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Physiological costs and carry-over effects of avian interspecific brood parasitism influence reproductive tradeoffs

Melissa M. Mark [*], Dustin R. Rubenstein

Department of Ecology, Evolution and Environmental Biology, Columbia University, 10th Floor Schermerhorn Extension, 1200 Amsterdam Avenue, New York, NY 10027, USA

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ABSTRACT

Although models of co-evolution between brood parasites and their hosts primarily focus upon the cost to hosts in the current reproductive bout, the impact of brood parasitism may carry over to future reproductive attempts by altering resource allocation. Glucocorticoid stress hormones help mediate resource allocation to reproduction, yet they have rarely been examined in brood parasitic systems. Here we determined if shifts in parental care and corticosterone had carry-over effects on future reproductive effort in the rufous-and-white wren (*Thryophilus rufalbus*), a host of the Central American striped cuckoo (*Tapera naevia*). We found that parasitized parents had significantly higher stress-induced, but not baseline, corticosterone than natural parents during the fledgling stage, which was associated with changes in parental care. The high investment in current reproduction while parasitized may be due to the value of fledged chicks in tropical systems. This maladaptive response by parasitized parents was associated with delayed re-nesting and a reduced likelihood of nesting in the subsequent breeding season. Although a reduction in future reproductive effort can result from a combination of factors, this work suggests that fitness costs of brood parasitism are mediated by changes in corticosterone and parental care behavior that carry over into subsequent breeding seasons.

Introduction

Parental care is a set of energetically costly behaviors that increase offspring survival, often at the expense of decreased survival or reduced future fecundity to the parents (Clutton-Brock, 1991, 1998). Obligate avian brood parasites have found a way to avoid the costs of parental care by laying their eggs in the nests of other species (Kruger and Davies, 2002). Hosts of evictor parasites transfer parental care entirely to the parasitic chick, which removes competition for host resources by ejecting or killing all host offspring. The transfer of parental care costs from parasitic birds to their hosts, and the selection for host defense to avoid these costs, form the basis of co-evolutionary models of brood parasitism in birds (Davies, 2000; Roldan and Soler, 2011; Rothstein, 1990). While most models of co-evolution between brood parasites and their hosts focus on costs of the current reproductive bout, brood parasitism may also incur a cost to future reproduction via carry-over effects. Carry-over effects are processes that occur in one season, but that influence the success of an individual in subsequent seasons (Harrison et al., 2011). Reproductive effort is a recognized driver of carry-over effects (Inger et al., 2010; Mitchell et al., 2012), but only a few studies have investigated the impact of non-evictor parasites on subsequent reproductive effort in hosts (Hauber, 2006; Hoover and Reetz, 2006), and to our knowledge none have examined evictor parasites.

One pathway between a brood parasitic event and a future cost to reproduction in hosts is via resource allocation between current reproduction and physiological maintenance for the next breeding event (Sibley and Calow, 1989). Resource allocation between physiological functioning and reproduction in birds can be mediated by changes in glucocorticoid stress hormones (Wingfield and Hunt, 2002). Corticosterone is the primary avian glucocorticoid and plays a central role in the endocrine response to a perceived stressor (Wingfield et al., 2008). Birds have been shown to mediate corticosterone levels in response to acute stressors depending upon the relative importance of present versus future reproduction (Bokony et al., 2009; Lendvai and Chastel, 2008). The energetic demands of reproduction can cause an increase in baseline corticosterone levels during critical stages of nestling provisioning (Bonier et al., 2009, 2011), but chronically high baseline corticosterone can also reduce survival (Haussmann and Marchetto, 2010). During an acute stress response, an increase in baseline levels of corticosterone redirects energy toward life-saving activities, often resulting in reduced parental effort (Angelier and Chastel, 2009; Breuner, 2011; Ouyang et al., 2011; Wingfield et al., 1998).

Any change in parental effort that is due to manipulation by cuckoo chicks may offset the trade-off between current and future reproduction for parasitized parents and result in reduced future reproductive capacity. There is evidence that cuckoo chicks may manipulate parasitized parents during the fledgling stage to provide extended care (Payne, 2005), and prolonged parental care can have energetic consequences that carry over into the subsequent breeding season,

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[*] Corresponding author.
E-mail address: mark.melissa@gmail.com (M.M. Mark).

