Video analysis of host–parasite interactions in nests of Darwin's finches

Jody A. O'Connor, Jeremy Robertson and Sonia Kleindorfer

Abstract Parasites place their hosts under strong selection for adaptive traits that increase parasite resistance. The initial impact of invasive parasites has rarely been observed and can be particularly strong on naïve hosts with limited prior exposure to parasites. *Philornis downsi* is an introduced fly to the Galapagos Islands whose parasitic larvae cause high mortality in nestlings of Darwin's finches. We used a within-nest camera system and nest monitoring data to examine this new host–parasite interaction in the wild. Many *P. downsi* flies entered finch nests with incubated eggs or nestlings but only when parent finches were not present. Parasitic *P. downsi* larvae were observed to emerge from the nest base at night to feed both internally and externally on nestlings. Adult and nestling Darwin's finches exhibit grooming and avoidance behaviours in the presence of *P. downsi* parasites. Specifically, in nests with high parasite intensity, nestlings increased self-preening behaviour, ate larvae and stood on top of one another. Female finches probed into their nestling's nares (first instar larvae reside in the nares) and probed into the nest base (second and third larvae reside in the nest base during the day). These findings shed light on the emergence of anti-parasite behaviour as well as host–parasite relationships after recent parasitism in a naïve host.

Keywords Darwin's finches, Galapagos, host–parasite interaction, larvae, mortality, *Philornis downsi*, video analysis

This paper contains supplementary material that can be found online at http://journals.cambridge.org

Introduction

Birds can develop and adapt their parasite defences under long-term continued exposure to a particular parasite (Jarvi et al., 2001; Foster et al., 2007) but can be extremely vulnerable on initial contact with a novel parasite (Warner, 1968). Island taxa are particularly vulnerable to introduced pathogens because they evolved in isolated, often pathogen-depauperate environments, with little need for defences until parasites and diseases are introduced (Wikelski et al., 2004).

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The majority of infectious avian pathogens on the Galapagos Islands have been introduced via the importation of poultry and pigeons (Gottdenker et al., 2005). Of the c. 34 avian pathogens currently identified on the Galapagos (Fessl et al., 2001; Wikelski et al., 2004; Dudaniec et al., 2005; Gottdenker et al., 2005; Soos et al., 2008), the invasive parasite, the fly *Philornis downsi*, presents the most imminent threat to the survival of Darwin's finches. In 1997 blood-filled larvae of *P. downsi* were discovered in the nests of Darwin's finches (Fessl et al., 2001). Retrospective examination of insect collections has found that the fly was present on the Galapagos Islands as early as 1964 (Causton et al., 2006). Adult *P. downsi* flies are vegetarian and lay their eggs in bird nests, where the three larval stages are free-ranging and feed on the blood and tissues of nestling birds (Plate 1; Fessl et al., 2006b). On average, finch nests are infested with 30–50 *P. downsi* larvae (Fessl & Tebbich, 2002; Dudaniec et al., 2007; O'Connor et al., 2010a,b) but up to 182 parasites have been found in a single nest (Fessl & Tebbich, 2002).

For Darwin's finches the fitness costs of *P. downsi* are severe, with 16–95% brood mortality over 1998–2008 (Dudaniec & Kleindorfer, 2006; Fessl et al., 2006b; Huber, 2008; O'Connor et al., 2010a,b), reduced blood haemoglobin concentrations (Dudaniec et al., 2006), multiple body wounds and infections, substantial blood loss (18–55%; Fessl et al., 2006b), grossly deformed nasal openings (nares; Galligan & Kleindorfer, 2009) and reduced growth rates and fledging success (shown experimentally; Fessl et al., 2006a). Potential host responses such as increased parental care and nestling defensive behaviours are yet to be examined between Darwin's finches and *P. downsi* (Huber, 2008) but may represent an important dynamic in this new host–parasite interaction. For example, when parasitism is specific to the nestling phase of the host, critical anti-parasite defences are usually underdeveloped (Lung et al., 1996; Smits & Bortolotti, 2008) and host parents typically provide extra care in the form of increased preening and feeding (Tripet & Richner, 1997; Hurtrez-Boussès et al., 1998).

