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BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Parasitism by an invasive nest fly reduces future reproduction in Galápagos mockingbirds

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Abstract

Organisms allocate limited resources to competing activities such as reproduction, growth, and defense against parasites and predators. The introduction of a novel parasite may create new life history trade-offs. As hosts increase their investment in self-maintenance or defense, the cost of parasitism may carry over to other aspects of host biology. Here, in an experimental field study, we document delayed effects of an introduced nest parasite, *Philornis downsi,* on reproduction of Galápagos mockingbirds (*Mimus parvulus*). Parasitism of first nests reduced both the number and size of chicks that parents hatched when they re-nested several weeks later. The delayed effect of *P. downsi* on future reproduction may have been mediated by behavioral shifts by the parents to avoid or resist parasitism. Our results demonstrate that effects of parasitism can persist even after immediate exposure ends. We draw attention to the potential implications that introduced parasites have for host reproductive strategies.

Keywords Life history · *Philornis downsi* · *Mimus parvulus* · Parental compensation · Tropics

Introduction

The fictional Darwinian demon—an organism that develops rapidly, has infinite offspring, and never ages—forces the recognition of trade-offs at the core of life history theory (Gustafsson et al. 1994). In reality, activities such as reproduction and self-maintenance are costly; limited resources force organisms to invest in one activity at the expense of others (Stearns 1976; van Noordwijk and de Jong 1986; Gustafsson et al. 1994; Zera and Harshman 2001). Parasites and pathogens can increase the severity of life history trade-offs (Gustafsson et al. 1994; Branson 2003; Descamps et al. 2009). Defense against parasitism demands additional resources; hosts may repay the costs directly, in the form of decreased survival, or indirectly, through trade-offs in current or future reproduction (Richner and Tripet 1999; Zuk and Stoehr 2002; Hanssen 2006; Asghar et al. 2015).

Whether parasitized hosts trade defense for survival or reproduction may depend on future opportunities for reproductive success (Agnew et al. 2000). If infection inevitably reduces the likelihood of survival or future reproductive opportunities, then parasitized hosts should invest earlier and more heavily in reproduction, often called "terminal investment" (Clutton-Brock 1984; Forbes 1993; Michalakis and Hochberg 1994; Agnew et al. 2000; Fredensborg and Poulin 2006). Evidence for terminal investment in reproduction in response to parasitism has been observed in diverse hosts including insects (Polak and Starmer 1998; Adamo 1999; Leventhal et al. 2014), crustaceans (Chadwick and Little 2005), mollusks (Minchella and Loverde 1981; Thornhill et al. 1986), mammals (Willis and Poulin 1999; Kristan 2004; Schwanz 2008; Jones et al. 2008), lizards (Sorci et al. 1996), and birds (Bonneaud et al. 2004; Podmokła et al. 2014).

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Terminal investment is predicted when infection is chronic and decreases residual reproductive value (Schwanz 2008). However, some parasites only use the host for a short period of time and have little effect on the likelihood of future reproductive opportunities (Forbes 1993; Telfer et al. 2005). Examples of such parasites include ectoparasitic species of mites, fleas, flies, and other arthropods that live in birds' nests, feeding on nestling birds and their parents. Nest parasites diminish reproductive success of their hosts by reducing the number, quality, or fledging success of the offspring (Moss and Camin 1970; Brown and Brown 1986; Møller 1993; Christe et al. 1996; Fitze et al. 2004; McNew and Clayton 2018). Exposure to nest parasites is typically limited to the nesting period and generally does not directly affect parent survival. Because hosts can expect future reproductive opportunities, some theory predicts that hosts should shift investment towards parasite defense and survival, and away from reproduction in response to nest parasites (Forbes 1993). Consistent with this hypothesis, nest parasites can cause parents to lay smaller clutches (Moss and Camin 1970), fewer clutches (de Lope and Møller 1993) or even abandon nests all together (Duffy 1983).

In other cases, however, parents instead intensify reproductive efforts in response to nest parasites (Perrin et al. 1996). For instance, parents may increase provisioning rates to help nestlings compensate for parasitism (Christe et al. 1996; Richner and Tripet 1999; Bouslama et al. 2002; Banbura et al. 2004; Hund et al. 2015). This additional effort may allow parents to maintain some current reproductive success; however, it can also negatively affect future reproduction (Johnson and Albrecht 1993; Perrin et al. 1996; Bize et al. 2004). For example, blue tits (*Parus caeruleus*) increase provisioning rates in response to hen fleas (*Ceratophyllus gallinae*), but parasitized parents pay a cost for these extra efforts in terms of lower return rates and reproductive success the following year (Richner and Tripet 1999). Still, parents do not always increase reproductive effort in response to parasites (Morrison and Johnson 2002; Gallizzi et al. 2008) and even when they do, an increase in effort does not always have costs for future reproduction (Fitze et al. 2004). In sum, parental compensation may allow parents to moderate fitness losses to parasites; however, it is unclear how common compensation is, or if compensation inevitably has carry-over consequences itself.

