Endangered White-breasted Thrashers (*Ramphocinclus brachyurus*) reject mimetic Shiny Cowbird (*Molothrus bonariensis*) eggs

Gunnar R. Kramer^{1,2}* and Jennifer L. Mortensen^{1,3}

ABSTRACT—Brood parasitism can decrease the reproductive success of host species and contribute to population declines, especially in small populations with naturally low fecundity. The ability of host species to recognize foreign eggs varies, as do the behavioral responses of hosts to brood parasitism. We experimentally tested the ability of a putative host, the White-breasted Thrasher (*Ramphocinclus brachyurus*), to recognize and reject the eggs of a recently established generalist brood parasite. The White-breasted Thrasher is an endangered songbird restricted to 2 small Caribbean islands that are not known to ever have supported obligate brood parasites. We experimentally parasitized active nests within the stronghold of the species' distribution in Saint Lucia and found that White-breasted Thrashers rejected 83% of mimetic Shiny Cowbird (*Molothrus bonariensis*) eggs (i.e., wooden eggs painted to look like Shiny Cowbird eggs) within 5 d of being parasitized. Rejection of mimetic eggs was not associated with nest initiation date, distance to habitat edge or agricultural area, nest-attempt number, or presence of helpers or dependent young. We conclude that White-breasted Thrashers can detect foreign eggs and possess behavioral adaptations to counter brood parasitism, and propose that these anti-parasitism traits are likely retained from ancestors that evolved in the presence of brood parasites. Our results suggest that brood parasitism by Shiny Cowbirds is unlikely to become a major threat to the White-breasted Thrasher in Saint Lucia. However, ongoing anthropogenic land alteration is likely to increase contact between the 2 species, warranting continued monitoring of their nascent relationship. *Received 4 February 2019. Accepted 12 March 2020.*

Key words: brood parasitism, egg rejection, endangered species, Saint Lucia

Le Moqueur Gorge-blanche (*Ramphocinclus brachyurus*) en voie de disparition rejette les œufs mimétiques du Vacher Luisant (*Molothrus bonariensis*)

RÉSUMÉ (French)—Le parasitisme de couvée peut diminuer le succès de reproduction chez les espèces d'hôtes et contribuer au déclin des populations, en particulier dans les petites populations avec la fécondité naturellement faible. La capacité des espèces d'hôtes à reconnaître les œufs étrangers varie, comme toutes les réponses comportementales des espèces d'hôtes au parasitisme de couvée. Nous analysâmes la capacité d'une espèce d'hôte putative, le Moqueur Gorge-blanche (*Ramphocinclus brachyurus*), à reconnaître et de rejeter les œufs d'un oiseau parasite et généraliste qui est récemment établi. Le Moqueur Gorge-blanche est un oiseau chanteur en voie de disparition limité à deux petites îles des Caraïbes ; on ne sait pas si les moqueurs avoir jamais soutenu des parasites de couvée obligatoires. Nous parasitâmes expérimentalement des nids actifs au milieu de l'aire de répartition de cette espèce à Sainte-Lucie et nous constatâmes que les moqueurs rejetaient 83% des œufs mimétiques de Vacher Luisant (*Molothrus bonariensis*) (c.-à-d., des œufs en bois peints pour ressembler à des œufs de Vacher Luisant) dans un délai de cinq jours d'être parasité. Le rejet des œufs mimétiques n'était pas associé à la date de début du nid, à la distance à l'orée d'habitat ou à la zone agricole, au nombre de tentatives de nidification, ou à la présence d'aides du nid ou de oisillons dépendants. Nous concluons que les moqueurs peuvent détecter les œufs étrangers et possèdent des adaptations comportementales pour contrer le parasitisme de couvée ; nous proposons que ces traits antiparasitaires soient probablement conservés des ancêtres qui ont évolué en présence de parasites de couvée. Nos résultats suggèrent qu'il est peu probable que le parasitisme de couvée par le Vacher Luisant devienne une menace majeure pour le Moqueur Gorge-blanche à Sainte-Lucie. Cependant, l'altération anthropique et continue des terres pourrait augmenter le contact entre ces deux espèces, justifiant la surveillance continue de leur interactio

Mots-clés: espèce en voie de disparition, parasitisme de couvée, rejet d'œufs, Sainte-Lucie

Brood parasitism is a reproductive strategy in which one species exploits host parents of another species to care for and raise parasitic young (Rothstein 1990). Parasitism is costly to hosts (e.g., Lyon 2003, Peterson et al. 2012) and selection has led to the evolution of behaviors to combat brood parasitism in some host species (Rothstein 1990). Shiny Cowbirds (*Molothrus bonariensis*) are obligate, generalist brood parasites that lay eggs in nests of many host species instead of specializing on one or a few hosts (Kattan 1997). Over the past 100 yr, Shiny Cowbirds have expanded their range north from their historical distribution in South America and now occur throughout the Caribbean and the southern United States, affecting local populations of native species in various ways (Cruz et al. 1985). At one extreme, Shiny Cowbird parasitism rates can lead to steep population declines of host species via decreases in reproductive success, as seen in the Yellow-shouldered Blackbird (*Agelaius*

