentified (2)	-	Italy	Naulleau & Bonnet (1995); Capula & Luiselli (2002)
<i>Zamenis scalaris</i>	Ladder snake	<i>Burhinus oedicephalus</i>	Eurasian Stone-curlew	Spain	Solis & Lope (1995)
		Unidentified	-	Spain	Pleguezuelos et al. (2007)
Elapidae					
<i>Bungarus fasciatus</i>	Banded krait	<i>Gallus gallus</i>	Red Junglefowl	India	Slowinski (1994)
<i>Denisonia devisi</i>	De Vis's banded snake	<i>Chrysococcyx basalii</i>	Horsfield's Bronze Cuckoo	Australia	Linton (1930)
<i>Laticauda colubrina</i>	Yellow-lipped sea krait	<i>Sterna sumatrana</i>	Black-naped Tern	Borneo	Pitman (1962a)
<i>Naja anchietae</i>	Anchieta's cobra	<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	Namibia	Maritz & Maritz (2020)
<i>Naja annulifera</i>	Snouted cobra	<i>Gallus gallus domesticus</i> [‡] (6)	Domestic Chicken	South Africa; Zimbabwe	Pitman (1958b); Broadley (1959); Newman (1965); Haagner (1993); Shine et al. (2007); Otto (2020) [†]
		Unidentified	-	South Africa	Hewitt & Power (1913)
<i>Naja haje</i>	Egyptian cobra	<i>Gallus gallus domesticus</i> [‡] (2)	Domestic Chicken	Kenya; Sudan	Corkill (1935); Pitman (1958b)
<i>Naja kaouthia</i>	Monocled cobra	<i>Anas platyrhynchos</i>	Mallard	Thailand	Chaitae (2011)
<i>Naja melanoleuca</i>	Central African forest cobra	<i>Dendrocygna javanica</i>	Lesser Whistling Duck	Thailand	Chaitae (2011)
		<i>Chroicocephalus cirrocephalus</i>	Gray-hooded Gull	Uganda	Pitman (1958b)
		<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	Uganda	Pitman (1958b)
		Unknown duck	-	Uganda	Pitman (1962a)
<i>Naja mossambica</i>	Mozambique spitting cobra	<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	South Africa	Maritz & Maritz (2020)
<i>Naja naja</i>	Spectacled cobra	<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	Sri-Lanka	Pitman (1962a)
<i>Naja nigricincta</i>	Western barred spitting cobra	<i>Numida meleagris</i>	Helmeted Guineafowl	Sri-Lanka	Pitman (1962a)
		<i>Nymphicus hollandicus</i> [‡]	Cockatiel	Namibia	Theart (2020) [†]
<i>Naja nigricollis</i>	Black-necked spitting cobra	<i>Anser domesticus</i> [‡]	Domestic Goose	Zambia	Maritz & Maritz (2020)
		<i>Columba guinea</i>	Speckled Pigeon	Kenya	Pitman (1958b)
		<i>Gallus gallus domesticus</i> [‡] (2)	Domestic Chicken	Zimbabwe	Pitman (1958b); Pitman (1962a)
<i>Naja nivea</i>	Cape cobra	<i>Burhinus capensis</i>	Spotted Thick-knee	South Africa	Pitman (1962a)
		<i>Coturnix coturnix</i>	Common Quail	South Africa	Stander (2021) [†]
		<i>Eupodotis caerulescens</i>	Blue Korhaan	South Africa	Pitman (1962a)
		<i>Gallus gallus domesticus</i> [‡]	Domestic Chicken	South Africa	Heyns & Smith (2018) [†]
		<i>Philetairus socius</i> (3)	Sociable Weaver	South Africa	Maclean (1973); Covas et al. (2008); Greuel (2020)
		<i>Pterocles namaqua</i> (2)	Namaqua Sandgrouse	South Africa	Pitman (1962a); Lloyd et al. (2001)
		<i>Upupa epops</i>	Eurasian Hoopoe	South Africa	Layloo et al. (2017)
<i>Notechis scutatus</i>	Tiger snake	Unidentified	-	Australia	Shine (1987a)
<i>Pseudechis australis</i>	Mulga snake	Unidentified	-	South Australia	Shine (1987b)
<i>Walterinnesia aegyptia</i>	Desert cobra	<i>Dendrocopos syriacus</i>	Syrian Woodpecker	Palestine	Al-Safadi (2004)
Psammophiidae					
<i>Malpolon monspessulanus</i>	Montpellier snake	<i>Burhinus oedicephalus</i>	Spotted Thick-knee	Spain	Solis & De Lope (1995)
		<i>Carduelis carduelis</i>	European Goldfinch	Spain	Monrós (1997)
		<i>Carduelis chloris</i>	European Greenfinch	Spain	Monrós (1997)
		<i>Emberiza cirius</i>	Cirl Bunting	Spain	Monrós (1997)

