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BREEDING PHENOLOGY AND NEW HOST LIST OF THE BLACK-HEADED DUCK (*HETERONETTA ATRICAPILLA*) IN ARGENTINA

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ABSTRACT.—The Black-headed Duck (*Heteronetta atricapilla*) is a unique interspecific brood parasite among birds where the host species provides parental care for incubation only. Despite this unique system, there are few studies on this species biology and the list of hosts remains incomplete. We present information about breeding phenology of the Black-headed Duck and an updated list of hosts obtained from a comprehensive review of egg collections deposited in the most important natural science museums of Argentina. We include five new hosts to the list: Great Grebe (*Podiceps major*), Maguari Stork (*Ciconia maguari*), White-cheeked Pintail (*Anas bahamensis*), South American Stilt (*Himantopus mexicanus*), and Long-winged Harrier (*Circus buffoni*). We found that solitary nesting host species were more likely to be parasitized earlier during the breeding season than colonial nesting species. The Black-headed Duck has an extended breeding season in central Argentina (Aug–Feb) as it is able to use a variety of hosts that breed in different times during the breeding season. With this contribution, the new list rises to 23 documented hosts of the Black-headed Duck belonging to eight different waterfowl orders. Received 17 March 2016. Accepted 1 July 2016.

Key words: breeding biology, egg collections, host list, interspecific brood parasitism, parasitic egg, waterfowl.

Avian brood parasites lay eggs in nests of other species (hosts) that incubate the parasite eggs and, in most cases, feed the parasite chicks (Davies 2000). Many interspecific avian brood parasite species are obligately parasitic and are completely dependent on a host to reproduce (Ortega 1998, Davies 2000). These females do not possess the ability to build nests, incubate eggs, or feed their nestlings (Sealy et al. 2002). Less than 1% of bird species are obligately parasitic, and this reproductive strategy has evolved independently at least seven times within birds (Rothstein 1990). Brood parasites generally reduce the reproductive success of their hosts (see Rothstein and Robinson 1998, Reboreda et al. 2003), generating a selection pressure that favors the evolution of antiparasitic defenses (Dawkins and Krebs 1979, Segura and Reboreda 2012).

The Black-headed Duck (*Heteronetta atricapilla*) is the only interspecific brood parasite species within the order Anseriformes (Madge and Burn 1988, Davies 2000). It is endemic to the Neotropical region, and its distribution mainly covers the central region of Chile and Argentina, Uruguay, southeastern Brazil, Paraguay and Bolivia (Carboneras 1992). Black-headed Ducks inhabit swamps, lakes, pools and marshes of permanent fresh waters with abundant emergent

vegetation. Adult birds are usually paired from September to January (breeding season), and during winter, they gather in groups of up to 40 individuals (Madge and Burn 1988, Carboneras 1992, Cofré et al. 2007). There are few data on the breeding biology of Black-headed Ducks with most of the accounts relating to central-east Argentina (Rees and Hillgarth 1984; Carboneras 1992; Lyon and Eadie 2004, 2013).

The Black-headed Duck parasitizes a wide variety of species (Madge and Burn 1988, Lowther 2013) and presents a unique characteristic among brood parasites: the cost of parasitism for the host is restricted to the egg-laying and incubation stages, as the ducklings are able to care for themselves just a few hours after hatching (Weller 1968, Rees and Hillgarth 1984, Lyon and Eadie 1991, Davies 2000). To date, there is scarce information about the breeding biology of this species and in particular, on the list of hosts that this duck is able to parasitize.

In this study, we present information about some aspects of the breeding phenology of the Black-headed Duck and its hosts, and present an updated version of the list of hosts obtained from a comprehensive review of egg collections deposited in the most important natural science museums of Argentina.

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METHODS

We inspected the Museo Argentino de Ciencias Naturales Bernardino Rivadavia (MACN) and

Museo de La Plata (MLP) egg collections extensively. These egg collections included information such as site, locality, province and country, date of egg collection, nest species, number of host and parasite eggs, state of incubation (early/late incubation) and collector. We also inspected other egg collections from Argentinian museums, but they did not have any data about hosts of Black-headed Ducks. The most significant contribution belongs to Mr. Ronald Runnacles, an amateur ornithologist who conducted numerous studies in eastern Buenos Aires province (36° 22' S, 57° 01' W) during 1932–1941. Mr. Runnacles collected numerous eggs with the aim of creating a private bird egg collection of the region. His collection was donated to MACN and MLP, along with all the original written records (manual forms and field notes). Field notes included additional information as weather conditions, nesting site characteristics, nest shape, nest material, adults (hosts or parasites) in the nest surroundings, and any evidence of recent incubation (adult flushing from the nest or warm eggs).