¹ Department of Biology, Tufts University, Medford, MA, USA

² Current address: Department of Environmental Sciences, University of Toledo, Toledo, OH, USA

³ Current address: Department of Biological Sciences, University of Arkansas, Fayetteville, AR, USA

^{*} Corresponding author: gunnarrkramer@gmail.com

xanthomus; Post and Wiley 1977, Miller et al. 2016) and Puerto Rican Vireo (Vireo latimeri; Faaborg et al. 1997, Woodworth 1999). Other species are apparently unaffected by Shiny Cowbirds either because they are not targeted as hosts (e.g., Bananaquit [Coereba flaveola]; Cruz et al. 1985) or because they exhibit anti-parasitism defense behaviors such as abandoning parasitized nests, removing parasitic eggs, or behaving aggressively toward Shiny Cowbirds (e.g., Yellow-hooded Blackbird [Chrysomus icterocephalus]; Cruz et al. 1985). Human activity and changes in land use (i.e., deforestation, fragmentation) may further facilitate the expansion of Shiny Cowbirds, which occur in open or semiopen landscapes and rapidly colonize deforested areas (Lowther and Post 2020). The fragmentation of contiguous forests may also increase the accessibility of previously isolated interior forestdwelling species to brood parasitism. Thus, the effects of Shiny Cowbirds on endemic species that have not co-occurred with obligate brood parasites in recent evolutionary history remain unclear (Payne 1977, Lovette et al. 2012).

The White-breasted Thrasher (Ramphocinclus brachyurus; Family Mimidae) is an endangered, range-restricted, cooperative-breeding songbird endemic to the islands of Saint Lucia and Martinique (Mortensen et al. 2017, BirdLife International 2018). The White-breasted Thrasher is considered a habitat specialist (Mortensen et al. 2020). It occurs year-round in deciduous seasonal dry forest with a canopy >5 m and tends to avoid shrubby or scrub forest and open areas (Temple 2005). The species faces an array of threats including habitat loss, fragmentation, and degradation; exposure to nonnative invasive predators; and stochastic events that affect small populations (Temple 2005, Mortensen et al. 2017). The degree to which White-breasted Thrashers may be susceptible to negative effects of brood parasitism by Shiny Cowbirds is unknown. Of 619 Whitebreasted Thrasher nests reported in the literature from 1995 to 2014, none were reported to be parasitized (Freeman 2015, Mortensen 2016, Mortensen et al. 2017), suggesting that either this species (1) is not currently selected by Shiny Cowbirds as hosts, (2) is very infrequently parasitized, or (3) quickly employs anti-parasitism behaviors (e.g., egg ejection, nest abandonment). Shiny Cowbirds and White-breasted Thrashers currently co-occur in dry forest on the east coast of Saint Lucia (Post et al. 1990), an area with ongoing habitat fragmentation (Mortensen et al. 2017) that might facilitate contact between the 2 species. Consequently, the threat of brood parasitism by Shiny Cowbirds to White-breasted Thrashers is unknown and warrants investigation.

Here, we tested whether White-breasted Thrashers reject foreign eggs from active nests. Due to a lack of recent evolutionary co-history with obligate brood parasites (Cruz et al. 1985, Lovette et al. 2012), we predicted that White-breasted Thrashers would accept mimetic Shiny Cowbird eggs (i.e., wooden eggs painted to look like Shiny Cowbird eggs) and would not display behavioral adaptations against brood parasitism (i.e., clutch burying, nest abandonment, or egg ejection). We then assessed whether a suite of temporal, spatial, and brood-specific predictors influenced the mimetic egg acceptance rate in this endangered bird.

Methods

We studied White-breasted Thrashers in the core of their Saint Lucian range in July–August 2013. Our study area was a ~650 ha portion of the Mandelé Important Bird Area (BirdLife International 2017) on the east coast of Saint Lucia (13.89°N, 60.89°W). Land cover in this area was primarily second growth deciduous seasonal ("dry") forest within a greater landscape matrix containing littoral scrub, shrubland, and semievergreen seasonal forest (Mortensen and Reed 2016). Our study areas also contained anthropogenic cover types including gardens, pastures, clearings for charcoal production, and land cleared for construction of a resort and golf course that has since been abandoned.