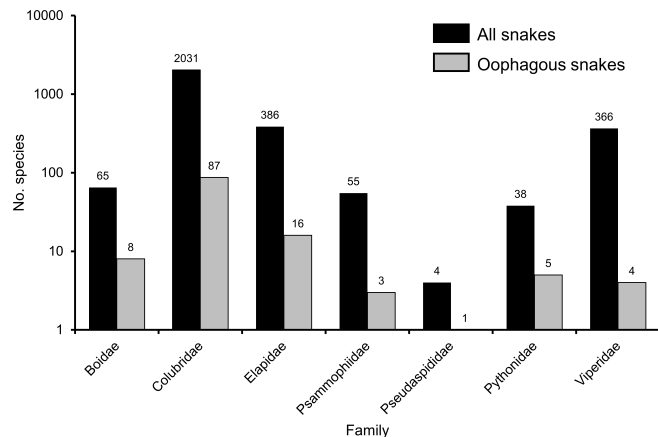
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<i>Psammodius phillipsi</i>	Phillips' whip snake	<i>Turdus merula</i>	Eurasian Blackbird	Spain	Monrós (1997)
<i>Psammodius schokari</i>	Schokari Sand Racer	Unknown heron	-	Spain	Pitman (1962a)
Pseudaspidae		<i>Merops breweri</i>	Black-headed Bee-eater	Gabon	Schmidt & Branch (2005)
<i>Pseudaspis cana</i>	Mole snake	<i>Pterocles orientalis</i>	Black-bellied Sandgrouse	Morocco	Znari et al. (2008)
		<i>Haematopus moquini</i>	African Oystercatcher	South Africa	Calf (2004)
		<i>Larus hartlaubii</i>	Hartlaub's Gull	South Africa	Dyer (1996)
		<i>Numida meleagris</i> (2)	Helmeted Guineafowl	South Africa	Dyer (1996); Van der Westhuizen (2020) [†]
		<i>Pavo cristatus</i>	Indian Peafowl	South Africa	Maritz & Maritz (2020)
		<i>Prinia maculosa</i>	Karoo Prinia	South Africa	Nalwanga et al. (2004)
		<i>Sphenescus demersus</i>	African Penguin	South Africa	Dyer (1996)
		Unidentified	-	South Africa	Maritz & Maritz (2020)
Pythonidae		Unidentified	-	Australia	Shine & Slijp (1990)
<i>Liasis fuscus</i>	Water python	<i>Anser anser</i> (2)	Graylag Goose	Australia	Shine & Fitzgerald (1996); Fearn et al. (2001)
<i>Morelia spilota</i>	Carpet python	<i>Gallus gallus</i>	Red Junglefowl	Australia	Fearn et al. (2001)
<i>Python bivittatus</i>	Burmese python	<i>Aramus guarauna</i>	Limpkin	USA	Dove et al. (2012)
		<i>Eudocimus albus</i>	White Ibis	USA	Orzechowski et al. (2019)
		<i>Numida meleagris domesticus</i> [‡]	Domestic Guineafowl	USA	Dove et al. (2012)
		Unidentified	-	USA	Dove et al. (2012)
<i>Python natalensis</i>	Southern African python	<i>Alopothen aegyptiaca</i>	Egyptian Goose	South Africa	Alexander (2012)
		<i>Numida meleagris</i>	Helmeted Guineafowl	South Africa	Koen (2021) [†]
<i>Python sebae</i>	African rock python	Unknown goose	-	-	Spaws et al. 2018
Viperidae		Unidentified (2)	-	Argentina; Trinidad and Tobago	Skutch (1985); Menezes & Marini (2017)
<i>Bothriechis schlegelii</i>	Eyesh viper	<i>Argya caudata</i>	Common Babbler	Iran	Moosavi et al. (2011)
<i>Echis carinatus</i>	Saw-scaled viper	<i>Chondestes grammacus</i>	Lark Sparrow	USA	Brush & Ferguson (1986)
<i>Sistrurus catenatus</i>	Massasauga	<i>Colinus virginianus</i>	Northern Bobwhite	USA	Applegate (1995)
<i>Vipera berus</i>	European adder	<i>Linaria cannabina</i>	Common Linnet	United Kingdom	Pitman (1962a)

[†]Unpublished Facebook record

[‡]Domesticated bird

Fig. 1. Counts of all species and oophagous species per each snake family with bird egg predators as reported from 471 predation records (n = 123 oophagous snake species).



