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Chapter 6
Obligate Brood Parasitism on Neotropical Birds

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6.1 Introduction

Obligate brood parasites do not build their nests nor do feed and take care of their nestlings. Instead, they lay their eggs in nests of individuals of other species (hosts) that rear the parasitic progeny. For behavioral ecologists interested in coevolution, obligate brood parasites are pearls of the avian world. These species represent only 1% of all the living avian species, and their peculiar reproductive strategy imposes on them permanent challenges for successful reproduction. At the same time, the hosts are under strong selective pressures to reduce the costs associated with parasitism, such as the destruction of eggs by parasitic females and the potential fitness costs of rearing foreign nestlings. These selective pressures may result in parasites and hosts entering in a coevolutionary arms race, in which a broad range of defenses and counterdefenses can evolve. Females of most species of parasites have evolved behaviors such as rapid egg laying and damage of some of the host's eggs when they visit the nest (Sealy et al. 1995; Soler and Martínez 2000; Fiorini et al. 2014). Reciprocally, as a first line of defense, hosts have evolved the ability to recognize and attack adult parasites (Feeney et al. 2012). Parasitic eggs typically hatch earlier than host eggs decreasing host hatching success and nestling survival (Reboreda et al. 2013), but several host species have evolved recognition and rejection of alien eggs, which in turn selected for the evolution of mimetic eggs in the parasite (Brooke and Davies 1988; Gibbs et al. 2000). Parasitic young are often morphologically and behaviorally adapted to manipulate host's parental effort, but sometimes host parents are able to discriminate against them (Liang et al. 2017). In addition to tricking hosts into raising them by mimicking gape markings (Payne et al. 2001), plumage

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color (Langmore et al. 2011), and begging calls (De Mársico et al. 2012), brood parasites also face the challenge of recognizing their conspecifics to interact and reproduce in the future. Yet, how parasitic juveniles identify and join their own kind is poorly understood.

Over the past 50 years, avian brood parasitism has been the focus of a plethora of studies that have substantially contributed to our understanding of the evolution of adaptations between parasites and their hosts, encompassing all the stages of the parasites' lifecycle (for a recent and comprehensive review, see Soler 2017). There are about 100 obligate brood-parasitic species worldwide distributed in seven phylogenetically independent groups (Sorenson and Payne 2002). In the Neotropics, eight species have been described in three of these groups: four cowbirds (*Molothrus*, Icteridae), three New World cuckoos (*Dromococcyx* and *Tapera*, Cuculidae, subfamily Neomorphinae), and the black-headed duck (*Heteronetta atricapilla*, Anatidae), which is the only precocial obligate brood parasite (Table 6.1). In this chapter, we present a compendium of the characteristics and behaviors of these species that aid our understanding of how natural selection shapes the interactions between parasites and their hosts.

Neotropical parasites reflect a wide range of strategies, from specialization to extreme generalization in host use, from nestmate tolerant to nestmate killing, and the unique nidifugous brood parasite. Unfortunately, most of these species have been incompletely studied and the extension devoted to each one in this chapter reflects this unbalance in the available information.

6.2 Family Icteridae

*6.2.1 Shiny Cowbird (*Molothrus bonariensis*)*

6.2.1.1 Species Characteristics

Shiny cowbirds are widespread throughout much of South America and the Caribbean. They occur from southern Argentina (Chubut province) to eastern Panama, with the exception of most areas above 2000 m and extensively forested regions such as the Amazon rainforest. They are also found in Chile, from Aysén to Atacama. During the early 1900s, they expanded their range to include the West Indies, and were first recorded in Peninsular Florida in 1987, where they are considered permanent residents since 1991 (Cruz et al. 1998; Lowther 2011).

This species occurs in open or semi-open habitats and are attracted to deforested areas like fields and pastures with scattered patches of trees and shrubs, or tree groves near farms, gardens and plantations (Cavalcanti and Pimentel 1988; Mason 1985). They also may be found in undisturbed habitats such as mangroves (Post and Wiley 1977). Their diet includes a wide variety of arthropods and seeds. Adults feed on the ground, usually in association with cattle and other large grazing mammals, and pick insects from the backs of grazers (Ortega 1998). Shiny cowbirds may show seasonal variation in diet, depending on the most readily available items. For example, they can consume mainly arthropods during the breeding season and then feed on grains and feed-mixtures in feedlots during the winter (Cruz et al. 1990; Lowther 2011).

Shiny cowbirds are sexually dimorphic in plumage coloration and body size. Males are entirely glossy black with blue and purple iridescence (Ortega 1998). Females are dull brown throughout most of the species' distribution, but in some areas they are dark brown or black (Friedmann 1929; Mahler et al. 2010). Males are larger than females, but body size varies geographically across subspecies (Table 6.1).

Table 6.1 Characteristics of the Neotropical obligate brood parasites

Parasite family	Species	Adult body mass	Incubation period	Number of hosts	Range of host body mass	Nestling/chick behavior
Icteridae	*Molothrus bonariensis*	Smallest subspecies: *M.b. minimus*[a] Female: 34.1–36.4 g Male: 37.9–40.0 g Largest subspecies: *M.b. cabanissi*[a] Female: 45.2–55.6 g Male: 49.0–63.7 g Argentinean subspecies: *M.b. bonaerensis*[b] Female: 46.8 g Male: 51.6 g	12–13 days[c]	268 victims 97 effective hosts[d]	10–80 g[e]	Nestmate tolerant[f]
	Molothrus rufoaxillaris	Female: 43.6–55 g[g,h] Male: 50.8–65 g[g,h]	12 days[i,j]	5[d]	40–90 g[k,l,m]	Nestmate tolerant[n]
	Molothrus oryzivorus	Female: 74–129 g[o], 156 g[n] Male: 120 g[o], 212 g[n]	10–13 days[a]	11[d]	40–232 g[m]	Nestmate tolerant[n]
	Molothrus aeneus	Female: 57 g[o], 59 g[n] Male: 69 g[n,o]	11–13 days[a]	102[d]	20–222 g[m]	Nestmate tolerant[n]

(continued)

Table 6.1 (continued)

Parasite family	Species	Adult body mass	Incubation period	Number of hosts	Range of host body mass	Nestling/chick behavior
Cuculidae	*Tapera naevia*	Females and males: 52 g[p]	15 days[q]	22[d]	7–37 g[m]	Nestmate killing[q]
	Dromococcyx pavoninus	Females and males: 48 g[p]	No information	7[d]	No information	Nestmate killing[o]
	Dromococcyx phasianellus	Females and males: 80 g[p]	No information	No information	No information	Nestmate killing[o]
Anatidae	*Heteronetta atricapilla*	Female:565 g[n] Males: 513 g[n]	21–22 days[r]	23[s]	394–1080 g[m]	Nidifugous[p]