We also include data on parasitism by Black-headed Ducks that occurred during a monitoring project on mixed breeding colonies of the Long-winged Harrier (*Circus buffoni*) and Cinereous Harrier (*C. cinereus*) in northeastern Patagonia (40°06'S, 64°27'W) during the breeding season of 2012–2013.

Width and length of parasite eggs were measured to the nearest 0.05 mm using Vernier calipers. Egg volumes were calculated using Hoyt's (1979) equation: volume = 0.51 x (length) x (width)². We estimated the date parasitism occurred related to the date of our first parasitism event detected (day 1 = 2 Aug), and we tested the relationship between egg measurements and date of the breeding season. We tested the relationship between the body mass of the host species (Dunning 2008) and parasite egg measurements. We also tested the relationship between the date of the breeding season and host nesting habits (i.e., solitary and colonial nesting species). For analysis purposes, we use the date of egg collection as an approximate date of parasitism, as all collected eggs were fresh. In addition to our data, we also used the parasitism date from Höhn (1975) and de la Peña (1987), since they were the only ones to report this data.

We consider as hosts the species in whose nest at least one egg of a Black-headed Duck was observed and/or collected whether the nest was active or abandoned. To compile the host list, we used also the available information published to date about the hosts of Black-headed Ducks (see Table 1). Reported values are means ± S.E. Tests were two-tailed and differences were considered significant at $P < 0.05$.

RESULTS

The egg collection at MACN contained 45 eggs from Black-headed Ducks, but only 24 of them had the host species data. The MLP contained 34 eggs, and 32 of them had the host species data. A complete host list of the Black-headed Ducks based in these collections is detailed in Table 1.

During the breeding monitoring project of harriers on the southern coast of the Río Negro, northeastern Patagonia (see Methods), we observed a parasitism event in an abandoned Long-winged Harriers' nest. On 28 December 2012, a pair of Long-winged Harriers was observed building their nest on a flooded area with dense cattail (*Typha latifolia*). On 2 January 2013, there were two Long-winged Harrier eggs in the nest, and 4 days later the nest was abandoned with three Long-winged Harrier eggs and one egg from a Black-headed Duck.

Black-headed Ducks' eggs were 59.4 ± 0.4 mm in length (range = 54.4–65.1 mm; $n = 39$ eggs) and 44.3 ± 0.3 mm in width (range = 40.7–48.9 mm; $n = 39$ eggs). Mean egg volume was 59.7 ± 0.9 cm³ (range = 49.9–71.9 cm³; $n = 39$ eggs). Parasite egg dimensions did not vary within breeding season (Spearman's rank correlation: length, $\rho = -0.23$, $P = 0.17$; width, $\rho = -0.14$, $P = 0.39$; volume, $\rho = -0.17$, $P = 0.32$; $n = 36$ eggs), nor with hosts body mass (Spearman's rank correlation: length, $\rho = -0.07$, $P = 0.67$; width, $\rho = 0.08$, $P = 0.62$; volume, $\rho = 0.09$, $P = 0.58$; $n = 39$ eggs) or nesting habits (solitary vs. colonial nesting species; Mann-Whitney U -test: length, $z = -0.18$, $P = 0.85$; width, $z = 1.44$, $P = 0.15$; volume, $z = 0.95$, $P = 0.34$; $n = 39$ eggs).

We found that parasitism in typically solitary nesting species (i.e., Great Grebe *Podiceps major*, Maguari Stork *Ciconia maguari*, Black-necked Swan *Cygnus melanocoryphus*, Coscoroba Swan

TABLE 1. List of hosts of the interspecific brood parasitic Black-headed Duck. We provide each host Order, Family, Species, and the list of studies that have contributed with data. Question marks (?) indicate that authors only gave the genera, parenthesis () indicate the number of parasitized nests, and asterisks (*) indicate the new species reported in this study.