Predation of bird eggs by snakes was reported on all continents on which snakes are distributed as well as on several archipelagos and small islands (Fig. 2). The majority of these observations (~75%) occurred at low elevations < 500 m above sea level. Sampling frequencies of feeding records varied between geographical regions (Fig. 3) as most predation events were observed in North America (37% of all records) and Africa (24% of all records). At the national level, most records disproportionately represented the relatively well-studied United States of America (35% of all records) and South Africa (14% of all records) respectively. Species richness of snake predators and bird egg prey also both varied regionally and were

similarly proportioned to the spread of predation records (Fig. 3). Approximately 29% of recorded snake predators were from North America, 20% from Asia, and 17% from Africa. Similarly, 31% of identified bird taxa whose eggs were consumed were from North America, and 23% were from Africa.

Which snakes eat bird eggs?

In Africa, the common egg-eater (*Dasypeltis scabra*), was responsible for most reports of egg-eating and was most reported for any snake species (N = 53, 11% of all records, Table 1). Common egg-eaters consumed the eggs of at least 40 species of birds throughout southern and East Africa, ranging from the southernmost regions of South Africa to Uganda. Other important oophagous African snakes included various species of cobras (*Naja* spp.), boomslang (*Dispholidus typus*), and mole snakes (*Pseudaspis Cana*) that were predominantly from southern Africa. Southern and East African pythons (*Python natalensis* and *Python sebae*) were also confirmed as bird egg consumers.

In North America, various rat snakes (*Pantherophis* spp.) were the principal consumers of bird eggs, collectively accounting for 15% of all records (Table 1). Other frequently reported species included several species of bullsnakes (*Pituophis* spp.), kingsnakes (*Lampropeltis* spp.), and eastern racers (*Coluber constrictor*). Collectively, snakes from the above genera consumed the eggs of at least 66 species of bird across the USA (Fig. 2). In particular, these snakes were most frequently observed raiding hen-houses for the eggs of Domestic Chickens (*Gallus gallus domesticus*) and often consumed the eggs of Black-capped Vireos (*Vireo atricapilla*), Field Sparrows (*Spizella pusilla*), Northern Bobwhites (*Colinus virginianus*), and several species of ducks and geese. In Florida, the invasive Burmese python (*Python bivittatus*) consumed the eggs of Limpkins (*Aramus guarauna*), American White Ibises (*Eudocimus albus*), and introduced Helmeted Guinea Fowl (*Numida meleagris*).

Fig. 2. Map of locations of predation events between snakes and bird eggs where coordinates could be determined.