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reducing future reproductive effort (Harrison et al., 2011; Inger et al., 2010). The fledgling stage is the least studied area of host–parasite interaction (Feeney et al., 2012) and host defense is considered less likely to evolve in the later stages of parasitism, as evolutionary pressure decreases once the hosts' chicks are lost (Britton et al., 2007; Planque et al., 2002). However, if parasitism incurs a cost to future reproduction, then the evolution of late-stage defenses may enable host parents to escape the costs of extended fledgling care and subsequent reduction in reproductive output.

Here we determine if parasitism by the Central American striped cuckoo (*Tapera naevia*) incurs any changes to parental care behaviors and physiological function that carry over and impact the future reproduction in its host, the rufous-and-white wren (*Thryophilus rufalbus*). Carry-over effects from the fledgling stage may be particularly evident in tropical birds, as fledged chicks are of high value due to high nest predation and high adult survival rates (Ricklefs, 2010; Tarwater and Brawn, 2010). If parasitized parents invest heavily in a fledged parasitic chick, then we would expect to observe changes in glucocorticoid stress hormones that influence the trade-off between current and future reproduction. We measured baseline and stress-induced corticosterone levels and parental care behaviors in parasitized parents raising a cuckoo chick or natural parents raising their own young. Although we could not directly assess the impact of a parasitism event on future reproductive output, we examined if parasitism was associated with the changes in body condition over the nesting season, rates of re-nesting within a season, and return rates for the following season. To our knowledge, this is the first study of whether behavioral and hormonal consequences of brood parasitism in a current reproductive event can carry over into subsequent breeding seasons.

Materials and methods

Study system

This study was conducted in the Pacific slope of Nicaragua (6° 55′ N, 43° 24′ W; elevation = 1100 m) from May to October 2010 and 2011. The rufous-and-white wren is a small insectivorous passerine found commonly in riparian forests and shade coffee plantations (Stiles and Skutch, 1989). It breeds from May to October during the rainy season and lays 2–4 eggs (mean brood size = 2.6). Breeding pairs re-nest after predation events, and may fledge up to two broods in a season. The rufous-and-white wren is the sole host at the study site for the Central American striped cuckoo, an evictor parasite whose chicks kill host nestmates and are raised alone (Morton and Farabaugh, 1979; Payne, 2005).

Active nests (n = 157 nests across both years) were monitored every 2–4 days during the breeding season. The rates of brood parasitism were 13.8% in 2010 and 33.7% in 2011. The rates of nest predation were 66% in 2010 and 75% in 2011. Parents were captured at active nests with passive mist-netting between 05:30 and 10:30 at three stages of reproduction: (i) incubation stage; (ii) nestling stage (chicks 9–11 days of age); and (iii) and fledgling stage (3–5 days post-fledging). All birds were sampled using a standardized capture/restraint protocol (Wingfield, 1994). Briefly, baseline corticosterone samples were taken from the jugular vein within 3 min of hitting the mistnet. Birds were then stored in a cloth bag until maximal stress-induced corticosterone sample (see Supplemental materials) were taken 30 min after capture from the brachial vein. Birds were weighed to the nearest 1 g, and tarsus and wing lengths were measured to the nearest 0.5 mm. All work was approved by Columbia University's Institutional Animal Care and Use Committee (AC-AAAB3709).

Hormone assay

Blood samples were centrifuged at 7000 RPM for 3 min immediately after collection, and plasma was decanted and kept on wet ice for up to 4 h before being stored at −80 °C until assay. Samples were measured in duplicate by enzyme immunoassay (Enzo Life Sciences, Farmingdale, New York) using 6 μl plasma samples diluted to a concentration of 1:40 with assay buffer. Dilution and extraction protocols were optimized for this species prior to assay using a pooled plasma sample (see Supplemental materials). Intra- and inter-assay variation were 3.9% and 5.5%, respectively.

Parental care

In 2010 and 2011, we measured parental care during the nestling stage by recording feeding visits during 1 h focal observations. We visited each nest two times at chick ages 10 and 12 days, and recorded visits by both parents between the hours of 07:00–09:00 (n = 14 natural nests; n = 11 parasitized nests). Parental care during the fledgling stage was only measured in 2011; within two days fledging, we conducted a continuous focal observation of both parents and the nearest chick for 60 min, or until the parents could no longer be located (n = 9 natural nests; n = 6 parasitized nests). Because feeding visits were difficult to observe at this stage, particularly for cuckoo chicks, we instead recorded behaviors associated with parental care, including the distance of parents from the nearest chick, the numbers of foraging bouts, hops, flights, contact calls, and begging calls of the brood.