	Daguerra		Weller 1968	Höhn 1975	de La Peña 1987	Lyon		This study				
	1920 and 1923	Wilson 1923				& Eadie 2013	Lowther 2013	Harriers Project	Runnacles field notes	MACN collection	MLP collection	
Podicipediformes												
Podicipedidae												
<i>Podiceps major</i> (1)*									X			X
Pelecaniformes												
Ardeidae												
<i>Nycticorax nycticorax</i>						X	X		X	X		X
Threskiornithidae												
<i>Phimosus infuscatus</i>					X					X		
<i>Plegadis chihi</i>	X		X		X	X	X		X			X
<i>Platalea ajaja</i>							X		X			X
Ciconiiformes												
Ciconiidae												
<i>Ciconia maguari</i> (1)*									X			
Anseriformes												
Anatidae												
<i>Dendrocygna bicolor</i>				X			X		X	X		X
<i>Anas bahamensis</i> (1)*									X			X
<i>Netta peposaca</i>			X		X	X	X			X		
<i>Coscoroba coscoroba</i>	X					X	X		X			X
<i>Cygnus melanocoryphus</i>						X	X		X	X		X
Anhimidae												
<i>Chauna torquata</i>	X					X	X		X			X
Falconiformes												
Falconidae												
<i>Milvago chimango</i>	X	X					X					
Accipitriformes												
Accipitridae												
<i>Rostrhamus sociabilis</i>				X	X	X	X			X		
<i>Circus buffoni</i> (1)*								X				
Gruiformes												
Aramidae												
<i>Aramus guarana</i>	X			X	X	X	X		X			X
Rallidae												
<i>Fulica leucoptera</i>	?				X							
<i>Fulica rufifrons</i>	?		X		X	X	X		X	X		
<i>Fulica armillata</i>	?		X			X	X		X	X		X
<i>Pardirallus sanguinolentus</i>	X								X			X
<i>Pardirallus maculatus</i>	X						X					
Charadriiformes												
Recurvirostridae												
<i>Himantopus mexicanus</i> (1)*									X			
Laridae												
<i>Chroicocephalus maculipennis</i>		?	X		X	X	X		X	X		

Coscoroba coscoroba, Southern Screamer *Chauna torquata*, Limpkin *Aramus guarana* and *Fulica* spp.) occurred earlier in the breeding season than the typically colonial nesting ones (i.e., Black-crowned Night-Heron *Nycticorax nycticorax*, Bare-faced Ibis *Phimosus infuscatus*, White-faced

Ibis *Plegadis chihi*, Roseate Spoonbill *Platalea ajaja* and Brown-hooded Gull *Chroicocephalus maculipennis*) (Mann-Whitney *U*-test: $z = 2.13$, $P = 0.03$; Fig. 1). However, according to existing data within the same egg collection, there were no significant differences throughout the breeding

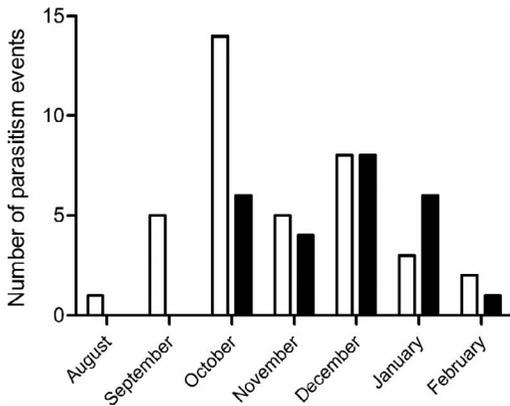


FIG. 1. Number of parasitism events of Black-headed Ducks at different times of the breeding season in central-east Argentina. Bars show solitary (white bars) and colonial (black bars) nesting host species.

season between availability of these solitary and colonial nesting species (Mann-Whitney U -test: $z = 1.86$, $P = 0.24$; Fig. 2).