Most studies of parental responses to nest parasites have focused on temperate birds (Hund et al. 2015). Moreover, evidence for parental compensation comes almost exclusively from one group of birds, tits (Paridae). Tropical birds are generally considered to have higher annual survival rates than temperate birds and therefore more lifetime opportunities to reproduce (Martin 1996; Robinson et al. 2010; Muñoz et al. 2018). Thus, nest parasites may mediate different trade-offs between current and future reproduction in tropical hosts. Compared to temperate birds, tropical birds may have less incentive to compensate for nest parasitism because they are more likely to have future reproductive opportunities and therefore should instead maintain their own condition and survival first (Ardia 2005).

In this study, we investigate the effects of a recently introduced nest parasite on reproductive investment of a Neotropical passerine bird, the Galápagos mockingbird (*Mimus parvulus*). The nest fly *Philornis downsi* has been recorded in nests of Galápagos passerines since the late 1990s (Fessl et al. 2001). Adult *P. downsi* are free-living; however, the larval flies live in birds' nests and feed on nestling birds, often killing them (Koop et al. 2011; Kleindorfer and Dudaniec 2016; McNew and Clayton 2018). *P. downsi* larvae also feed on adult female birds while incubating and brooding the nest (McNew and Clayton 2018), but no instances of parent mortality due to parasitism are known. Adults are much larger than nestlings, which presumably reduces the direct cost of parasitism. In addition, adults may have defenses against parasitism that the nestlings do not possess, including immune responses (Huber et al. 2010; Koop et al. 2013b) and the ability to avoid contact with parasites by leaving the nest or reducing brooding (Koop et al. 2013b; Knutie et al. 2016).

Effects of *P. downsi* on Galápagos mockingbird reproductive success vary among years and are more severe in dry conditions (McNew et al. 2019). Mockingbirds may increase provisioning in response to *P. downsi* (Knutie et al. 2016); however, this response is not seen in all years (McNew et al. 2019). Furthermore, it is unknown whether compensation results in trade-offs in other areas, such as future reproduction or survival. To investigate these potential carry-over consequences of parasitism, we experimentally manipulated the presence of *P. downsi* in mockingbird nests and measured the effects of parasitism on the condition, behavior, next-year survival, and re-nesting investment of parent mockingbirds. We used these data to test two hypotheses: First, under the "parental compensation" hypothesis, parents will respond to nest parasites by increasing investment in provisioning and care of nestlings. This increased effort may come at the expense of parental survival or condition. Alternatively, under the "cut and run" hypothesis, parents will respond to nest parasites by reducing investment in reproduction, thus prioritizing their own condition, survival, and long-term reproductive potential.

Materials and methods

Study system

The study was conducted in January–May 2015 and 2016 on Santa Cruz Island in the Galápagos, Ecuador. The field site, El Garrapatero, is a 3 × 4 km region of arid scrub habitat. Galápagos mockingbirds are common, year-round residents at the site. Breeding occurs during the rainy season, typically January–April. Mockingbirds lay between one and five eggs, which are incubated by the female alone for roughly 15 days. After hatching, nestlings are fed by both parents until the nestlings fledge at approximately 14 days of age (Knutie et al. 2016). Mockingbirds may re-nest if their initial clutch fails or if the rainy season is long enough (Curry and Grant 1990); however, they do not reuse the same nest. Demographic studies estimate that mockingbirds double nest in approximately one out of every three to four seasons (Curry and Grant 1989). In 2015, most pairs of mockingbirds nested twice, first in February–March and then again in April–May. Rains increased over the course of the season, as a result the first reproductive attempt occurred during drier conditions than the second (Supplemental Fig. 1).

Experimental manipulation

Active nests were checked every other day. When nestlings hatched, they were removed briefly and weighed while the nest was fumigated with 1% aqueous permethrin (Permectrin™ II), or "sham-fumigated" with water as a control. Treatment of the first nest was decided by coin flip. Subsequent nests were assigned to alternating treatments as their nestlings hatched, so that treatments would be relatively matched in date. Correspondingly, the earliest and latest hatch dates for nests in each treatment were identical (5 March and 22 March, respectively). Permethrin has been used in several previous studies to eliminate *P. downsi* larvae from nests (Fessl et al. 2006; Koop et al. 2013b; O'Connor et al. 2014; Knutie et al. 2016). Permethrin has little or no effect on nestlings (Causton and Lincango 2014; López-Arrabé et al. 2014). Nests were fumigated soon after the first nestling hatched and then a second time 5–6 days later. At 10–11 days of age, nestlings were banded with an individually numbered Monel band and a unique combination of three plastic color bands. At 5–6 days and 10–11 days, nestlings were weighed and measured; nestling growth data are reported in McNew et al. (2019). Fledging success was determined by re-sighting banded individuals after they left the nest. We did not observe any signs of nest depredation (e.g., the loss of an entire healthy clutch, destroyed nests, predators captured on nest videos). Therefore, we assume that *P. downsi* was the primary cause of nestling mortality. Second nests of each pair were treated (for a separate study) with the same experimental treatment as their first, i.e., second nests were fumigated or sham-fumigated shortly after nestlings hatched. Thus, carry-over effects of *P. downsi* could only be assessed before treatment of the second nest.

In total, we studied 35 breeding pairs of mockingbirds. Of these, 22 pairs (63%) re-nested after their first breeding attempt. Three re-nesting attempts were excluded from study, because they were discovered too late. Fledging success was not analyzed for two additional second nest attempts, because treatment was inadvertently switched between attempts. Of the 19 pairs whose second nest was included in the study, 11 were in the fumigated treatment and 8 in the sham-fumigated treatment. All 35 first nests were included in analyses, along with 19 second nest attempts.