[a] Lowther (2011)
[b] Reboreda et al. (1996)
[c] Fiorini et al. (2005)
[d] Lowther (2018)
[e] De Mársico et al. (2010a, b)
[f] Gloag et al. (2012)
[g] Mason (1987)
[h] Cabezas et al. (2011)
[i] Fraga (1998)
[j] De Mársico et al. (2010b)
[k] Fraga (1992)
[l] Mermoz and Reboreda (2003)
[m] Dunning (1993)
[n] Ortega (1998)
[o] Payne (2005)
[p] Davies (2000)
[q] Morton and Farabaugh (1979)
[r] Lyon and Eadie (2004)
[s] Cabrera et al. (2017)

The shiny cowbird is the most generalist parasite of the *Molothrus* clade, parasitizing more than 260 species of 26 families (Lowther 2018). Less than half of these species have reared parasitic nestlings (Table 6.1). Hosts vary broadly in body mass, from the tiny house wren (*Troglodytes aedon*) to the large brown-and-yellow marshbird (*Pseudoleistes virescens*) (Table 6.1). At individual level, host use by shiny cowbird is not random. In eastern Argentina, some genetic differences exist between females that parasitize the house wren, which is a cavity-nester, and those parasitizing three other common hosts that build open nests (Mahler et al. 2007). This result suggests that host preference of shiny cowbird females might be mainly guided by host's nest type (Mahler et al. 2007), although some individual females in the population parasitize both cavity- and open-nesting hosts (Gloag et al. 2014; de la Colina et al. 2016).

6.2.1.2 Behaviors and Adaptations of the Shiny Cowbird and Host Antiparasitic Defenses

Adults

During the breeding season, female shiny cowbirds use relatively constant areas, in which they search for nests to parasitize (Gloag et al. 2013; Scardamaglia and Reboreda 2014). They are also faithful to one communal roost throughout the breeding season, which is located near their diurnal home-range (Scardamaglia et al. 2018). Daily and cumulative morning ranges of females are about half the size of those of males (22 *vs.* 45 ha and 70 *vs.* 185 ha, respectively), which is consistent with males mating with multiple females and a socially polygynous or promiscuous mating system (Scardamaglia and Reboreda 2014). Nevertheless, information on the genetic mating system is needed to confirm this observation.

Most parasitism occurs before sunrise (90% of parasitic events) but there are parasitic events until 30 min after sunrise (Gloag et al. 2013). Females make at least one prelaying visit to a nest that they parasitize (range 1–8 visits), which is normally located within the area that they used on previous days (Scardamaglia and Reboreda 2014; Scardamaglia et al. 2017). On the laying day, females fly directly from the roost to the target nest, which indicates that they have already acquired information about where to lay through previous prospecting visits (Scardamaglia and Reboreda 2014; Scardamaglia et al. 2017, 2018). Video recording of shiny cowbird females visiting nests of a primary host, the chalk-browed mockingbird (*Mimus saturninus*), revealed that laying visits last less than 30 s on average. During this time, the female first punctures the eggs before laying quickly while being mobbed by the hosts (Gloag et al. 2013; Fiorini et al. 2014). Mobbing does not reduce the probability of parasitism, but it decreases the chance of host eggs being punctured (Gloag et al. 2013). Experiments performed in several host species consisting in the presentation to breeding pairs of taxidermic models of female shiny cowbirds and a control species show that they are able to recognize the parasite as a threat (for a review see Reboreda et al. 2013).

In chalked-browed mockingbird and house wren nests, female shiny cowbirds lay their eggs either standing in the nest, with the legs partially or fully extended, or perched on the rim of the nest. These positions result in cowbird eggs being dropped from about 4–7 cm to the nest floor or onto the other eggs (Ellison et al. in press). This laying behavior may benefit the female cowbird, as a thickly shelled egg laid from a certain height can damage existing eggs in the nest and therefore reduce the competition at the nestling stage (López et al. 2018; Ellison et al. in press).

Female shiny cowbirds do not defend exclusive territories. Individual females overlap in their ranges (Scardamaglia and Reboreda 2014) and two or more females laying eggs in the same nest are common (Mason 1986a; Mermoz and Reboreda 1999; Gloag et al. 2012). Moreover, in chalk-browed mockingbird nests, almost 40% of the parasitic events recorded were cases of same-day multiple parasitism (Gloag et al. 2014). Evidence of other parasite–host systems shows that brown-headed and bronzed cowbirds also present same-day multiple parasitism

(Ellison et al. 2006). For shiny cowbirds, around one-third of these events involved a second female closely tailing a preceding female to the nest (Gloag et al. 2013). This "tailing" behavior might have arisen as a strategy used for the second female to evade mockingbird attacks when approaching the nest. Another possibility is that tailing females, lacking information on suitable nests to parasitize, follow a conspecific from the communal roost (Gloag et al. 2013).

Once a female shiny cowbird parasitizes a nest, she does not visit it again (Gloag et al. 2014; Scardamaglia and Reboreda 2014; but see de la Colina et al. 2016). This pattern is consistent with a “bookkeeping” mechanism (Clayton et al. 1997), that is, the cowbird female has a mental inventory of suitable nests to parasitize and this inventory is updated periodically by eliminating the nests she already has parasitized. In this way, the parasite benefits by remembering the location and status of each nest and her own act of laying in them, avoiding the costs of repeated parasitism, such as sibling competition and damaging her own previously laid eggs (Gloag et al. 2014). Nevertheless, as in brown-headed cowbird, whereby females sometimes return to parasitize the same nest (McLaren et al. 2003), de la Colina et al. (2016) found that in an area of low density of nests of its main host, female shiny cowbirds did not avoid laying in the same nest they had parasitized (i.e., repeated parasitism).

Shiny cowbirds spend morning hours on breeding grounds watching host behavior and use the host’s nest building activity as a cue for finding nests (Wiley 1988). Female cowbirds may also locate host nests by using conspicuously noisy searching (i.e., flushing the host from its nest) (Wiley 1988) or by searching systematically through the habitat (Kattan 1997; Svagelj et al. 2003; Fiorini and Reboreda 2006). Hosts could reduce the risk of nests being detected by choosing more concealed nesting sites. Nevertheless, increased nest concealment seems not to decrease the probability of shiny cowbird parasitism (Svagelj et al. 2003; Fiorini et al. 2009a, 2012). The host laying sequence itself is not a cue for eliciting parasitism and shiny cowbirds need to observe host activity at the nest before parasitizing it (Fiorini and Reboreda 2006).

Shiny cowbirds synchronize parasitism with laying of the host. Nevertheless, the degree of the synchronization varies across host species. In medium- and large-sized and open-nester hosts, the percentage of synchronized parasitic events is high (70–80%; Massoni and Reboreda 1998; Mermoz and Reboreda 1999; Fiorini and Reboreda 2006; Astié and Reboreda 2009), whereas in nests of the small-sized and close-nester house wren, synchronization decreases (47–57% of parasitism events during host’s laying period; Kattan 1998; Fiorini et al. 2009b; Tuero et al. 2007). In hosts whose eggs have longer incubation period than cowbird eggs, laying synchronization secures that they will hatch first, thereby giving a head start to the parasitic nestlings (Mermoz and Reboreda 1999; Fiorini et al. 2005). This advantage is critical in nests of larger hosts, where parasitic nestlings are more likely to be outcompeted for food, than in nests of small-sized hosts (Mermoz and Reboreda 2003; Fiorini et al. 2009b; Gloag et al. 2012).