DISCUSSION

Reviewing the egg collections from MACN and MLP, we found four host species not included in the pre-existing lists: Great Grebe, Maguari Stork, White-cheeked Pintail (*Anas bahamensis*), and South American Stilt (*Himantopus mexicanus*) (Table 1). The egg collection data yielded 16 different hosts of Black-headed Ducks. Other documented lists of host species include those of Daguerré (1920, 1923): 8 hosts, Wilson (1923): 2 hosts, Weller (1968): 5 hosts, Höhn (1975): 3 hosts, de la Peña (1987): 8 hosts, Lyon and Eadie (2013): 11 hosts and the online version of Lowther (2013) with 15 hosts. The Maguari Stork had been listed as a host by Gibson (1920), but supposed parasitic eggs were later identified as Rosy-billed Pochards' eggs (see Weller 1968).

The observation of nest parasitism by Black-headed Ducks in a nest of Long-winged Harriers is unexpected, as usually harriers are predators of some waterfowl, including the Black-headed Duck (Madge and Burn 1988, Bó et al. 1996). We suggest that the parasitic event could have occurred after the nest was abandoned.

In Europe, Rees and Hillgarth (1984) experimentally introduced six Neotropical potential hosts (Rosy-billed Pochard, Lake Duck *Oxyura vittata*,

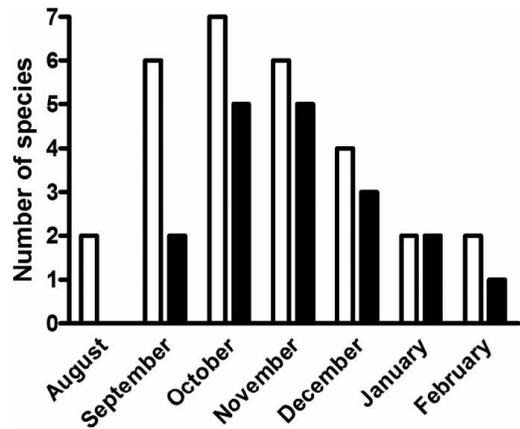


FIG. 2. Number of host species available for Black-headed Ducks at different times of the breeding season in central-east Argentina. Bars show solitary (white bars) and colonial (black bars) nesting host species.

Silver Teal *Anas versicolor*, Red Shoveler *A. platalea*, Black-necked Swan and Common Moorhen *Gallinula chloropus*) and two exotic potential hosts (Wild Duck *A. platyrhynchos* and Gadwall *A. strepera*) in a large enclosure in order to observe the behavior of the Black-headed Duck. In this captivity context, authors only observed the use of the Rosy-billed Pochard as a host. Similarly, other studies in captivity conditions also reported the Rosy-billed Pochard, Red Shoveler, Common Moorhen, Cinnamon Teal (*A. cyanoptera*), and Silver Teal as hosts of the Black-headed Duck (Powell 1979, Todd 1979). These studies were not included in Table 1, because they were based in a captive environment and the host selection strategies may have been altered.

Solitary nesting host species were more parasitized early during the breeding season (Aug, Sept, and Oct), while colonial nesting ones were more parasitized between the middle and the end of the breeding season (mainly Nov to Feb). This strategy cannot be explained by simple differences in host availability, since we did not find any difference in that regard for solitary and colonial hosts throughout the season. On the one hand, it is quite accepted among researchers that waterfowl that nest early in the breeding season tend to have greater success in relation to those that nest late (Blums et al. 2002). On the other hand, colonial nesting waterfowl have lower predation costs than solitary ones (Picman et al. 2002). Would it be

possible that Black-headed Ducks are taking advantage of both scenarios for maximizing their own breeding success? We cannot speculate accurately on the functionality of this strategy, because there are not enough available data on the effect of breeding season date on host and parasites' reproductive success for these Neotropical waterfowl. What is clear is that Black-headed Ducks have a very extensive breeding season (Aug–Feb) to take advantage of a variety of host nesting times.

With this contribution, we are adding valuable information on the breeding phenology of Black-headed Ducks and reporting five new host species (three unreported families of waterfowl), completing a list of 23 hosts of eight different waterfowl orders. Apparently, the Black-headed Duck is not a specialized brood parasite (but see Weller [1968] and Lyon and Eadie [2004] that suggested there is a marked preference for two effective hosts: the Red-gartered Coot and the Red-fronted Coot). It is very likely that the host list is considerably wider, since there have not been many systematic and comprehensive studies in waterfowl breeding biology, resulting in a potential underestimation of the host list. Further studies on this particular brood parasite are necessary to clarify the real number of its suitable hosts and to highlight the host selection strategies used by Black-headed Ducks.

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