White-breasted Thrashers are medium-sized (range = 53-66 g; Temple 2005) dry forest specialists that breed from April to September depending on environmental conditions (Mortensen et al. 2017). They are facultative cooperative breeders, with some breeding pairs receiving help from closely related individuals (usually offspring from the previous year; Temple et al. 2009). The species builds conspicuous open-cup nests constructed of twigs and leaves, lined with dried grass and roots, typically placed 1–3 m high in the crown of a small sapling or shrub (most often

Myrcia citrifolia or *M. deflexa*; Mortensen et al. 2014). They lay a 2-egg clutch $(1.96 \pm 0.03 \text{ [SE]})$, range = 1–4; Temple 2005, Mortensen et al. 2017) and may attempt up to 5 clutches during a breeding season, often constructing a new nest for each attempt (Mortensen et al. 2017).

White-breasted Thrasher and Shiny Cowbird eggs differ in color and size. White-breasted Thrasher eggs are immaculate with a bright turquoise ground color (Mortensen et al. 2020). Shiny Cowbirds lay both immaculate (usually white) and spotted (pale buff ground color with brown or reddish-brown blotches or spots) eggs (Lowther and Post 2020), although we only encountered the latter egg type at our field site (GRK and JLM, 2013, pers. observ.). Our model eggs were made of lightweight wood (sensu Rothstein 1975) and painted with acrylic paints such that they visually resembled the size (22.3 \times 15.9 mm, 2.2 g; Ankney and Johnson 1985), shape, and color of spotted Shiny Cowbird eggs observed in nests of other host species in Saint Lucia and described in the literature. We measured our mimetic eggs with digital calipers and collected colorimetric data with a hue-saturationbrightness (HSB) color model by photographing eggs with white light on a white background. Mimetic cowbird eggs measured 22.4×15.7 mm, weighed 2.1 g, had a ground color of 25° hue and 14% saturation, and spots with 12° hue and 50% saturation. We also made model eggs that resembled the size, shape, and color of Whitebreasted Thrasher eggs (real egg = 30.0×20.05 mm; Western Foundation of Vertebrate Zoology Catalogue #EN-188784; mimetic thrasher egg = 33.9×21.8 mm, 5.6 g, 188° hue and 50%saturation) to attempt to determine whether thrashers would reject any foreign object (e.g., egg) placed in their nest, or if they reject only cowbird eggs. Similarly, we constructed a model egg that was the size and shape of a Whitebreasted Thrasher egg but painted to visually resemble a Shiny Cowbird egg (large cowbird egg).

We simulated brood parasitism by placing a single mimetic Shiny Cowbird egg into active White-breasted Thrasher nests during the laying or early incubation period (as determined by candling; GRK and JLM, 2013, unpubl. data). We deposited each mimetic egg within 5 hr of sunrise while the nest was unattended. Due to the

endangered status of White-breasted Thrashers, we did not remove viable host eggs as cowbirds often do when parasitizing nests (Rothstein 1975). We checked nests every 24-48 h following simulated brood parasitism to determine the fate of the mimetic egg, except for a few nests that were checked over longer intervals due to logistical constraints. If a mimetic egg vanished during an extended nest-check interval (i.e., >48 h), we assumed the egg was ejected at the midpoint of the interval (Mayfield 1961, Johnson 1979). We considered the mimetic egg rejected if it disappeared from an otherwise active nest (i.e., still contained White-breasted Thrasher egg[s] or nestling[s] that were being incubated or brooded) within 5 d of simulated parasitism (Rothstein 1975). When logistically possible, we tried to remove mimetic eggs from nests if they had not been rejected after 5 d. Nests depredated within 5 d of simulated parasitism were omitted from analysis. We followed the same protocol when adding both other types of eggs (i.e., mimetic Whitebreasted Thrasher eggs, thrasher-sized mimetic Shiny Cowbird eggs) to active thrasher nests.

We used R 3.4.1 (R Core Team 2017) for all statistical tests. We used an exact binomial test and an α of 0.05 to test the hypothesis that the rate of acceptance of mimetic Shiny Cowbird eggs was significantly different from expectations if Whitebreasted Thrashers were egg accepters (i.e., rejected at a rate $\leq 20\%$ sensu Peer and Sealy 2004). We then used logistic regression and an information-theoretic approach to assess whether a suite of temporal, spatial, and brood-specific factors affected egg acceptance rates. We modeled the effects of nest initiation date (temporal) and nest distance to the nearest habitat edge and agricultural area (spatial). We also investigated the effects of brood-specific parameters related to breeding experience, including nesting attempt number, presence of recently fledged dependent young, and number of helpers at the nest (Canestrari et al. 2009, Feeney et al. 2013), and built single, additive, and multiplicative models with these parameters. We used the AICcmodavg package (Mazerolle 2019) to compare models in our set using their second-order Akaike's Information Criterion (AIC) adjusted for small sample size (AIC_c) and Akaike weights (ω ; Burnham and Anderson 2003, Arnold 2010). Finally, we used principal components analysis (package factoex-