The detrimental impacts of *P. downsi* on Darwin's finches are well documented but because larval parasitism occurs within finch nests at night (Fessl et al., 2006a) there are few observations of the host–parasite interaction in the wild. Developing effective control methods requires a more detailed understanding of within-nest activity such as the fly's reproductive characteristics, larval feeding strategies and finch anti-parasite defences. Meanwhile, the threat this parasite poses to endemic birds is steadily increasing. Since

PLATE 1 Recently deceased nestling with larval damage to beak and 1st instar larvae present, feeding in beak cavity.

first being discovered on Santa Cruz Island *P. downsi* has spread to 12 Galapagos islands (Wiedenfeld et al., 2007; also S. Huber & R. Grant, pers. comms), and larvae have been found in 64–100% of nests (Fessl & Tebbich, 2002; Fessl et al., 2006b; Dudaniec et al., 2007; Huber, 2008; O'Connor et al., 2010a,b) of 11 of the 14 species of Darwin's finches on the Galapagos (Wiedenfeld et al., 2007). We used infrared video cameras inside nests to monitor fly visitation and finch responses to the presence and activity of the fly and larvae. We provide the first observational data of within-nest interactions between Darwin's finches and *P. downsi* in the wild.

Study area and species

Flies and finches were studied at the height of the finch breeding season between February and April 2008 in the arid zone (00°44 S, 090°18 W) of Santa Cruz Island and both the arid (01°16 S, 090°29 W) and humid highland (01°17 S, 090°27 W) zones of Floreana Island. We monitored nests of three common finch species that have comparable inter-species variation in *P. downsi* intensity (number of parasites per nest; Dudaniec et al., 2007): the small ground-finch *Geospiza fuliginosa*, medium ground-finch *Geospiza fortis* and small tree-finch *Camarhynchus parvulus*. The location, general characteristics and video recording details of each nest are provided in Table 1.

Methods

We monitored nest activity with a battery-powered video monitoring system that included four cameras, a multiplexer and a digital video recorder (DVR). Each of the Jaycar monochrome CCD security cameras were fitted with two infrared LEDs with shaven ends to diffuse light more evenly within the nest. This light is not visible and does not affect nest activity or predation (Pierce & Pobprasert, 2007) but enables cameras to function day and night. A 15-mm diameter hole was cut through the roof material of the dome-shaped nests to insert the camera lens and infrared LEDs, leaving the small camera body (60 g) outside supported by roof material. Camera insertion caused no structural damage, gaps were sealed with waterproof material and video and power cables were firmly secured to branches to avoid weighing down the nest. Each camera was connected by video cable to a multiplexer that combines up to four signals into a single quad split-screen input recorded onto an Archos 605 DVR that was programmed to record continuously in 2-hour segments. DVR and cable malfunctions interrupted video recordings for between 1 and 12 hours at different nests (Table 1) and, in the case of a complete DVR breakdown, a Sony digital camcorder was used to record an LCD monitor displaying the camera outputs. The remoteness of the sites prevented the possibility of repair or equipment replacement. Recordings were analysed with the software *Quicktime Pro v. 7.4* (Apple Inc., Cupertino, USA).

The intensity of *P. downsi* per nest was determined using established methods (Fessl & Tebbich, 2002; Dudaniec et al., 2006). Empty nests or those containing dead nestlings were considered inactive and were removed from the nesting tree, sealed in plastic bags and later dismantled. All larvae, pupae and pupae cases were preserved in 95% ethanol and summed for total *P. downsi* intensity.

All parasite–host behaviours were counted from either 1 hour of video recording or, if there was sufficient video footage, behaviour frequency was averaged over 2 randomly selected hours during the day and/or night. Table 2 provides an overview of the behaviours inside the nest that were observed and quantified for *P. downsi* flies, fly larvae, nestlings and parent birds. For statistical analysis nests were categorized according to total *P. downsi* intensity (low, 0–9; medium, 18–25; high, 52–74; no nests contained a parasite intensity that was either between or above these categories) and nestling age (young, 1–4 days; old, >7 days). We did not film any nestlings aged 5–7 days because either nestlings had died before Day 5 or cameras were placed in nests when nestlings were already >7 days old.

Results

Adult fly activity

Of the nests monitored, *P. downsi* flies were videoed entering one of two nests with incubating eggs and seven of nine nests with nestlings (Table 2). No fly activity was observed in (1) a nest with recently abandoned eggs, (2) in the hour before or 24 hours after nestlings had fledged from four nests, and (3) one nest with 10-day-old nestlings in the Floreana arid zone, where *P. downsi* intensity was low (eight larvae in the nest). Flies walked over all inner nest surfaces and remained

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Table 1 Description of nests fitted with in-nest cameras on Santa Cruz (SC) and Floreana (F) Islands in 2008.