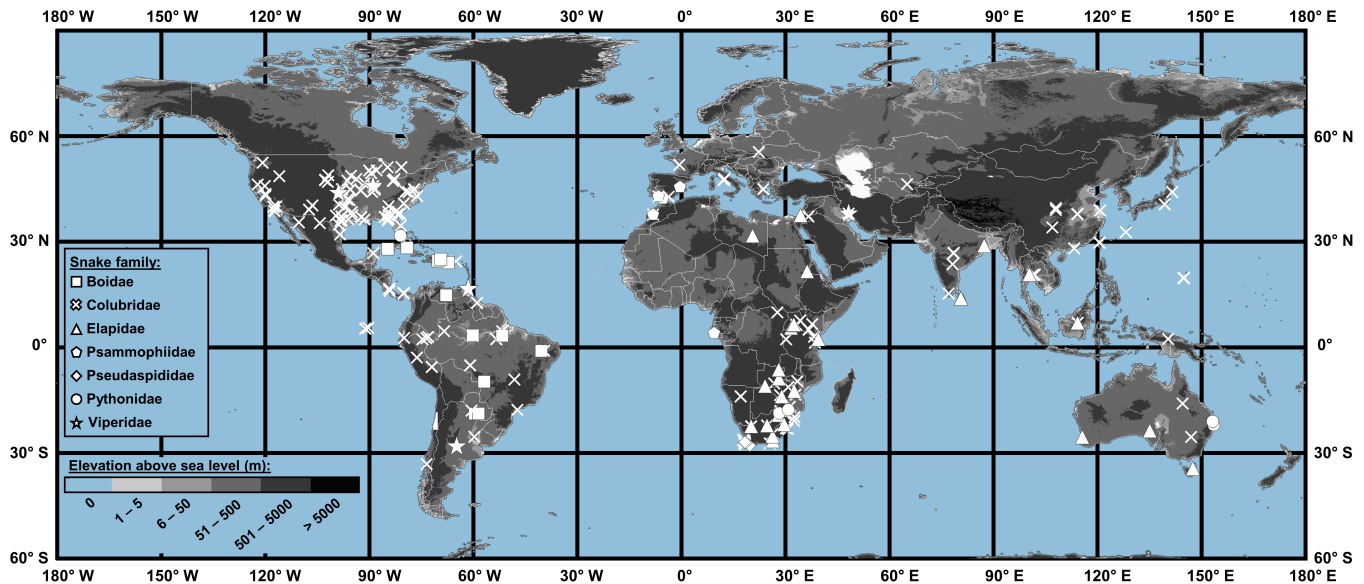
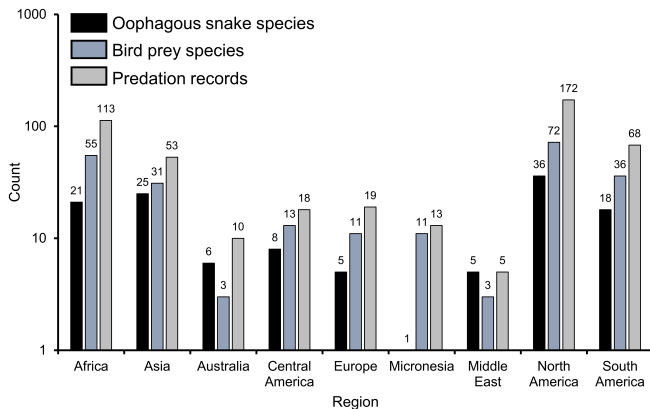


Fig. 3. Summary of the numbers of feeding records of snakes eating bird eggs across major continental regions. Values above each bar represent count data.



Other notable North American oophagous snakes included common garter snakes (*Thamnophis sirtalis*), eastern indigo snakes (*Drymarchon couperi*), and massasaugas (*Sistrurus catenatus*), the only viperid from North America included on our list.

Neotropical snakes from Central and South America that consumed bird eggs mostly included several species of colubrids (Table 1). Western indigo snakes (*Drymarchon corais*), several species of puffing snakes (*Phrynonax* spp.), and both species of chicken snakes (*Spilotes pullatus* and *S. sulphureus*) were the principal egg predators in these regions. Records involving those species were largely restricted to regions in Brazil and Peru but extended as far south as Chile and as far north as Costa Rica (Fig. 2). Collectively, Neotropical colubrids consumed the eggs of at least 20 species of birds. Large boas and anacondas of the genera *Boa*,

Epicrates, and *Eunectes* were observed consuming the eggs of at least seven species of birds in various habitats in Brazil and Argentina. Similarly, in the Caribbean, several species of Antillean boas (*Chilabothrus* spp.) were notable bird egg predators.

In Europe, only five species of snakes were reported consuming bird eggs (Table 1). The most frequently reported species were the four-lined snake (*Elaphe quatuorlineata*) in Italy and the Montpellier snake (*Malpolon monspessulanus*) in Spain. The European adder (*Vipera berus*) in the United Kingdom, the Aesculapian snake (*Zamenis longissimus*) in Italy and Poland, and the ladder snake (*Zamenis scalaris*) in Spain were also confirmed as oophagous. Those snakes were frequently recorded consuming the eggs of Common Pheasant (*Phasianus colchicus*), Great Tit (*Parus major*), Common Linnet (*Linaria cannabina*), and Common Babbler (*Argya caudata*). We only found one record of bird egg predation in the Middle East which was of the Arabian tiger snake (*Telescopus dhara*).

Across the oceanic region of Asia, Australia, and Micronesia, cat snakes of the genus *Boiga* were the predominant bird egg predators. Records of these snakes accounted for 6% of our dataset (Table 1). More than half of those observations were of the invasive brown tree snake (*Boiga irregularis*; $N = 16$) on the island of Guam (Fig. 2). Predations by other cat snakes (*B. cyanea*, *B. cynodon*, *B. dendrophilia*, *B. kraepelini*, *B. ochracea*, and *B. siamensis*) were observed on several islands and coastal regions of South-East Asia. Asian rat snakes (*Elaphe* spp.) were important predators of bird eggs in habitats across China and offshore Japan. In India and surrounding areas, the bird egg specialist Indian egg-eater (*Elachistodon westermanni*) purportedly consumed the eggs of several species of birds similarly to African *Dasyeltis*. However, few feeding records for these snakes have been published. Lastly, while few observations were reported from Australia, at least two species of pythons (*Liasus fuscus* and *Morelia spilota*) and three species of elapid snakes (*Denisonia devisi*, *Notechis scutatus*, and *Pseudechis australis*) consumed bird eggs in this region.

