OLD ENEMIES WITH NEW PROBLEMS? INVESTIGATING THE ECOLOGICAL RELATIONSHIP BETWEEN RIDGWAY’S HAWK AND THE PARASITIC NEST FLY *PHILORNIS PICI*

by

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DEDICATION

To my family: my nine siblings for honing my survival skills, Mom for teaching me to love the outdoors, and Dad for teaching me to love science.

To Mojave, my daughter, who keeps me honest.

To Thomas, my husband, helper, best friend, and confidant, who loves unconditionally and always encourages me to grow, test myself, and never stop trying new things.

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ABSTRACT

Modern conservation efforts tend not to focus on individual species, but rather on the entire ecosystem of a species in peril. Many ecological factors can affect a species' ability to maintain healthy populations. Parasites, which derive nutrients at the expense of their hosts, can reduce host fitness and limit population growth, acting as biological controls in healthy ecosystems. The negative impacts of parasites on their hosts can be exacerbated by climate change and anthropogenic land-use practices in ways that may limit recovery or drive host species to extinction. Introduced parasitic nest flies in the genus *Philornis* (Diptera: Muscidae) are threatening the extinction of bird species in the Galápagos, yet almost nothing is known about *Philornis*-host ecology in systems where the fly is native. To fill this knowledge gap, we examined the ecological relationship between the parasitic nest fly *Philornis pici* and its host, the Critically Endangered Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park in the Dominican Republic. We excluded nest flies from some Ridgway's hawk broods and compared fledging success with that of control broods, from which flies were not excluded. Treated young had an 89% lower infestation rate and were 179% more likely to fledge than were untreated (control) young. Further, because of the recent history of deforestation in the region, we measured biotic variables around untreated Ridgway's hawk broods and compared these values with abundance and prevalence of nest fly infestation in nestling hawks. We found *P. pici* infestation was negatively associated with grass-cover around hawk nests, which suggests that managing certain aspects of land cover may be a way to

mitigate parasitism levels of Ridgway's hawks. Our work is novel in that we offer the first measurable impact of nest fly infestation on survival or productivity in a non-passerine host. Our findings suggest that *P. pici* parasitism of hawk nestlings could be a factor in the decline of the Ridgway's hawk.

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CHAPTER ONE: NATIVE PARASITIC NEST FLY IMPACTS REPRODUCTIVE SUCCESS OF AN ISLAND-ENDEMIC HOST

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Abstract

Parasitic nest flies (*Philornis* spp.) are a driving force threatening the extinction of bird species endemic to Neotropical islands such as the Galápagos, where introduced *Philornis downsi* negatively impacts reproductive success of naïve avian hosts. Elsewhere in the Neotropics, such as in the Caribbean region where *Philornis* nest flies are native, effects of *Philornis* on host productivity are poorly known. We manipulated parasitism by the native Hispaniolan nest fly *Philornis pici* on a critically endangered endemic host, Ridgway's hawk (*Buteo ridgwayi*) to study the impact of nest fly myiasis on hawk breeding success with the goal of providing a management option for endangered species until broad-scale solutions can be found. Our treatment protocol was enough to reduce *P. pici* abundance by 89% and increase probability of fledging by 179% for treated nestlings. Our results indicate that parasitism by nest flies decreases survival and fledging success of nestling Ridgway's hawks and is a possible factor in the decline of the species. To our knowledge, this work represents the first quantitative evidence of nest fly impact on survival or productivity in a non-passerine host.

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Capítulo Uno: Moscas parásitas nativas impactan negativamente la reproducción de un hospedador endémico de una isla

Resumen en Español

Las moscas parásitas del género *Philornis* constituyen una amenaza que puede llevar a la extinción a numerosas especies de aves endémicas de islas neotropicales; tal como sucede en las islas Galápagos. Allí, la introducida *Philornis downsi* afecta negativamente el éxito reproductivo de aves que no han sido expuestas con anterioridad a parásitos similares. Sin embargo en otros lugares de los Neotrópicos, como en la región del Caribe donde las moscas de este género son nativas, los efectos de estos parásitos sobre la productividad de los hospedadores son escasamente conocidos. El gavilán de la española (*Buteo ridgwayi*) especie endémica y críticamente amenazada que habita la isla de la Española, ha sido reportada como hospedador de la también nativa *Philornis pici*. Mediante la manipulación del parasitismo hemos estudiado el impacto de estas moscas parásitas en el éxito reproductivo del gavilán de la española con el objetivo de proveer una opción de manejo para especies altamente amenazadas hasta que puedan ser encontradas soluciones de largo plazo. Nuestro tratamiento posibilitó reducir la abundancia de *P. pici* en un 89% e incrementar la producción de volantones en un 179%. Nuestros resultados indican que el parasitismo de esta especie de moscas parásitas reduce la supervivencia y las tasas de producción de volantones del gavilán de la española y podría constituir un factor de relevancia en la declinación poblacional de esta especie. Hasta donde es de nuestro conocimiento, este trabajo representa la primera evidencia

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cuantitativa sobre el impacto en la supervivencia y productividad en un hospedador no paseriforme.

Introduction

Although many avian parasite species are described in the literature, their effects on host fitness are poorly known, thus limiting our understanding of host population dynamics (Toft 1991). For example, *Philornis* Meinert (Diptera: Muscidae), a genus of flies that are obligate parasites of nestling birds in much of the Neotropics (Couri 1999; Teixeira 1999; de Carvalho et al. 2005; Dudaniec & Kleindorfer 2006), contains about 50 described species, yet few data exist regarding *Philornis* host-parasite relationships. Adult *Philornis* flies are non-parasitic, but larvae live in nest material or under the skin of nestling birds, feeding on blood and other fluids (Dudaniec & Kleindorfer 2006). Recent work in the Galapagos indicates that myiasis (infection of living tissue by fly larvae) caused by introduced *Philornis downsi* negatively affects reproductive success of previously unexposed avian host species (henceforth "naïve hosts"), and is a driving force threatening the extinction of several endemic bird species (Koop et al. 2011, 2015; Knutie et al. 2014). *Philornis downsi*, introduced to the Galápagos ca. 1960 (Causton et al. 2006, Causton, Cunninghame & Tapia 2013; Dudaniec & Kleindorfer 2006; Kleindorfer & Sulloway 2016), negatively affects fledging rates in eight species of Darwin's finches (Fessl & Tebbich 2002; Fessl, Kleindorfer & Tebbich 2006, Fessl et al. 2010). Now considered invasive, *P. downsi* has been implicated in the rapid decline of at least two critically endangered species, the mangrove finch (*Camarhynchus heliobates*) and the medium tree finch (*Camarhynchus pauper*; Fessl & Tebbich 2002; Fessl et al.

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2010; O’Connor et al. 2010b), and likely contributed to the local extinction of Darwin’s warbler finch (*Certhidea fusca*) on Floreana Island (Grant et al. 2005).

Elsewhere in the Neotropics, less is known about *Philornis*-host relationships within the native ranges of hosts and parasites. The Caribbean is a recognized biodiversity hotspot (Stattersfield et al. 1998; Mittermeier et al. 1999; Myers et al. 2000), and recent declines of endemic birds in the region are troubling. Of the ca. 770 bird species found on Caribbean islands, 73 are threatened with extinction and 12 are considered Critically Endangered (BirdLife International 2016). Although parasitism by *Philornis* spp. is known to occur in Caribbean birds, parasite-host ecology remains almost completely unquantified except in two native songbird species (see Knutie et al. 2017). Improving our understanding of *Philornis*-host relationships may prove important to bird conservation.

Ridgway’s hawk (*Buteo ridgwayi*) is a medium-sized raptor endemic to the island of Hispaniola and satellite islands in the Caribbean (Wiley & Wiley 1981). The hawk formerly occurred in a variety of woodland and edge habitat types from 0–1800 masl, and currently breeds in a mosaic of secondary forest, small agricultural and pastoral plots, and disturbed landscapes (Wiley & Wiley 1981; Thorstrom et al. 2005, Thorstrom, Almonte & Balbuena 2007; Woolaver 2011; Anderson et al. 2017). In recent years, Ridgway’s hawk has suffered dramatic population declines. As of 2009, the single extant natural population of the hawk was estimated at fewer than 109 pairs, decreasing at a rate of 21% between 2006 and 2009, and calculated to be on track for extinction within 20 years (Thorstrom et al. 2007; Woolaver 2011). Reasons for the species’ decline remain speculative (Woolaver 2011), but biologists working for The Peregrine Fund on

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Hispaniola in 2011 began noticing high rates of parasitism and associated nestling mortality from the native nest fly *Philornis pici*, raising concern that parasitism is a contributing factor to hawk population declines.

The genus *Philornis* was first described with the discovery of *P. pici* on Hispaniola in 1854 (Macquart), thus establishing its native range within that of Ridgway's hawk. Wiley and Wiley (1981) reported subcutaneous-dwelling *Philornis* larvae infesting young in a single Ridgway's hawk nest, but no previous effort has been made to quantify the effects of *Philornis* spp. in Ridgway's hawk or any other non-passerine bird.

Given the possibility that *Philornis* nest flies may be adversely affecting Ridgway's hawk populations, the present study aimed to quantify the effects of *P. pici* on nestling mortality and number of offspring fledged per pair (i.e., reproductive success) of Ridgway's hawk, and to test a method for reducing parasitism in nestling birds in the field. Specifically, we applied the broad-based insecticide fipronil to hawk nests and nestlings and physically removed nest fly larvae from nestlings to reduce the abundance (number of larvae per nestling) of *P. pici*. We then modeled the effect of *P. pici* abundance on survival and fledging success in untreated and treated nestlings. To confirm the efficacy of our treatment in reducing parasite abundance in nestling birds, we first evaluated the effect of treatment on the abundance of *P. pici* larvae on nestlings. Further, we hypothesized that (1) the reduction in parasite load accomplished by treatments would increase the number of young fledged per pair, and (2) that the survival of nestlings would be negatively related to larval load.

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Methods

Study Area

Los Haitises National Park encompasses ca. 600 km^2 (reduced from 1600 km^2 in 2004) in northeast Hispaniola. With an elevation range of 0–380 masl, the region is defined by steep rolling hills and sinkhole valleys formed from limestone karst (Monroe 1966). Los Haitises is an area of high biological diversity. However, due to logging to build infrastructure for sugar cane production in the 1960s, and the subsequent establishment of smallholder farming and cattle communities within the park, it is also an area of moderate to high levels of anthropogenic disturbance (Marizán 1994; Brothers 1997a, 1997b). The combined effects of forest conversion to agriculture and pasture, and associated forest fires, had fragmented and reduced primary vegetation coverage to 10-17% of the park as of 1989 (Dirección Nacional de Parques 1991; Brothers 1997b), an amount that has certainly diminished in the 29 intervening years.

Data Collection

We identified nesting pairs of Ridgway's hawk from January through May, 2015 and 2016. When pairs of hawks laid eggs and began incubation, we randomly assigned them to either control (n = 42) or treatment (n = 64) groups; the probability of a pair being assigned to a treatment group = 0.5 independent probability. Unequal number of pairs in the control and the treatment groups was due to some pairs failing during the incubation period or before we recorded nestlings in the nest. After eggs hatched, we visited nests weekly to examine individual nestlings and to tally the number of subcutaneous-dwelling *P. pici* larvae. Larvae of *P. pici* are easily seen or felt beneath nestling skin and feathers because each larva forms a lump and remains at its point of

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entry until it is ready to emerge and pupate (Manzoli et al. 2013). We sprayed nests in the treatment group weekly with ca. 5 cc of fipronil (0.25% solution) to prevent the emergence of any nest fly pupae already inhabiting the nest. We removed nestlings and any prey remains prior to spraying and returned them after the nests had dried (approximately 10 minutes). We did not manually remove any larvae or pupae from nests, only from nestlings. Larvae of *P. pici* do not inhabit the nest material except to pupate; to search for and remove pupae from the nest material would have destroyed nests.