Shiny cowbird females peck eggs during nest visits to puncture them and render them unviable. In chalk-browed mockingbird nests, such egg-pecking behavior begins immediately upon arrival and continues, on average, for about 12 s, though the duration depends on whether cowbirds are mobbed (mean: 2.6 s) or not (15.9 s) (Fiorini et al. 2014). Egg puncturing reduces host's clutch size and, in cases where the host is larger than the parasite, it increases the survivorship of the parasitic nestlings (Mermoz and Reboreda 2003; Sackmann and Reboreda 2003; Astié and Reboreda 2009; Fiorini et al. 2009b; Gloag et al. 2012). Indeed, there is some evidence that shiny cowbird females strategically modulate their puncturing behavior according to the clutch size and eggshell thickness (Cossa et al. 2017). For example, they peck more at larger mockingbird clutches (Tuero et al. 2012; Fiorini et al. 2014), in which parasitic nestlings are more likely to be outcompeted for food (Fiorini et al. 2009b). In addition, under both natural and laboratory conditions, females peck more frequently at clutches containing thicker-shelled cowbird eggs than at those containing less resistant host eggs (Fiorini et al. 2014; Cossa et al. 2017). In brown-headed and bronzed cowbirds, the puncture behavior is used by females that found host nests late in the nesting cycle, to induce host to renest and create new opportunities for parasitism (i.e., nest farming) (Arcese et al. 1996; Peer and Sealy 1999a; Swan et al. 2015). On the contrary, females of shiny and screaming cowbird puncture eggs in association with parasitism (De Màrsico and Reboreda 2014; Fiorini et al. 2014) and do not puncture all the eggs at complete clutches (Cossa et al. 2017), supporting the hypothesis of reduction of competition with host nestlings. Therefore, the puncture behavior seems to have different functions depending on the parasitic species and probably on the ecological context (Peer 2006).

Eggs

The eggs of the shiny cowbird are adapted to their brood-parasitic lifestyle. Eggshells are thicker than expected for the egg volume and thicker than the eggshells of their hosts (Spaw and Rohwer 1987; Mermoz and Ornelas 2004; López 2013; López et al. 2018). Increased eggshell thickness provides greater resistance against puncturing by other parasitic females (Hudson 1874; Mermoz and Ornelas 2004; Gloag et al. 2012; Fiorini et al. 2014) and decreases the probability of cowbird eggs being damaged when laid from an elevated position, meanwhile inflicting damage to host eggs (López et al. 2018). Moreover, the thicker eggshell protects cowbird eggs from being damaged by eggs that are laid in the nest by subsequent female cowbirds (López et al. 2018). It has been hypothesized that this increased resistance is an adaptation of cowbird eggs to minimize the ejection of hosts that need to puncture the egg before rejecting it (puncture-ejecters) (Spaw and Rohwer 1987). Nevertheless, ejection of parasitic eggs is rare among shiny cowbird hosts (9 species; Mason 1986b, Reboreda et al. 2013); and only two host species are known to puncture-eject foreign eggs: the red-crested cardinal, *Paroaria coronata* (Segura and Reboreda 2012), and the fork-tailed flycatcher, *Tyrannus savana* (Tuero et al. unpublished data).

Each shiny cowbird female lays eggs of consistent appearance (Gloag et al. 2014), but at the population level, the eggs vary widely in background color and spotting pattern, from unspotted to highly spotted (Ortega 1998; Mahler et al. 2007; Hanley et al. 2019). Shiny cowbird eggs mismatch in size and coloration of the eggs of most of their hosts. Therefore, it would be expected that hosts eject parasitic eggs. However, among hosts tested, only two species ejected the spotted and unspotted (white) shiny cowbird eggs, and four species only ejected the unspotted eggs (Reboreda et al. 2013). Besides, hosts smaller than shiny cowbirds are non-ejectors, probably because they are unlikely to remove parasitic eggs from their nests (but see Underwood and Sealy 2006 for a small host that grasp-eject brown-headed cowbird eggs). Small hosts do not usually desert their nests in response to parasitism either (Mason 1986b; Reboreda et al. 2013).

Nestlings and Fledglings

Shiny cowbird nestlings do not evict host eggs or nestlings; therefore, the number and relative size of their nestmates affect their survival and growth dynamics. In nests of small-sized hosts, the major problem faced by cowbird nestlings is to elicit sufficient parental provisioning to meet their needs (Massoni and Reboreda 1998; Tuero et al. 2007). Under this scenario, cowbird nestlings benefit from the presence of host nestlings because, collectively, they induce higher provisioning rates and parasitic nestlings monopolize the extra food (Fiorini et al. 2009b; Gloag et al. 2012, Fig. 6.1). By contrast, in nests of large hosts where competition for food is more intense, cowbird nestlings often grow more slowly with lower survival when reared alongside host nestmates (Astié and Reboreda 2009; Fiorini et al. 2009b; Gloag et al. 2012). Unlike other brood parasites (Payne 1973), the shiny cowbird

Fig. 6.1 Shiny cowbird (*Molothrus bonariensis*) nestling sharing the nest with four smaller house wren (*Troglodytes aedon*) nestlings. Photo: Vanina D. Fiorini

has not evolved shorter incubation periods or faster growth rates than expected by allometric regressions (Mermoz and Ornelas 2004). Nevertheless, their incubation period is shorter than that of many of their hosts (Kattan 1995; Mermoz and Reboreda 1994; Fiorini et al. 2005; but see Astié and Reboreda 2009). In large-sized hosts, such as brown-and-yellow marshbird and the chalk-browed mockingbird, hatching ahead of host young enhances the survival (Fig. 6.2). This is because early hatching decreases the size difference relative to the larger host nestlings or allows the cowbird to be the largest nestling in the brood during most of the nestling period (Dure Ruiz et al. 2008; Mermoz and Reboreda 2003; Fiorini et al. 2009b).

Shiny cowbird nestlings do not mimic the appearance or begging calls of any particular host (Gloag and Kacelnik 2013; Tuero et al. 2016; Bortolato et al. in preparation). Nevertheless, they appear to be highly efficient in stimulating provisioning in a wide range of host species. This ability is partly due to their relatively long and tremulous begging calls that can stimulate parental feeding, even in non-host species (Gloag and Kacelnik 2013). Moreover, shiny cowbird nestlings modulate the intensity of their begging behavior based on their perceived level of intrabrood competition. Tuero et al. (2016) experimentally showed that shiny cowbird nestlings reared in chalk-browed mockingbird nests begged more intensively, faster, and for longer periods of time than those reared in house wren nests. The body condition of cowbird nestlings was similar in both host species; hence, the authors suggested that they adjusted their begging effort to allow them to secure sufficient provisioning without incurring extra energetic costs (Tuero et al. 2016). Gochfeld (1979) and Lichtenstein (1997) also described the begging calls of shiny cowbirds as louder and longer than host's begging calls. A drawback of such exaggerated behavior is that noisy cowbird nestlings may render host nests more detectable to potential

Fig. 6.2 One shiny cowbird (*Molothrus bonariensis*) exhibiting its red gape and three chalk-browed mockingbird (*Mimus saturninus*) nestlings. The parasitic cowbird has hatched before host nestlings and all have a similar body size. Photo: Vanina D. Fiorini

predators (Massoni and Reboreda 1998) as it also happens in brown-headed cowbirds (Dearborn 1999).