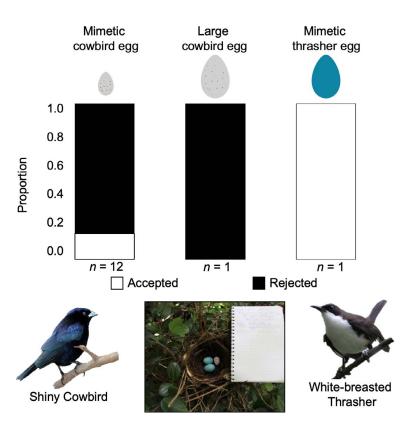


Figure 1. Proportion of mimetic eggs accepted and rejected by White-breasted Thrashers at nests in Saint Lucia July–August 2013. We painted artificial, wooden eggs to resemble Shiny Cowbird eggs (top left), large cowbird eggs (top center), and White-breasted Thrasher eggs (top right) and deposited them in active thrasher nests (bottom center). We monitored the nests to determine the fate of mimetic eggs (i.e., accepted or rejected). Shiny Cowbird photo courtesy of Wikimedia Commons (Charles J. Sharp).

tra; Kassambara and Mundt 2017) to visualize differences between the mimetic egg rejecters and accepters in multi-dimensional parameter space.

Results

We experimentally simulated brood parasitism by Shiny Cowbirds in 13 White-breasted Thrasher nests. We checked 77% of nests (10/13) within 2 d of adding a mimetic egg and 92% (12/13) within 5 d (range 1–7 d). We omitted one nest from analysis because it was depredated <24 h after manipulation, and we were unable to determine if the egg was removed by the predator or ejected by the breeders prior to the depredation event. Of the remaining 12 nests, White-breasted Thrashers rejected the mimetic Shiny Cowbird egg in 83% (10/12) and accepted the egg in 17% (2/12; Fig. 1). Observed counts of egg rejection and acceptance differed significantly from expected values if White-breasted Thrashers were egg accepters (i.e., rejected at a rate $\leq 20\%$ sensu Peer and Sealy 2004; exact binomial test, P < 0.001). Due to the small population size and endangered status of White-breasted Thrashers, the availability of active nests, and logistical constraints we were unable to attain meaningful sample sizes that would allow us to statistically compare the fates of different types of mimetic eggs. However, one mimetic Whitebreasted Thrasher egg was accepted into an active thrasher nest and incubated alongside an inviable thrasher egg for 19 d. One thrasher-sized mimetic Shiny Cowbird egg was added to a thrasher nest and rejected after 4.5 d.

Of White-breasted Thrashers that rejected mimetic Shiny Cowbird eggs (n = 10), 80% did so within 48 h of simulated brood parasitism. No host eggs were damaged or missing following

Table 1. Competing models of effects of temporal, spatial, and brood-specific variables on White-breasted Thrasher
acceptance rate of mimetic Shiny Cowbird eggs ($n = 12$ clutches). Criteria for comparing models include K (number of
estimated parameters), ΔAIC_c , and ω (AIC _c weight).

Model	K	ΔAIC_{c}	ω
Null (intercept-only)	1	0	0.24
Nest distance to agricultural area	2	0.19	0.21
Presence of dependent young	2	1.12	0.14
Within-season nesting attempt	2	1.65	0.10
Nest initiation date	2	2.10	0.08
Nest distance to habitat edge	2	2.12	0.08
Presence of helpers	2	2.87	0.06
Dependent young + within-season nesting attempt	3	4.16	0.03
Within-season nesting attempt + presence of helpers	3	4.30	0.03
Dependent young + presence of helpers	3	4.61	0.02
Dependent young + within-season nesting attempt + helpers	4	8.28	0.00
Dependent young * within-season nesting attempt	4	8.88	0.00
Within-season nesting attempt * presence of helpers	4	9.32	0.00

rejection of the mimetic egg. We observed no instances in which the host species abandoned a nest following simulated brood parasitism or buried a clutch containing a mimetic egg; therefore, we assume all cases of behavioral egg rejection involved the physical ejection of mimetic eggs. We considered 2 White-breasted Thrasher nests to have accepted the mimetic Shiny Cowbird egg. Adults at one nest incubated a clutch containing 2 thrasher eggs and a mimetic egg for 7 d before the nest was depredated. At the second nest, adults incubated a clutch containing 2 thrasher eggs and a mimetic egg for 14 d after which we removed the mimetic egg.