Statistical analysis

All analyses were performed in SPSS Statistics 20.0 (IBM, New York). We measured the effect of environmental and reproductive variables on baseline and stress-induced corticosterone using linear mixed models suitable for repeated measures with an unbalanced design with restricted maximum likelihood estimation. We included rainfall and body condition, parent type (parasitized or natural), nesting stage (incubation, nestling, fledgling), sex, and all two-way interactions as fixed effects. Body condition was estimated as the residuals of a linear mixed model with mass as the dependent variable, tarsus length and sex as the independent variables, and individual as a random factor (Garcia-Berthou, 2001). To account for repeated measures within a season, and that six birds were sampled in both seasons but not at all stages, we included two random effects: individual identity nested within brood identity, and year. Separate models were run with square root transformed baseline and stress-induced corticosterone as dependent variables. We sequentially removed non-significant variables (rainfall and body condition) from the model until only significant variables remained.

Due to predation, inability to capture both parents, or inability to collect a blood sample before 3 min, the sample sizes used in the analysis were as follows: for 21 total nests of natural parents, we analyzed baseline and stress-induced samples from 8 females and 5 males in the incubation stages, 14 females and 9 males in the nestling stage, and 9 females and 9 males in the fledgling stage; for 25 nests of parasitized parents, we analyzed baseline and stress-induced samples from 5 females and 7 males in the incubation stage, 11 females and 11 males in the nestling stage, and 8 females and 13 males in the fledgling stage.

To estimate parental effort during the nestling stage, we took the average number of feeding visits per hour for each parent, and compared these rates between natural and parasitized parents using a non-parametric Mann–Whitney *U* test. Non-parametric tests were used when the dependent variables were not normally distributed. We compared the change in body condition over the reproductive bout between parasitized and natural parents that fledged young, as well as difference in weight and age of fledged broods using a general linear model. During the fledgling stage, evidence of parental effort was measured by distance between parents and chicks, movement and foraging behaviors, and contact calls to chicks. We performed individual non-parametric tests with parent type as a grouping factor and the following parental behaviors as dependent variables: (1) pecks/min; (2) hops/min; (3) flights/min; and (4) contact calls/min. We also compared the frequency of chick begging calls and the distance of parent from the nearest chick using Mann–Whitney *U* tests. We used t-tests to compare perching height in the understory and distance from open areas for parasitized and natural parents and their chicks.

To determine if raising a cuckoo chick influenced future reproduction, we compared the probability to re-nest within a season using a Mann–Whitney *U* test and the latency to re-nest within a season using a chi-square test for natural and parasitized parents. To evaluate if parasitism resulted in reproductive carry-over effects into the following season, we used a Mann–Whitney *U* test to compare the probability that natural and parasitized parents monitored in 2010 would re-nest in 2011. We also examined changes in body condition over the breeding cycle for natural and parasitized parents using t-tests.

Results

Hormones

Baseline corticosterone levels increased across nesting stages for all parents ($F_{89} = 6.91$, $p = 0.002$; Fig. 1a). For both parasitized and natural parents, baseline corticosterone was significantly higher in the fledgling stage than in the incubation stage (post-hoc Tukey's HSD: $p = 0.004$). There was a significant interaction between sex and parent type ($F_{89} = 4.61$, $p = 0.035$); baseline corticosterone in natural parents was significantly higher for females than for males overall ($F_{1,47} = 5.95$, $p = 0.025$), but when examined by stage, the only significant relationship was in the nestling stage ($t = 2.40$, $df = 21$, $p = 0.026$). There was no sex difference in baseline corticosterone for parasitized parents ($F_{1,48} = 0.078$, $p = 0.783$). Stress-induced corticosterone levels in parasitized parents increased across nesting stages (nesting stage: $F_{72.36} = 9.06$, $p = 0.001$; parent type: $F_{77.63} = 4.42$, $p = 0.039$; nesting stage × parent type: $F_{72.36} = 7.52$, $p = 0.001$; Fig. 1b); parasitized parents experienced higher maximal levels of stress-induced corticosterone in the fledgling stage than in both incubation and nestling stages (post-hoc Tukey's HSD: all $p < 0.001$). While all parents were sampled within five days of fledging, the chicks were not of uniform age: cuckoo chicks fledged between 12 and 28 days (mean ± SE = 17.1 ± 1.85 days), while wren chicks fledged between 14 and 17 days (mean ± SE = 16.7 ± 1.69 days). To ensure that the stress-induced corticosterone levels during the fledgling stage were not related to age, we assessed the correlation of age of all fledged chicks to stress-induced corticosterone levels in the parents and found no relationship ($r_{35} = 0.06$, $p = 0.36$).