Most shiny cowbird hosts do not discriminate against parasitic nestlings. An exception is the firewood-gatherer (*Anumbius annumbi*), which seems to reject shiny cowbird nestlings shortly after hatching (Delhey et al. 2011). Cowbird nestlings in firewood-gathered nests were found dead inside the nest within the first 48 h post-hatching, probably due to insufficient feeding, whereas host nestlings that hatched later were raised until fledging or predation. Hosts may have recognized the parasitic nestlings as foreign and rejected them. Alternatively, it could be a case of "discrimination without recognition" (*sensu* Grim et al. 2003). In this host, shiny cowbird eggs hatched 4–5 days before host eggs; thus, it is possible that host parents begin to provision their young after a certain incubation period and failed to feed nestlings that hatch too early (Delhey et al. 2011). These alternatives remain to be tested.

There is little information for shiny cowbirds pertaining to the fledgling stage, particularly how parasitic fledglings begin to associate with adult conspecifics and disperse away from the natal territory. Recent observations of shiny cowbirds fledged from chalk-browed mockingbird and house wren nests show that survival rate until independence is 45–60% (Crudele et al. unpublished data). Fledglings departed from the host's territory at about 35 days of age and occasionally they associate with adult conspecific females within the natal range (Crudele et al. unpublished data). Adult females could facilitate the socialization of parasitic juveniles (Soler and Soler 1999), but this idea has not been tested and it is not known whether shiny cowbird juveniles disperse solitarily or in groups.

*6.2.2 Screaming Cowbird (*Molothrus rufoaxillaris*)*

6.2.2.1 Species Characteristics

The screaming cowbird is the most specialized of the five *Molothrus* species (Table 6.1). It inhabits savannahs, grasslands, and suburban areas throughout most parts of Argentina (excluding central-south Patagonia and the Andean region), Uruguay, Paraguay, southeastern Bolivia, and southeastern Brazil (Ortega 1998). Its geographic distribution overlaps completely that of the closely related shiny cowbird and the two species frequently forage together in mixed flocks. Adult screaming cowbirds are readily recognizable by their glossy black plumage that lacks the iridescence of male shiny cowbirds. Sexual dichromatism is subtler in the screaming cowbird than in other cowbird species. Males and females are alike in plumage except for the rufous axillary patch that is more noticeable in males. They do show sexual dimorphism in body size, with males being visibly larger than females. Screaming cowbirds are also characterized by their vocalizations, a harsh and loud call note uttered by both sexes as a contact call. Contrary to shiny cowbirds, they are suspected to be socially monogamous. Males and females are typically seen in pairs and both capture–recapture and radio-tracking data suggest that pair bonds last the entire breeding season (Mason 1987; Scardamaglia and Reboreda 2014). It is still unclear why they form stable sexual associations in the absence of parental care (see Hauber and Dearborn 2003).

6.2.2.2 Host Use at Population and Individual Level

The screaming cowbird has four known effective hosts, grayish baywing (*Agelaioides badius*; Hudson 1874), chopi blackbird (*Gnorimopsar chopi*; Sick 1985; Di Giacomo and Reboreda 2014), brown-and-yellow marshbird (Mermoz and Reboreda 1996; Mermoz and Fernández 2003), and austral blackbird (*Curaeus curaeus*; Lowther 2018). Two other species are suspected hosts in Brazil based on online photographic records, yellow-rumped marshbird (*Pseudoleistes guirahuro*; Sessegolo 2014) and the pale baywing (*Agelaioides fringillarius*; Mota 2010), yet these reports require confirmation. These species differ in body size, incubation period, and nest characteristics, but all breed cooperatively (Orians et al. 1977; Fraga 1991; Mermoz and Fernández 2003; Ursino et al. 2011; Di Giacomo and Reboreda 2014). This suggests a non-random association of screaming cowbird parasitism and the presence of helpers-at-the-nest that deserves further inquiry (Feeney et al. 2013). The scarlet-headed blackbird (*Amblyramphus holosericeus*) was added to the host list based on a single record (Lowther 2018), which, if confirmed, would be the first non-cooperatively breeding host species. Screaming cowbird parasitism also has been reported in nests of solitary cacique (*Cacicus solitarius*) and cattle tyrant (*Machetornis rixosa*), but that parasitism is attributed to recognition errors made by laying females attempting to parasitize baywing or chopi blackbird nests (Di Giacomo et al. 2010). Interestingly, such “recognition errors” reveal a potential mechanism through which screaming cowbird females may have colonized their hosts, or could switch to new host species in the future. Using mtDNA, Mahler et al. (2009) reported in an area of sympatry that haplotype frequency distribution differed between screaming cowbird eggs laid in baywing and chopi blackbird nests, which suggested females are host-specific and host switches would have occurred more than once over evolutionary time.

From the host species reported so far, the grayish baywing (hereafter baywing) is the primary host across most of the screaming cowbird’s geographic range. This cavity-nester breeds mostly in bulky stick nests constructed by many furnariid species (e.g., *Anumbius annumbis*, *Phacellodomus* sp.), domed nests of rufous horneros (*Furnarius rufus*) and great kiskadees (*Pitangus sulphuratus*), and excavated nest holes of woodpeckers (e.g., *Colaptes melanochloros and C. campestris*). In eastern Argentina, baywings breed later than most other passerines, from late November to mid-February. It is quite common to see pairs of screaming cowbirds arriving at or departing from baywings’ nesting sites throughout the breeding season. Each season, more than 90% of baywing nests are parasitized by screaming cowbirds, with a mean of about five parasitic eggs per parasitized nest (De Mársico et al. 2010a).

Despite such heavy parasitism pressure, the costs of screaming cowbird parasitism to baywing's reproductive success seem to be relatively benign, and baywings usually fledge all or most of their own young alongside one or two screaming cowbird nestlings (De Mársico and Reboreda 2014). Screaming cowbirds are so tightly linked to baywings that it would be almost impossible to understand many aspect of their biology without considering how they interact with each other. What follows is an overview of the screaming cowbird's parasitic behavior and various reciprocal adaptations undergone by screaming cowbirds and baywings at different stages of the nesting cycle.