Body lengths and habitat use of oophagous snakes

Oophagous snakes averaged 2057 mm in maximum length, ranging by an order of magnitude in size from 600 mm (*Denisonia devisi*) to 6000 mm (*Python bivittatus*). However, most of these species ranged between 1500 mm to 2000 mm in maximum length. The distribution of maximum body lengths of oophagous snakes differed significantly from snakes in general ($D = 0.671$, $P < 0.001$; Fig 4.A). Oophagous snakes were significantly larger in maximum length on average compared to other snakes (Phylogenetic ANOVA: $F_{1,3501} = 307.322$, $P < 0.001$). Body size thus appears to be an important component of bird egg consumption by snakes.

Most snake species in our list were terrestrial (60% of all 123 taxa) rather than semi-arboreal (21% of all 123 taxa) or arboreal (17% of all 123 taxa). Only two species (*Laticauda colubrina* and *Thamnophis hammondi*) were aquatic (~2% of all 123 species), and none of the species in our list was fossorial. We found no differences in the body sizes of snakes of differing habitats (Phylogenetic ANOVA: $F_{3,105} = 2.117$, $P = 0.339$). Thus, differences in body size of oophagous and non-oophagous snakes are unlikely driven by differences in habitat use. Additionally, we found a low phylogenetic signal for oophagy in snakes (Blomberg's K value of 0.065; $P = 0.504$), indicating that this trait evolves independently of phylogenetic relatedness.

Sizes of consumed bird eggs

Consumed bird eggs snakes ranged between 10 mm (Zebra Finch, *Taeniopygia guttata*) and 58 mm (Domestic Goose, *Anser domesticus*) in average diameter. Approximately 64% of the eggs consumed by snakes were on average narrower than the mean of this range (24.38 mm, back-transformed from log widths). Overall, the relative distribution of egg diameters did not differ between consumed eggs and all other eggs ($D = 0.061$, $P = 0.602$, Fig. 4B). The same pattern was found when comparing 100 samples randomly drawn from each distribution ($D = 0.091$, $P = 0.813$). Moreover, average egg diameters of both groups were statistically similar in size (Phylogenetic ANOVA: $F_{1,2342} = 0.570$, $P < 0.723$; Fig. 4B).

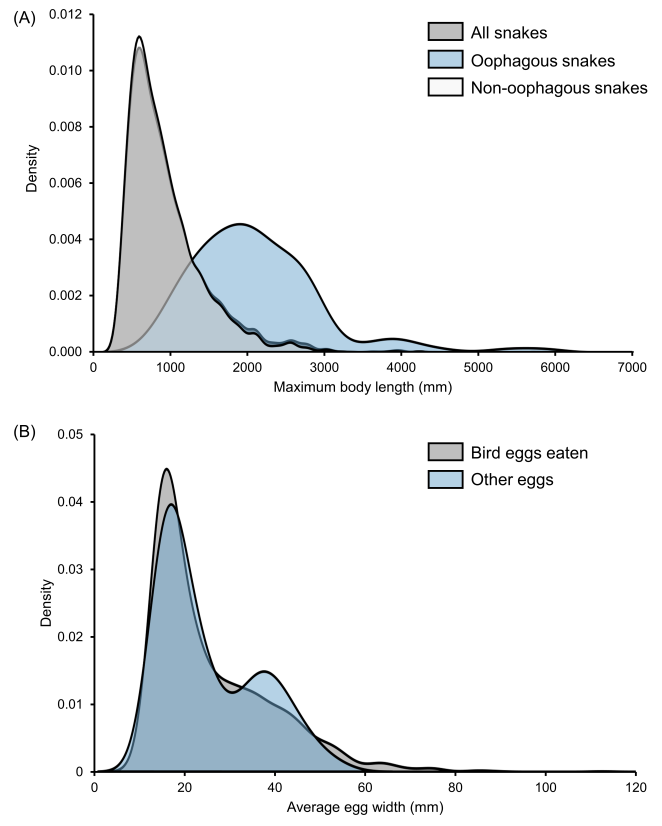
Relationship between snake-size and bird egg-size

With the exception of predation events involving the uniquely adapted, bird egg specialist *Dasypeltis*, snake species in the lowest size classes (i.e., < 2 m in length) mostly consumed narrow bird eggs (< 20 mm; Fig. 5). Larger-bodied species mostly consumed narrow and moderately-sized eggs but also consumed bulkier eggs inaccessible to most other smaller-bodied species.