Effect of parasitism on parental care in current reproductive bout

Feeding rates of natural and parasitized parents did not differ during the nestling stage ($U = -0.32$, $N = 43$, $p = 0.75$). The mean age at fledging did not differ between natural and parasitized nests, indicating that cuckoo chicks were not fed in the nest for longer than wren chicks ($t = -0.82$, $df = 19$, $p = 0.43$). However, cuckoo chicks were more variable in their fledge age than wren chicks (Levene's test for equality of variances: $F_{1,19} = 6.06$, $p = 0.030$). Moreover, the average fledging weight of a cuckoo chick was greater than that of an entire fledged wren brood ($t = -3.05$, $df = 19$, $p = 0.004$).

Once chicks fledged from the nest, differences were observed in both chick and parental behaviors. Cuckoo chicks perched closer to open areas ($U = -4.44$, $N = 15$, $p = 0.001$; Fig. 2a) and higher in the understory ($t = -3.23$, $df = 13$, $p = 0.007$; Fig. 2b) than wren chicks. A single fledged cuckoo chick gave almost twice as many begging calls per minute as an entire fledged wren brood of up to four chicks ($U = 3.01$, $N = 15$, $p = 0.001$; Fig. 2c), and remained nearly stationary throughout all observations. Parasitized parents remained in closer proximity to their chick than natural parents ($U = -2.94$, $N = 29$, $p = 0.003$; Fig. 2d), usually because one parasitized parent guarded the immobile cuckoo chick while the other parent was absent, presumably foraging. Natural parents engaged in more hops ($U = -2.19$, $N = 30$, $p = 0.02$), flights ($U = -4.23$, $N = 30$, $p = 0.001$), and contact calls ($U = -2.30$, $N = 30$, $p = 0.02$) with their chicks, moving with their brood through the understory, suggesting that wren chicks began to forage earlier than cuckoo chicks.

To evaluate if proximity to chicks or proximity to open areas influenced maximal corticosterone levels, we examined these relationships separately in natural and parasitized parents. We found that the distance between natural parents and their chicks did not predict high levels of stress-induced corticosterone in parents ($\beta = -0.77$, $t = 2.79$, $df = 10$, $p = 0.11$; adjusted $r^2 = 0.69$), but when chicks moved closer to open areas, natural parents experienced higher maximal corticosterone levels ($\beta = -0.92$, $t = -4.150$, $df = 10$, $p = 0.03$; adjusted $r^2 = 0.81$). We found a similar

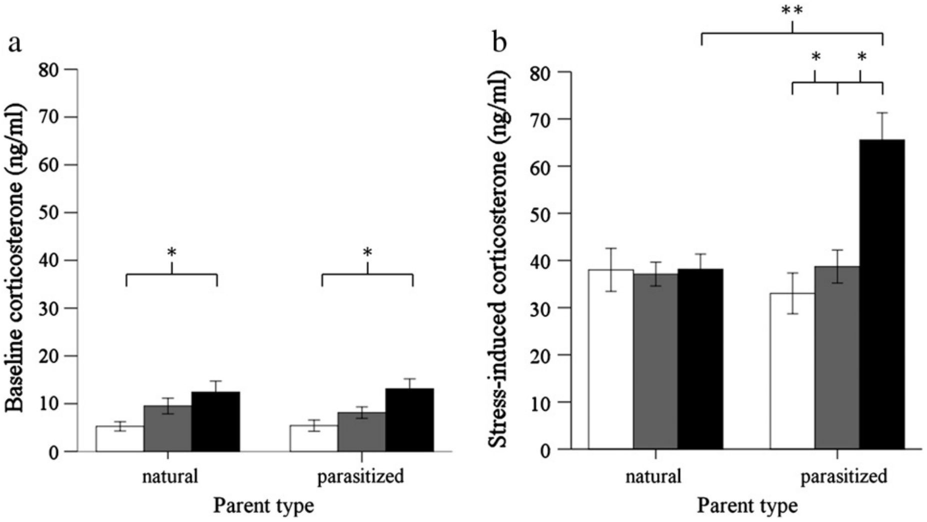

Fig. 1. The effects of nesting stage (incubation = white, nestling = gray, fledgling = black) on (a) baseline and (b) stress-induced corticosterone levels for natural and parasitized parents. Stress-induced corticosterone levels were highest in parasitized parents during the fledgling stage. Data are means ± SE. *$p < 0.01$, **$p < 0.001$.