We used topical application of fipronil for nestling hawks upon recommendation of the Santo Domingo Zoo, because they have successfully used this method for many years in both adult and young raptors as well as other birds (A. Nuñez, pers. com). To our knowledge, current literature on negative effects of fipronil in birds is limited to ingestion studies (Gibbons, Morrissey & Mineau 2014). Fipronil ingestion seems to have a wide range of effects in birds, from being practically non-toxic in mallard ducks, *Anas platyrhynchos* (LD_{50} 2,150 mg/kg), to highly toxic in gallinaceous birds such as the Northern bobwhite quail, *Colinus virginianus* (LD_{50} 11.3 mg/kg; Tingle et al. 2003). In rats (*Rattus* sp.), topical application of fipronil was absorbed at a rate of less than 1% of the administered dose (FAO & WHO 1998). For the present study, we used the minimum effective topical dose for prevention of *P. pici* infestation of Ridgway's hawks, based on preliminary trials (T. I. Hayes & C. D. Hayes, unpubl. data). To date we are not aware of any other study of fipronil use in raptors. We treated nestlings topically with 14mg/kg fipronil once per week for the first three visits, and on alternating weeks thereafter. We applied fipronil to the exposed skin of nestlings, between feather tracts, as evenly as

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possible over the body while avoiding orifices, using a 1-cc or 5-cc syringe and a blunt-point application needle.

We removed and saved for identification any larvae found parasitizing nestlings in the treatment group. We used this approach because previous work found that, post treatment, any larvae that remained in nestling integument would inevitably die and decompose in situ, causing bacterial infections and pus-filled inclusion cysts with the potential to deform nestlings and affect their health (T. I. Hayes & C. D. Hayes unpubl. data). Because the primary goal of the present study was to test for effects of *P. pici* on reproductive success of hawks, rather than testing the effect of fipronil per se, the removal of larvae from treated nestlings was used to ensure that the effect of interest – abundance of *P. pici* – was indeed reduced by the treatment, while also minimizing the risk of infection in nestlings due to decomposition of larvae killed by fipronil.

We recorded nestling age in days for each visit. When nestlings reached ca. 30 days of age we banded them with uniquely coded, color-anodized aluminum leg bands (Acraft©). Fledging was confirmed by identifying banded young after they left the nest. We operated this study under Boise State University IACUC protocol 006-AC15-020.

Statistical Analyses

We conducted three analyses to evaluate our hypotheses regarding the effect of *P. pici* larvae on Ridgway's hawk nestlings. (1) To confirm that our treatment did indeed result in lower loads of *P. pici* larvae on nestlings, we compared the count of *P. pici* larvae per nestling per visit between control and treatment groups using generalized linear mixed models with Poisson distributions built in R (R Core Team 2017) and package lme4 (Bates et al. 2015). To control for repeated sampling of broods and

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nestlings, the *P. pici* model included random effects of individual nestlings nested within each brood and fixed effects of treatment and year. (2) To test our hypothesis about the effect of treatment on fledgling production, we compared the number of offspring fledged per pair between control and treatment groups using a generalized linear model with a Poisson distribution including treatment and year as predictor variables. We used this model to develop a model-based prediction of fledglings produced from the control versus treatment groups according to the formula $n_{2015} * (\exp(\beta_0 + \beta_{Treat}) – (\exp(\beta_0)) + n_{2016} * (\exp(\beta_0 + \beta_{Treat} + \beta_{year}) – (\exp(\beta_0 + \beta_{year})$, where n is the number of nests treated in a given year, β_0 is the intercept, β_{Treat} is the treatment coefficient, and β_{year} is the effect of year 2016 compared to year 2015. We calculated the median as the point estimate and 2.5th and 97.5th percentiles as the 95% confidence interval of 1000 non-parametric bootstraps. (3) To test our hypothesis about the effect of *P. pici* abundance on nestling survival, we used a generalized linear mixed model with a binomial distribution and logit link (Hedlin & Franke 2017). This binomial model included a random effect of brood and fixed effects of year and maximum count of *P. pici*. We calculated R^2 values using the method described by Nakagawa and Schielzeth (2013) with the package MuMIn (Barton 2016).

During field studies of avian productivity, failed nests are often underrepresented because researchers are more likely to find successful nests (Mayfield 1961). This phenomenon can bias productivity estimates if not controlled for during analysis (e.g., Heisey, Shaffer & White 2007; Johnson 2007; Converse et al. 2013) or study design (Johnson & Shaffer 1990). Because we only considered nests monitored from hatching onwards (for our purposes termed “nesting attempt”), the probabilities of detecting failed

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and successful nests are equal—thus negating the need to adjust our estimates for different sampling periods (Johnson 2007).

Results

We observed 106 nesting attempts (42 control, 64 treatment) and 186 nestlings (71 control, 115 treatment). Regarding the effects of *P. pici* larvae on Ridgway's hawk, we found the following.

Treatment with fipronil combined with manual removal of nest fly larvae reduced *P. pici* abundance significantly (Table 1.1). Average maximum count of *P. pici* larvae was 16.44 in untreated nestlings (range 0 – 84, SD = 15.58), and 1.73 in treated nestlings (range 0 – 26, SD = 4.44; Fig. 1.1A, Table 1.2). Prevalence (presence/absence) of *P. pici* parasitism in untreated nests averaged 88% (Table 1.2).

There was a significant effect of treatment on fledgling production per pair (Table 1.1). The average number of nestlings fledged per pair was 0.48 ± 0.74 in the control group and 1.41 ± 0.75 in the treatment group (Fig. 1.1B, Table 1.2).

Parasitism significantly lowered survival of nestlings to fledging; the probability of a nestling surviving to fledge for both 2015 and 2016 combined was 0.28 for the control group and 0.78 for the treatment group, resulting in 59.59 (95% CI = 38.43—77.03) more nestlings fledging in the treatment group (Table 1.2). Treated nestlings contained 89% fewer parasites than untreated nestlings and this was associated with a 179% ((0.78-0.28)/0.28) increase in the probability of a single nestling fledging. Odds of a nestling surviving to fledge decreased by 14% (1 - odds ratio for slope coefficient; SE = 5%) with each one-larva increase in maximum *P. pici* count per nestling (Fig. 1.1C). An

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effect of year was apparent only for the number of *P. pici* larvae per nestling per visit (Table 1.1).

Discussion

Our findings support the hypothesis that parasitic nest flies can reduce the reproductive success of an island-endemic host in the shared, native range of both species. Productivity of Ridgway's hawk pairs declined with increasing levels of parasitism by *P. pici*. Our results provided no indication that short-term, topical use of fipronil 0.25% solution negatively affected survival of young when used at a rate of 14mg/kg. Although sub-lethal effects of the treatment may exist, the benefit of increased survival seems to outweigh potential costs to nestlings. Indeed, based on our analysis, we predict that the increase in nestling survival in response to the treatment resulted in production of roughly 60 Ridgway's hawk fledglings that otherwise would have potentially died. Although previous reports exist of *Philornis* parasitism in raptors (Wiley & Wiley 1981; Delannoy 1984; Leite et al. 2009; Reyes & Astudillo-Sánchez 2017), to our knowledge we provide the first quantitative data describing nest fly effects on survival and productivity in raptors or any non-passerine host.

In both introduced and native ranges of nest flies, host response to parasitism varies by host species. mockingbird (*Mimus* spp.) nestlings in the Galápagos, where nest flies are introduced, and on Tobago, where they are native, demonstrated immune and behavioral responses to parasitism, and survived heavy nest fly loads (Knutie 2014; Knutie et al. 2017). In contrast, Darwin's finches (Galápagos) and black-faced grassquits (*Tiaris bicolor*, Tobago) suffered severe declines in productivity due to nest flies (Koop et al. 2011; Knutie et al. 2017). In Puerto Rico, pearly-eyed thrasher (*Margarops*

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fuscatus) nestlings survived infestations of >60 nest fly larvae (Arendt 1985), whereas infestations as low as two nest fly larvae were associated with mortality in a non-passerine host, Puerto Rican sharp-shinned hawk (*Accipiter striatus venator*, Delannoy & Cruz 1991).

Ridgway's hawk life history traits may partially explain severe effects of nest flies on hawk fitness. Interspecific differences of nest fly abundance have been attributed to clutch size (Fessl & Tebbich 2002) and host body size (Dudaniec, Fessl & Kleindorfer 2007; O'Connor, Robertson, Kleindorfer 2010a). The small clutch size (1 to 3 eggs), large mass (280 to 450g), and long nestling period (about 45 days) in Ridgway's hawk may put its nestlings at increased risk of severe infestations by concentrating larvae loads in few large nestlings and allowing for multiple generations of flies to exploit the same brood.

Previous studies have also used nest fumigation as a means of parasite control, including to increase reproductive success of birds in other conservation efforts (Fessl et al. 2006; Knutie et al. 2014, and reviewed in Causton & Lincango 2014). Increasing reproductive output through management of nests can affect growth, or decline, of a population (Catry et al. 2009; Altwegg et al. 2014; McClure et al. 2016). For example, the addition of nest platforms for aplomado falcons (*Falco femoralis*) in Texas nearly doubled pair productivity, which reversed the population growth rate from declining to increasing (McClure et al. 2016). The near tripling of productivity for Ridgway's hawks in the present study supports the efficacy of our treatment for management of nest fly infestations. Whether the treatment used in our study boosts productivity enough to substantially improve population growth rate of Ridgway's hawk remains to be

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determined. Future studies are needed to verify if Ridgway's hawk population can still grow under the pressure of *P. pici* or if intervention is crucial for the continued survival of the species. Recent work suggests that post-fledging survival rates for Ridgway's hawk are relatively high in comparison to other *Buteo* spp., (McClure et al. 2017), which might buffer the effect of nestling mortality on population growth rate (Sæther & Bakke 2000). Future efforts to understand the relationship between nest parasites and Ridgway's hawk productivity should include the development of a population model to assess the effects of nest treatment at the population level.

Knutie et al. (2017) suggest that the natural enemies of nest flies help to control their numbers in native populations, with prevalence (presence/absence) of parasitism by nest flies in native systems tending to be below 50%, whereas prevalence is between 80-100% in systems where the flies have been introduced. In our study, nest fly prevalence in untreated Ridgway's hawk nests averaged 88% (Table 1.2). Manzoli et al. (2013) found that *Philornis torquans* prevalence in the temperate pampas of Argentina was inversely related to average forest height and positively correlated with shrub coverage, both associated with forest clearing. Le Gros, Stracey & Robinson (2011) found that the proportion of nests parasitized by *Philornis porteri* in humid, subtropical Florida, USA, increased with some aspects of urbanization, such as residential areas and pastureland and decreased with others, such as parking lots. Further investigation is needed to examine the role of landscape change and other anthropogenic activities in Los Haitises (Dirección Nacional de Parques 1991; Marizán 1994; Brothers 1997a, 1997b; Rivera, Zimmerman & Aide 2000) in relation to the prevalence and abundance of *P. pici* and its natural enemies (see Knutie et al. 2017). In contrast to the enemy release hypothesis, the

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observed preference of *Philornis* spp. for some bird species that can sustain high levels of parasitism can create a phenomenon of reservoir hosts (Antoniazzi et al. 2010; Quiroga, Reboreda & Beltzer 2012; Manzoli et al. 2013; Knutie 2014) that drive nest fly prevalence and morbidity in other, less resilient host species. Further investigation is needed to determine if *P. pici* is benefitting from either enemy release or the increased presence of a reservoir host species on Hispaniola.

