ethology international journal of behavioural biology

Ethology

RESEARCH PAPER

Darwin's Finch Begging Intensity Does Not Honestly Signal Need in Parasitised Nests

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Received: May 15, 2013
Initial acceptance: July 23, 2013
Final acceptance: November 10, 2013
(M. Herberstein)

doi: 10.1111/eth.12196

Keywords: *Philornis downsi*, introduced species, parental care, bird, tasty chick hypothesis, signal of need

Abstract

Parental care should be selected to respond to honest cues that increase offspring survival. When offspring are parasitised, the parental food compensation hypothesis predicts that parents can provision extra food to compensate for energy loss due to parasitism. Chick begging behaviour is a possible mechanism to solicit increased feeding from attending parents. We experimentally manipulated parasite intensity from *Philornis downsi* in nests of Darwin's small ground finch (*Geospiza fuliginosa*) to test its effects on chick begging intensity and parental food provisioning. We used in-nest video recordings of individually marked chicks to quantify nocturnal parasite feeding on chicks, subsequent diurnal chick begging intensity and parental feeding care. Our video analysis showed that one chick per brood had the highest parasite intensity during the night (supporting the tasty chick hypothesis) and weakest begging intensity during the day, which correlated with low parental care and rapid death. We observed sequential chick death on different days rather than total brood loss on a given day. Our within-nest video images showed that (1) high nocturnal larval feeding correlated with low diurnal begging intensity and (2) parent birds ignored weakly begging chicks and provisioned strongly begging chicks. Excluding predation, all parasite-free chicks survived (100% survival) and all parasitised chicks died in the nest (100% mortality). Weak begging intensity in parasitised chicks, which honestly signalled recent parasite attack, was not used as a cue for parental provisioning. Parents consistently responded to the strongest chick in both parasitised and parasite-free nests.

Introduction

Haematophagous nest parasites such as fly larvae, fleas and mites consume the blood of altricial chicks and can reduce the growth, health and fledging success of their hosts (Møller 1990; Richner et al. 1993; Hurtrez-Boussès et al. 1997; Dudaniec et al. 2006; Fessl et al. 2006a). However, these effects of nest parasites can be highly variable and sometimes negligible (Gold & Dahlsten 1983; Roby et al. 1992; Johnson & Albrecht 1993; Miller & Fair 1997; Thomas & Shutler 2001), especially when biotic conditions and host adaptations reduce parasite impact (Clark & Mason 1988; Merino & Potti 1996). For example, the parental food compensation hypothesis predicts that when there are sufficient resources, parents increase the food provisioning to their young to compensate for the costs of parasitism and thereby maintain chick growth rates (Johnson & Albrecht 1993; Tripet & Richner 1997; Tripet et al. 2002). While the parental food compensation hypothesis can be generally tested by monitoring feeding visits to nests, complementary hypotheses that predict parental allocation decisions are important to understand food distribution per chick and individual chick survival rather than brood survival.

We use Darwin's small ground finch (*Geospiza fuliginosa*) on Floreana Island, Galapagos Archipelago, as a model system to test predictions of the parental food compensation hypothesis. Darwin's finches experience high fitness costs from introduced *Philornis downsi* fly larvae parasites, which reside in the nest material and emerge to feed nocturnally on the blood and flesh of developing chicks (Fessl et al. 2006b;

O'Connor et al. 2010b). Annual chick mortality due to parasitism has been shown to vary between 13% and 100% (Fessl & Tebbich 2002; Dudaniec & Kleindorfer 2006; Fessl et al. 2006a; Dudaniec et al. 2007; Huber 2008; O'Connor et al. 2010a,d), but interestingly, it is not always predicted by the number of parasites per nest (Huber 2008; O'Connor et al. 2010a,b). For example, some chicks will fledge from heavily infested nests containing 60–90 larvae, whereas others die in nests containing fewer than 20 larvae (O'Connor et al. 2010b; J. A. O'Connor and S. Kleindorfer unpubl. data). There is also evidence for considerable variation in the age of death for sibling chicks under equal levels of parasitism (J. A. O'Connor and S. Kleindorfer unpubl. data; Fessl & Tebbich 2002), whereby some chicks are able to survive the effects of *P. downsi* longer than their siblings.