None of our models explained meaningful amounts of variation in mimetic egg acceptance (Table 1). The null model was the top model in the set, receiving 24% of the weight. The models with spatial, temporal, or brood-specific parameters were uninformative (i.e., did not outperform the intercept-only model based on AIC_c) and did not improve the ability to predict whether Whitebreasted Thrashers would accept mimetic eggs. Nevertheless, accepter nests tended to be close to agricultural areas and habitat edges, and to have relatively early nest initiation dates and few previous nesting attempts. A principal components analysis showed that while there is substantial overlap between the nest types in multivariate space, the 2 accepter nests were more similar to each other than to most of the rejecter nests (Fig. 2).

Discussion

Contrary to our prediction, we found that Whitebreasted Thrashers rejected foreign eggs. Our suite of temporal, spatial, and brood-specific predictors were not useful in explaining the small amount of observed variation in egg rejection among clutches. This intraspecific variation in rejection rate may be linked to other factors that we did not consider or were unable to test sufficiently. For example, parasitism rates and anti-parasitism behavior in other bird species can be influenced by breeder age and lifetime experience (e.g., Smith and Arcese 1994, Hauber et al. 2006), but these data were not available for all individuals in our study. Instead, we used the number of broods initiated within a single breeding season, presence of dependent young, and number of helpers (philopatric offspring in this system; Temple et al. 2009) as proxies for experience, which turned out to be poor predictors of egg ejection.

Performing manipulative experiments with endangered species poses certain challenges. Logistical constraints and the availability of active nests at the correct stage of egg development limited our ability to conduct more elaborate experiments. Determining whether White-breasted Thrashers reject all foreign eggs from their nests (Prather et al. 2007), if mimetic egg material influences rejection (Prather et al. 2007, Honza and Moskát 2008), the role of ultraviolet (UV) reflectance in egg recognition (Šulc et al 2016), or how thrashers

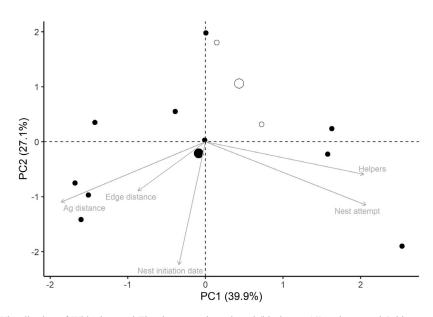


Figure 2. Visualization of White-breasted Thrasher nests that rejected (black, n = 10) and accepted (white, n = 2) mimetic Shiny Cowbird eggs in multivariate parameter space. The large circles corresponded to group centroids. Data were too sparse to construct confidence ellipses.

would respond to parasitism with real cowbird eggs (Prather et al. 2007, Honza and Moskát 2008) are all important questions for further work. These factors are known to influence egg rejection behavior in other systems with smaller-bodied host species (e.g., Village Weavers [Ploceus cucullatus], Prather et al. 2007; Great Reed Warblers [Acrocephalus arundinaceus], Honza and Moskát 2008) and may be addressed in future studies of White-breasted Thrasher egg rejection behavior. However, that White-breasted Thrasher pairs in our study rejected 83% of mimetic Shiny Cowbird eggs and 0% of mimetic White-breasted Thrasher eggs suggests that the removal of foreign eggs we observed is not simply a response to clean the nest of a foreign object, but is a more typical behavioral adaptation to counter brood parasitism (i.e., egg rejection).

Most Mimidae studied to date have been classified as foreign-egg rejecters (>75% of experimental eggs rejected; Peer and Sealy 2004). The majority of anti-brood parasitism research in mimids comes from field studies in North America and consequently highlights co-evolutionary relationships with Brown-headed (*Molothrus ater*) and Bronzed cowbirds (*M.*

aeneus). The Gray Catbird (Dumetella carolinensis; Rothstein 1975, Lorenzana and Sealy 2001), Sage Thrasher (Oreoscoptes montanus; Rich and Rothstein 1985), Brown Thrasher (Toxostoma rufum; Rothstein 1975, but see Haas and Haas 1998), Curve-billed Thrasher (T. curvirostre; Carter 1986), and Crissal Thrasher (T. crissale; Finch 1982) are North American species that reject parasitic eggs. The Northern Mockingbird (Mimus polyglottos) is classified as an "intermediate rejecter" with reported rejection rates of 25-100% in studies of different populations (Rothstein 1975, Post et al. 1990, Peer et al. 2002, Quinn and Tolson 2009). In contrast, LeConte's Thrasher (T. lecontei; Rich and Rothstein 1985) and California Thrasher (T. redivivum; Rich and Rothstein 1985) are North American egg accepters. Investigations of egg rejection behavior in South American and Caribbean mimids are limited. Chalk-browed Mockingbirds (M. saturninus) are a common host of Shiny Cowbirds in South America and accept foreign eggs (Fraga 1985). In the West Indies, Pearly-eyed Thrashers (Margarops fuscatus) breeding in Puerto Rico reject Shiny Cowbird eggs (81% rejection rate; Cruz et al. 1985), but experimentally parasitized Scaly-breasted Thrashers (*Allenia fusca*) and Tropical Mockingbirds (*M. gilvus*) breeding in Saint Lucia accept them (14% and 0% rejection rate, respectively; Post et al. 1990).