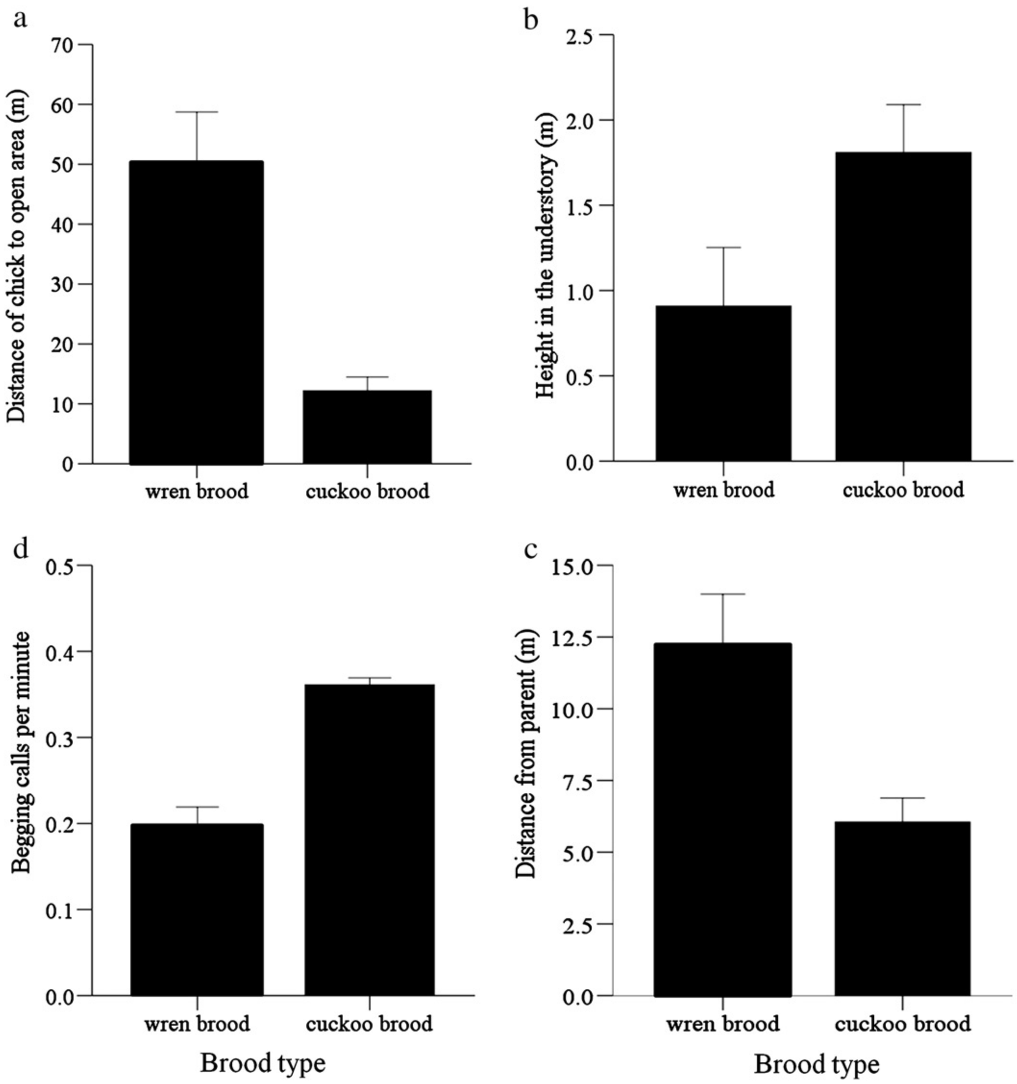

Fig. 2. Fledgling behavior differed significantly between cuckoo and wren broods. Cuckoo chicks (a) perched closer to open areas ($p < 0.01$) and (b) higher in the canopy ($p < 0.01$), (c) begged more frequently ($p < 0.01$), and (d) remained closer to parents than wren chicks ($p < 0.05$). Data are means ± SE.