Parasite quantification

Once nestlings had died or fledged, the nest was collected and dissected to quantify the parasites in it. *P. downsi* abundance was the total number of larvae and pupae found in the nest (Koop et al. 2013a, b; Knutie et al. 2016). Pupae were reared to the adult stage to confirm that they were *P. downsi*; no other fly species were found in nests. Parasite abundance and fledging success for the mockingbirds' first reproductive attempts are also reported in (McNew et al. 2019).

Parental identification and condition

Parents were opportunistically captured with mist nets during their first reproductive attempt. We banded 53 parent mockingbirds during the breeding season, 30 of which were captured during incubation and provisioning of their first nest. Parents were sexed using skeletal size and the presence/absence of a brood patch. They were banded with an individually numbered Monel band and a unique combination of color bands. We quantified adult body condition, following the scaled body mass method described by Peig and Green (2009) which scales body mass to skeletal size (tarsus length). We collected a small blood sample via brachial venipuncture to quantify immune response to *P. downsi*. We estimated next-year survival for parents by re-sighting color-banded parents about a year later when the same study area was surveyed on a daily basis from January–April 2016 (McNew et al. 2019). The identity and location of all color-banded mockingbirds was recorded as they were re-sighted or recaptured. Replicate data on the effects of *P. downsi* on parental body condition and immune responses were collected in 2016 from 48 parent mockingbirds. Mockingbirds in 2016 only attempted one nest, so carry-over effects on reproduction were not replicated that year.

Behavior

We used small surveillance cameras (31 × 36 mm; Sony SC-IRB) suspended above nests and attached to a portable digital video recorders (Lawmate PV700 Hi-res DVR) to record behavior of mockingbirds at a haphazard sample of nests between the hours of 0600 and 1000 (McNew et al. 2019). The mean ± SE video length was 2.13 ± 0.10 h. We recorded 18 videos during the first nesting period and 15 during the second. Behavior was scored using the program Boris (version 3.60) by one author (SMM). The following mutually exclusive parental behaviors were scored according to definitions described in Knutie et al. (2016): provisioning, allopreening nestlings, nest sanitation, brooding nestlings, and standing upright in the nest. Each behavior was scored as a percentage of total video time. Total time present at the nest was the sum of all behaviors. Allopreening and nest sanitation were combined for analysis, because they could occasionally be difficult to distinguish in videos. Provisioning data from mockingbirds' first attempts were previously reported (McNew et al. 2019).

Parental immune response

We used enzyme-linked immunosorbent assays (ELISAs) to quantify *P. downsi*-binding antibodies in parent mockingbirds following methods in Knutie et al. (2016). Ninety-six well plates were coated in 100 µl/well of *P. downsi* protein extract (capture antigen) diluted 1:100 in carbonate coating buffer, followed by incubation for 1 h on an orbital table. Plates were then washed and coated with 200 µl of blocking buffer (bovine serum albumin), followed by incubation for 30 min. Next, plates were washed and coated with 100 µl of mockingbird plasma diluted 1:100 in sample buffer and incubated for an hour, followed by washing and coating with 100 ul of Goat-αBird-IgG (diluted 1:10,000) (Antibodies Online, Atlanta GA, USA). Plates were incubated with the detection antibody for 1 h, and then washed. Finally, wells were filled with 100 µl of peroxidase substrate tetramethylbenzidine, TMB, Bethyl Laboratories, Montgomery, TX, USA) and incubated for exactly 15 min. The reaction was stopped using 100 µl/well of stop solution (Bethyl Laboratories).

Optical density (OD) was measured with a spectrophotometer (BioTek, Winooski, VT, USA; PowerWave HT, 450-nanometer filter). Samples were run in triplicate on each plate. Each plate also included a positive control sample of pooled adult plasma, which was used to control for inter-plate variation. Each plate also included three other methodological controls: (1) wells in which *P. downsi* antigen and the detection antibody were added but no plasma was added, to test for non-specific binding (NSB) of the detection antibody to the antigen; (2) wells in which the antigen was excluded but the rest of the procedure was followed to ensure that samples were binding exclusively to the antigen; and (3) blank wells, in which coating, sample, and blocking buffers were added, without antigen or plasma, followed by the detection antibody, to ensure that the buffers were uncontaminated. OD values were calculated as the mean OD from each sample minus the mean NSB value for that plate, scaled to the positive control OD to control for inter-plate variation. Higher OD values correspond to higher antibody binding levels.

Analyses

We used generalized linear mixed models (GLMMs) to analyze clutch size (number of eggs laid), brood size (number of nestlings hatched), nestling mass at hatching, parasite abundance, and reproductive success (number of fledglings per nesting attempt and percent fledging success). GLMMs included the fixed effects of treatment, nesting attempt, and treatment × nesting attempt, and the random effect of mockingbird pair. A significant interaction term indicates that the change in the response variable between reproductive attempts depended on treatment. Nestling mass was modeled with a gaussian error distribution. Clutch size was modeled with a Conway–Maxwell–Poisson distribution (Lynch et al. 2014). Brood size (hatching success) was analyzed using a binomial distribution, where the response variable was a paired vector of the number of eggs that hatched and the number of eggs that failed to hatch for each nest (Zuur et al. 2009; Crawley 2012). Parasite abundance was modeled using a zero-inflated GLMM with a negative binomial error distribution. Total number of fledglings was modeled using a negative binomial error distribution. Fledging success (proportion of nestlings that fledged) was modeled with a binomial distribution where the response variable was a paired vector of the number of nestlings that fledged and the number of nestlings that died for each nest.