DISCUSSION

Our search for reports of snakes consuming bird eggs produced 471 feeding records from 238 individual data sources. From those reports, we produced a global list of oophagous snakes spanning 123 species, 58 genera, and seven families. Our list greatly exceeds prior attempts at cataloguing predatory interactions between snakes and bird eggs but is similarly geographically biased to a few well-sampled regions. For instance, we compiled nearly five times more records of snakes consuming bird eggs than Grundler (2020), 98 records across 50 snake taxa, but 60% of our records were from North America and southern Africa together. Collectively, the snakes on our list consumed the eggs of at least 210 species of birds across a variety of different families and orders. Our examination of traits of identified snake species and

Fig. 4. Distributions of (A) maximum body lengths (in mm) of all snakes, snakes that consume eggs, and snakes that do not, and (B) average diameters of bird eggs (in mm) consumed and not consumed by snakes.

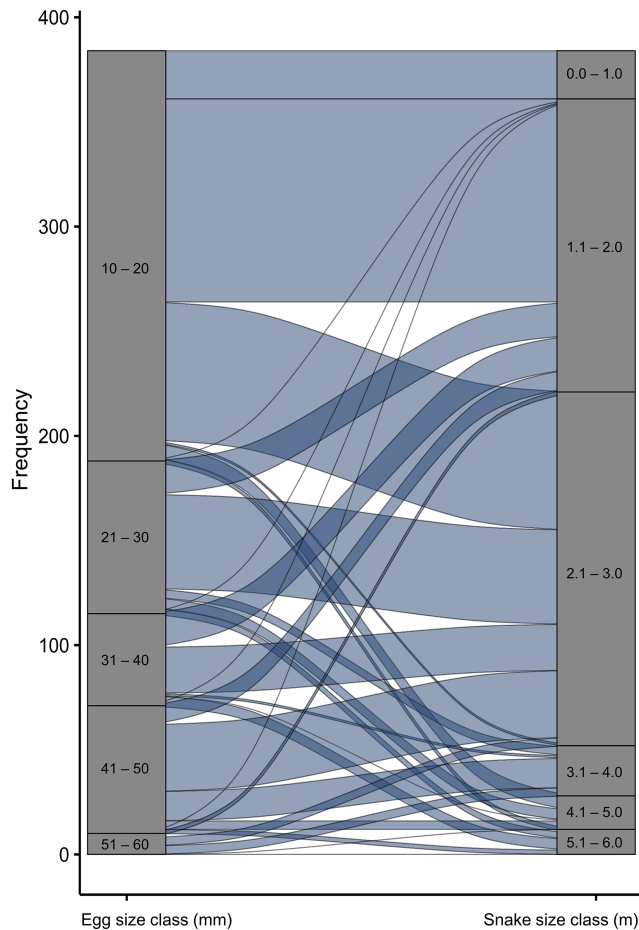


bird egg prey revealed that most oophagous snakes are large-bodied terrestrial species and that narrow bird eggs are most frequently, but not disproportionately, consumed. We identified several trends in the data that we hope will form the basis for testable hypotheses and serve as indicators of sampling bias that needs to be addressed.

What we know about bird egg feeding by snakes

There are currently 3921 recognized species of snakes (Uetz et al. 2021) distributed across the globe, all of which are predators (Greene 1997, Cundall and Greene 2000). Excluding the 471 species of invertebrate specialist Scolecophidian snakes (i.e., the blind snakes and thread snakes), the vast majority of the remaining 3450 species feed on vertebrate prey. Our list of 123 snake taxa represents a meagre 4% of those species. Bird eggs thus appear to be an uncommon source of prey for snakes overall. However, our list is undeniably an under-representation of the full range of snakes that consume bird eggs. Many congeners and close relatives of several taxa in our list almost certainly also consume bird eggs but have yet to be directly reported as doing so. For example, despite all 16 members of the genus *Dasypeltis* being known as obligate bird egg specialists (Bates and Little 2013, Bates and Broadley 2018), we only found feeding records for four of these species.

Fig. 5. Sankey diagram depicting the association between snake lengths and the widths of consumed bird eggs across 384 reported predation events. All snakes mostly consumed small eggs but only large snakes and *Dasypeltis* consumed bulky eggs.