From an evolutionary standpoint, egg rejection behavior in the White-breasted Thrasher is likely either an ancestral behavior that has been retained despite the loss of utility (i.e., behavioral relic; Coss et al. 1993, Rothstein 2001) or a recently evolved trait that arose following Shiny Cowbird colonization of Saint Lucia. Shiny Cowbirds were first reported in small numbers in Saint Lucia in 1931, slowly increased in abundance over ~70 yr, and currently occur in relatively low densities compared to other West Indian islands (e.g., Puerto Rico; Post and Wiley 1977, Post et al. 1990). Given the (1) relatively short time interval and limited exposure since cowbird colonization and (2) lack of consistent behavior among sympatric mimids (Cruz et al. 1985, Post et al. 1990), it is unlikely that egg rejection rapidly evolved in White-breasted Thrashers following initial contact with a generalist brood parasite (Rothstein 2001). Instead, parasitic egg recognition and rejection in this species are likely retained ancestral traits (Rothstein 2001, Peer and Sealy 2004, Peer et al. 2007, Grim et al. 2011). Furthermore, contemporary maintenance of these traits in the thrasher system may be associated with ongoing selective pressure resulting from conspecific brood parasitism or jointnesting behavior (Temple 2005). However, the prevalence of these pressures and any relationship they have to interspecific egg recognition or rejection behavior in White-breasted Thrashers remains unknown.

Lack of observed brood parasitism in our system may be a result of egg ejection, but it is also possible that White-breasted Thrashers are not targeted as hosts. Thrashers appear to be a suitable host for Shiny Cowbirds; they build among the most conspicuous and accessible nests in Saint Lucia's dry forest (often nesting <20 m from the forest edge; Mortensen 2009), they exhibit relatively low nest attendance during incubation and therefore may be less likely to chase cowbirds away from nests (Mortensen and Reed 2018), and their breeding season coincides with and incubation period exceeds that of the Shiny Cowbird (Wiley 1988, Temple 2005, Lowther and Post 2020, Mortensen et al. 2020). However, the absence of observed brood parasitism may be linked to the presence of more suitable hosts (e.g., Yellow Warblers [*Setophaga petechia*] and Blackwhiskered Vireo [*Vireo altiloquus*]; Post et al. 1990, Wiley 1988), or host-specific traits like a history of egg rejection leading to the avoidance of a specific host species or nest dimensions that cause poor survival of cowbird nestlings (Peer and Bollinger 1997, Grim et al 2011).

Nevertheless, understanding behavioral responses to potential brood parasites is important for predicting future risk and focusing limited conservation resources available for this taxon. Whitebreasted Thrashers have a global population size of <2,000 individuals, are extremely range-restricted, disperse short distances, and have relatively low fecundity-all traits that increase their extinction risk (Mortensen and Reed 2016). Our results suggest that White-breasted Thrashers may be susceptible to brood parasitism by Shiny Cowbirds. However, due to the low rate at which thrashers accepted mimetic cowbird eggs in our study (17%) and the lack of observations of natural brood parasitism (Mortensen et al. 2017), Shiny Cowbirds likely do not currently pose a severe conservation risk to White-breasted Thrashers in Saint Lucia.

Future changes to the landscape through anthropogenic development and clearing (White et al. 2012, Caribbean News Now 2015) may alter the relatively nascent relationship between these 2 species (e.g., through the loss of other preferred host species, greater accessibility to nests). Given the small population size and limited range of the White-breasted Thrasher, continued vigilance for signs of brood parasitism by Shiny Cowbirds is warranted, as are efforts to further understand the effects of relatively low rates of brood parasitism on the thrasher's reproductive success and population dynamics.

Acknowledgments

We thank the Saint Lucia Forestry Department (Ministry of Agriculture, Fisheries, Physical Planning, Natural Resources, and Co-operatives) for research permissions, logistical support, and technical assistance, and DCG Properties Limited for site access. This work was partially supported by the Tufts Institute of the Environment and a P.E.O. Scholar Award to JLM. We are grateful to SE Fischer, RK Pagel, and JM Reed for providing constructive feedback on earlier versions of this manuscript.