Probability of re-nesting was evaluated with a binomial GLM with treatment and first nest clutch size as fixed effects. Time between nesting attempts was evaluated with a LM with treatment, date of first nest, and first nest clutch size as fixed effects. Mockingbird behaviors were individually analyzed using LMMs with treatment, nesting attempt, and treatment × nesting attempt as fixed effects, and mockingbird pair as a random effect. To differentiate total time spent provisioning from per-nestling provisioning, we additionally modeled provisioning behavior including the fixed effect of brood size.

Variation in parental condition and *P. downsi* antibody binding response (measured as optical density, OD) were analyzed using linear models (LMs) with treatment, sex, clutch size, and age of nestlings at capture as fixed effects. We limited analysis of condition and immune response to just those parents that were captured during incubation or provisioning of nestlings. We combined adults captured in both 2015 and 2016 for analyses of parental condition and immune response. Parental survival from 2015 to 2016 was analyzed using a binomial GLM with treatment, sex, first clutch hatch date, and first clutch size as fixed effects. Statistical analyses were conducted in RStudio (2016, version 1.0.136; R version 3.3.3) using the packages car, lmer4, MASS and smatr and glmmTMB. Degrees of freedom and *P* values for LMMs were calculated using a Satterthwaite approximation with the lmerTest package. Significant *P* values and estimates are from the minimal model, while non-significant values are those obtained before removing the variable from the full model (Crawley 2012). Non-significant interaction terms are presented in tables for completeness; however, if the interaction term was not significant, main effects estimates and *P* values are from the additive model after removing the interaction term.

Results

Breeding attempts summary

We followed reproductive success of 35 nests in the first reproductive attempt and 19 nests in the second. The probability of re-nesting did not differ between treatments (odds ratio estimate: 0.56, 95% CI 0.15–2.14, $P = 0.397$). The mean ± SE time between fledging or failure of the first clutch and the laying date of the second clutch (inter-nest interval) was 27 ± 1.17 days. There was no significant difference between treatments in inter-nest interval (effect size estimate β: 1.11 days, 95% CI − 3.69–5.92, $P = 0.65$). As expected, fumigating nests almost completely eliminated *P. downsi* (mean ± SE abundance in fumigated nests: 0.89 ± 0.27, sham-fumigated: 58.5 ± 7.4, $P < 0.001$). *Philornis downsi* abundance did not differ between reproductive attempts (sham-fumigated only, mean ± SE abundance first attempt: 57.3 ± 8.7, second attempt: 61.4 ± 14.9, $P = 0.44$).

Reproductive success and carry-over effects

Clutch and brood sizes did not differ between treatments during mockingbirds' first nesting attempt (Fig. 1a, b; Table 1). Parents in both treatments increased their clutch size when they re-nested (Fig. 1a; Table 1). However, there was a significant interaction between nesting attempt and treatment in hatching success (Table 1). Consequently, the second broods of sham-fumigated parents were 30% smaller than those of fumigated parents, an average of one fewer nestling per brood (Fig. 1b). There was also a significant interaction between treatment and nesting attempt in 1–2 day old nestling mass (Fig. 1c; Table 1). Masses were initially slightly higher for nestlings in sham-fumigated nests, but during second attempts nestlings in sham-fumigated nests were approximately 10% smaller than nestlings in fumigated nests (Fig. 1c). Thus, parents whose nest was sham-fumigated during their first attempt hatched fewer and smaller nestlings during the second nesting attempt, compared to fumigated parents. These differences occurred before the second nests were treated (because treatments were applied shortly after hatching).

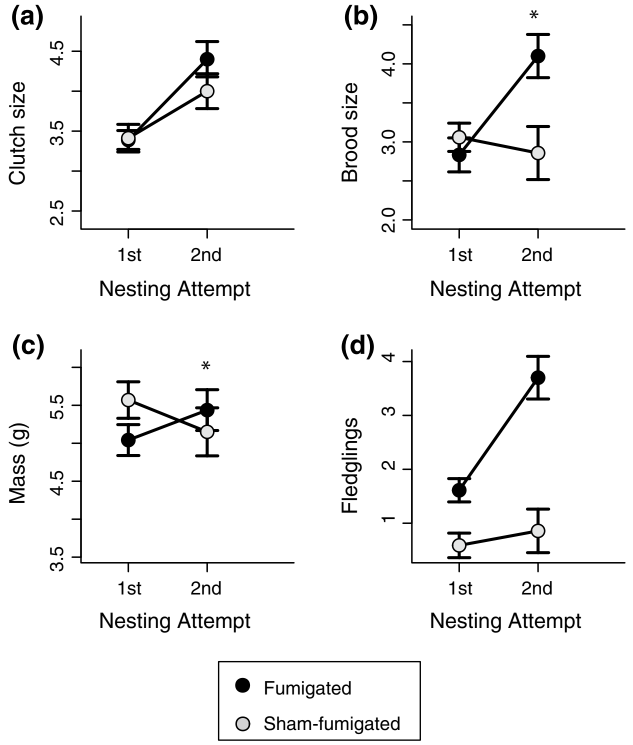

Fig. 1 Mean ± SE of raw values of **a** clutch size, **b** brood size, **c** nestling mass at hatching, and **d** number of fledglings for fumigated (black) versus sham-fumigated (gray) nests in first and second nesting attempts of mockingbirds. Data are from 18 fumigated and 17 sham-fumigated nests in the first attempt and 11 fumigated and 8 sham-fumigated nests in the second (see methods for details). Asterisks indicate significant interactions between treatment and nesting attempt