The differential mortality of parasitised chicks may be explained by (1) targeted feeding by parasites on particular chicks (the tasty chick hypothesis: Christe et al. 1998), (2) sibling competition to avoid being consumed by parasites (O'Connor et al. 2010b) and (3) differences in parental food provisioning of particular chicks (Wright et al. 1998). We predict that parent birds respond to chick begging intensity as a cue for provisioning and provide more feeds to chicks with high begging intensity, as these chicks may have the highest need (see Godfray 1991, 1995; Kilner & Johnstone 1997). Conversely, parasitised chicks with the highest need for provisioning could have the weakest begging intensity and would therefore receive less food from their parents and die sooner (see Christe et al. 1996). The theory of parent–offspring conflict predicts that chicks are competing for parental care, and parents are incorporating multiple indicators to assess the honesty of the chick's begging signal (Trivers 1972; Dor & Lotem 2010). Here, we test whether parasite attacks on chicks correlate with begging intensity, to test whether chick begging intensity honestly reflects the need for parental provisioning.

The tasty chick hypothesis predicts that a single chick will be targeted by parasites, whereas the parental food compensation hypothesis predicts that parental provisioning occurs in response to the nestling need. The two hypotheses address different 'actors': the parasite (which chick does it feed on) and the parent (which chick does it feed). We use within-nest video surveillance to quantify (1) nocturnal feeding of larvae on each chick, (2) diurnal begging intensity of each chick and (3) parental provisioning of chicks in naturally parasitised and experimentally parasite-free nests. We measure chick body size and mass, and compare age at death and synchrony of chick mortality across the nesting phase. There is ample evidence of high chick mortality (44–100% annual mortality since 1998) in small ground finch nests infested with *P. downsi* (Fessl et al. 2006a,b; Dudaniec et al. 2007; O'Connor et al. 2010a,b). Intriguingly, the pattern of chick mortality has been sequential across days rather than total brood loss on a single day (Fessl & Tebbich 2002; Fessl et al. 2006b; Huber 2008; O'Connor et al. 2010b,d). Based on these findings, we aim to test whether parasites affect particular chicks more so than others, whether parasite attacks predict chick begging intensity and whether parents are most likely to provision heavily parasitised chicks or chicks with the strongest begging intensity. We test the following predictions: (1) nocturnal larval feeds will be concentrated on one chick per brood, as evidenced by the proportion of larvae feeding on a given chick (tasty chick hypothesis); (2) given asymmetry in larval feeding (tasty chick hypothesis), we predict asymmetry in chick begging intensity to solicit parental provisioning (parental food compensation hypothesis): chicks with the most parasite attacks will be weakened and consequently have the weakest begging, or conversely, these chicks could have the strongest begging intensity to stimulate parental feeding to compensate for their weakened state; (3) parental provisioning will be correlated with begging intensity (parental food compensation hypothesis) and (4) chick mortality will be correlated with parental provisioning.

Methods

Study Site and Species

The small ground finch is common across the Galapagos Archipelago (Grant 1999; Sulloway & Kleindorfer 2013) and is the most abundant finch on Floreana Island (O'Connor et al. 2010c). We conducted this study from Feb. to Apr. in 2010 at two study sites on Floreana Island, Galapagos: (1) lowland scrub around the township of Puerto Velasco Ibarra (1°16′28S, 90°29′13W) and (2) highland forest at the base of Cerro Pajas volcano (1°17′46S, 90°27′06W) (sites fully described in O'Connor et al. 2010a). We recorded rainfall at an elevation of 6 m in our lowland study site (1°16′20.5″S, 90°29′16.5″W) and 343 m in our highland study site (1°17′48.4″S, 90°27′07.0″W). Compared with 2004–2006 (see O'Connor et al. 2010a,d), there was high rainfall in 2010 in the lowlands (306 mm) and highlands (635 mm).

Philornis downsi Life Cycle

Adult *P. downsi* flies feed on fruit and organic matter; only the larvae are parasitic on birds (Fessl et al. 2006b). Multiple *P. downsi* flies enter active finch nests (containing eggs or chicks) and lay eggs on inner nest surfaces when parents are absent (Dudaniec et al. 2010; O'Connor et al. 2010b). The *P. downsi* eggs hatch into parasitic larvae, whereby first- and early second-instar stages feed within the nares of chicks (Fessl et al. 2006b). Late-instar larvae (second and third) reside in the nest base during the day and emerge at night to feed on the blood and tissues of chicks by external attachment and by entering through the nares to feed internally on chicks (O'Connor et al. 2010b). Larvae pupate in the nest base after 4–7 d of feeding on chicks (J. A. O'Connor and S. Kleindorfer, unpubl. data) and emerge as flies after 7–18 d (P. Lincango and C. Causton, unpubl. data). Previous evidence shows that parasitised chicks can appear healthy right up to their death and then die suddenly (O'Connor et al. 2010b). Dead chicks are commonly found with flesh wounds, damage to vital internal organs, open body cavities sometimes devoid of any blood or flesh, enlarged nares and loss of internal beak structure (Fessl & Tebbich 2002; Fessl et al. 2006b; Huber 2008; O'Connor et al. 2010b,d).