relationship for parasitized parents: proximity of the chick to open areas predicted high levels of stress-induced corticosterone ($\beta = 0.80$, $t = 3.51$, $df = 16$, $p = 0.01$; adjusted $r^2 = 0.59$), while distance between parasitized parent and chick did not ($\beta = -0.77$, $t = -2.09$, $df = 16$, $p = 0.13$; adjusted $r^2 = 0.66$). These data suggest that a chick's proximity to the forest edge was a stressor, likely due to increased predation risk (Vitz and Rodewald, 2010).

Effect of parasitism on future reproduction

There was no difference in body condition between parasitized and natural parents during any of the three nesting stages (incubation: $t = 0.29$, $df = 21$, $p = 0.78$; nestling: $t = 0.84$, $df = 40$, $p = 0.39$; fledgling: $t = 0.70$, $df = 35$, $p = 0.94$). Both parent types experienced a reduction in body condition between the laying and fledgling stage, and did so at the same rate ($t = -2.61$, $df = 19$, $p = 0.79$). Although both natural and parasitized parents were equally likely to re-nest in the same season ($X^2 = 0.12$, $N = 24$, $p = 0.53$), the latency to re-nest was significantly longer for parasitized parents ($U = 2.28$, $N = 11$, $p = 0.008$; Fig. 3). Moreover, parasitized parents in 2010 were less likely to re-nest in 2011 than natural parents ($X^2 = 4.34$, $N = 38$, $p = 0.037$). Thus, rufous-and-white wren pairs who fledged a cuckoo chick reduced their future breeding attempts, demonstrating a prolonged negative impact of brood parasitism on reproductive success.

Discussion

This is the first study to detail the differences in parental care behaviors in parasitized and non-parasitized hosts of an evictor parasite during the fledgling stage, as well as the hormonal and reproductive consequences of those differences. We found that cuckoo chicks coerced parasitized parents into increasing parental investment via behavior that was markedly different than that of wren chicks. Parasitized parents displayed altered parental care behaviors compared to natural parents; while natural parents foraged together with their brood through the understory, parasitized parents engaged in chick guarding, remaining close to the nearly immobile cuckoo chick which gave frequent begging calls and did not attempt to forage. The cuckoo chicks perched away from the riparian areas where rufous-and-white wrens prefer to forage, and which have been shown to be areas of high food abundance for insectivorous forest birds (Chan et al., 2008). Cuckoo chicks also perched near to open areas which have been shown to have high rates of predation for juvenile birds (Cohen and Lindell, 2004; King et al., 2006), but those are also the natural habitat for adult striped cuckoos. An increase in

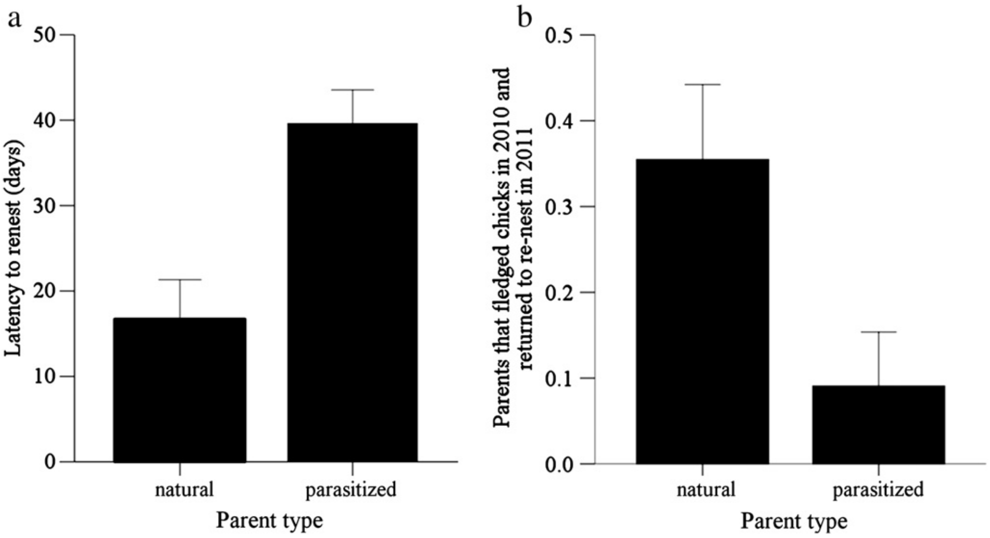

Fig. 3. Carry-over effects of brood parasitism. Parasitized parents (a) took longer to re-nest after brood fledging than natural parents ($p < 0.05$) and (b) were less likely to re-nest the following year ($p < 0.05$). Data are mean ± SE.