Parents of fumigated nests fledged significantly more nestlings than parents of sham-fumigated nests in both reproductive attempts (Fig. 1d; Table 1). Both treatments fledged more nestlings in their second nesting attempt (Fig. 1d; Table 1); the interaction of treatment and attempt was not significant. The mean ± SE fledging success for fumigated parents was 59.25% ± 7.3% in their first nesting attempt and 89.33% ± 7.4% in the second attempt. The mean ± SE fledging success for sham-fumigated parents was 19.11% ± 7.4% in their first attempt and 23.81% ± 11.4% in their second attempt (Table 1).

Parental behavior

There was no difference between treatments in the total amount of time that parents spent provisioning their first nests (Fig. 2a; Table 2). In contrast, parents of fumigated nests increased total provisioning time when they re-nested, whereas parents of sham-fumigated nests spent less time

Table 1 GLMM estimates for measures of reproductive success of fumigated and sham-fumigated nests during first and second nesting attempts

Response variable	Error distribution	Predictors	Estimates[a]	95% CI	*P*
Clutch size	COM–Poisson				
		(Intercept)[b]	3.49	3.24 to 3.75	< 0.001
		Treatment S	0.95	0.87 to 1.04	0.27
		Attempt 2	1.23	1.12 to 1.35	**< 0.001**
		Treat. × Att.	0.86	0.72 to 1.04	0.122
Hatching success	Binomial				
		(Intercept)	1.74	0.93 to 2.55	< 0.001
		Treatment S	0.55	−0.62 to 1.71	0.36
		Attempt 2	1.09	−0.29 to 2.47	0.122
		Treat. × Att.	−2.22	−4.07 to −0.37	**0.018**
1–2 Day old nestling mass	Gaussian				
		(Intercept)	5.07	4.52 to 5.61	< 0.001
		Treatment S	0.52	−0.23 to 1.28	0.179
		Attempt 2	0.3	−0.36 to 0.96	0.373
		Treat. × Att.	−1.06	−2.06 to −0.06	**0.04**
Fledglings	Negative binomial				
		(Intercept)	1.69	1.21 to 2.36	0.002
		Treatment S	0.3	0.17 to 0.51	**< 0.001**
		Attempt 2	2.1	1.36 to 3.24	**0.001**
		Treat. × Att.	0.63	0.21 to 1.89	0.413
Fledging success	Binomial				
		(Intercept)	0.49	−0.24 to 1.22	0.187
		Treatment S	−2.48	−3.65 to −1.31	**< 0.001**
		Attempt 2	1.74	0.67 to 2.81	**0.001**
		Treat. × Att.	−1.5	−3.37 to 0.37	0.115

Bold values indicate statistically significant of *P* values ($P \leq 0.05$)

[a] Estimates are untransformed from raw output for Gaussian variables, exponentiated from outputs of negative binomial and COM–Poisson GLMMs, and presented as log-odds for binomial GLMMs

[b] The intercept in each case is the estimate for fumigated nests during the first attempt. Contrasts show estimates for sham-fumigated nests (S), second nesting attempts, and the interaction of treatment × attempt

provisioning (Fig. 2a; Table 2). Brood size had a significant effect on provisioning behavior. When brood size was included in provisioning models (i.e., provisioning after controlling for differences in brood size), there was no difference in provisioning time either between treatments, between nesting attempts, or the interaction of treatment × attempt (Table 2). There was no significant difference between treatments or between nesting attempts in the amount of time that parents spent brooding their nestlings (Fig. 2b; Table 2). The time spent allopreening and sanitizing the nest did not differ significantly between treatments in the first breeding attempt, nor did it increase significantly between attempts for parents of fumigated nests (Fig. 2c; Table 2). However, there was a significant interaction between treatment and attempt; the amount of time that parents of sham-fumigated nests spent allopreening nestlings and sanitizing the nest increased substantially between first and second attempts (Fig. 2c; Table 2). Mockingbirds did spend more time standing upright in their second nests compared to their first nests; however, there was no difference in percent standing time between treatments (Fig. 2d; Table 2). The total time present at the nest was higher for sham-fumigated parents and increased for both treatments in the second attempt (Table 2).