Nest Monitoring

We located 14 active small ground finch nests. We monitored nests every day to determine the nesting activity and the age of chick at death. The average nestling period for Darwin's finches is 14 d (Grant 1999). After all chicks had died or fledged from a nest, the nesting material was dismantled and all *P. downsi* larvae, pupae and pupal cases were counted to calculate the total number of parasites per nest (see Fessl & Tebbich 2002; Dudaniec et al. 2006). Chicks that had recently died were immersed in alcohol so that larvae within the body would float out and could be counted. Parasite intensity could not be determined in two nests: one nest was completely depredated by an owl (whole nest was missing) and the other by fire ants (*Wasmannia auropunctata*), which remove *P. downsi* larvae from the nest (O'Connor et al. 2010b).

Chick Body Size and Mass

We tested the effect of *P. downsi* intensity on chick body size and mass. We measured the following variables every second day for each chick in each nest: tarsus, beak length head, beak length naris, naris diameter, wing length and body mass. Morphological measurements were taken to the nearest 0.01 mm using calipers. Mass was measured to the nearest 0.01 g using portable electronic scales. For consistency, all measurements were taken between 9–10 am. The difference in chick mass was calculated every 2 d for each chick. To determine the range of intra-brood chick mass, we calculated the difference between the lightest and heaviest chick in each brood at day 4 after hatching.

Experimental Treatments and Video Monitoring

The 14 nests were videoed and randomly assigned to one of the two treatments: parasitised (seven nests) or experimentally parasite-free (seven nests). For the naturally parasitised group, we removed 2-d-old chicks, sprayed the nest interior with water and returned the chicks after 10 min. For the experimentally parasite-free nests, we removed 2-d-old chicks, sprayed the nest interior with 1% pyrethrin solution and returned the chicks after 10 min. Pyrethrin is non-toxic to birds and virtually eliminates larvae that are already present in the nest (Fessl et al. 2006a). Because *P. downsi* flies do not enter pyrethrin-treated nests, there is no subsequent infestation (J. A. O'Connor pers. obs.). The parasite-treatment was carried out on day 2 after hatching. We quantified begging intensity in relation to parasite intensity on day 3–5 after hatching. The sample size was 20 chicks in the seven nests with parasites and 23 chicks in the seven nests without parasites.

To film within nests, the lens of a small surveillance camera was inserted through the roof of each dome-shaped nest. We used an Archos 605 180-GB media device and Archos 5 250-GB media tablet with the Archos DVR station (O'Connor et al. 2010b). Chicks in the videoed nests were uniquely marked by colouring parts of the beak and toes with non-toxic black marker. These marks allowed us to identify individual chicks when quantifying begging intensity and parental care from video recordings and for identification of individuals when taking morphological measurements.

Behavioural Observations: Chick Begging, Parental Care and Larval Attacks

We quantified chick begging behaviour and parental feeding care (insertion of parent beak into chick's beak) from video recordings. For this analysis, we used data from the first five feeding visits on a single day (either day 3 or 4 post-hatching). We quantified the frequency of parental visits to the nest per hour and the number of beak insertions provided to each chick for the first five feeding events from 6 am onwards on the day of observation. For every feeding event, each chick was assigned to one of the three begging intensity categories: (1) weak – chick's body was not extended and gape opened <30% of maximal capacity; (2) medium – chick's body was partially extended and gape opened ~30–90% of maximal capacity or (3) strong – chick's body was fully extended and gape opened >90% of maximal capacity. We used the average of the five observations per chick to assign a begging intensity per chick. To determine intra-brood range in beak insertions for each feeding event, we calculated the difference between the least and the most number of parental beak insertions per chick within the brood. To calculate the duration of parental beak insertions per nest visit (rather than time spent sitting at the nest, for example), we divided the duration of the feeding visit to the nest (in seconds) by the total number of beak insertions.