6.2.2.3 Parasitic Behaviors of Screaming Cowbirds and Host Antiparasitic Defenses

Laying Period

Brood parasites must locate suitable host nests and parasitize them at the right time to produce offspring. If parasitism occurs too early, parasitic eggs are more likely to be rejected, and if it occurs too late, the eggs may not hatch or the parasitic nestlings may be outcompeted by their older nestmates. For screaming cowbird females, synchronizing parasitism with baywing's egg-laying period is not straightforward because this host may start to lay eggs at virtually any time, between 1–2 days and 2–3 weeks, following nest completion (Fraga 1998; De Mársico and Reboreda 2008). During this prelaying period baywings defend the nest as aggressively as would after laying eggs; thus, they do not provide any obvious behavioral clue for screaming cowbirds (or researchers!) to reliably assess when egg laying will commence (De Mársico and Reboreda 2008). As a result, nearly one-third of all screaming cowbird eggs laid in baywing nests appear before the hosts have initiated laying and are almost invariably rejected by baywings, i.e., they are literally kicked out from the nest (De Mársico and Reboreda 2008; De Mársico et al. 2013). In addition, baywings often reject the entire clutch when parasitic eggs outnumber their own and lay a replacement clutch in the same nest after, again, a variable prelaying period (De Mársico et al. 2013). These prelaying and clutch rejection strategies allow baywings to limit the number of parasitic eggs they ultimately incubate and, thus, potential fitness costs of parasitism (De Mársico et al. 2010a). Interestingly, screaming cowbirds synchronize parasitism better in nests of their alternative host species than in baywing nests and, conversely, the host-generalist shiny cowbirds synchronize parasitism well in their primary hosts but not in baywing nests. This further supports the role of baywing's egg-laying behavior as an evolved defense against brood parasitism (De Mársico and Reboreda 2008).

Synchronizing parasitism with an unpredictable host correlates with the screaming cowbird's nest prospecting behavior. Studies involving monitoring of radio-tagged screaming cowbird females revealed that they maintain constant areas to search for host nests, and that parasitism of baywing nests occurs within a narrow time-window, from roughly 30 to 60 min before sunrise (Scardamaglia and Reboreda

2014; Scardamaglia et al. 2017). Consistent with multiparasitism in baywing nests, parasitic females overlap extensively in their individual morning ranges, which confirms non-exclusive use of breeding territories (Scardamaglia and Reboreda 2014). Scardamaglia et al. (2017) used a novel digital radio-tracking technology to record nest visits by screaming and shiny cowbird females prior and during the host's egg-laying period. For both species, parasitism events were always preceded by at least one visit to the targeted nest, providing direct evidence that cowbird females prospect host nests before laying eggs. The frequency of nest visits was higher among screaming than shiny cowbird females, suggesting that the former required more prospecting visits to gather information about the status of baywing nests (Scardamaglia et al. 2017). Furthermore, screaming cowbird females often revisited the nest where they had laid an egg and occasionally parasitized the nest twice, contrary to shiny cowbirds that seldom revisit nests and typically avoid parasitizing already parasitized nests (Gloag et al. 2014; Scardamaglia et al. 2017; but see de la Colina et al. 2016). These differences likely reflect adaptive strategies of the host-specialist screaming cowbird for synchronizing egg laying with its unpredictable host and keeping track of baywing nests for new opportunities of parasitism.

During nest visits, screaming cowbirds, like shiny cowbirds, may puncture host eggs, a behavior that presumably serves to reduce competition among parasitic offspring (Fiorini et al. 2009b; Cossa et al. 2017). The most obvious host defense against egg puncturing would be to prevent parasitic females from accessing the nest in the first place, but apparently this is seldom achieved. Although baywings recognize adult screaming cowbirds as a specific threat and respond aggressively to them (De Mársico and Reboreda 2008), the high frequency of parasitism on baywing nests clearly indicates that screaming cowbirds are able to overcome host nest defense. Video recordings of baywing nests show that when screaming cowbird females arrive to lay, the host female is almost always inside the nest, sitting tightly on the nest chamber (De Mársico et al. 2013). This "tight sitting" behavior is useless to prevent parasitism because, despite host efforts, screaming cowbird females manage to lay their egg, and they do so quickly, sometimes on the head or back of the host. Instead, tight sitting may serve to protect host eggs from being punctured by blocking access of cowbird females to the nest contents, but this hypothesis needs to be tested (De Mársico et al. 2013; see also Hobson and Sealy 1989). Moreover, parasitic females may have difficulty puncturing baywing eggs, due to these species' thicker eggshells than expected from allometry, which has been proposed as an adaptation to increase egg resistance against cowbird attacks (Hudson 1874; Spaw and Rohwer 1987; Mermoz and Ornelas 2004).

Nestling and Fledging Periods

Host–parasite interactions encompass the entire nesting cycle, but it is during the nestling and fledgling stages that the most striking adaptations of screaming cowbirds become apparent. Unlike their cowbird relatives, young screaming cowbirds mimic their hosts (Hudson 1874). They resemble baywings so closely that, by the age of 4–5 days, nestlings of the two species are almost impossible to distinguish, even for the trained eye (Fraga 1979). The parasitic juveniles retain their baywing-like plumage until well after they have attained nutritional independence, by the age of 37 days post-hatching (Ursino et al. 2012). At that time, they initiate molt into the adult black plumage and reveal their true identity. Hudson (1874) was the first to note the parasitic habit of screaming cowbirds after identifying molting juveniles in a flock of baywings. He was astonished by the sight of those birds that "appeared to be undergoing the process of transmutation into another species" (p. 162). An adaptive explanation for the remarkable similarity between screaming cowbird and host fledglings came much later from a series of field observations and cross-fostering experiments that show that adult baywings refuse to care for non-mimetic fledglings of the shiny cowbird as soon as they leave the nest, but provision screaming cowbird fledglings until independence (Fraga 1998; De Mársico et al. 2012).

Screaming cowbirds also precisely match the begging call structure of baywing nestlings. Recent cross-fostering experiments suggest that the development of baywing's species-specific acoustic signals occurs independently of the social experience of parasitic nestlings (Rojas Ripari et al. 2018). Ursino et al. (2017) tested the response of adult baywings to begging calls of screaming cowbird (mimetic), shiny cowbird (non-mimetic), and conspecific nestlings. They supplemented six-day-old broods with playbacks of each call type and found that baywings increased nest provisioning rates in response to screaming cowbird and conspecific begging calls, but not in response to non-mimetic calls. These results provide support of the adaptive value of vocal similarity between screaming cowbird and baywing nestlings and its role in manipulating host parental behavior (Ursino et al. 2017). In addition, screaming cowbird nestlings beg more intensely than host nestlings at similar hunger levels, which might also serve to effectively compete for food (Lichtenstein 2001; Ursino 2016). Some recent experiments further suggest that host-specific call structure and exaggerated begging displays are critical for parasitic fledglings to capture the attention of adult baywings after leaving the nest (Lama et al. unpublished data).

At some point after attaining nutritional independence, parasitic fledglings must abandon their foster parents and join their conspecifics to find potential mates, but very little is known about this transition in cowbirds and other brood parasites (reviewed recently in De Mársico et al. 2017). This knowledge gap is likely due to the difficulties inherent in following mobile juveniles. Preliminary data from radio-tagged fledglings suggest that screaming cowbird juveniles remain with their foster parents for 40–60 days after fledging, and that they come in contact with conspecifics before dispersing (Rojas Ripari et al. unpublished data). Interactions with conspecific adults could facilitate natal dispersal and socialization of cowbird juveniles, but this hypothesis has not been tested (e.g., Hahn and Fleischer 1995; Lorenzana and Sealy 1998). Also not known is the mechanism of conspecific recognition, although species-specific vocal cues are presumably involved (e.g., Hauber et al. 2001). Clearly, more work is needed to disentangle how young parasites join their own after having been reared by heterospecific hosts.