Parental condition, immune response, and next-year survival

Scaled mass of parents decreased over the nestling period (Fig. 3; Table 3). Parent sex, clutch size, and treatment all had no significant effect on scaled mass. Antibody binding activity (optical density, OD) was higher in females than males; however, there was no difference in OD between treatments or with age of nestlings when females were captured (Table 3). Twenty-six out of 53 banded parents were re-sighted the following year (2016). Males were more likely to be re-sighted the following year than females, but the

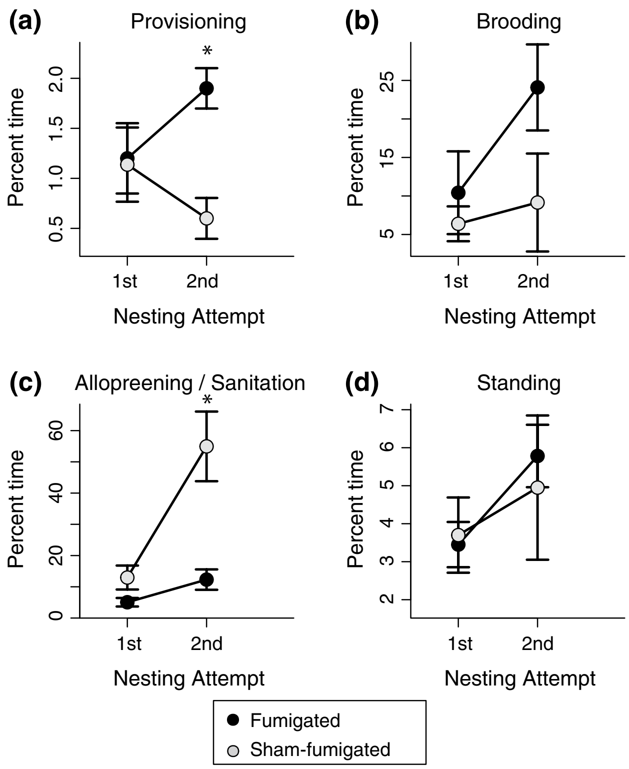

Fig. 2 Behaviors of parents at fumigated and sham-fumigated nests during their first and second reproductive attempts. All behaviors are scored as a percentage of total video time. Mean ± SE were calculated from raw data. Behavioral data were produced from 10 fumigated and 11 sham-fumigated videos recorded during the first breeding attempt, and 8 fumigated and 4 sham-fumigated videos during the second attempt (see "Materials and methods" for details). Asterisks indicate a significant interaction between treatment and nesting attempt

probability of re-sighting did not differ between treatments (Table 3).

Discussion

Nest parasites can mediate trade-offs with survival or future reproductive success as hosts shift resource allocation in response to parasitism (Richner and Tripet 1999). Here, we tested whether mockingbirds would increase reproductive effort to help nestlings compensate for energy lost to parasites or whether they would decrease investment in reproduction to devote energy to self-maintenance and parasite defense. We manipulated *P. downsi* abundance in mockingbird nests to test the effects of parasitism on mockingbird condition, behavior, survival, and reproductive investment. Overall, we did not find evidence for parental compensation; instead, mockingbirds appeared to "cut and run." *P. downsi* affected short-term future reproduction of mockingbirds by reducing both the number and size at hatching of nestlings when mockingbirds re-nested. Thus, our data demonstrate that trade-offs associated with parasitism are not limited to the period of exposure but can also carry over to future reproductive success.

After their first breeding attempt, sham-fumigated parents had significantly lower hatching success and, moreover, the nestlings that did hatch were smaller. The change in 1–2-day-old nestling mass between nesting attempts of sham-fumigated parents was particularly striking, because in the first attempt sham-fumigated nestlings tended to be slightly heavier than fumigated nestlings. If anything, this pattern suggests that despite randomization of treatment, parents of sham-fumigated nests tended to be in slightly better reproductive condition in their first attempt compared to fumigated parents. Nevertheless, instead of their reproductive investment increasing over the course of the season, as it did for fumigated parents, it decreased.

In contrast to other studies of nest parasites, including in this system, *P. downsi* did not cause parents to increase provisioning behavior during their first nesting attempt (Christe et al. 1996; Knutie et al. 2016). Because of the dry conditions during the first attempt, there may not have been enough food in the environment to support compensation (McNew et al. 2019). Indeed, provisioning rates during the first breeding attempt were lower than in other 2 years in which mockingbirds were more tolerant to *P. downsi* (McNew et al. 2019). Mockingbirds adjust clutch sizes across years according to environmental conditions, indicating that investment in reproduction depends on the number of offspring they estimate they can feed (Curry and Grant 1989). Some compensation may be possible in wetter years of higher food abundance (Knutie et al. 2016). However, in most years, the tight relationship between environment and reproductive effort likely leaves little room for accommodating the extra costs of parasitism.

The improved environmental conditions later during the second nesting attempt should have allowed parental compensation in response to parasitism. Parents of fumigated nests had larger broods when they re-nested and increased total provisioning time proportionally. In contrast, parents of sham-fumigated nests did not increase brood size or either per-nestling or total provisioning of their second broods. The difference between treatments in provisioning behavior shows that environmental conditions were not the limiting factor for provisioning behavior during the second nesting attempt. The fact that parents of sham-fumigated nests did not increase provisioning to their second broods suggests that some costs of parasitism carried over from first to second nesting attempts and limited parental investment in reproduction when they re-nested.