	Geospiza fortis	*Camarhynchus parvulus*	*Geospiza fuliginosa*								
Nest number (ID)	1	2	3	4	5	6	7	8	9	10	11
No. of young chicks in nest		2			3	2	4	2			6
No. of old chicks in nest	2								2	4	
Eggs (incubated or unhatched)		1		5	2	2					
Eggs (abandoned)			3								
Hours of footage	55	1	40	1	14	14	6	4	2	12	12
Footage during day &/or night	Day/ night	Day	Day/ night	Day	Day/ night	Day/ night	Day	Day/ night	Day	Night	Night
Island	SC	F	SC	F	F	F	F	F	F	F	F
Habitat	Low	High	Low	High	High	High	High	High	Low	Low	Low
Total *Philornis downsi*	74	0	0	1	21	22	52	33	4	8	18

in a nest for up to 10 minutes. Mean duration of fly activity in nests was 1.34 ± SE 0.43 minutes and was similar for nests with eggs and nestlings. Flies were only observed entering nests with young nestlings during the day (mean entry frequency 0.63 ± SE 0.18 h^{-1}, n = 8), and nests with old nestlings during the night (mean entry frequency 1.6 ± SE 1.6 h^{-1}, n = 5), when adult finches were absent. Finches did not display fly-repelling behaviours (see Hart, 1997).

White eggs were observed at the rear of female flies in two nests and were deposited on the base of a nest with eggs and a nest with 2- to 3-day-old nestlings. Oviposition probably occurred in all eight nests with fly activity but could not always be confirmed because of the angle of the camera lens. Flies barely touched nestlings or finch eggs (maximum 3-second contact per nest visit). We did not observe egg laying directly on the nares of nestlings, where first instar larvae are first found (Fessl et al., 2006b) but 13 fly eggs were found clumped on the naris of a < 1-day-old chick in a nest where we did not film. *Philornis* spp. larvae can hatch within a few hours following hatching of host eggs (Spalding et al., 2002) and navigate to the nares of nestlings to begin feeding; hence, it may not be necessary for flies to lay their eggs directly on the nares of nestlings. Fly mating was not observed.

Table 2 Overview of Darwin's finches and *P. downsi* host/parasite interactions observed on video during the day and night. We filmed at two nests with eggs and nine nests with nestlings. Corresponding nest ID details and characteristics are given in Table 1.

	Activity	No. of nests	ID of nest(s)	Frequency (mean hr^{-1})	Duration (mean minutes hr^{-1})
Day					
Adult finch	Probe nest	6	1,2,5,6,8,11	4.3	
	Nest sanitation	3	5,6,11		5.7
	Preen chick feathers	2	1,11	23.5	
	Preen chick nares	1	1	11	
Adult fly	Enter nest	6	2,4,5,7,8,11	1.2	
	Land on chick	5	2,4,5,8,11	1	
	Land on eggs	3	2,4,5	1	
	Land on nest material	7	2,4,5,7,8	1	
	Deposit eggs	2	2,8	1	
Night					
Adult finch	Probe nest	4	5,6,8,11	17	
Finch Nestling	Self preen	2	1,10	30.5	
	Stand on top of sibling(s)	1	1	10	9.6
Adult fly	Enter nest	1	1	8	
	Land on chick	1	1	4.5	
	Land on nest material	2	1,11	1	
Fly larvae	Enter chick nares	2	1,7	1.8	
	Minutes feeding in nares	2	1,7		16.4
	Minutes attached to chick	3	1,5,11		1.9

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Larval activity

Larvae were only observed in nests with nestlings and were not observed in nests during the 24 hours post fledging. Larval activity was observed at the surface of the nest base between nightfall (18.00) and sunrise (06.00; Appendix: Video 1) when parent finches did not visit the nest, although larvae were occasionally seen for short periods during the day. Larvae were observed crawling over and between young nestlings that were being brooded by their mother at night. A maximum of 40 large larvae were seen emerged from the base of nests with old nestlings at any one time. Larvae spent a mean 14.3 minutes squeezing in and out of nares (n = 17 larvae, two nests; Appendix: Video 2), and a maximum of five large larvae emerged from the nares of one nestling within a 10-minute period. The larvae had presumably resided in the nestling for at least 1 hour, as the larvae were not observed externally. Larvae attached to nestlings for external feeding for 1–3 minutes and entered nares of nestlings a mean of 2.5 times ± SE 0.5 h^{-1}, n = 2; Table 2).