Unsurprisingly, most of the species on our list were represented by only a handful of feeding records. Only ten species had ten or more records, and nearly half of the species were represented by only a single observation. This paucity of feeding records, of which a large proportion represent apparently novel observations, highlights our limited understanding of bird egg predation by snakes. Moreover, additional factors like method-specific biases in feeding data collection also limit the extent of this knowledge. Several studies have highlighted the propensity at which different sampling techniques can affect the quality and quantity of collected dietary information for snakes (Rodríguez-Robles 1998, Glaudas et al. 2017, Maritz and Maritz 2020). As a result, even the diets of species that are relatively “well-known” may be incomplete because the methods used to collect feeding data for those taxa may have been unfavourable towards detecting prey like bird eggs. From this perspective, it is clear that continued reporting of novel feeding records, increased publications of descriptive studies of snake diets, and especially investigations of nest predation will lead to additional identifications of species suitable for inclusion in our list.

Most of the observed predations between snakes and bird eggs took place in the USA. However, at similarly high latitudes east of the Atlantic Ocean, exceedingly few records were reported. Moreover, there were no records at latitudes exceeding 60° N. The paucity of records at high latitudes regions can likely be explained by the limited numbers of snake species that occur in those regions. Snake species richness at high latitudes is relatively low compared to regions closer to the equator and in the southern hemisphere. For example, while there are around 200 species of snakes distributed across the USA there are fewer than 30 species in Canada (Ernst and Ernst 2003). Similarly, in most of northern Europe, there are fewer than 10 species of snakes, and in Russia, there are fewer than 45 species (Uetz et al. 2021). The lack of records from these areas is therefore not surprising given that egg consumption is uncommon in snakes and even in areas with high species richness, there are few records.

External factors unrelated to snake occurrences may also have inhibited records from being published. Several regions with high snake species richness are represented by only a few records of egg consumption (for example, West Africa, North Africa, India, and China). In some of those areas, the financial constraints on publishing may make it difficult to report on observations (see Mekonnen et al. 2021) since it may simply be too expensive to publish, especially for standalone observations like dietary feeding records. Additionally, sampling biases caused by a lack of interest in avian or reptile ecology may also have hindered observations of oophagy being reported.

Why don't more snakes eat bird eggs?

While detailed dietary records are not available for many species (Grundler 2020), the feeding habits of most snakes are either at least generally known or can be inferred from life-history traits and the diets of their close relatives (Greene 1997, Cundall and Greene 2000). While not without exception, such inferred generalized assertions of snake feeding habits are often supported by detailed dietary studies (Bates and Little 2013, Maritz et al. 2019, Maritz et al. 2021a). Many species of snakes can be ruled out as consumers of bird eggs because they occur in areas where other prey types may be more abundant, easier to forage, or less difficult to consume. Alternatively, these snakes may lack the necessary morphology or physiology to consume eggs. Egg-specialist species like *Dasypeltis* possess unique adaptations that facilitate egg swallowing such as reduced teeth and vertebral modifications (Gans 1952) that most other snakes do not have. Factors like limitations in gape size, active selection of different prey, differences in encounter rates, and variable habitat use each contribute to the selectivity of different prey types, including bird eggs (de Queiroz and Rodríguez-Robles 2006).

Our results demonstrate that most snakes that consume bird eggs are large-bodied, exceeding 2000 mm in maximum length. Comparatively, the average maximum length of snakes overall is only ~800 mm (Feldman et al. 2016). Snake body size appears to play an important role in the inclusion of bird eggs in snake diets. Longer snakes tend to have larger gapes, and as a result, larger snakes are generally able to consume bulkier and heavier prey than smaller snakes (Arnold 1993, Cundall and Greene 2000). The ovoid shapes and wide cross-sectional diameters of eggs relative to snake head dimensions make them difficult for snakes with narrow gapes to handle and ingest (de Queiroz and Rodríguez-Robles 2006). Some small-bodied species like those in

the genera *Dasypeltis* and *Elachistodon* overcome these mechanical constraints using specialized morphological features (Bates and Little 2013, Dandge and Tiple 2016) but most other small-bodied snakes are morphologically ill-equipped to ingest this type of prey (Gartner and Greene 2008).