Instead of investing more energy in reproductive efforts, parents of sham-fumigated nests may have allocated more energy to self-maintenance and/or parasite defense. Nest parasites can cause harm to brooding mothers themselves,

Table 2 GLMM estimates for parental behaviors of fumigated and sham-fumigated nests during first and second nesting attempts

Response variable	Predictors	Estimates	95% CI	*P*
Provisioning (total)				
	(Intercept)[a]	1.19	0.56 to 1.83	0.001
	Treatment S	−0.1	−1.08 to 0.89	0.851
	Attempt 2	1.08	0.50 to 1.66	**0.002**
	Treat. × Att.	−1.49	−2.55 to −0.43	**0.013**
Provisioning (controlling for brood size)				
	(Intercept)	−0.35	−1.23 to 0.52	0.434
	Treatment S	−0.14	−0.87 to 0.59	0.712
	Attempt 2	−0.61	−1.25 to 0.04	0.075
	Brood size	0.64	0.38 to 0.90	**< 0.001**
	Treat. × Att.	−0.38	−1.48 to 0.73	0.511
Brooding				
	(Intercept)	12.35	3.75 to 20.94	0.009
	Treatment S	−8.37	−19.40 to 2.66	0.147
	Attempt 2	9.99	−0.66 to 20.65	0.076
	Treat. × Att.	−10.91	33.48 to 11.67	0.351
Allopreening/sanitation				
	(Intercept)	4.73	−2.58 to 12.03	0.217
	Treatment S	8.51	−2.63 to 19.66	0.149
	Attempt 2	7.97	−0.73 to 16.68	0.085
	Treat. × Att.	33.42	17.94 to 48.89	**< 0.001**
Standing				
	(Intercept)	3.64	2.17 to 5.12	<0.001
	Treatment S	−0.18	−2.07 to 1.71	0.853
	Attempt 2	1.97	0.14 to 3.80	**0.043**
	Treat. × Att.	−1.08	−5.00 to 2.83	0.592
Present				
	(Intercept)	17.03	6.93 to 27.13	0.002
	Treatment S	16.58	3.63 to 29.54	**0.018**
	Attempt 2	31.74	19.23 to 44.26	**< 0.001**
	Treat. × Att.	21.39	−4.39 to 47.16	0.115

Bold values indicate statistically significant of *P* values ($P \leq 0.05$)

[a] The intercept in each case is the estimate for fumigated nests during the first attempt. Contrasts show estimates for sham-fumigated nests (S), second nesting attempts, and the interaction of treatment × attempt

producing stress and inflammatory or other immune responses (Sorci and Faivre 2009; Owen et al. 2010; Fowler and Williams 2017). These responses, in turn, can negatively affect egg hatchability and other measures of reproductive success (Saino et al. 2005; Bize et al. 2008; Love and Williams 2008; Fowler and Williams 2017). In contrast to studies of other Galápagos hosts of *P. downsi* (Huber et al. 2010; Koop et al. 2013b), we did not find evidence that mockingbirds were investing in immune defense against *P. downsi*. However, relatively dry conditions and associated resource limitation may have diminished the ability of parents to mount an immune response (Schmid-Hempel 2011; McNew et al. 2019). Exposure of mockingbirds to parasites in previous years may have also masked differences between treatments. Still, other physiological mechanisms that we did not characterize may have mediated the trade-offs between maternal condition and second nestling quality.

Behavioral responses to *P. downsi* show signs that parents were trying to avoid parasitism, which may also have had downstream effects on nestling hatching success and nestling quality. Female birds in the Galápagos often reduce brooding of nests parasitized by *P. downsi*, presumably to avoid being fed upon by larvae (Koop et al. 2013b; Knutie et al. 2016). During second nesting attempts, females of sham-fumigated nests spent less time brooding on average than females of fumigated nests, though the difference was not statistically significant. Many sham-fumigated nests failed before we could record behavior, especially during mockingbirds' second nesting attempts, thus our ability to detect behavioral changes was limited. We did not record

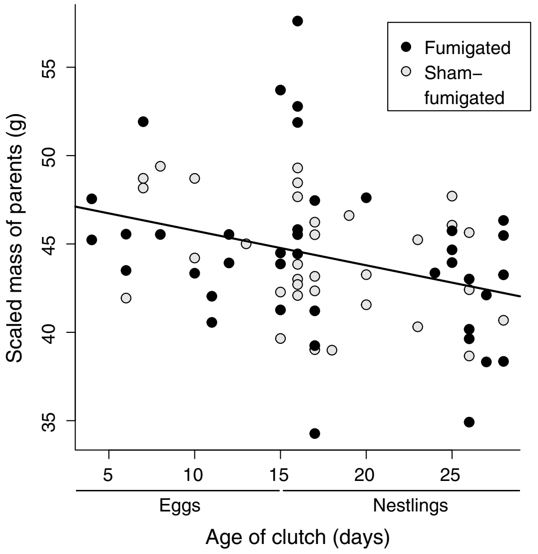

Fig. 3 Scaled mass of mockingbird parents during incubation of eggs and caring for nestlings (first nesting attempts only). Each point is an individual. Data are combined from parents captured in 2015 and 2016

behavior during incubation, even though nests are often infested before the nestlings hatch (McNew and Clayton 2018). Reduced or inconsistent incubation by females can lead to failure of eggs to hatch (Arnold et al. 1987; Cooper et al. 2005). Continued study of brooding behavior could determine whether changes in incubation in response to *P. downsi* inhibit nestling development.