Literature cited

- Ankney CD, Johnson SL. 1985. Variation in weight and composition of Brown-headed Cowbird eggs. Condor 87:296–299.
- Arnold, TW. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.
- BirdLife International. 2017. Important Bird Areas factsheet: Mandelé Dry Forest [cited 10 Oct 2017]. http://www. birdlife.org
- BirdLife International. 2018. Species factsheet: Ramphocinclus brachyurus [cited 10 Oct 2017]. http://www. birdlife.org
- Burnham KP, Anderson DR. 2003. Model selection and multimodal inference: A practical information-theoretic approach. New York (NY): Springer-Verlag.
- Canestrari D, Marcos JM, Baglione V. 2009. Cooperative breeding in Carrion Crows reduces the rate of brood parasitism by Great Spotted Cuckoos. Animal Behaviour 77:1337–1344.
- Caribbean News Now. 2015. St. Lucia installs test tower for potential wind farm. http://www.caribbean360.com/ business/st-lucia-installs-test-tower-for-potential-windfarm
- Carter MD. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. Condor 88:11–25.
- Coss RG, Gusé KL, Poran NS, Smith DG. 1993. Development of antisnake defenses in California ground squirrels (*Spermophilus beecheyi*): II. Microevolutionary effects of relaxed selection from rattlesnakes. Behaviour 124:137–162.
- Cruz A, Manolis T, Wiley JW. 1985. The Shiny Cowbird: A brood parasite expanding its range in the Caribbean region. Ornithological Monographs 36:607–620.
- Faaborg J, Dugger KM, Arendt WJ, Woodworth BL, Baltz ME. 1997. Population declines of the Puerto Rican Vireo in Guánica forest. Wilson Bulletin 109:195–202.
- Feeney WE, Medina I, Somveille M, Heinsohn R, Hall ML, et al. 2013. Brood parasitism and the evolution of cooperative breeding in birds. Science 342:1506–1508.
- Finch DM. 1982. Rejection of cowbird eggs by Crissal Thrashers. Auk 99:719–724.
- Fraga RM. 1985. Host–parasite interactions between Chalkbrowed Mockingbirds and Shiny Cowbirds. Ornithological Monographs 36:829–844.
- Freeman KF. 2015. Impacts of habitat fragmentation, parental care, and social context on reproductive success in the White-breasted Thrasher [master's thesis]. Villanova (PA): Villanova University.
- Grim T, Samaš P, Moskát C, Kleven O, Honza M, et al. 2011. Constraints on host choice: Why do parasitic birds rarely exploit some common potential hosts? Journal of Animal Ecology 80:508–518.
- Haas CA, Haas KH. 1998. Brood parasitism by Brownheaded Cowbirds on Brown Thrashers: Frequency and rates of rejection. Condor 100:535–540.
- Hauber ME, Moskát C, Bán M. 2006. Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. Biology Letters 2:177–180.

- Honza M, Moskát C. 2008. Egg rejection behavior in the Great Reed Warbler (*Acrocephalus arundinaceus*): The effect of egg type. Journal of Ethology 26:389–395.
- Johnson DH. 1979. Estimating nest success: The Mayfield method and an alternative. Auk 96:651–661.
- Kassambara A, Mundt F. 2017. factoextra: Extract and visualize the results of multivariate data analyses. R package version 1.0.5. https://CRAN.R-project.org/ package=factoextra
- Kattan GH. 1997. Shiny Cowbirds follow the 'shotgun' strategy of brood parasitism. Animal Behaviour 53:647–654.
- Lorenzana JC, Sealy SG. 2001. Fitness costs and benefits of cowbird egg ejection by Gray Catbirds. Behavioral Ecology 12:325–329.
- Lovette IJ, Arbogast BS, Curry RL, Zink RM, Botero CA, et al. 2012. Phylogenetic relationships of the mockingbirds and thrashers (Aves: Mimidae). Molecular Phylogenetics and Evolution 63:219–229.
- Lowther PE, Post W. 2020. Shiny Cowbird (*Molothrus bonariensis*), version 1.0. Birds of the World (Billerman SM, editor). https://doi.org/10.2173/bow.shicow. 01
- Lyon BE. 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature 422:495– 499.
- Mayfield H. 1961. Nesting success calculated from exposure. Wilson Bulletin 73:255–261.
- Mazerolle MJ. 2019. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.2–2. https://cran.r-project.org/package= AICcmodavg
- Miller PS, Lacy RC, Medina-Miranda R, López-Ortiz R, Díaz-Soltero H. 2016. Confronting the invasive species crisis with metamodel analysis: An explicit, twospecies demographic assessment of an endangered bird and its brood parasite in Puerto Rico. Biological Conservation 196:124–132.
- Mortensen JL. 2009. Short-term behavioral and demographic responses of the White-breasted Thrasher (*Ramphocinclus brachyurus*) to habitat loss and fragmentation [master's thesis]. Villanova (PA): Villanova University.
- Mortensen JL. 2016. Multifaceted characterization of extinction risk in the endangered, cooperatively breeding White-breasted Thrasher (*Ramphocinclus brachyurus*) [dissertation]. Medford (MA): Tufts University.
- Mortensen JL, Freeman KF, Morton MN. 2020. Whitebreasted Thrasher (*Ramphocinclus brachyurus*), version 1.0. Birds of the World (Schulenberg TS, editor). https://doi.org/10.2173/bow.whbthr1.01
- Mortensen JL, Morton MN, Haynes P, Tschirky J, Felix M, Reed JM. 2017. Current status of the endangered White-breasted Thrasher (*Ramphocinclus brachyurus*), a dry-forest songbird endemic to Saint Lucia and Martinique. Journal of Caribbean Ornithology 30:39– 48.
- Mortensen JL, Reed JM. 2016. Population viability and vital rate sensitivity of an endangered avian cooperative breeder, the White-breasted Thrasher (*Ramphocinclus brachyurus*). PLOS One 11:e0148928.