*6.2.3 Giant Cowbird (*Molothrus oryzivorus*)*

6.2.3.1 Species Characteristics

As its name denotes, the giant cowbird is the largest species in the genus *Molothrus* and one of the larger New World blackbirds. It has a long rounded tail, black feet, and has a conspicuous ruff of feathers around the neck that makes the head look small (Jaramillo and Burke 1999). The bill is long and black with a shape unlike to the bill of other cowbirds. The maxilla expands into a flat frontal shield rounded at the base, which is absent in the other cowbird species, but occurs in the giant cowbird's hosts. Males are larger and heavier than females (Table 6.1) and this sexual dimorphism extends to the plumage. The male is black with a violet iridescence, whereas the female is dark brown to black. The neck ruff is more conspicuous in males (Ortega 1998).

The giant cowbird is quiet, though noisy in flight (Jaramillo and Burke 1999). Its geographic range is wide, from southern Mexico south to northern Argentina. It is associated with open woodlands and cultivation, but it is also the only cowbird species found deep in the forest (Jaramillo and Burke 1999). It usually forages in flocks and consumes arthropods, fruit, and nectar (Robinson 1998). Giant cowbirds feed on the ground, near water, on top of trees (branches and foliage), and on the back of large herbivores such as capybaras (*Hydrochoerus hydrochoerus*) (Robinson 1998).

Eleven host species are known for this parasite (Lowther 2011; Table 6.1). Its better-known hosts are colonial nesting blackbirds: two species of caciques (*Cacicus* sp.) and four species of oropendolas (*Psarocolius* sp.) (Friedmann 1929; Robinson 1998; Jaramillo and Burke 1999). These species are the same size or larger than giant cowbirds. Most host species remain unstudied and little is known about host–parasite interactions, possibly because host nests are difficult to access as most colonies are placed on top of very tall, isolated trees (Fraga 2011).

6.2.3.2 Host–Parasite Interactions

Contrary to other cowbird species that approach nests stealthily and lay eggs around sunrise, giant cowbirds lay in host nests during the day and visit colonies in groups, where males appear to distract hosts while females enter the nests. It has also been observed that single females or pairs visit host colonies at times of the day when caciques and oropendolas were most likely to be absent (Robinson 1998). Hosts aggressively defend the nest when giant cowbirds approach their colonies (Webster 1994; Robinson 1998).

Giant cowbird's eggs are oval and have the largest relative volume among those of the parasitic cowbirds. They vary from immaculate white to dark-spotted on white, pale or green backgrounds (Fleischer and Smith 1992). Most hosts have not been studied yet, but their eggs are apparently not mimetic to any particular host. Fraga (2011) suggested some resemblance in color, but not in size, between the spotted egg morph and cacique's eggs in northeastern Argentina; in this area, the unspotted white egg was the more common morph.

In general, nests are parasitized with a single egg, but multiparasitism is also common (Fraga 2011). Giant cowbirds damage host eggs, which may have selected for increased clutch size in the Montezuma oropendola (*P. montezuma*) (Cunningham and Lewis 2006; Fraga 2011). This host is an obligate brood-reducer that does not raise more than one chick per brood; however, most clutches are of two eggs (Cunningham and Lewis 2006). Montezuma oropendolas apparently benefit from laying this "extra" egg because cowbird females often remove or damage one host egg when they parasitize the nest. Therefore, hosts are more likely to fledge their own nestling in two-egg clutches (Cunningham and Lewis 2006). This host species rejects up to 72% of model giant cowbird eggs placed in their nests, regardless of whether there were own eggs present for comparison (Cunningham and Lewis 2006).

Giant cowbird nestlings have white bills and a pale frontal casque like those of their oropendola hosts. Bills turn to the usual cowbird-black after fledglings become independent (Redondo 1993). The pale bill may be a phylogenetically retained feature because it is found in the closely related screaming cowbird (Fraga 1979). The casque is retained in adult giant cowbirds, but it becomes smaller and black. Due to the resemblance between the casque of giant cowbirds and oropendolas, Webster (1994) proposed this could be a case of mimicry. However, the evolutionary origin of the frontal casque as well as its potential fitness benefit to giant cowbird nestlings remains to be studied.

A controversial study proposed that parasitism by the giant cowbird is advantageous for the host species (Smith 1968). Nevertheless, results of other studies have not supported this hypothesis (Robinson 1998; Webster 1994). Moreover, Cunningham and Lewis (2006) described a giant cowbird nestling unable to remove *Philornis* larvae from host nestlings, which was the main benefit proposed for this parasitic system (Smith 1968). Finally, giant cowbirds infested with *Philornis* spp. were observed in Argentina (Fraga 2011).

*6.2.4 Bronzed Cowbird (*Molothrus aeneus*)*

6.2.4.1 Species Characteristics

The bronzed cowbird owes its common name to the plumage color of the males; they are dark bronzed-brown with iridescent black on the wing and tail. Like giant cowbirds, males have elongated feathers in the neck forming a conspicuous ruff. Females are brownish black and lack the males' distinctive bronze color, but its color varies among the three subspecies. Bronzed cowbirds are also known as red-eyed cowbirds due to the red iris that males exhibit in summer. Female's iris color is brownish orange, similar to males in winter (Ortega 1998). The bill is one of the longest among cowbirds.

The geographic range extends from the southern United States to Mexico, western Panamá, and northeast Colombia. There are three subspecies and an isolated population on the Caribbean coast of Colombia that is sometimes treated as a separate species, the bronze-brown cowbird (*M. armenti*) (Ortega 1998; Fraga 2016). The bronzed cowbird occurs in open and semi-open fields, agricultural fields, and forest parches (Ortega 1998). It often forages alone, but also with conspecifics in small flocks or in mixed flocks with other blackbirds. They are omnivorous and search for food on tree branches, the ground, and on the back of large grazing mammals (Carter 1986).

This is a generalist parasite with more than 100 known host species (Table 6.1), mainly icterids and flycatchers (Sealy et al. 1997; Lowther 2018). Hosts are smaller and larger than the cowbird (Table 6.1). Eggs are immaculate pale blue, bluish green, greenish blue, and white and, like other cowbird species, the shells are thick (Carter 1986; Ortega 1998).