Woolaver (2011) listed reasons for conservation concern for Ridgway's hawk, including human persecution and habitat loss. Although habitat loss is often given as a primary reason for species decline, it is hard to rationalize the near extinction of a habitat and dietary generalist such as Ridgway's hawk solely, or even primarily, by habitat disturbance. We speculate that parasitism by *P. pici* may have an additive effect when presented with these other elements. Efforts to understand the underlying causes of Ridgway's hawk population declines should include a focus on factors that may affect distribution and density of *Philornis* spp. on Hispaniola. Understanding recent shifts in ecological systems and how they relate to avian myiasis may be an essential step in long-term conservation of island biodiversity in the Neotropics.

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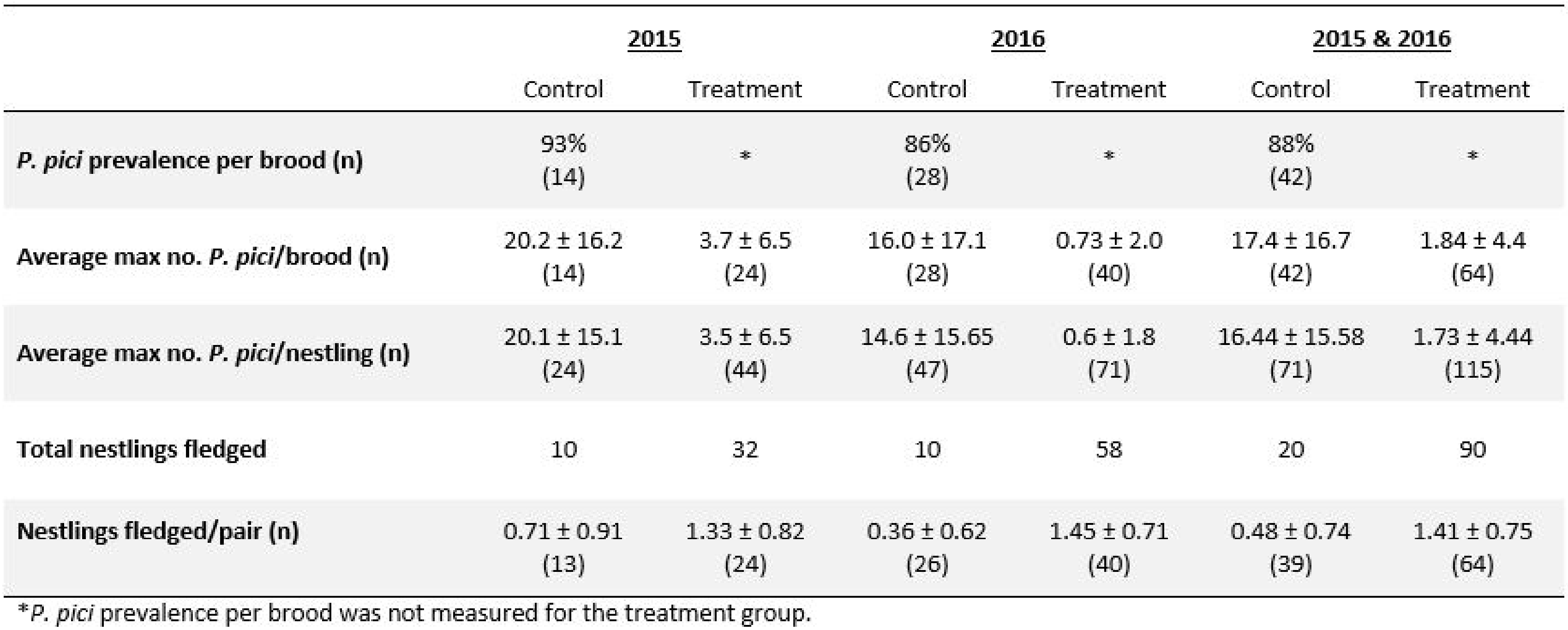
Tables and Figures

Table 1.1 For Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park, Dominican Republic, 2015 and 2016: Generalized linear mixed model results for differences between control and treatment (with larvae experimentally reduced) groups. Confidence intervals were bootstrapped.

Model	R^2	Coefficient	B	SE	p	CI (95%)
No. larvae	0.224	Intercept	2.059	0.336	**<0.001**	1.381, 2.720
		Treatment	-3.844	0.370	**<0.001**	-4.614, -3.147
		Year	-1.077	0.323	**<0.001**	-1.728, -0.447
No. fledged	0.169	Intercept	-0.701	0.258	**0.007**	-1.238, -0.224
		Treatment	1.08	0.247	**<0.001**	0.618, 1.593
		Year	-0.062	0.196	0.754	-0.442, 0.330
Nestling survival	0.846	Intercept	3.205	1.414	**0.023**	1.193, 10.046
		No. larvae	-0.154	0.061	**0.011**	-0.363, -0.065
		Year	-1.115	1.09	0.306	-3.711, 1.190

No. Larvae = number of *P. pici* larvae per nestling per visit (dependent variable) for each group (independent variable) random effects of individual nestlings nested within each brood and fixed effects of treatment and year. No. fledged = number of nestlings fledged per pair that successfully hatched nestlings (dependent variable) for each group (independent variable), treatment and year as predictor variables. Nestling survival = individual nestlings that survived to fledge (dependent variable) compared with that individual's maximum larva count (independent variable), random effect of brood and fixed effects of year and maximum number of larvae. *P*-values <0.05 are in **bold.**

Table 1.2 For Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park, Dominican Republic, 2015 and 2016: Percent prevalence (presence/absence) of *Philornis pici* for untreated broods as well as average maximum counts of *P. pici* larvae for individual nestlings and broods, total nestlings fledged for each group by year, and average productivity (number of fledglings/pair that successfully produced nestlings) all with standard deviation. In the treatment group we experimentally removed *P. pici* larvae (see Methods). Note: most nestlings with *P. pici* larvae counts in the treatment group derive from nestlings prior to receiving their first treatment of fipronil. We calculate fledglings per pair rather than per brood, because some pairs had more than one brood before either discontinuing to breed, or successfully fledging young.



	2015		**2016**		**2015 & 2016**	
	Control	Treatment	Control	Treatment	Control	Treatment
***P. pici* prevalence per brood (n)**	93% (14)	*	86% (28)	*	88% (42)	*
Average max no. *P. pici*/brood (n)	20.2 ± 16.2 (14)	3.7 ± 6.5 (24)	16.0 ± 17.1 (28)	0.73 ± 2.0 (40)	17.4 ± 16.7 (42)	1.84 ± 4.4 (64)
Average max no. *P. pici*/nestling (n)	20.1 ± 15.1 (24)	3.5 ± 6.5 (44)	14.6 ± 15.65 (47)	0.6 ± 1.8 (71)	16.44 ± 15.58 (71)	1.73 ± 4.44 (115)
Total nestlings fledged	10	32	10	58	20	90
Nestlings fledged/pair (n)	0.71 ± 0.91 (13)	1.33 ± 0.82 (24)	0.36 ± 0.62 (26)	1.45 ± 0.71 (40)	0.48 ± 0.74 (39)	1.41 ± 0.75 (64)

**P. pici* prevalence per brood was not measured for the treatment group.

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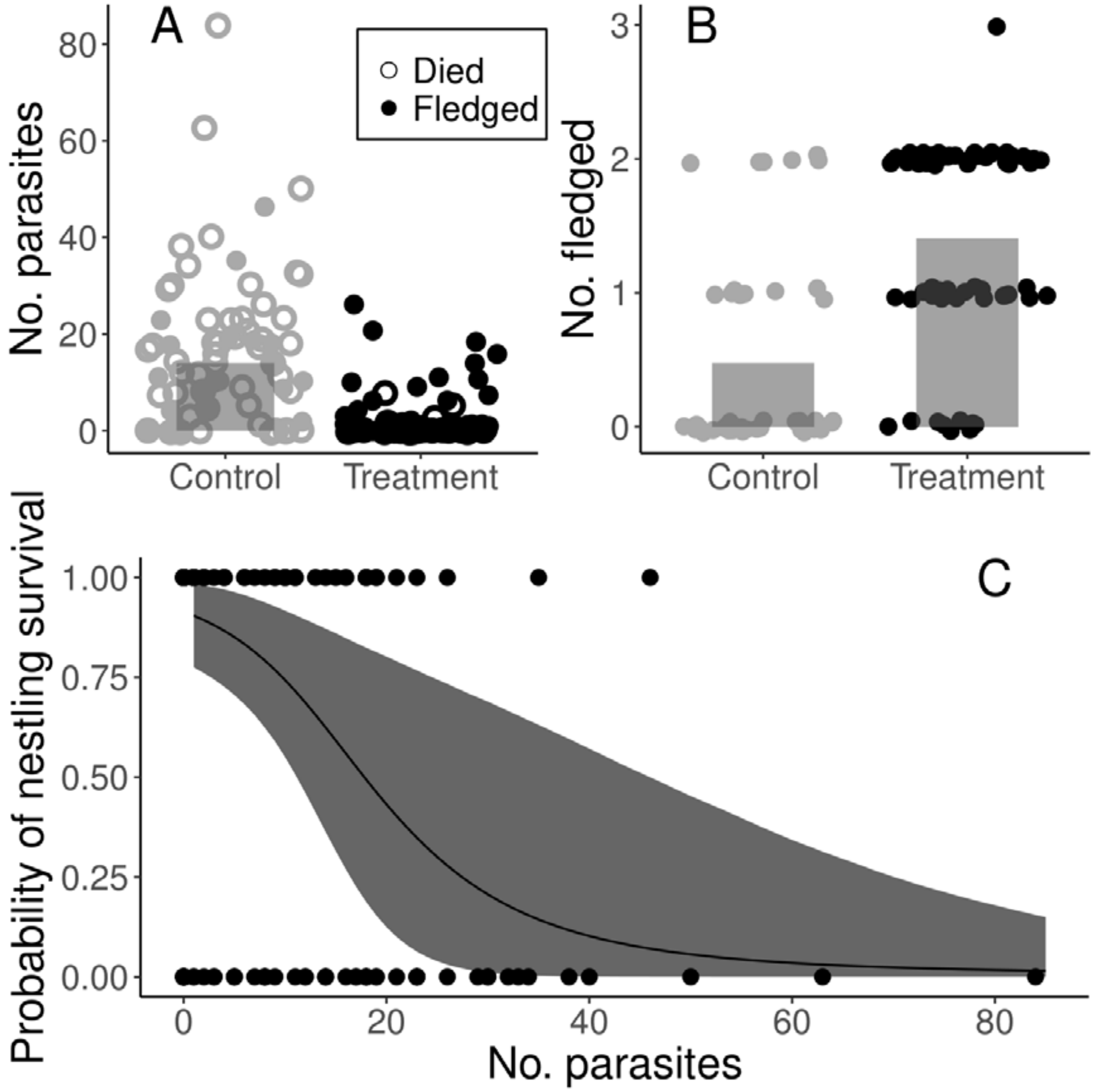

Figure 1.1 For Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park, Dominican Republic, 2015 and 2016. A) Maximum counts of *Philornis pici* larvae for hawk nestlings in untreated control nests (gray points) and treatment nests (black points) in which *P. pici* abundance was controlled by spraying nests and nestlings with 0.25% fipronil solution and manual removal of larvae from nestlings. Open points show nestlings that died before fledging and closed points show nestlings that survived to fledge. B) Average number of hawk nestlings fledged per pair for control (gray points) and treatment (black points). In A) and B) bars represent means, and points are jittered for visibility. C) The relationship between nestling survival and maximum larva count on a given nestling. Gray shading is the 95% confidence interval. Note that in A) all *P. pici* larva counts ≥ 8 in the treatment group derive from nestlings prior to receiving their first treatment of fipronil (see Methods).