To quantify larval feeding per chick, we scored the relative percentage of larvae feeding externally per chick from 10 pm to 6 am. Larval feeding data per chick were analysed as proportions per chick and were analysed in relation to subsequent diurnal begging intensity (scored from 7 am to 9 am) and diurnal mortality. To calculate the proportion of larvae feeding on each chick, we scored the total number of larvae in view of the camera and calculated the percentage of larvae per chick (this was considered a reasonable approach because larvae reside in the nest base and not all larvae emerge to feed at the same time). We scored the proportion of larval attacks per chick per hour and used the average score. The sample size was 14 chicks from six parasitised nests for which we had data on number of external larvae attached to the chick body and begging intensity, the next morning (we could not observe larval feeding at one nest because of consistently poor visibility due to female brooding).

Statistical Analyses

All analyses were carried out with SPSS 17.0 for Mac. We used an unpaired *t*-test to quantify the outcome of our planned experimental reduction in parasites using pyrethrin. The percentage data for larval feeding per chick and chick begging intensity were acrsin square-root transformed for all analyses. To test for the effect of chick begging intensity (weak, moderate, strong) on parental feeding care (proportion of first feeds), we used a chi-squared test, with nest as a covariate. To test for the effects of nest treatment (parasitised, parasite-free) and brood size on number of parental beak insertions and other measures of parental feeding care [mean duration (s) per feeding visit; mean duration (s) per beak insertion], we used ANOVA. We tested for patterns of chick mortality (individual, total brood loss) in relation to nocturnal parasite feeding using binary logistic regression analysis. We used linear regression analysis to compare the percentage of nocturnal parasite feeding on a given chick and the diurnal begging intensity of that chick. For the analysis of chick morphology and chick age, we used mean values from each nest at each age to avoid pseudoreplication. We used MANOVA for the statistical analysis, with all morphological variables as the dependent variables and treatment (parasitised, parasite-free) as the fixed factor. We restricted our analyses of morphological data to day 2, 4 and 6 after hatching, because all parasitised nests died by day 9, and there was a very high mortality after day 6.

Results

Chick Mortality

In parasitised nests, all chicks showed signs of *P. downsi* larval feeding (dark, enlarged nares and body wounds). No parasitised chicks fledged (all 20 chicks found dead in seven nests with signs of *P. downsi* parasitism) (Table 1). The mean age at death was 4.2 ± 0.3 d for the parasitised chicks. There was daily mortality of single chicks at all parasitised nests rather than total brood loss on a single day (Fig. 1). Video footage confirmed that parents removed dead, parasitised chicks from the nest. For the parasite-free nests, one was depredated by an owl on day 7, one was consumed by fire ants and the remaining five nests fledged or survived until day 8 post-hatching (we stopped monitoring on day 8 at two nests) (Table 1).

Chick Begging Intensity and Parental Care

Spraying nests with pyrethrin to remove *P. downsi* larvae was successful and resulted in a significant difference in parasite intensity between treatment groups ($t = 3.9$, $n = 14$, $p = 0.001$) (Table 1). Next we examined begging behaviour by chicks in nests with and without parasites. There was no significant difference in begging intensity across treatments ($\chi^2 = 0.76$, df = 1,14, $p = 0.76$): strong begging behaviour was

Table 1: Overview of nesting outcome, parental care and parasite intensity in small ground finch nests video-recorded on Floreana Island in 2010

	Parasitised nests	Parasite-free nests
Number of nests	7	7[a]
Brood size (x̄ ± SE)	3.1 ± 0.27	3.3 ± 0.33
% Depredated nests	0% (0/7)	28% (2/7)
% Nests with in-nest chick mortality across days	100% (7/7)	0% (0/7)
% Nests with fledglings	0% (0/7)	73% (5/7)[b]
Male nest visits (x̄ ± SE) per hour	3.05 ± 0.27	2.80 ± 0.28
Female nest visits (x̄ ± SE) per hour	2.45 ± 0.30	2.15 ± 0.41
Chick preens per hour (x̄ ± SE) by the female	1.12 ± 0.29	0.25 ± 0.19
Beak insertions per chick (x̄ ± SE) per feeding visit	10.97 ± 1.33	6.09 ± 0.58
Beak insertions per chick (range) per feeding visit	0–51	0–45
Parasite intensity per nest (x̄ ± SE) day 3 post-hatching	22.7 ± 3.9	0.17 ± 0.01
Parasite intensity per nest (range) day 3 post-hatching	12–60	0–2

[a] Nesting outcome is not known for two nests that were still active 8 d post-hatching.

[b] This value includes the two nests with uncertain nesting outcome.