The relationship between snake body size and bird egg prey sizes further illustrates the importance of relative prey bulk in facilitating these interactions. Most snakes, including several large-bodied boas and pythons, consumed relatively narrow eggs compared to their own lengths. This pattern reflects the findings of Gartner and Greene (2008) who quantified the egg-eating performance of *Lampropeltis getula* and found that adult specimens could only ingest modestly sized eggs relative to the dimensions of their feeding apparatus whereas juveniles could not ingest eggs at all. Those results highlight the body-size mediated mechanical difficulty of bird egg consumption for snakes and support the general predator-size, prey-size pattern found here. However, this pattern is not without exception given that several snakes consume bulky chicken, duck, and goose eggs.

Apart from body size and gape size limitations, specific predispositions towards hunting particular prey also preclude several species of snakes from predating bird eggs. In snakes, the habit of eating the eggs of an animal tends to arise from first eating the corresponding laying animal (de Queiroz and Rodríguez-Robles 2006, Maritz et al. 2021c). This is thought to be because the eggs of an animal share chemical cues with the parent animal, and so 1) this allows snakes to recognize the eggs as suitable food, and 2) leads to greater encounter rates of those organisms (de Queiroz and Rodríguez-Robles 2006). As a result, because relatively few species of snakes consume birds (Greene 1997, Cundall and Greene 2000), few species consume the eggs of birds because they do not associate them as appropriate prey.

Snakes may also actively exclude bird eggs from their diet in favour of other prey. Relative to their size, bird eggs are filled with calories, lipids, proteins, and water (Sotheland and Rahn 1987) but because of their size and associated high handling costs offer lower energetic payoffs to most other vertebrate prey (Greene et al. 2013). Snakes that prey on bird eggs can compensate for this by eating multiple eggs in a single meal, a trend that our data suggests occurs often. However, most species of birds lay small clutches with few eggs (Baicich and Harrison 2005, Tarboton 2011). Moreover, bird eggs are sedentary and nests are often difficult to locate (Nalwanga et al. 2004). For many species of snakes, the energetic costs of searching for nests with eggs likely outweigh the costs of foraging other, more easily detectable and energetically profitable prey. As a result, it is likely optimal for most snakes to exclude bird eggs in favour of other prey. In particular, large snakes should theoretically prefer singular, heavy prey items that provide a surplus of energy whereas smaller-bodied snakes probably prefer less bulky prey that are easier to consume (Shine 1991a).

Differences in foraging mode (i.e., active foraging versus ambush foraging) and lifestyle habits between snakes also greatly affect the chances of species encountering sedentary prey like bird eggs (Greene 1997, Alencar et al. 2013). Sit-and-wait foraging snakes probably only rarely encounter nesting birds and even less so bird eggs. Similarly, aquatic and fossorial species will encounter bird

eggs considerably less often than arboreal and terrestrial species. Surprisingly, the majority of the species in our list were terrestrial rather than arboreal or semi-arboreal. However, we suspect that this is likely an artefact of sampling bias rather than a reflection of true biological patterns as terrestrial snakes are easier to detect than arboreal species (Pizzatto et al. 2007). Additionally, most occurrences of egg predation took place in habitats at low elevations (< 500 m above sea level) which could also be indicative of biased sampling efforts since high altitudes are generally difficult to access.

Importance of identifying snake predators of bird eggs

Identifying the snake predators of bird eggs is a key first step toward understanding the extent of their roles in nest predation and the potential implications thereof (Weatherhead and Blouin-Demers 2004, Lahti 2009; Menezes and Marini 2017). By knowing which snakes occur in a given area and which of those species eat bird eggs, researchers can consider species-specific hypotheses informed by existing knowledge of the demographics, ecologies, and natural histories of those particular species (for example Barends and Maritz 2021). Ultimately, this will lead to investigations that further our understanding of the relative importance of different snakes towards avian breeding success and more broadly, their impacts on ecosystem functioning (Reidy and Thompson 2012, DeGregorio et al. 2016a). Importantly, these investigations can also inform conservation strategies that seek to manage or protect endangered or vulnerable species of birds (Carter et al. 2007, Thompson and Ribic 2012).

Our primary objective of this review was to compile a comprehensive list of snake species unambiguously categorized as predators of bird eggs. We hope that this list can act as a baseline for further research seeking to understand patterns of nest predation by snakes and their impacts on avian ecology. By searching through the literature, citizen science reports, and social media, we provide a summary of accounts of bird egg predation by snakes that can act as a foundation for a consolidated database for further research.

Responses to this article can be read online at:

<https://journal.afonet.org/issues/responses.php/88>

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Data Availability:

Supplementary electronic datasets are available on Figshare <https://doi.org/10.6084/m9.figshare.19508938>.

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