CHAPTER TWO: ECOLOGICAL CORRELATES OF THE PARASITIC NEST FLY *PHILORNIS PICI* ABUNDANCE IN RIDGWAY'S HAWK (*BUTEO RIDGWAYI*) IN THE DOMINICAN REPUBLIC

Abstract

Shifts in climate and human land-use practices alter ecosystem functioning, benefiting some organisms and disadvantaging others. Parasites function as a biological control for their host species in some ecosystems and parasites that are ecologically advantaged can limit host recovery or even drive the host species toward extinction. Understanding parasite-host ecology is increasingly important for conservation efforts in a changing world. Nest flies in the genus *Philornis* (Diptera: Muscidae) have been implicated in the decline of Darwin's finches in the Galápagos and are also known to negatively impact breeding success of the Critically Endangered Ridgway's hawk (*Buteo ridgwayi*) on the island of Hispaniola. Despite the importance of these effects on hosts, the ecology of Philornid nest flies is poorly understood. We examined biotic factors related to *Philornis* nest fly infestations of nestling Ridgway's hawks in the Dominican Republic, where both fly and hawk are native. We found that grass-cover was negatively associated with *Philornis pici* infestations, which is interesting in light of recent landscape-level changes to Ridgway's hawk habitat. Anthropogenic activities in Los Haitises National Park, the last strong-hold of Ridgway's hawk, have shifted the landscape from primary forest to a fragmented secondary forest with grassy patches. Our goal was to provide information on the ecology of nest flies in their native habitat that

would inform conservation efforts and allow us to make recommendations for future research.

Introduction

Parasites adversely affect their hosts by deriving nutrients at the hosts' expense (Price 1977). The study of parasite-host ecology is important for species management and conservation because parasitism contributes to the natural regulation of populations (Haldane 1990). Parasitism can threaten biodiversity, especially where changes to landscapes diminish the quality of host habitats and increase host exposure to outside elements (May 1988). Fragmented, diminished habitats can heighten the detrimental consequences parasitism has on a host species for example by increasing stress to the host, concentrating hosts so that parasite transmission between individuals is increased, and in some cases, parasitism can drive host species towards extinction (Myers 1979; Holmes 1996). For rare host species, the consequences of parasitism may be particularly severe because any adverse effect of parasitism on survival or recruitment could increase the host species' risk of extinction (Grzybowski & Pease 1999). Thus, understanding the causes and consequences of parasitism is important for the management and conservation of rare or threatened species affected by parasites. In the present study, we focused on identifying the biotic factors that influence the abundance and prevalence of a nest fly parasite of Ridgway's hawk (*Buteo ridgwayi*) an endangered raptor native to the Caribbean island of Hispaniola. As an island raptor in a developing country, Ridgway's hawk is in a category designated by recently published work as especially vulnerable to extinction (McClure et al. 2018; Buechley et al. 2019).

Parasite-host interactions may be particularly important for island species because these species are naturally isolated and historically more vulnerable to extinction than are mainland species (Diamond 1989; Smith et al. 1993; Loehle & Eschenbach 2012). In birds, the vulnerability of island species to extinction is especially pronounced, with > 90% of bird extinctions in the past 500 years having been in island birds (Loehle & Eschenbach 2012). Island bird species are often ecologically specialized and non-migratory with a narrow latitudinal range, making them more susceptible than mainland species to extinction due to anthropogenic effects and climate change (Julliard et al. 2003; Crick 2004; Thomas et al. 2004). Other risks to island birds include the introduction of non-native pathogens and parasites (Lafferty et al. 2005). For example, the parasitic nest fly *Philornis downsi* (Diptera: Muscidae), introduced to the Galápagos islands ca. 1960, is driving naïve host species toward extinction (Koop et al. 2011, 2015; Knutie et al. 2014). However, in parts of the world where Philornid nest flies are native, less is known about the potential of these organisms to influence host populations.

Members of the genus *Philornis* Meinert, of which there are about 50 known species, are parasites of nesting birds (Couri 1999). Only the larval stages are parasitic. These larvae live in the nest substrate of their hosts, feeding externally (semi-haematophagous lifestyle) or internally (subcutaneously or intramuscularly) on blood and other body fluids of their host (Teixeira 1999). By contrast, adult *Philornis* feed on nectar, fruits, and decaying matter (Teixeira 1999).

Philornis nest flies were first described on the island of Hispaniola in 1853 (Macquart 1853) and are native to the Caribbean as well as other parts of the Neotropics. Despite their widespread distribution and known parasitic habits (Teixeira 1999), there is little information about *Philornis* ecology in the Caribbean except in Tobago (Knutie et al. 2017). Factors that affect the abundance (intensity, quantity per sample unit; Koop et al. 2011) and prevalence (incidence, number of cases per sample unit; Knutie et al. 2017) in native hosts are poorly known. In Argentina, vegetative composition of the natural landscape was correlated with prevalence and abundance of *Philornis* parasitism of nestling passerines (Manzoli et al. 2013). Specifically, Manzoli et al. (2013) examined nests of 57 different species of forest passerines and found that abundance of *Philornis torquans* was correlated positively with presence of shrubs and inversely to grass height and tree height around nests. Anthropogenic modification of landscapes may also play a role in *Philornis* activity. In Florida, *Philornis porteri* parasitism of nestling northern mockingbirds (*Mimus polyglottos*) had higher prevalence and abundance in moderately-vegetated suburban areas than in highly urbanized city landscapes or nature reserves (Le Gros et al. 2011). The mechanisms by which habitat characteristics influence parasitism are unclear. For example, vegetation and other physical characteristics of landscapes may influence landscape use by adult *Philornis*, or they may affect the microclimate around nests and therefore the conditions experienced by *Philornis* larvae, or both. Vegetation may also be associated with parasitism because of its influence on key abiotic factors, such as temperature and humidity. Fluctuations in dipteran fly populations have been associated with temperature and humidity (Goulson et al. 2005) and *P. torquans* parasitism of passerines in Argentina was also associated with temperature and rainfall (Antoniazzi et al. 2010; Manzoli et al. 2013).

In addition to the effects vegetation or other habitat characteristics may have on *Philornis* abundance and prevalence, host species that are unaffected by the parasite may serve as reservoirs that promote nest fly populations and harm hosts more sensitive to parasitism (Knutie et al. 2016). Contemporary anthropogenic changes to landscapes may affect the distribution, density, and ecology of reservoir host species for *Philornis*, with cascading effects on less resilient host species.

Research on the island of Hispaniola has shown that the native nest fly *Philornis pici* negatively impacts breeding success of the endemic and IUCN-designated Critically Endangered Ridgway's hawk (BirdLife International 2018; Hayes et al. 2018). The hawk was formerly distributed across Hispaniola and despite having a wide prey base and a history of using a variety of landscapes, the sole wild population of ca. 200 breeding pairs is now isolated in the northeast sector of the Dominican Republic (Woolaver 2011; Woolaver et al. 2013; Anderson et al. 2017). Identifying biotic factors that influence parasite-host interactions, such as vegetative coverage or the abundance of potential reservoir hosts near hawk nests, may have important conservation implications for the Ridgway's hawk. Thus, the goal of our research was to identify biotic factors that correlate with parasitism by *P. pici* in Ridgway's hawk nestlings on Hispaniola in an effort to better inform conservation efforts, provide land managers with actionable information to improve the survival prospects of Ridgway's hawks, and furnish groundwork for future research. Because previous studies have identified vegetation as an important parameter that influences *Philornis* numbers, we included in our analysis measurements of percent cover and height of vegetation as well as the number of nest fly larvae parasitizing nestling Ridgway's hawks. We also investigated whether prevalence and abundance of nest fly parasitism in nestling hawks might be linked to a reservoir host (as in Knutie et al. 2016). For this goal, we chose to investigate the palmchat (*Dulus* *dominicus*), a common bird species that builds large communal nest structures that are often cohabited by Ridgway's hawk (Wiley & Wiley 1981; Woolaver 2011).

Methods

Study Area

Los Haitises National Park (henceforth "Los Haitises") in northeastern Dominican Republic is an area rich in biodiversity despite anthropogenic changes to the landscape (Zanoni et al. 1990; Marizán 1994). For an in-depth description of the landscape structure and vegetative composition of Los Haitises see Zanoni et al. (1990). Organized deforestation of the region began in the 1960s to build infrastructure for sugar cane production, making the area more accessible to settlement by smallholder farmers and cattle ranching (Brothers 1997a, 1997b). Since its declaration as a forest reserve in 1968 and subsequent upgrade to National Park in 1976, Los Haitises has been almost continuously plagued by social, economic, and environmental conflicts (Zanoni et al. 1990; Marizán 1994; Brothers 1997a, 1997b). The park boundary, as well as the area it encompasses, have changed several times, from as little as 208 km^2 in 1976 up to 1600 km^2 in 1992. Currently, Los Haitises measures ca. 600 km^2 (Dominican Law: Ley 202-04). The park has a limestone karst topography described as "egg crate" with rounded "*mogote*" hills and sinkhole valleys, ranging from 0 – 380 m above sea level (Monroe 1966; Zanoni et al. 1990; Marizán 1994). Average annual rainfall in Los Haitises is the highest in the Dominican Republic - about 2700 mm annually. Average humidity is 70 – 75%, and average high and low temperatures are 32.5 and 25.5 ^{o}C (Marizán 1994). Climate does not vary much by season, though highest rainfall occurs between May and October and nighttime temperatures during these months may dip as much as 10 ^{o}C below daytime levels (Wiley & Wiley 1981; Marizán 1994). Despite high rainfall, Los Haitises has little standing water due to the permeability of its karst landscape (Wiley & Wiley 1981). The park's botanical diversity is the highest in the Caribbean, with > 700 species of vascular plants and several endemic vertebrates, including the solenodon (*Solenodon paradoxus*), a small mammal, and several bird species that include the palmchat, Dominican parrot (*Amazona ventralis*), and Ridgway's hawk (Marizán 1994). There are over 50 species of non-native plants that have been introduced to the area, many for agriculture (Zanoni et al. 1990). The royal palm (*Roystonea borinquena*) is native, but was not common in the area historically and was planted in forest clearings by park settlers, who valued the palm for its wood and for food (J. Polanco pers. comm.). Now many clearings have at least one, if not several, mature royal palms, which frequently contain nests of palmchat and Ridgway's hawk (Woolaver 2011, C. Hayes, pers. obs.). The palmchat, a frugivorous passerine most closely related to silky-flycatchers (*Ptiliogonatidae*) and waxwings (*Bombycillidae*, Fleischer et al. 2008; Spellman et al. 2008) is monotypic in the family *Dulidae*. palmchats construct cavity nests inside stick-based communal nest structures, sometimes as large as 1-meter across (C. Hayes unpublished data). Other bird species, including Ridgway's hawk, often build their own nests atop palmchat nest structures (Wiley & Wiley 1981; Curti et al. 2018).

<u>Data Collection</u>

This study is part of a larger effort by The Peregrine Fund to conserve the Ridgway's hawk including the use of prophylactic treatments of nests and nestlings to prevent parasitism by nest flies. Our field methods for finding and observing Ridgway's hawk nesting pairs are described in detail in Hayes et al. (2018). Briefly, between January

– May, 2016 and 2017, we located and followed breeding pairs of hawks during weekly visits through incubation. Pairs of hawks (n=42) were randomly selected from the Ridgway's hawk population in Los Haitises. When nestlings hatched we visited nests weekly to count nest fly larvae, which form a noticeable lump beneath the skin of nestlings and are easily detected by sight or by touch via a gentle massage. We defined abundance of larvae as the number of larvae per nestling on a given date. We defined prevalence of infestation as the probability of presence of nest fly larvae in a Ridgway's hawk nest (see Koop et al. 2011). In instances when a nesting attempt failed, we dissected the nest to record if *P. pici* pupae were present in the nesting substrate – an indication that nestlings had likely been infected, especially useful when we did not recover dead nestlings (Koop et al. 2011).