6.2.4.2 Host–Parasite Interaction

Females parasitize host nests a few minutes before sunrise with egg laying lasting a few seconds (Peer and Sealy 1999b). Small hosts, like the hooded oriole (*Icterus cucullatus*) and orchard oriole (*I. spurius*), are frequently at their nests when cowbird females arrive to lay, and attempt to remain there defending the nest while bronzed cowbirds peck their eggs. However, host nest defense often does not prevent parasitism (Ellison and Sealy 2007). Bronzed cowbirds, similar to shiny and screaming cowbirds, pierce host eggs during laying visits. Egg puncturing may have different functions but the evidence suggests that it serves to force renesting, when bronzed cowbird females locate a nest that is too advanced for successful parasitism (Peer and Sealy 1999b). In addition, egg puncturing may decrease competition when parasitizing larger hosts (Peer and Sealy 1999b). Multiparasitism is common and same-day laying at a single nest has been observed, indicating that more than one female can lay an egg in the same nest (Carter 1986; Peer and Sealy 1999b). Through genetic analyses, Ellison et al. (2006) confirmed that multiparasitism is the result of different females laying in the same nest and that most females did not parasitize nests again. Some females parasitized more than one host species, acting as generalists (Ellison et al. 2006).

This species generally synchronizes laying with the host's laying, but parasitism after the onset of incubation sometimes occurs (Carter 1986; Ellison et al. 2006). Egg rejection has been documented in several host species (Sealy 1999; Sealy and Underwood 2004); Rasmussen et al. 2012). An interesting case is that of grackles (*Quiscalus* spp.), many of which have retained a 100% of rejection behavior towards bronzed cowbird eggs in the absence of parasitism (Peer and Sealy 2004). Conversely, rejection occurs only in 18% of nests of clay-colored thrushes (*Turdus grayi*) in Costa Rica, where reports about parasitism by bronzed cowbirds are infrequent, suggesting the existence of a mixture of acceptor and ejector individuals in this population (Rasmussen et al. 2012).

There are few descriptions of the nestling stage of bronzed cowbirds. The cowbird egg can hatch before, on the same day, or after the host's eggs. If the parasitic nestling hatches before or within 36 hs after the host eggs, it has a better chance of fledging than if it hatches later (Carter 1986). Bronzed cowbirds have a rapid development that allows them to outcompete its host nestmates and to become alone in the nest of small-sized hosts. On the other hand, large-sized hosts can raise the parasitic nestling alongside its own nestlings, but cowbirds that hatch too late, generally die (Carter 1986).

6.3 Family Cuculidae, Subfamily Neomorphinae

*6.3.1 American Striped Cuckoo (*Tapera naevia*)*

6.3.1.1 Species Characteristics

The striped cuckoo owes its common name to its striped blackish and rufous shaggy crest. Adult females and males are similar in appearance. The upper parts are brown streaked buff and black. The alula is long and black and it is exhibited during courtship. The wings are brown to rufous with a white base noticeable in flight. It has a long tail and its face has a white streak above the eyes and a black whisker line (Payne 2005).

This cuckoo occurs in open habitats as pastures and llanos from southern Mexico to northern Argentina. This is a solitary and shy species, which uses counter-singing and duets in reproduction and territory defense. Individuals are often heard singing from bushes and trees, but are difficult to find. They forage amid vegetation or near the ground, where they feed primarily on large insects (Howell and Webb 1995). The striped cuckoo is a generalist parasite with 22 known host species (Table 6.1). Its hosts are small passerines that build open or domed nests, especially the ovenbirds (Furnariidae). The breeding biology of the striped cuckoo is little known (Payne 2005; Mark 2013).

6.3.1.2 Host–Parasite Interaction

The intensity of parasitism is usually one egg and sometimes two. Among the New World cuckoos, only the striped cuckoo lays eggs that mimic host eggs in color. Eggs may be white, bluish white, or greenish blue, depending on the geographic area (Payne et al. 2005). In most of South America, striped cuckoos lay white eggs that are identical to those of its host species. In Central America, however, striped cuckoos lay blue eggs that mimic those of a different suite of hosts. There is an area where the ranges of these two-host groups overlap and striped cuckoo eggs are polymorphic. The other cuckoo species in the striped cuckoo's clade lay white eggs. Therefore, white eggs were probably the ancestral condition for striped cuckoos and blue color may have evolved as courter-defense to the host egg rejection (Payne 2005). However, the defense and counterdefense between striped cuckoo and its hosts have been poorly studied. There is only one experimental study that has explored host defenses against striped cuckoo eggs (Mark 2013). Using reflectance spectrometry, Mark (2013) showed that cuckoo eggs matched the coloration of the immaculate blue-green eggs of its host, the rufous-and-white wren (*Thryophilus rufalbus*). Visual mimicry of host eggs would be adaptive for the cuckoo because it reduces host rejection of parasitic eggs (Mark 2013). Another infrequently used host species that lays white eggs, the plain wren (*Cantorchilus modestus*), accepts both mimetic and non-mimetic eggs (Mark 2013). Curiously, striped cuckoo's eggs accurately match the blue-green appearance of rufous-and-white wren eggs despite differences in pigment composition and concentration, suggesting that egg mimicry can arise from alternative chemical pathways (Dainson et al. 2018).

As in most of the Old World cuckoos, the striped cuckoo kills its nestmates (Table 6.1) but, unlike its relatives, striped cuckoo nestlings slash host nestlings to death with a sharp bill hook, soon after hatching (Morton and Farabaugh 1979). As a result, the parasitic nestling is reared alone in the nest, losing the bill hook as it grows (Morton and Farabaugh 1979).

The young cuckoo leaves the nest at 16–18 days of age, remains flightless for a week, and may be cared for the hosts until it is one month of age (Payne 2005). Brood parasitism by the striped cuckoo leads to changes of rufous-and-white wren host behaviors because parasitic fledglings move away from the center of the host territory, towards forest edges and open areas that are not used by the host (Mark and Gamez-Rugama 2015). Moreover, there is evidence that parasitized parents are more stressed than non-parasitized ones (Mark and Rubenstein 2013). The physiological costs of being parasitized can carry over into subsequent nesting attempts, as suggested by the positive association between parasitism status and the latency to renest in the same breeding season and the negative association between parasitism and the likelihood of nesting in the subsequent breeding season (Mark and Rubenstein 2013).

The post-fledging stage is poorly studied in birds in general and even less so in brood parasites. An observational study involving three radio-tracked striped cuckoo fledglings discovered that juveniles might associate with adult conspecifics. Adults often initiate the social interactions; the resulting juvenile–adult pairs move and forage together, and even counter-singing and duetting (Mark and Gamez-Rugama 2015).

*6.3.2 Pavonine Cuckoo (*Dromococcyx pavoninus*)*

6.3.2.1 Species Characteristics

Female and male are alike. The face is rufous with a short rufous crest. The back is brown with feathers edged in white and the long graduated tail is spotted with white. The pavonine cuckoo also has a long alula and wing covers edged with whitish tinge. Its belly is white. The bill is black above and gray below and the feet are gray to gray brown (Payne 2005).

This species is solitary and uncommon, and their distribution is discontinuous in South America east of the Andes, from Colombia, Venezuela, Guyana, and French Guyana south to eastern Ecuador, eastern Peru, Bolivia, Brazil, and northeastern Argentina. Its habitats include understory forests, mountain forests, and thickets with dense secondary woodland at height elevations (Payne 2005). Pavonine cuckoos seem to be sensitive to human avoiding their settlements.