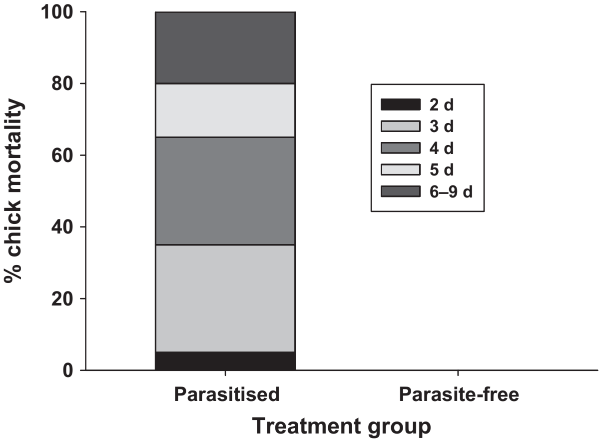

Fig. 1: The percentage of chicks found dead in the nest each day after hatching in parasitised nests (n = 20 chicks at seven nests) and parasite-free nests (n = 23 chicks at seven nests). All chicks died by 9 d post-hatching in parasitised nests. The mean age at death was 4.2 ± 0.3 at parasitised nests, whereas no chicks were found dead in parasite-free nests. Two nests were depredated (all chicks missing on a single day) on day 5 and 9 post-hatching (see Table 1) and were not included in our calculation of the percentage of in-nest mortality presented here.

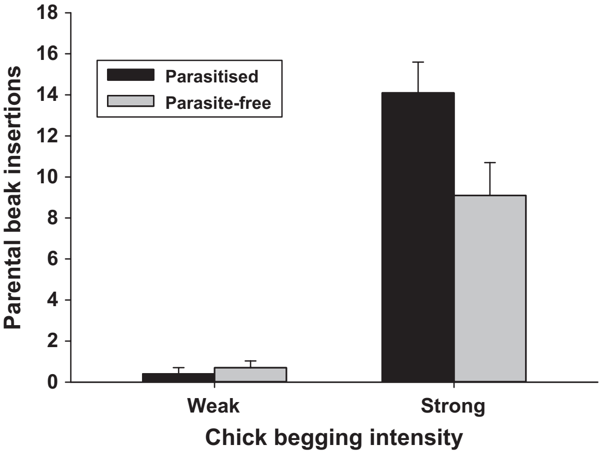

Fig. 2: The number of parental beak insertions (x̄ ± SE) per chick and per feeding visit is shown in relation to the vigour of chick begging behaviour. The data are shown for seven parasitised nests (n = 20 chicks) and seven parasite-free nests (n = 23 chicks) on Floreana Island in 2010. The number of parental beak insertions was calculated from five feeding visits on a single day of observation per nest on either day 3 or 4 post-hatching (see Methods).

found for 56% of cases in parasitised nests and 58% of cases in parasite-free nests. In both treatments, chicks with strong begging behaviour were fed first more frequently (Likelihood ratio = 12.09 df = 5, 43, p = 0.03) and had more beak insertions per feeding event (ANOVA, $F_{1,42}$ =5.95, p = 0.02) (Fig. 2). Parasitised chicks that begged strongly were more likely to survive to at least 5 d after hatching (ANOVA: nest: $F_{1,20} = 4.6$, p = 0.04; survival category $F_{1,20} = 9.7$ p = 0.01), although all parasitised chicks died by 9 d after hatching. The proportion of weakly or strongly begging chicks was not related to brood size (Likelihood ratio = 4.1, n = 14, p = 0.25).

Parents visited nests to 'feed chicks' (inserted their beaks into chicks' beaks) about three times per hour in both treatments (Table 1), but female parents did so more often than males in both treatments (ANOVA: treatment $F_{1,14} = 0.5$, p = 0.82, sex $F_{1,14} = 25.43$, $p \leq 0.001$, interaction effect $F_{1,14} = 0.06$, p = 0.81) (Table 1). From the video recordings, we observed that parent birds inserted their beaks into those of the chicks nearly twice as often for parasitised than parasite-free nests (ANOVA: nest treatment $F_{2,14} = 7.60$, p = 0.03, brood size $F_{3,14} = 0.68$, p = 0.59, interaction effect $F_{2,14} = 0.09$, p = 0.92) (Fig. 2; Table 1). Neither the mean length of feeding visits, mean number of beak insertions to the entire brood per feeding visit, nor mean duration of beak insertions were significantly different across treatments or brood sizes (all p > 0.05). Intra-brood variation in beak insertions (with nest as a covariate) was not significantly different across treatments (ANOVA treatment: $F_{1,14} = 0.95$, p = 0.36; brood size:

$F_{2,14} = 0.59$, $p = 0.64$; interaction $F_{2,14} = 3.1$, $p = 0.11$). Only female parents visited the nest solely for cleaning or preening chicks and did so five times more often in parasitised nests (ANOVA: $F_{1,14} = 6.29$, $p = 0.03$) (Table 1).