Around each Ridgway's hawk nest, we surveyed four 50-m linear transects that radiated from the nest tree in each cardinal direction. Every 10 m along each transect, we recorded above-ground height of each of five classes of vegetation commonly encountered near hawk nests: tree, shrub, herbaceous, grass, and bare ground. If more than one vegetation class was represented at a given point, we measured the dominant (taller) vegetation class (i.e., overstory) and recorded the presence only of that class. Thus, we measured 20 points per nest and used these data to establish percent coverage and mean height of vegetation. We used percent cover as well as height of vegetation classes because we wanted to include the variation between both tall and short vegetation as well as the amount of ground covered by that vegetation (0-100%). We also recorded whether a hawk nest was constructed exclusively by the hawks or constructed atop a palmchat nest and if so, whether the palmchat nest was concurrently in use by palmchats.

Statistical Analysis

We conducted all analyses in R version 3.5.1 (R Core Team 2018) and organized our data using tidyverse (Wickham 2016). We built linear mixed-effects regression (lmer) models with maximum likelihood using the automated model selection function “dredge” (package MuMIn, Barton 2018) to assess a global model composed of all vegetation variables of interest as well as nestling age and visit date. We then used the dredge function (package MuMIn, Barton 2018) to similarly assess a global lmer model of principal components (PCA) derived out of a correlation of the original vegetation variables of interest using R packages caret (Kuhn 2018), psych (Revelle 2018), and FactoMineR (Le et al. 2008). In all models we used log +1 of the maximum count of nest fly larvae for individual nestlings as our response variable and included brood as a random effect. In the event that the larva count for a given nestling was zero for all visits, or if on two or more visits a nestling had an equal maximum count of larvae, we chose the latter visit. Over the course of this study, nestlings < 3 days of age were never parasitized by nest fly larvae, thus we excluded them from analyses to prevent the introduction of false zeros into the data set. We used Akaike's Information Criterion with small-sample correction (AICc) to rank and compare the top models and a null model.

We considered models to be competitive if they were ≤ 2 ΔAICc of the top model (Burnham & Anderson 2002). We verified our top models by assessing the adequacy of residual plots (Zuur et al. 2009) as well as following the “nesting rule” which eliminates any model that has a higher AICc value when compared with a similar, more parsimonious model (Burnham & Anderson 2002; Richards 2008; Arnold 2010; Richards et al. 2011). Although model averaging is often recommended in this circumstance, we did not model average because, after eliminating these more complex models with higher weights, we found it more informative to examine individual covariates within the few top models, which we did using 85% confidence intervals (Arnold 2010) on models built using restricted maximum likelihood.

To assess whether palmchat construction of the hawk primary nest structure or concurrent use of the nest structure by palmchats and hawks correlated with either *P. pici* abundance or prevalence in hawk nests, we used a two-sample t-test and a Pearson's chi-squared test with a simulated p-value based on 2000 replicates (R package: gmodels, Warnes et al. 2018). To determine if there was a difference between years in either nest fly abundance or prevalence we used a two-sample t-test and a Pearson's chi-squared test with Yates' continuity correction, respectively.

Results

Thirty-eight of the 42 nests had at least one hawk nestling infested by *P. pici* larvae and we found 12 *P. pici* pupae in one additional nest after the two nestlings had disappeared (Table 2.1). Of 66 total nestlings, 51 had ≥ 1 *P. pici* larva, and six additional nestlings died in nests where a sibling had ≥ 1 *P. pici* larva. Only three of 16 nestlings that successfully fledged were never infested by nest fly larvae (Table 2.1). We attributed 45 of 50 (90%) nestling mortalities to nest fly infestations, one to a fallen nest, and four to unknown causes. One of these unknown deaths was a possible siblicide. In this case, the nestling was not infected with *P. pici* up to the week before its disappearance; however, its older sibling in the nest was infected and survived to fledge. Thus, the total number of nestling deaths associated with nest fly infestation was 46 (Table 2.1).

Models within 2 ΔAICc of the top model are summarized in Table 2.2. Vegetation variables that were not included in the top model set were: coverage of bare ground, herbaceous-cover, herbaceous-height, shrub-height, and tree-cover. Models of PCA components were not competitive (≤ 2 ΔAICc) when compared with models containing the original vegetation variables (see Statistical Methods). In all models, age and visit date covariates were positively correlated with nest fly parasitism of nestling hawks (Table 2.3). Grass variables were consistently included in top models and are the only vegetation variables that we found to be informative of nest fly abundance. Model 1 had the lowest AICc and included the vegetation variables grass-cover and grass-height (Table 2.2). We infer from model 1 that for our population sample, grass-cover had a moderate inverse relationship with *P. pici* parasitism of Ridgway's hawk nestlings (Table 2.3). The relationship between grass-height and parasitism is weak (Table 2.3) so we caution against making inferences based on this covariate. We found that grass-cover and grass-height were positively correlated (0.70 (t = 7.8411, df = 64, p = 6.146e-11); however, variance inflation in model 1 (as compared with the null model), was not high, significance of individual variables was not diminished (Table 2.3), and the model remained stable (i.e., its coefficients did not fluctuate drastically when one grass variable or the other was omitted). Residual plots suggested that having both grass variables present contributed to a more appropriate model in terms of basic assumptions (see Zuur et al. 2009). However, we recognize that by including both grass-cover and grass-height in model 1, we limit the extent to which the predictors can be independently interpreted. Although shrub-cover and tree-height were included in models ≤ 2 ΔAICc of the top model, neither variable was informative (85% confidence intervals span 0, Tables 2.2 and 2.3).

Although palmchats were associated with 36 (86%) of 42 Ridgway's hawk nests, they did not appear to be a factor in nest fly infestation of Ridgway's hawk nestlings (Table 2.1). Abundance of *P. pici* was not associated with concurrent use of nests by palmchats ($t = 0.80457$, $df = 64$, $p = 0.424$) or nest construction by palmchats ($t = -0.19813$, $df = 64$, $p = 0.8436$). Similarly, *P. pici* prevalence was not associated with concurrent use or construction of nests by palmchats ($x^2 = 0.86562$, df = NA, *simulated p-value based on 2000 replicates* = 0.7131).

We found no difference between years 2016 and 2017 for either nest fly abundance ($t = 0.746$, $df = 64$, $p = 0.4584$) or prevalence ($x^2 = 0.98425$, $df = 1$, $p = 0.3212$).

Discussion

Our study of biotic variables and nest fly infestation of Ridgway's hawk nestlings in Los Haitises found that variation in vegetation was related to *P. pici* abundance and that grass-cover was the single vegetation variable most associated with reduced fly infestation. Nestling age and visit-date were positively correlated with nest fly abundance. This relationship makes sense even for a random search strategy by flies – i.e., the longer a host is available and the larger it grows, the more likely that a nest fly will find it. The same relationship between nestling age and nest fly abundance was true for passerines in Argentina (Segura & Reboreda 2011; Manzoli et al. 2013). Our results did not support palmchats as reservoir hosts in terms of either prevalence or abundance of nest flies.

Grass was the strongest predictor of nest fly abundance once we controlled for nestling age. Specifically, grass-cover was moderately associated with a decreased abundance in *P. pici* parasitism whereas grass-height showed a positive correlation with parasitism. However, because our sample size was small and the association weak, we recommend further investigation of the grass-height – nest fly relationship before inferences are made. In Argentina, abundance of the nest fly *P. torquans* in passerine bird broods was inversely related to grass-height (Manzoli et al. 2013). Percent coverage of grass was not measured in that study; however, there was no correlation between grass presence and *P. torquans* abundance (Manzoli et al. 2013). Rainfall, leading to increased humidity, was positively associated with the prevalence of nest fly *P. torquans* in Argentina (Antoniazzi et al. 2010; Manzoli et al. 2013). It is possible that the negative association we found between *P. pici* abundance and grass-cover was due to vegetation-related variation in humidity. Grass-grown areas in Los Haitises tend to be more open, receive more direct sunlight, and have lower humidity than forested areas (C. D. Hayes, unpubl. data), all of which may negatively affect the microclimate of *P. pici* larvae in nests. An alternative, but not mutually exclusive explanation is that grass, in comparison to other vegetation, may offer limited cover to *P. pici* adults, benefiting insectivorous predators.

Variation in shrub-cover around nests did not significantly correlate with nest fly parasitism of hawk nestlings in Los Haitises. In Argentina, Manzoli et al. (2013) observed a positive relationship between presence of shrubs around nests and *P. torquans* abundance. In Florida, Le Gros et al. (2011) found that nest flies were more abundant in pastures and residential areas than in highly developed, urban or heavily vegetated, nature reserves. These findings by Le Gros et al. (2011) may be related to a greater density of shrubbery and other mid-level vegetation in suburban landscapes. It may be that shrub-cover is not related to *P. pici* abundance in the Los Haitises system; however, in light of the significance of shrub-covered landscapes from both Le Gros et al. (2011) in Florida and Manzoli et al. (2013) in Argentina, we recommend further investigation of shrub-cover and nest fly abundance in the *P. pici* ecosystem on Hispaniola.

It appears that tree-height is also not a factor in nest fly parasitism of Ridgway's hawk nestlings as tree-height in Los Haitises was not associated with nest fly abundance. By contrast, Manzoli et al. (2013) found a significant inverse relationship between tree height and *P. torquans* abundance in broods of nestling passerines, except in forests dominated by an introduced, non-native, honey locust tree (*Gleditsia triacanthos L.*), where nest fly abundance was positively correlated with tree-height. Manzoli et al. (2013) also found that abundance of nest flies per brood correlated with forest composition. Specifically, nest fly abundance was higher when some tree species were the predominant vegetation as compared to others (Manzoli et al. 2013). The recent history of landscape-level changes to vegetation structure in Los Haitises (Marizán 1994; Brothers 1997a, 1997b; J. Polanco pers. comm.) could be important for the abundance and prevalence of *P. pici* parasitism of nestling birds in the park. Further study is needed to determine if *P. pici* may be influenced by forest composition of either native tree species, such as royal palm, or the presence of other commonly encountered, introduced non-native trees such as the African tulip tree (*Spathodea campanulata*) or agriculture.

Palmchats did not seem to influence nest fly abundance or prevalence, although the small sample size in our study may have made such a relationship difficult to detect.

Only six of the 42 Ridgway's hawk nests in our study were not associated with palmchat use or construction. palmchats are ubiquitous in Los Haitises, and can be found in small flocks in almost any forest clearing (C. Hayes pers. obs.). There are no historical data of palmchat use of the park, and it is possible that the documented landscape-level changes to Los Haitises have benefited the park's palmchat population. It is also possible that the prevalence or abundance of *P. pici* in Los Haitises is influenced by some other reservoir host species. Knutie et al. (2016, 2017) found that Galápagos mockingbird (*Mimus parvulus*) in the Galápagos and tropical mockingbird (*Mimus gilvus*) in Tobago were tolerant of *P. downsi* and *Philornis trinitensis* infestations, respectively; thus, each bird species is a potential driver of *Philornis* parasitism in their corresponding ecosystem. northern mockingbird is native to Hispaniola, where it is common (BirdLife International 2017). It is possible that the northern mockingbird, rather than the palmchat, may influence *P. pici* infestations of Hispaniolan birds, including Ridgway's hawk.