During their second reproductive attempt, parents of sham-fumigated nests increased allopreening and nest sanitation behaviors, which may have been an attempt to resist or avoid parasitism (O'Connor et al. 2010, 2014). However, there is no evidence that these behaviors are effective at reducing *P. downsi* abundance or improving fledging success (O'Connor et al. 2014; McNew and Clayton 2018). If the increased time devoted to resistance behaviors came at the expense of foraging or provisioning time, mockingbirds may have inadvertently exacerbated the costs of *P. downsi* to reproductive success. *P. downsi* is a recently introduced parasite, thus behavioral responses to parasitism may not be entirely adaptive.

Galápagos mockingbirds are likely under selection to limit investment in any particular reproductive attempt. When the likelihood of future reproductive opportunities is high, birds should invest in self-maintenance over current reproduction (Forbes 1993; Ardia 2005). For example, tree swallows (*Tachycineta bicolor*) in Alaska, which have low annual survival, respond to experimentally enlarged broods by increasing reproductive efforts, at the expense of immune function (Ardia 2005). In contrast, swallows in Tennessee, which have higher survival rates, maintain immune function at the expense of reproduction. Tropical birds are expected to have more opportunities to reproduce compared to temperate relatives (Robinson et al. 2010; Muñoz et al. 2018).

Table 3 GLM estimates for parent condition, immune response and survival

Response variable	Error distribution	Predictors	Estimates^a	95% CI	*P*
Scaled mass	Gaussian				
		(Intercept)	45.68	40.13 to 51.23	< 0.001
		Nest age	− 0.22	− 0.36 to − 0.08	**0.004**
		Sex M^b	− 0.5	− 2.36 to 1.36	0.601
		Treatment S	− 0.09	− 1.92 to 1.74	0.922
		First nest clutch size	0.76	− 0.53 to 2.05	0.254
Immune response	Gaussian				
		(Intercept)	0.57	0.29 to 0.86	0.024
		Sex M	− 0.16	− 0.23 to − 0.08	**< 0.001**
		First nest clutch size	− 0.05	− 0.11 to − 0.00	**0.052**
		Treatment S	0.05	− 0.03 to 0.12	0.24
		Nest age	0	− 0.01 to 0.00	0.376
Next-year survival	Binomial				
		(Intercept)	− 1.39	− 2.94 to 0.16	0.08
		Sex M	1.9	0.05 to 3.75	**0.045**
		Treatment S	− 0.14	− 2.16 to 1.87	0.888
		First nest clutch size	1.27	− 0.30 to 2.84	0.113
		First nest hatch date	− 0.15	− 0.40 to 0.10	0.241

Bold values indicate statistically significant of *P* values ($P \leq 0.05$)

[a] Estimates for survival are in log-odds

[b] Sex was coded as female (intercept) or male (contrast)

Thus, mockingbirds should limit investment in any particular reproductive opportunity, because their residual reproductive value is generally high. We do not have data on the relative ages of the adults in our study, but a long-term study of this resident population may reveal the dynamics of reproductive investment over individual lifetimes. Parental compensation may only be common for older pairs who are facing terminal investment, or when conditions are so favorable that compensation requires little additional effort.

Predicting the effects of introduced species on endemic Galápagos species is vital for determining conservation priorities (Jiménez-Uzcátegui et al. 2019). While several studies have now documented the effects of *P. downsi* on the reproductive success of Galápagos hosts (reviewed in Kleindorfer and Dudaniec 2016 and McNew and Clayton 2018), less is known about the potential long-term consequences of *P. downsi* for Galápagos bird populations (Koop et al. 2016). Population viability models demonstrate that carry-over effects of infection on future fecundity influence host population dynamics (Smith et al. 2008). However, empirical data from field studies are necessary to generate and validate such models. Our results are from just 1 year of experimental field work. Galápagos mockingbirds double nest in approximately 1 out of every 3 or 4 years (Curry and Grant 1989, SMM unpublished data), making replication of this experiment challenging. However, from a biological standpoint, this behavior is not uncommon and cumulative carry-over effects could reduce lifetime fitness of mockingbirds. Our results demonstrate that costs of *P. downsi* are not limited to the period of host exposure, and further question how “tolerant” mockingbirds really are to *P. downsi* (Knutie et al. 2016; McNew et al. 2019).

Introduced parasites and pathogens are a threat to wildlife populations worldwide (Daszak 2000). Following the outbreak of an emerging disease or the invasion of a novel parasite, attention often focuses on the pathology of infection and the direct effects on host survival or reproductive success. Few studies have investigated life-history shifts of hosts in response to novel parasites or pathogens (Jones et al. 2008). However, novel parasites have the potential to produce a cascade of effects on their hosts beyond the immediate cost of infection. The study of the long-term consequences of parasitism may reveal additional costs of infection, as well as potential adaptations of the host in response to attack.

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Author contribution statement SMM and DHC designed the research, SMM, GBG and JYR collected the data, SMM analyzed the data, and SMM and DHC wrote the paper with input from the other authors.

Data availability Data and code used in analyses are available at https://github.com/smcnew/delayed_effects.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethical approval All applicable institutional guidelines for the care and use of animals were followed.

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