Nocturnal Parasite Activity and Chick Begging

Of the six parasitised nests (n = 14 chicks) for which we have data on nocturnal parasite feeding, in all nests, one chick received the most larval feeding (percentage of larvae, percentage of time the larvae fed on the chick) (MANOVA:%larvae: $F_{1,14} = 29.79$, $p < 0.001$;%time: $F_{1,14} = 28.44$, $p < 0.001$). *Post hoc* tests (Tukey's HSD) showed significant differences between weak vs. strong begging chicks for %larvae ($p < 0.001$), but not for intermediate vs. strong begging ($p = 0.26$). The *post hoc* tests showed the same pattern for an effect of %time of larval feeding, namely a significant difference in weak vs. strong begging ($p < 0.001$). We then correlated nocturnal parasite activity with diurnal begging intensity and found a significant correlation: chicks with the most larvae feeding on them during the night (%larvae) had the weakest diurnal begging ($r = -0.86$, $t = -7.36$, n = 14, $p < 0.001$), and chicks that were consumed by larvae for the longest time period (%time of larval feeding) had the weakest diurnal begging ($r = -0.74$, $t = -4.85$, n = 14, $p < 0.001$) (Fig. 3).

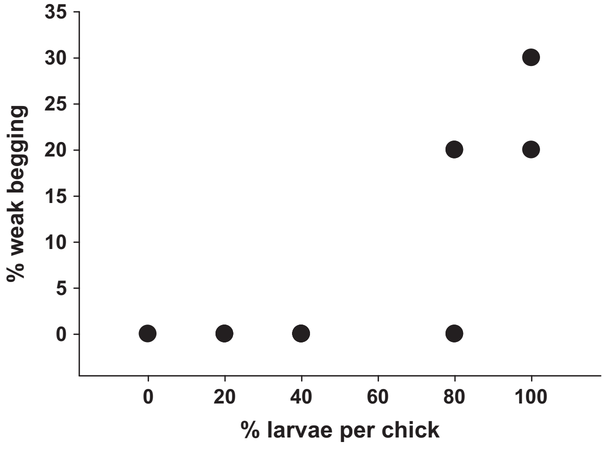

Fig. 3: The percentage of weak begging behaviour by chicks during the day in relation to the proportion of larval feeding on the chick during the night. The association was statistically significant: chicks with more larvae feeding on them during the night were more likely to show weak begging intensity the next day (see Results). The data are shown for 14 chicks from six parasitised nests (we excluded one nest due to poor visibility of larval feeding). Of the 14 chicks, eight had no parasite feeding and strong begging behaviour; the eight 'zero' values on the graph overlap.

Chick Morphology

We considered the effect of nest treatment (parasitised, parasite-free) on chick morphology for day 2, 4 and 6 from hatching. None of the morphological variables differed significantly – except for naris size on day 6, which was significantly larger in parasitised chicks (Table 2). Thus, there were no morphological cues until day 6 that parents could have used to inform their decision about beak insertion per chick (but note that parents could have used the presence of larvae in the nares, which we did not quantify at the time of beak insertions). The range in chick mass per nest was not significantly different between treatments (ANOVA treatment: $F_{1,6} = 0.02$, $p = 0.89$; brood size: $F_{3,6} = 1.05$, $p = 0.44$; interaction effect $F_{1,6} = 0.07$, $p = 0.80$).

Discussion

Using within-nest video analysis of larval parasite feeding, chick begging behaviour and parental provisioning, we show that parasite feeding was generally focused on one chick per night. This finding supports the tasty chick hypothesis, although it should be noted that sibling competition within the nest (chicks standing on top of one another with the consequence that the chick at the bottom of the pile receives most parasites) needs to be considered as an additional mechanism for the observed pattern (see O'Connor et al. 2010b). Parasite feeding was correlated with subsequent chick begging intensity during the day. Chicks that had been heavily parasitised in the previous hours had lower begging intensity. In both

Table 2: Statistical results (MANOVA) for a comparison of chick morphology in parasitised versus parasite-free nests on day 2, 4 and 6 after hatching. In the model, the morphological variables were the dependent variables and treatment (parasitised, parasite-free) was the fixed factor. Only naris diameter was significantly different between treatment groups at day 6