After killing one > 8-day-old nestling, larvae ate a hole through the rear of its body and consumed most of its internal tissues within 2 hours (saprophagous feeding). After this time, the larvae moved away from the dead nestling and congregated around the feet of the surviving nestling, after which the nestling perched at the nest entrance.

Nestling evasive behaviour

Night-time nestling evasive behaviour could be quantified from two nests with > 8-day-old nestlings that had markedly different parasite intensities. In a nest with low *P. downsi* intensity (eight parasites in a nest with four nestlings, Floreana arid zone), the nestlings spent 98% of the night resting, 2% repositioning and preened themselves an average of once per hour. In contrast, in a nest with high *P. downsi* intensity (74 parasites in a nest with two nestlings, Santa Cruz arid zone), nestlings spent 10% of the night resting, 90% repositioning and preened themselves a mean of 28.5 times per hour (Appendix: Video 3). Furthermore, in the nest with high parasite intensity, the older nestling frequently trampled on top of the younger nestling (while alive and for 2 hours after its death), forming a 'buffer' between itself and the larvae (Table 2). On one occasion a nestling (> 8 days old) was observed to pick a larva from under its wing and eat it. Nestlings used their beaks for preening but were never observed to use a foot to scratch their heads to reach ectoparasites inaccessible to their beaks (Moyer & Clayton, 2003).

Parental care

Female finches preened their nestlings' feathers, probed within nestlings' nares (Appendix: Video 4), probed nest material (Appendix: Video 5) and probed between nestlings, probably in an attempt to remove larvae from the nest (Table 2). Female finches will remove dead nestlings from the nest (J. O'Connor, pers. obs.), which would also discard any larvae in the nestling. There was no significant correlation between *P. downsi* intensity and the rate at which parents visited the nest to feed their nestlings (Spearman's rank order correlation $r = 0.25$, n = 8, $P > 0.5$).

Parasitism and fledging success in filmed nests

In the nine nests *P. downsi* intensity was 4–74 parasites per nest (mean 27.13 ± SE 8.5) and only 20.8% of nestlings fledged (5 of 24). However the relationship between parasite intensity and fledging success was not clear-cut ($\chi^2 = 1.2$, df = 8, $P = 0.15$). No fledglings left the nest before the expected minimum 14 days. Of the five fledglings, four were from a nest with only eight larvae, while only one fledgling survived from a heavily parasitized nest (74 parasites), presumably because it perched on top of its younger sibling before and after it died. Only one of the nine nests was free of *P. downsi* larvae and pupae and those chicks were found dead and covered with fire ants *Wasmannia auropunctata* within a day of hatching. It is possible that larvae were removed by ants in this nest but this cannot be confirmed because video recording stopped before the nestlings died. In another nest small ants were seen removing small *P. downsi* larvae from nesting material during the day and large ants were seen inspecting nares of live and dead chicks and removing small larvae at night.

Discussion

Most nests had multiple fly visitations throughout the finch incubation and nestling period (Table 2), which would contribute to high parasite numbers from several flies accumulating within the same finch nest. *Philornis carinatus* and *Protocalliphora* botflies have similarly been observed to randomly enter and oviposit in bird nests regardless of host nestling age (Gold & Dahlsten, 1983; Young, 1993). Recent microsatellite analyses provide genetic evidence that up to five *P. downsi* females contribute to the larvae within a single nest (Dudaniec et al., 2008).

Birds can reduce the impact of high ectoparasite intensity by preening (Cotgreave & Clayton, 1994). Female finches directed anti-parasite behaviour at areas of larval infestation by using their beak to probe directly into the nest base and within the enlarged nares and between feathers of parasitized nestlings. Nestlings rely on maternal anti-parasite defences for at least the first 4 days after hatching, when they are blind, featherless and have rudimentary motor control skills. Subsequently, older nestlings (> 8 days old) had to undertake their own anti-parasite behaviours because their parents did not visit the nests at night. Adults did not alter the rate at which they visited nests to

feed to compensate for the effects of parasitism, which contrasts with studies of blue tits *Parus caeruleus* in which parents increased food provisioning to parasitized nestlings (Tripet & Richner, 1997; Hurtrez-Boussès et al., 1998). We recommend further within-nest studies of Darwin's finches to examine the role of host species, island and parasite intensity on host–parasite behaviours.