Very little is known of *P. pici* ecology in any system and we know even less in systems where the fly is native (but see Knutie et al. 2017; Hayes et al. 2018). *Philornis* larvae are the immediate beneficiaries of parasitism, in addition to being a simpler study subject because of their sedentary life-history; for these reasons most ecological research of *Philornis* has focused on the larval stage. Investigation of adult *Philornis* life-history and behavior may give insight into *Philornis* ecological relationships beyond those immediately related to the host and should be a component of future research. While a primary goal of our study was to identify the biotic factors associated with *P. pici* abundance and prevalence so that actionable measures could be employed to mitigate the effects of the parasite on the Ridgway's hawk population, we recommend further study before initiating large-scale management actions in Los Haitises or any other system. As anthropogenic activities continue to modify and fragment landscapes, these activities have the potential to change the way pathogens and hosts interact across the globe making the study of parasite-host ecology increasingly important to conservation.

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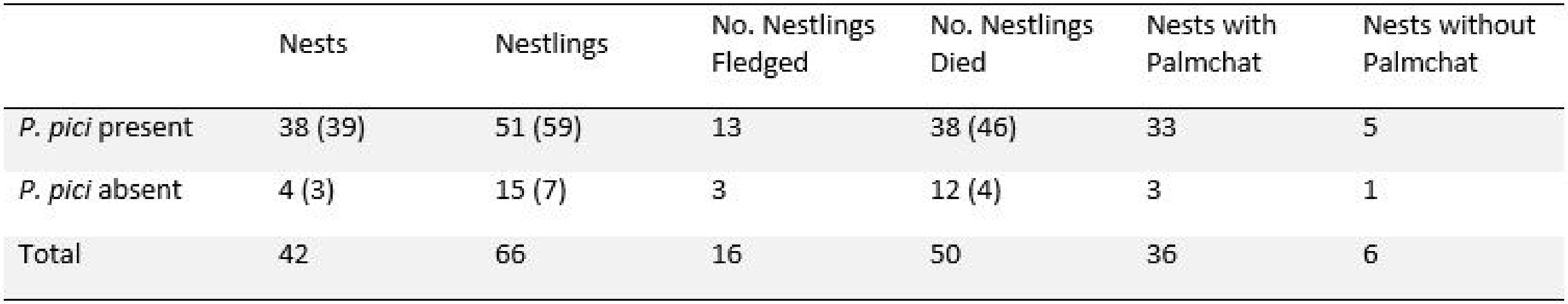
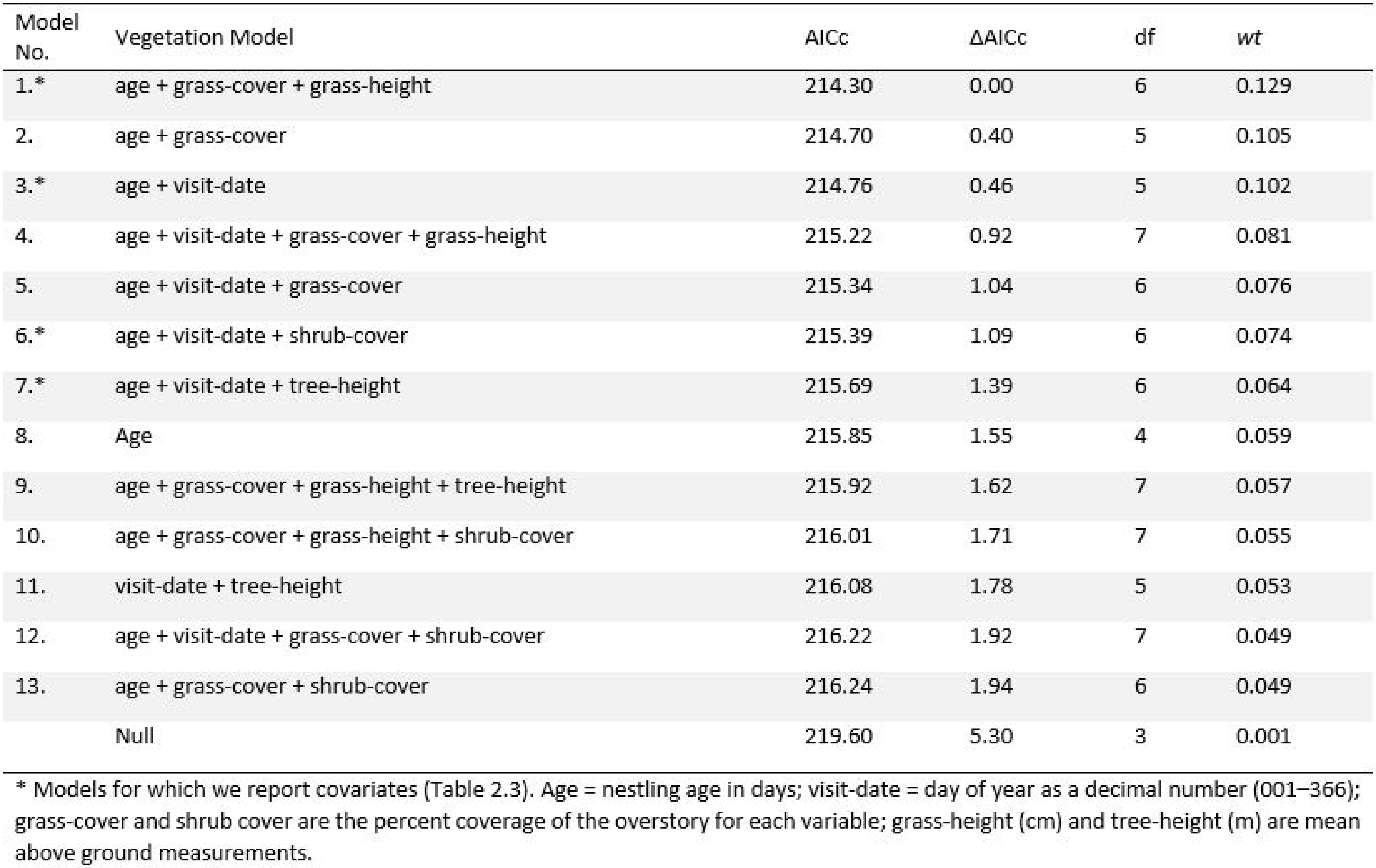
Tables

Table 2.1 For *P. pici* infestation and survival of Ridgway’s hawk (*Buteo ridgwayi*) nestlings in Los Haitises National Park, Dominican Republic, 2016 and 2017. Numbers in parentheses include nests where a sibling had ≥ 1 *P. pici* larva or where *P. pici* pupae were found in the nest cup substrate after nestlings had died (see methods). Palmchat (*Dulus dominicus*) columns are the number of Ridgway’s hawk nests that were either built by or inhabited by palmchats (with) and those that were not (without).



	Nests	Nestlings	No. Nestlings Fledged	No. Nestlings Died	Nests with Palmchat	Nests without Palmchat
P. pici present	38 (39)	51 (59)	13	38 (46)	33	5
P. pici absent	4 (3)	15 (7)	3	12 (4)	3	1
Total	42	66	16	50	36	6

Table 2.2 AICc results for linear mixed models comparing log+1 of *P. pici* larvae to vegetation variables as well as age and visit-date (see Methods) for Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park, Dominican Republic, 2016 and 2017.



Model No.	Vegetation Model	AICc	ΔAICc	df	*wt*
1.*	age + grass-cover + grass-height	214.30	0.00	6	0.129
2.	age + grass-cover	214.70	0.40	5	0.105
3.*	age + visit-date	214.76	0.46	5	0.102
4.	age + visit-date + grass-cover + grass-height	215.22	0.92	7	0.081
5.	age + visit-date + grass-cover	215.34	1.04	6	0.076
6.*	age + visit-date + shrub-cover	215.39	1.09	6	0.074
7.*	age + visit-date + tree-height	215.69	1.39	6	0.064
8.	Age	215.85	1.55	4	0.059
9.	age + grass-cover + grass-height + tree-height	215.92	1.62	7	0.057
10.	age + grass-cover + grass-height + shrub-cover	216.01	1.71	7	0.055
11.	visit-date + tree-height	216.08	1.78	5	0.053
12.	age + visit-date + grass-cover + shrub-cover	216.22	1.92	7	0.049
13.	age + grass-cover + shrub-cover	216.24	1.94	6	0.049
	Null	219.60	5.30	3	0.001

* Models for which we report covariates (Table 2.3). Age = nestling age in days; visit-date = day of year as a decimal number (001–366); grass-cover and shrub cover are the percent coverage of the overstory for each variable; grass-height (cm) and tree-height (m) are mean above ground measurements.

Table 2.3 Coefficients (β) of top models (see methods for model selection process) for linear mixed models ± standard error, comparing log+1 of *P. pici* larvae to vegetation variables as well as age and visit-date for Ridgway's hawk (*Buteo ridgwayi*) in Los Haitises National Park, Dominican Republic, 2016 and 2017. 85% confidence intervals are in parentheses.

Model No.	Intercept	Age	Visit-date	Grass-cover	Grass-height	Shrub-cover	Tree-height	ICC
1.	*1.532 (1.038, 2.047)	*0.039 (0.017, 0.059)	-	*-0.038 (-0.060, -0.017)	*0.006 (0.001, 0.012)	-	-	0.4298
3.	-0.150 (-1.390, 1.098)	*0.032 (0.010, 0.054)	*0.014 (0.003, 0.025)	-	-	-	-	0.4799
6.	-0.511 (-1.779, 0.774)	*0.031 (0.009, 0.053)	*0.016 (0.005, 0.027)	-	-	0.015 (-0.001, 0.031)	-	0.4644
7.	0.148 (-1.099, 1.423)	*0.027 (0.004, 0.049)	*0.016 (0.005, 0.026)	-	-	-	-0.041 (-0.090, 0.008)	0.4524

* 85% confidence intervals do not span 0. Age = nestling age in days; visit-date = day of year as a decimal number (001–366); grass-cover and shrub cover are the percent coverage of the overstory for each; grass-height (cm) and tree-height (m) are mean above ground measurement; ICC = intraclass correlation coefficient: [(within-nest covariance) / (within-nest covariance + overall variance)]. - Variable not included in model.

APPENDIX A

Photographs of study organisms and Los Haitises National Park, Dominican Republic

Figure A.1 *Philornis pici* **adult (Photo: Martín Quiroga)**

Figure A.2 Ridgway's hawk (*Buteo ridgwayi*) adult

Figure A.3 Three *Philornis pici* larvae in the left leg of a nestling Ridgway's hawk (*Buteo ridgwayi*).

Figure A.4 ***Philornis pici*** **larvae in the face of a nestling Ridgway’s hawk (*Buteo ridgwayi*).**

Figure A.5 Ridgway's hawk (*Buteo ridgwayi*) adult pair on their self-made nest in a deciduous tree (Photo: Thomas Hayes).