- Mortensen JL, Reed JM. 2018. Parental incubation patterns and the effect of group size in a Neotropical cooperative breeder. Auk 135:669–692.
- Payne RB. 1977. The ecology of brood parasitism in birds. Annual Review of Ecology and Systematics 8:1–28.
- Peer BD, Bollinger EK. 1997. Explanations for the infrequent cowbird parasitism on Common Grackles. Condor 99:151–161.
- Peer BD, Ellison KS, Sealy SG. 2002. Intermediate frequencies of egg ejection by Northern Mockingbirds (*Mimus polyglottos*) sympatric with two cowbird species. Auk 119:855–858.
- Peer BD, Rothstein SI, Delaney KS, Fleischer RC. 2007. Defence behaviour against brood parasitism is deeply rooted in mainland and island scrub-jays. Animal Behaviour 73:55–63.
- Peer BD, Sealy SG. 2004. Correlates of egg rejection in hosts of the Brown-headed Cowbird. Condor 106:580– 599.
- Peterson SM, Streby HM, Andersen DE. 2012. Effects of parasitism by Brown-headed Cowbirds may persist into post-fledging. Wilson Journal of Ornithology 124:179– 183.
- Post W, Nakamura TK, Cruz A. 1990. Patterns of Shiny Cowbird parasitism in St. Lucia and southwestern Puerto Rico. Condor 92:461–469.
- Post W, Wiley JW. 1977. The Shiny Cowbird in the West Indies. Condor 79:119–121.
- Prather JW, Cruz A, Weaver PF, Wiley JW. 2007. Effects of experimental egg composition on rejection by Village Weavers (*Ploceus cucullatus*). Wilson Journal of Ornithology 119:703–711.
- Quinn J, Tolson KM. 2009. Proximate mechanisms of parasite egg rejection by Northern Mockingbirds. Wilson Journal of Ornithology 121:180–183.
- R Core Team. 2017. R: A language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing.

- Rich T, Rothstein SI. 1985. Sage Thrashers reject cowbird eggs. Condor 87:561–562.
- Rothstein SI. 1975. An experimental and teleonomic investigation of avian brood parasitism. Condor 77:250–271.
- Rothstein SI. 1990. A model system for coevolution: Avian brood parasitism. Annual Review of Ecology and Systematics 21:481–508.
- Rothstein SI. 2001. Relic behaviours, coevolution and the retention versus loss of host defenses after episodes of avian brood parasitism. Animal Behaviour 61:95–107.
- Smith JN, Arcese P. 1994. Brown-headed Cowbirds and an island population of Song Sparrows: A 16-year study. Condor 96:916–934.
- Šulc M, Procházka P, Capek M, Honza M. 2016. Birds use eggshell UV reflectance when recognizing non-mimetic parasitic eggs. Behavioral Ecology 27:677–684.
- Temple H. 2005. Ecology, cooperative breeding and conservation of the White-breasted Thrasher *Ramphocinclus brachyurus* [dissertation]. Cambridge (UK): University of Cambridge.
- Temple HJ, Hoffinan JI, Amos W. 2009. Group structure, mating system and extra-group paternity in the cooperatively breeding White-breasted Thrasher Ramphocinclus brachyurus. Ibis 151:99–112.
- White RL, Baptiste TJ, Dornelly A, Morton MN, O'Connell MJ, Young RP. 2012. Population responses of the Endangered White-breasted Thrasher *Ramphocinclus brachyurus* to a tourist development in Saint Lucia— Conservation implications from a spatial modelling approach. Bird Conservation International 22:468–485.
- Wiley JW. 1988. Host selection by the Shiny Cowbird. Condor 90:289–303.
- Woodworth BL. 1999. Modeling population dynamics of a songbird exposed to parasitism and predation and evaluating management options. Conservation Biology 13:67–76.