Morphological variables	Day 2		Day 4		Day 6	
	F-value	p-Value	*F*-value	p-Value	*F*-value	p-Value
Tarsus	0.000	0.987	0.023	0.881	0.006	0.941
Beak length head	0.006	0.939	0.058	0.813	0.139	0.720
Beak length naris	0.000	0.988	0.304	0.592	0.580	0.471
Naris diameter	1.240	0.298	0.437	0.521	6.349	0.040
Wing length	0.004	0.951	0.153	0.703	0.050	0.830
Body mass	0.081	0.783	1.085	0.318	0.095	0.766

parasitised nests and in parasite-free nests, parents more often and more quickly inserted their beaks (presumably to provide feeding care) into the beaks of chicks that begged most strongly. Chicks that begged weakly did not receive parental beak insertions – despite having the highest need for provisioning. Weakly begging chicks in this study had been heavily parasitised as evidenced by larval feeding activity during the night. We found some support for the parental food compensation hypothesis, given the observation that parent birds inserted their beaks more often into the beaks of strongly begging chicks at parasitised nests compared with strongly begging chicks at parasite-free nests – but parental beak insertions did not correspond with recent parasite attack per chick.

Parental beak insertions were associated with chick begging behaviour, but not based on the putative need of the chick (see also Mock et al. 2005). The most heavily parasitised chicks had the weakest begging signal and were rarely 'fed' by parents. Those chicks that had the strongest begging intensity, in both parasitised and parasite-free nests, received the most beak insertions by parent birds. This pattern of parental response to the strongest begging chick has been found in many studies and supports the claim that parental care boosts the stronger offspring, not the weaker.

Surprisingly, there was no difference in the number of parental feeding visits to parasitised and parasite-free nests. But on the inside of the nest, using the video data, we could show that beak insertions by parent birds occurred twice as often for parasitised chicks compared with parasite-free chicks. Perhaps parents were seeking additional information about whether the chicks' crops were full, but this requires further research. If we assume that parent birds regurgitated food into the beaks of parasitised chicks twice as often as parasite-free chicks, then this interpretation is consistent with the hypothesis that parents attempt to compensate for parasitism through increased feeding (Johnson & Albrecht 1993; Tripet & Richner 1997). Clearly in this study, the higher within-nest parental feeding care did not compensate for the effects of *P. downsi* parasitism, because 100% of chicks in parasite-infested nests died. Chicks died after a $\bar{x}$ 4.2 d from hatching, which is the youngest mean age of death recorded for parasitised Darwin finch chicks (see Fessl et al. 2006b).

Parental Nest Visitation

Parental feeding visits were relatively infrequent (two to four visits per hour) and did not increase for parasitised nests. This contrasts with the studies of great and blue tits (*Parus major, Cyanistes caeruleus*), which found that parents increased feeding visits to nests by 24–65% if nests were infested with blowfly larvae and that total feeding rates could exceed 30 visits per hour (Christe et al. 1996; Tripet & Richner 1997; Hurtrez-Boussès et al. 1998). Interestingly, Kleindorfer (2007) also reported comparably low levels of parental care (2.6–3.6 visits per hour) in small ground finches on Santa Cruz Island (however, the 2.6 is mistakenly reported as 82.6 in Table 4). However, unlike our study, the Santa Cruz data were obtained during dry years (2000, 2004) when chick mortality due to *P. downsi* was low (8–30% mortality across nests). Comparing the two study sites and study years, we conclude that the frequency of parental feeding visits to the nests was not directly related to the presence or intensity of *P. downsi* larvae in nests (see O'Connor et al. 2010b), or rainfall (linked with food availability). The use of within-nest video surveillance allowed us to determine that parents may allocate more food to chicks in parasitised nests without increasing the frequency of nest visitation, as has been observed in nest-box studies of great tits (Christe et al. 1996). Of course, we cannot rule out that parents may be provisioning parasitised offspring with higher quality food. For example, parasitised corsican blue tit (*Parus caeruleus*) chicks are fed a significantly higher proportion of protein-rich caterpillars (Bańbura et al. 2004), and in house sparrows (*Passer domesticus*), prey size but not parental delivery rate predicted chick mass and recruitment (Schwagermeyer & Mock 2007).