Figure A.6 **Ridgway's hawk (*Buteo ridgwayi*) adult pair in their nest atop a palmchat (*Dulus dominicus*) communal nest structure in a royal palm (*Roystonea borinquena*).**

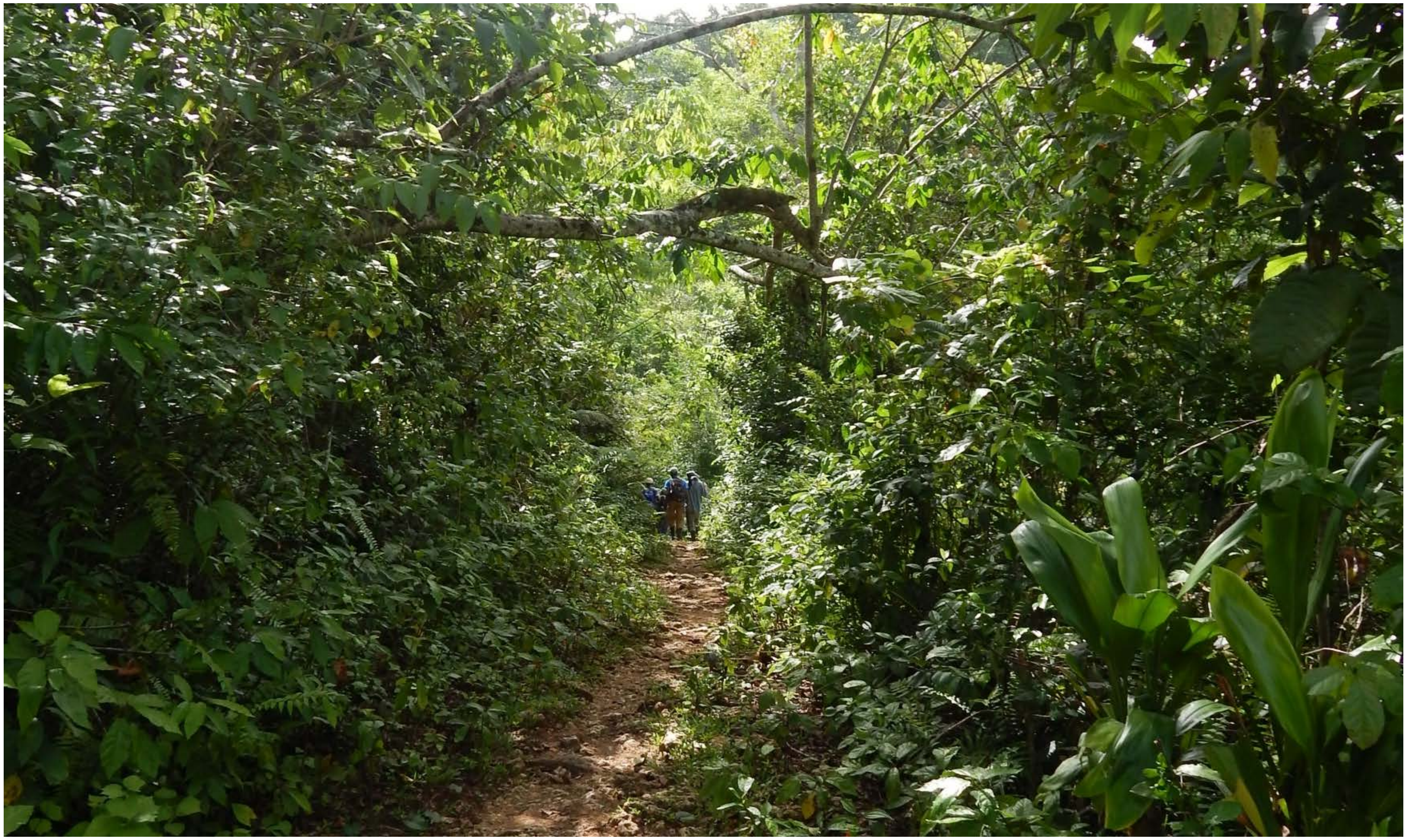


Figure A.7 Man-made path through forest vegetation in Los Haitises National Park, Dominican Republic.

Figure A.8 Cultivated valley between limestone karst hills with secondary forest vegetation in Los Haitises National Park, Dominican Republic.

Figure A.9 A climber accesses a Ridgway's hawk (*Buteo ridgwayi*) nest in a royal palm tree (*Roystonea borinquena*). The palm is in a small valley pasture and secondary forest growth is visible on the rocky karst hill in the background (Los Haitises National Park, Dominican Republic).

Figure A.10 Palmchat (*Dulus dominicus*) adult.

Figure A.11 View from below: palmchat (*Dulus dominicus*) communal nest structure in a coconut palm (*Cocos nucifera*).

Figure A.12 Climber, Thomas Hayes accessing a palmchat (*Dulus dominicus*) nest in a coconut palm (*Cocos nucifera*).

Figure A.13 Climber, Thomas Hayes, standing between two palmchat (*Dulus dominicus*) nests in a royal palm (*Roystonea borinquena*). The palm is located in a small-valley farm plot between low karst hills in Los Haitises National Park, Dominican Republic.

APPENDIX B

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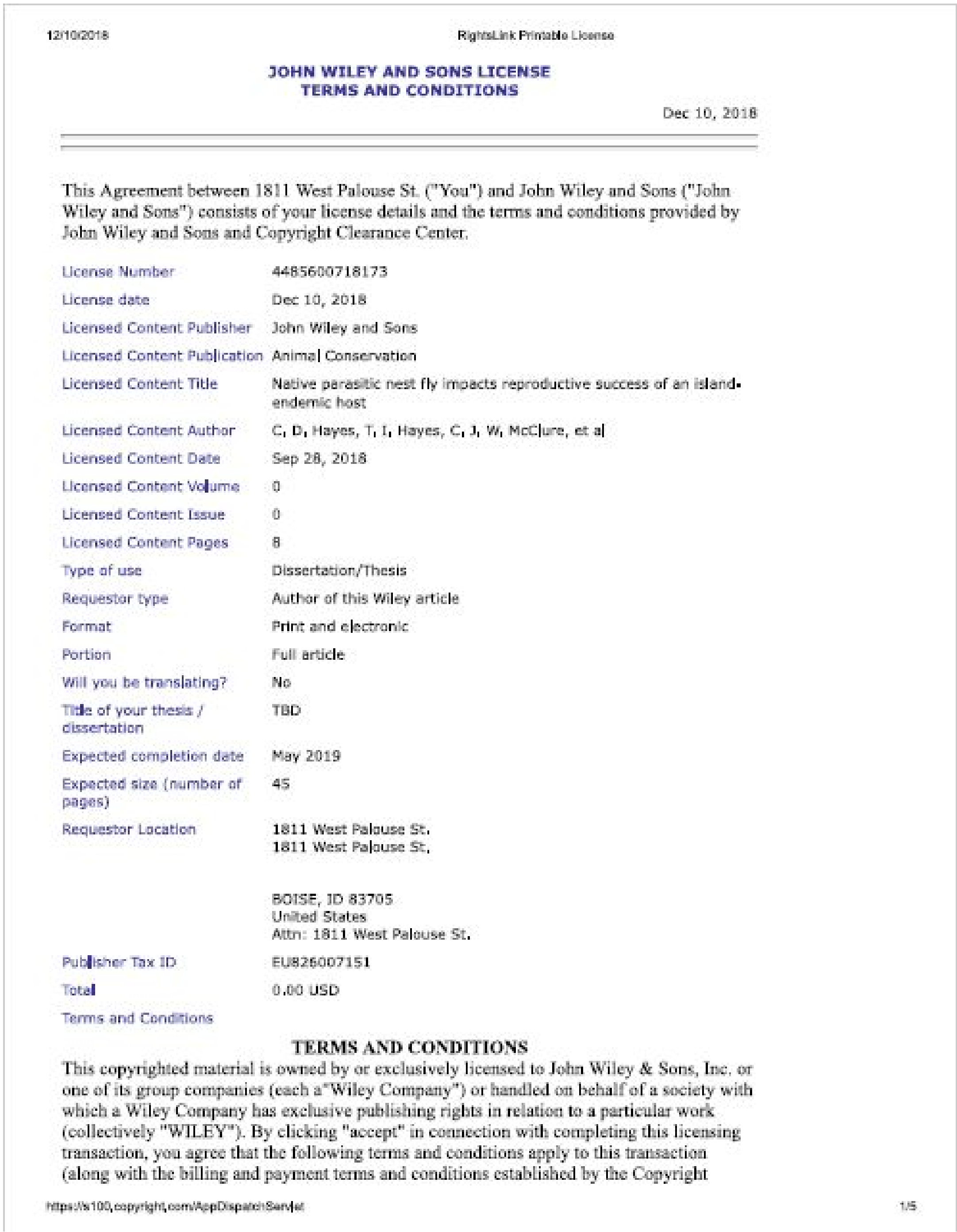

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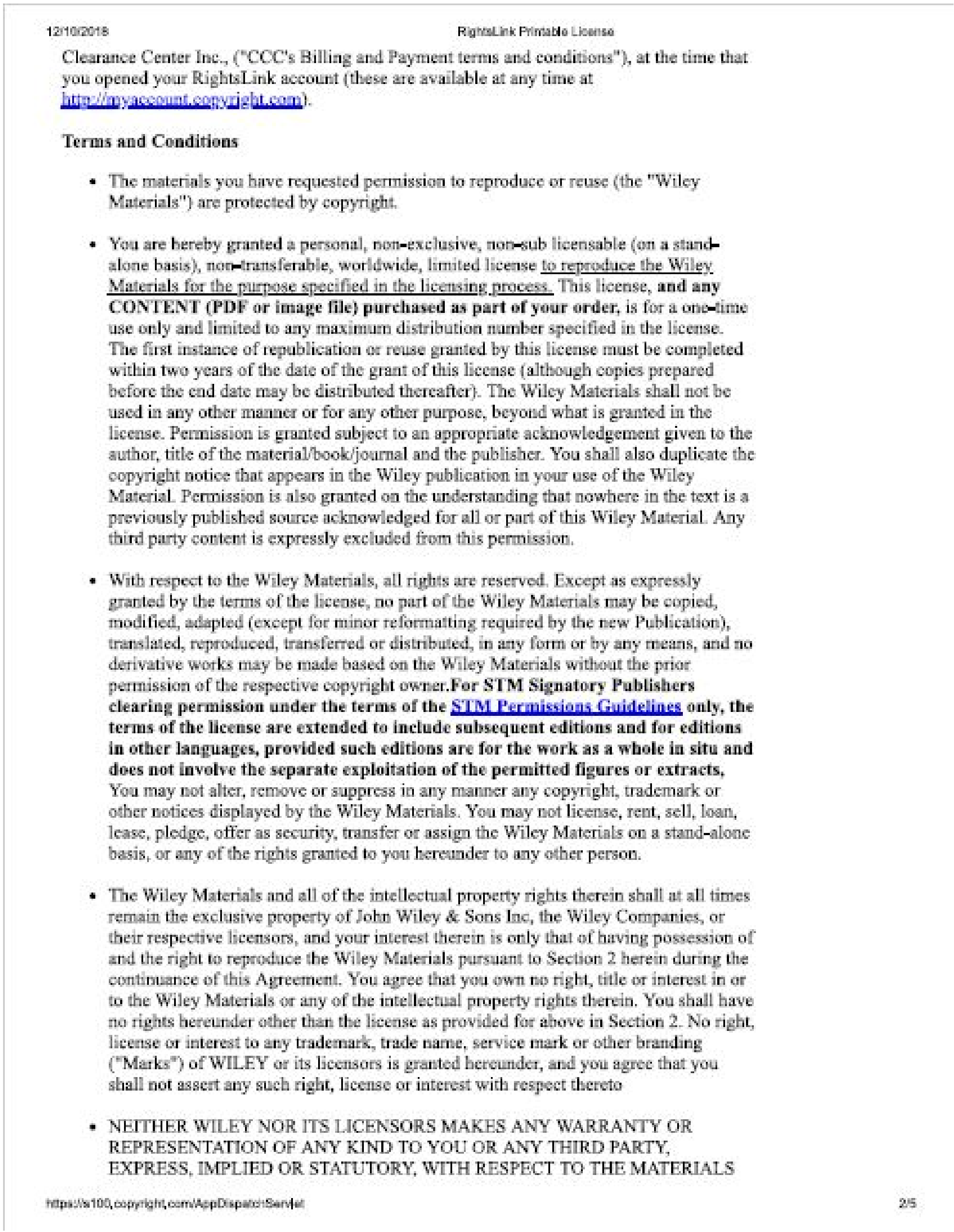