perceived predation risk to chicks in close proximity to open areas was associated with a high stress response in both parent types, and predation risk has been shown to drive alterations in parental care in other bird species (Zanette et al., 2011). Perceived predation risk for a cuckoo chick perched near forest edges (Butler et al., 2009) or increased foraging effort away from the territory center (Crossin et al., 2012) could be the primary cause of the significantly higher stress-induced corticosterone levels in parasitized parents.

Brood parasitism by the striped cuckoo led to changes in parental care behaviors, as well as stress-induced, but not baseline, corticosterone levels in parasitized parents. Similar to other avian studies, levels of baseline corticosterone increased moderately over the breeding cycle to allow parents to meet the energetic demands of reproduction (Bokony et al., 2009; Bonier et al., 2009). However, we documented that elevated stress-induced corticosterone levels in parasitized parents were associated with an increase in parental attentiveness, or chick guarding, which contradicts the current paradigm that an acute stress response reduces parental care in favor of self-maintenance (Angelier et al., 2007; Lendvai and Chastel, 2008). One possible explanation for the positive relationship between maximal corticosterone and parental attentiveness may be brood value. If brood value is very high, rather than suppress the corticosterone response to a stress-event, parents may modulate behavioral responses to high corticosterone to prevent the diversion of resources from reproduction. Fledgling chicks are of high value to tropical birds due to generally high nest predation and parents engage in chick guarding and brood division to increase survival during the fledgling stage (Tarwater and Brawn, 2008). In the case of parasitism, a single large chick such as a cuckoo may be perceived to be of particularly high value, prompting increased guarding behavior.

In the case of brood parasitism, continued investment in current reproduction via modulation of the stress response or parental care behavior is maladaptive. In this study, parasitized parents invested heavily in the current reproductive bout, which resulted in no offspring and contributed to reduced future productivity in the current and subsequent breeding seasons. Parasitized parents that fledged a cuckoo delayed re-nesting in the same season, suggesting that shifts in parental care for parasitized parents were energetically costly. Parasitized parents were also less likely to re-nest the following year, indicating that raising a parasitic chick can have carry-over effects on fitness (Harrison et al., 2011). Studies in other avian species have shown that an increase in corticosterone can decrease the likelihood of re-nesting (Angelier et al., 2009), that a stress event can reduce future reproductive success (Legagneux et al., 2012), and that increased reproductive effort can have carry-over effects (Done et al., 2011).

Evidence of carry-over effects from brood parasitism in hosts is inconsistent and likely species-specific. For example, prothonotary warbler hosts of a non-evictor parasite have reduced offspring recruitment and lower return rates (Hoover and Reetz, 2006), whereas parasitized black phoebe hosts show no reduction in subsequent clutch size (Hauber, 2006). Investigations like ours of hormonal stress response may serve to further our understanding of the costs of brood parasitism. Recently, researchers found a high corticosterone stress response in host chicks raised with a parasitic chick, which can negatively impact developing organisms (Ibanez-Alamo et al., 2012). Thus, endocrine responses to brood parasitism provide a pathway by which a parasitism event can influence future fitness via changes in resource allocation.

Conclusions

In summary, we found that parasitized rufous-and-white wrens raising a striped cuckoo chick experienced higher maximal corticosterone levels than natural parents raising wren chicks, likely due to markedly different parental care patterns and differences in chick behavior. Brood parasitism altered the energetic trade-off between investment in current versus future reproduction; parasitized parents invested heavily in current reproduction to maximize fitness, a maladaptive response that decreased both current and future fitness via carry-over effects. The perceived value of a fledged chick to a tropical host could explain why parasitized parents continued to care for a cuckoo chick at a cost to self-maintenance. Ultimately, this work suggests that brood parasitism can have negative consequences for hosts that carry over into subsequent breeding seasons. Thus, in addition to the obvious loss of current reproduction by an evictor parasite, there is likely to be a major cost of brood parasitism to future reproduction.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.yhbeh.2013.03.008.

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