Parental Misinterpretation of the Weak Begging Signal

Strongly begging parasitised chicks received more parental beak insertions than their weaker siblings and were also more likely to survive to at least 5 d after hatching. In parasitised nests, chicks targeted by parasites were too weak to beg, possibly as the result of high blood loss (Fessl et al. 2006b) or little sleep (O'Connor et al. 2010b). In contrast, weak begging may be a sign of satiation in parasite-free nests. Experimental studies have found that recently fed rock dove, *Columba livia,* barn swallow, *Hirundo rustica,* and magpie, *Pica pica,* chicks begged less intensely than food-deprived siblings (Redondo & Castro 1992; Mondloch 1995; Saino et al. 2000). Thus, heavily parasitised chicks that were too weak to beg may have been misinterpreted by parents as 'recently fed'. As parents only allocated food to chicks if they were begging, the begging behaviour may have been interpreted by parents as a 'signal of hunger' rather than a 'signal of need' (reviewed in Mock et al. 2011). Nevertheless, female parents appear to respond to the occurrence of parasitism because females at parasitised nests visited the nest five times more often than females with parasite-free nests to clean and preen their chicks.

Chick Condition and Growth

Parasitised chicks had significantly larger nares than chicks from parasite-free nests (see also Galligan & Kleindorfer 2009) – but only by day 6 post-hatching. Video analysis showed that first-instar larvae fed in the nasal cavities and second and third instar moved through the nares to feed internally (see Fessl et al. 2006b; O'Connor et al. 2010b). In this study, we show sudden changes in mortality: a chick that appears fine 1 d is heavily parasitised at night and dies the next, without any indication of being smaller prior to the parasite attack. Perhaps parents used other cues for low chick viability, such as flesh wounds or the presence of larvae inside the nares – which we have frequently noted when handling chicks for measurement. Although the interpretation of our results is limited by small sample sizes, studies of Darwin's medium ground finch (*Geospiza fortis*) have similarly found that *P. downsi* intensity had no significant effect on chick size or growth rates in parasitised vs. parasite-free (Huber 2008) or parasite-reduced nests (Koop et al. 2011). However, Koop et al. (2011) did find that chicks from parasite-reduced nests ($\bar{x}$ 22 parasites per nest) had significantly longer wing feathers than control nests ($\bar{x}$ 38 parasites per nest) at the time of fledging. Notably, Fessl et al. (2006a,b) found that Darwin finch chicks in parasite-free nests had significantly higher body mass than chicks in parasitised nests. The Fessl et al. (2006a,b) study was carried out in 2000 and 2001, when most finch chicks survived to at least 6 d post-hatching, even in parasitised nests. The mean age at death in parasitised nests is currently 4.2 d. Therefore, we may not be detecting a difference in mass between parasitised and parasite-free chicks for the following reason: chick mass for the first days post-hatching may be obfuscated by maternal investment into the egg, followed by parasite-induced mortality on days 3–5 post-hatching, and survivorship of a single chick in some cases until day 6–9; the single chick receives all parental provisioning, but then dies overnight from blood loss. Our measure of mass does not seem to reflect these possible changes in trajectory.

Conclusion

Our study showed that begging intensity was not an accurate measure of chick 'need' for adult provisioning. Parents always responded to the strongest begging chick most quickly with beak insertions (presumed feeds). Interestingly, strongly begging chicks in parasitised nests received more parental beak insertions than did strongly begging chicks in parasite-free nests. We suggest that parents could have been acquiring information from the crop contents of the chick rather than feeding the chick (which remains to be tested). Females showed more parental care than males and did all preening and grooming of parasitised chicks. As a result of increased parental care per nest visit (but no difference in the number of feeding visits), there may be a higher cost of parental care that could lead to trade-offs for future reproduction and survival. Clearly, Darwin's finches were unable to compensate for the negative effects of parasitism, and all parasitised chicks in this study died.

Acknowledgements

This research was supported by the Australian Research Council, Max Planck Institute for Ornithology, Adelaide Zoo, Australian Federation for University Women, Royal Society for the Protection of Birds/Birdfair, Mohamed bin Zayed Species Conservation Fund and Rufford Small Grants for Nature Conservation. TAME airlines provided reduced airfares. We thank the Galapagos National Park Service and the Charles Darwin Research Station for logistical support and for the opportunity to work in the Galapagos. We thank D. Butler, B. Jaensch, B. White and M. McKelvey for the development of field equipment, S. Cisneros, C & W. Cruz and the community of Floreana Island for logistical support and J. Forwood, C. Charlton, T. Clark and R. Dudaniec for field assistance. This publication is contribution number 2081 of the Charles Darwin Foundation for the Galapagos Islands.

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