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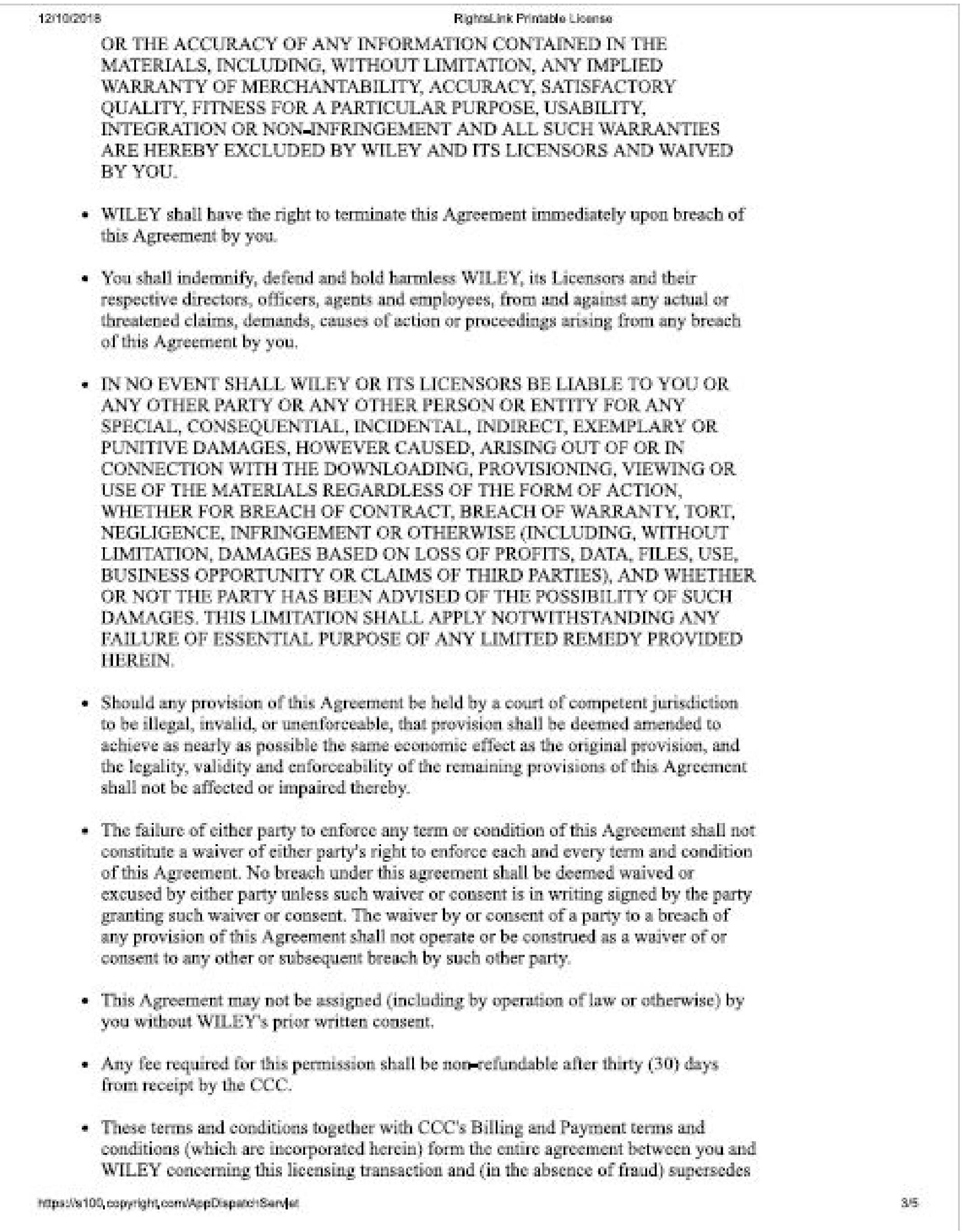

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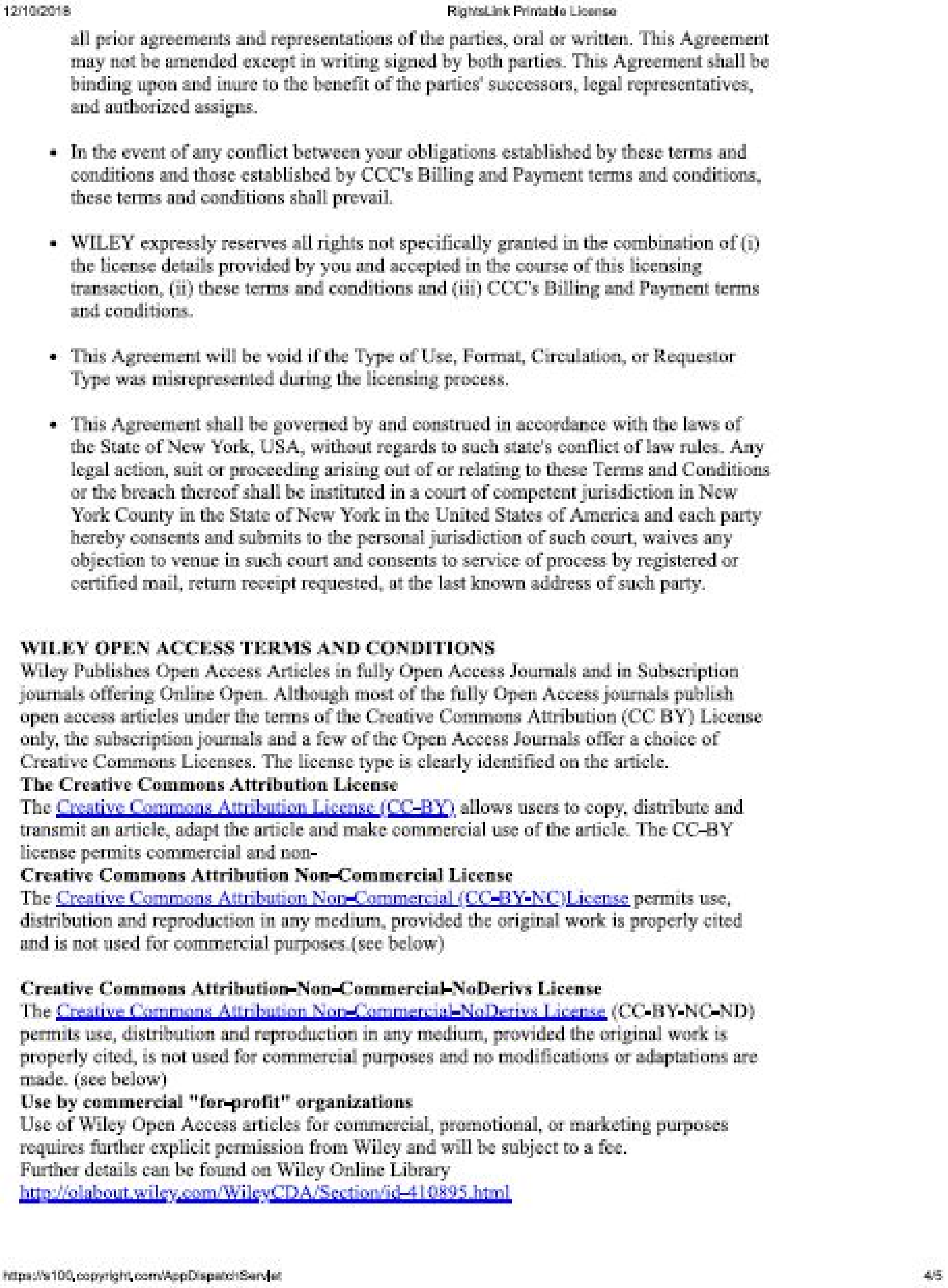

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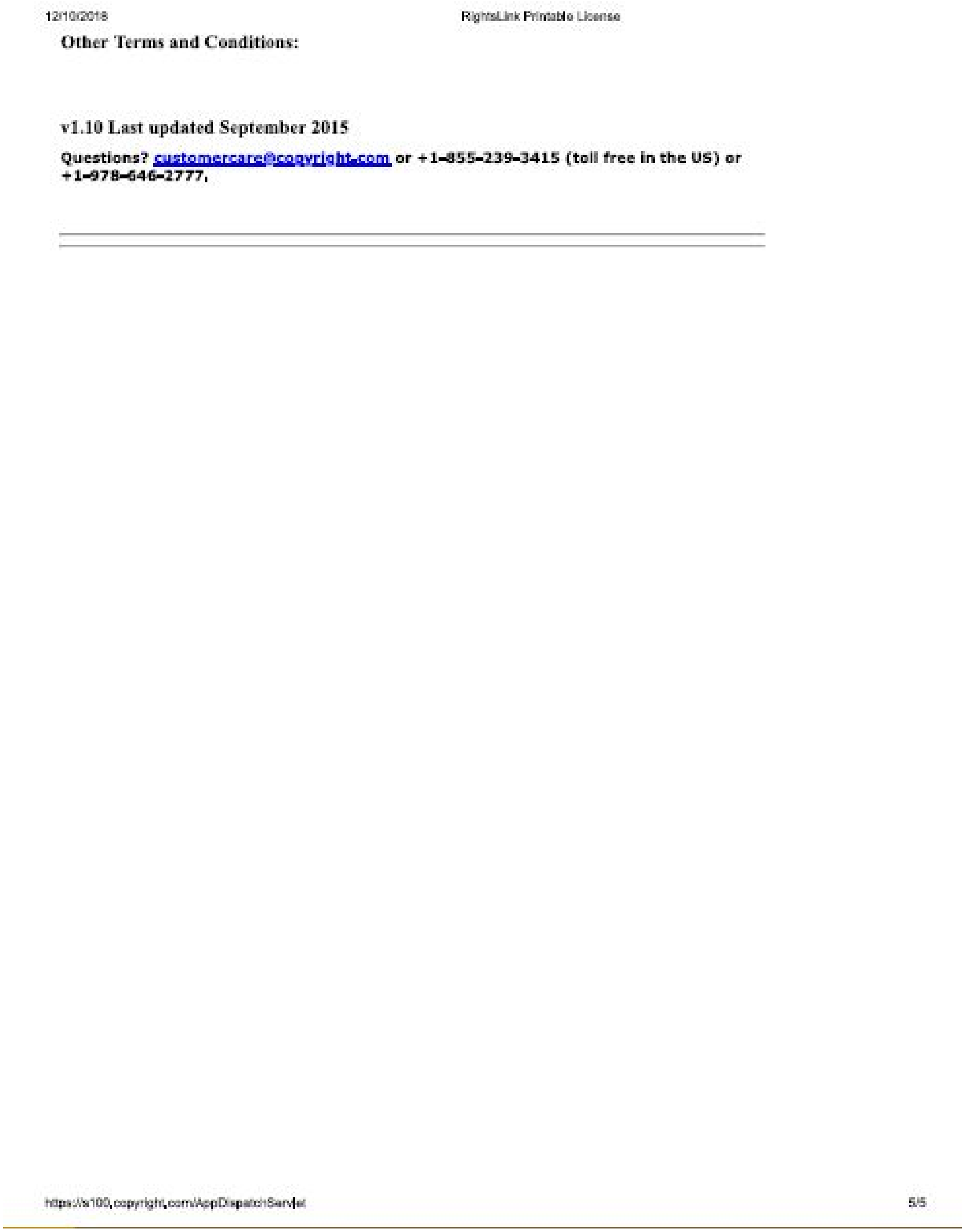

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