Larvae of most *Philornis* species are subcutaneous feeders (Dudaniec & Kleindorfer, 2006). *P. downsi* larvae are known as free-living semi-haematophagous feeders that feed externally on their host (Dudaniec & Kleindorfer, 2006) but our study indicates they also enter through the nares of nestlings to feed internally. Repeated larval movement through the nares is probably the cause of the gross enlargement of nasal openings observed in Darwin's finches (Fessl et al., 2006b; Galligan & Kleindorfer, 2009). In addition to external evidence of damage to nares we found many nestlings with an empty cavernous inner beak (Plate 1), devoid of a nasal septum and lacking the ciliated mucosa-covered turbinate projections that increase surface area to humidify respired air (Geist, 2000) and filter large particulate matter, which may increase the likelihood of dehydration during expiration and contraction of respiratory diseases. Beak deformation is also associated with high ectoparasite infestations and decreased preening efficiency in studies of other bird species (Clayton, 1991; Clayton et al., 1999).

A nestling's beak is essentially its only means for removing larvae: once larvae have entered the nares, nestlings are unable to prevent or obstruct their progress. Nestlings weakened by blood loss and constant repositioning often collapsed, and subsequently, their beak or face rested on the nest base, which facilitated larval attachment to the nape or entry into the nares. After a night attempting to avoid consumption by larvae, weaker nestlings may be unable to beg for food effectively when competing with stronger nestlings and thus further lose body condition. Simon et al. (2003) showed that weakened blue tit nestlings with lowered immunocompetence attract more feeding attacks by fly larvae, providing evidence for the 'tasty chick hypothesis'. Larval preference for weaker Darwin's finch nestlings could therefore select for the survival of nestlings that have strong immune defences and are competent at avoiding parasite attachment/nares entry. Huber et al. (2010) demonstrated that nesting female *G. fortis* can produce specific antibodies in response to *P. downsi* parasitism. This suggests that adult females are subject to some larval parasitism while brooding, and could possibly transfer immunological advantages to subsequent offspring (Huber et al., 2010).

Newly formed avian host–parasite systems are commonly characterized by large ectoparasite numbers and high fitness costs to the host (Clayton, 1991). This pattern is occurring in the effects of the recently introduced *P. downsi* on Darwin's finches in the Galapagos archipelago. The past 10 years of research have documented high levels of parasite intensity and nestling mortality (Fessl et al., 2006a,b; Dudaniec et al., 2007; Kleindorfer & Dudaniec, 2009; O'Connor et al., 2010a,b), indicating that Darwin's finches do not have sufficient defences against *P. downsi* parasitism. Given the iconic status of Darwin's finches and their relatively small populations (including two Critically Endangered species), development of a control method for *P. downsi* is essential. We recommend further research into fly trapping systems and long-term eradication using biological control or methods such as the sterile insect technique. Our observations on the behaviour of *P. downsi* flies, larvae, nestlings of Darwin's finches and parental care will facilitate the timing and application of control methods.

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Appendix

The Appendix for this article is available online at http://journals.cambridge.org

Biographical sketches

Jody O'Connor works on conservation issues for Darwin's finches in the Galapagos Archipelago, with a focus on the Critically

Endangered medium tree finch on Floreana Island. She specializes in studies of avian behaviour and population genetics, and monitoring the effects of invasive parasites and predators on island birds. JEREMY ROBERTSON'S current research includes the role of acoustic signals in sexual selection, assessing predation risks and speciation in birds, and developing new approaches to the analysis of acoustic signals. Through the Focus Conservation Fund he also promotes community projects that conserve habitats and biodiversity in Brazil. SONIA KLEINDORFER is studying *Philornis* parasitism in the Galapagos and also works on avian population ecology and behaviour in Australia. Her field research has significantly developed theoretical frameworks for the study of clinal variation in morphology and song, and the interplay between habitat characteristics, predation risk and parasitism using birds as model systems.

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