This cuckoo is a generalist brood parasite with seven known host species of suboscine passerines, mainly of the Tyrannidae family (Table 6.1). Its hosts build small closed or bag-shaped nests with a side entrance (Payne 2005; Lowther 2009). Given its large size, it is not clear how pavonine cuckoo females manage to lay their egg in such small host nests.

6.3.2.2 Host–Parasite Interaction

Dromococcyx species are the most poorly studied Neotropical parasites. Available information is mainly restricted to species lists and records of its presence. Recently, Sanchez-Martınez et al. (2017) looked for evidences of pavonine cuckoo parasitism in many potential hosts in the Peruvian Amazon. Over the seven-year-study, they found pavonine eggs in only nine out of 74 nests of three host species. Nests were parasitized in synchrony with host laying, with only one egg in each nest. There was no evidence for egg mimicry because pavonine cuckoo eggs were white with brown spots and host eggs were white and smaller in size. Some evidences of antiparasitic defenses were found in two host species: the ochre-bellied flycatcher (*Mionectes oleagineus*) and the sepia-capped flycatcher (*Leptopogon amaurocephalus*), where the hosts deserted one and three parasitized nests, respectively. However, in three nests, these species accepted cuckoo eggs. The reasons that hosts accept or desert parasitized nests have not been explored.

As in most other cuckoo species, pavonine cuckoo nestlings apparently are infanticidal (Table 6.1), based on the observation that host nestlings disappeared after the cuckoo hatched, or they were found dead under the nest (Payne 2005; Sanchez-Martınez et al. 2017). Nestling skin color differed substantially between one host, the sepia-capped flycatcher (pink), and the parasitic cuckoo (black). However, nestling plumage coloration is similar in both species (Sanchez-Martınez et al. 2017), suggesting a potential coevolutionary arms race that awaits study.

*6.3.3 Pheasant Cuckoo (*Dromococcyx phasianellus*)*

6.3.3.1 Species Characteristics

Similar to the other Neotropical parasitic cuckoos, the pheasant cuckoo is neither sexually dichromatic nor dimorphic. It has a small head, thin neck, and a long fan-shaped tail with white spots. Its face shows a white line through the eye. Its back is blackish-brown, the wing covers have white margins, and the alula is long. The tail covers end with a subterminal black band and a white spot (Payne 2005).

The pheasant cuckoo ranges from south Mexico through Central and South America to Paraguay, northeastern Argentina, and southeastern Brazil. It is a forest bird, frequently described as easy to hear but difficult to see. It often forages on the ground, feeding on insects and lizards (Davies 2000).

This species is among the most poorly understood cuckoo species in the world. It is a generalist with at least 5 documented host species (Table 6.1). Its hosts are small passerines birds, mainly tyranid flycatchers that construct open or closed nests (Davies 2000). The breeding biology, laying behavior, and egg characteristics of this parasite are unknown (Johnsgard 1997; Davies 2000; Payne 2005; Lowther 2010).

6.4 Family Anatidae, Subfamily Oxyurinae

*6.4.1 Black-Headed Duck (*Heteronetta atricapilla*)*

6.4.1.1 Species Characteristics

The black-headed duck (*Heteronetta atricapilla*) is unique in that it is the only precocial obligate brood parasite described. Black-headed ducks are able to care for themselves just a few hours after hatching (Davies 2000). It is a small, dark duck and females are larger and heavier than males (Table 6.1) (del Hoyo et al. 2011). The male has a black head, whereas the female is pale brown overall.

It is distributed in the central region of Argentina to Uruguay, southeastern Brazil, Paraguay, and Bolivia, and also, the central region of Chile (Carboneras 1992). Black-headed ducks inhabit swamps, lakes, pools, and marshes of permanent fresh waters with abundant emergent vegetation (Weller 1968; Carboneras 1992).

The black-headed duck is a generalist parasite with more than 20 known host species (Cabrera et al. 2017) (Table 6.1), mainly coots (*Fulica* spp.), but also swans and gulls (Madge and Burn 1988; Lowther 2011; Lyon and Eadie 2013). There are very few data on parasitism of black-headed ducks and most of the accounts are from central-east Argentina (Weller 1968; Rees and Hillgarth 1984; Carboneras 1992; Lyon and Eadie 2004, 2013).

6.4.1.2 Host–Parasite Interaction

Hosts of the black-headed duck provides incubation and protection for the parasitic eggs during the 24–25 days of the incubation period. Because black-headed ducks do not damage host eggs like other brood-parasite species, sophisticated host defensive behaviors are not expected during the laying and prelaying stages. Black-headed duck eggs are whitish to buff in color and unmarked, similar to those of the rosy billed pochard (*Netta peposaca*) (Davies 2000), but unlike other hosts' eggs

(Lyon and Eadie 2013, 2004). There is no evidence for egg rejection by rosy billed pochards but this behavior was described in other three main host species in the east-central Argentina: the red-gartered coot (*F. armillata*), red-fronted coot (*F. rufifrons*), and brown-hooded gull (*Chroicocephalus maculipennis*) (Lyon and Eadie 2013). Coots buried parasitic eggs in their nests (Lyon and Eadie 2004), whereas gulls eject eggs or often move them off to the side, so that duck eggs were not incubated.

The parasitic eggs hatch before host eggs. One or two days after hatching, black-headed ducks leave their brood mates because they are able to care for themselves without any assistance from the hosts (Weller 1968; Lyon and Eadie 2004).

6.5 Final Conclusions

Throughout this chapter, we presented the main characteristics and behaviors of Neotropical obligate brood parasites. These species show a wide range of adaptations to their exciting lifestyle but some of them have characteristics that do not fit any particular host. The nestling morphology and the behavior of female shiny, giant, and bronzed cowbirds allow them to succeed in a variety of hosts. Others, such as the screaming cowbird, that has a tight relation with its main host, mimics the appearance of their nestling and fledging and also their begging calls. Whereas cowbird species are nestmate tolerant, the New World cuckoos kill their nestmates. The black-headed duck is an outlier in the brood-parasite world, as it is the only precocial species and only needs the host for the incubation of the eggs. The asymmetry of the information available on the different species is marked. Shiny and screaming cowbirds were studied for the first time more than 130 years ago, by Hudson (1874), followed by Friedmann (1929) and Hoy and Ottow (1964). Later, research by Fraga (1979, 1985, 1998) and Ortega (1998) expanded the information on these cowbird species. During the last two decades there have been very many studies on the behavioral ecology of these species. Although there are still several questions to be answered, the advance of the last years has been evident.

The reasons why the other Neotropical parasitic species have not been extensively studied yet could be related to the difficulty to reach the areas of distribution of these species and to the low density of some of their populations. On the other hand, the lack of resources in the countries where these species are distributed may also limit the possibility to study them, due to low numbers of researchers and the lack of adequate equipment and funding to carry out investigations.

The information on Neotropical obligate brood-parasites species is subrepresented compared to Old World or North American species and this may skews the interpretations and conclusions on the adaptiveness of parasitic behaviors and on the results of the coevolutionary processes between them and their hosts. To better understand the variety of adaptations of the parasites, it is crucial to increase our knowledge on Neotropical parasites, which will give more comprehensive understanding of how species solve problems through different strategies.

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