

## Research



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# Female in-nest attendance predicts the number of ectoparasites in Darwin's finch species

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Selection should act on parental care and favour parental investment decisions that optimize the number of offspring produced. Such predictions have been robustly tested in predation risk contexts, but less is known about alternative functions of parental care under conditions of parasitism. The avian vampire fly (*Philornis downsi*) is a myiasis-causing ectoparasite accidentally introduced to the Galápagos Islands, and one of the major mortality causes in Darwin's finch nests. With an 11-year dataset spanning 21 years, we examine the relationship between parental care behaviours and number of fly larvae and pupae in Darwin's finch nests. We do so across three host species (*Camarhynchus parvulus*, *C. pauper*, *Geospiza fuliginosa*) and one hybrid *Camarhynchus* group. Nests with longer female brooding duration (minutes per hour spent sitting on hatchlings to provide warmth) had fewer parasites, and this effect depended on male food delivery to chicks. Neither male age nor number of nest provisioning visits were directly associated with number of parasites. While the causal mechanisms remain unknown, we provide the first empirical study showing that female brooding duration is negatively related to the number of ectoparasites in nests. We predict selection for coordinated host male and female behaviour to reduce gaps in nest attendance, especially under conditions of novel and introduced ectoparasites.

## 1. Introduction

Parental care functions to enhance offspring survival by satisfying offspring needs during growth and development, often at a cost to the parent [1–3]. Selection should act on parental care and favour parental investment decisions that optimize both the number and quality of offspring in relation to the current versus future reproductive opportunity of each parent [4,5]. Such predictions have been robustly tested in the context of predation risk, and parents generally adjust their level of parental defence behaviour towards a predation threat to themselves or their offspring, as predicted by life-history theory [6–9]. In the context of avian nest ectoparasites, the effects of parasitism on parental care have mostly been explored in relation to food delivery. Yet, when offspring are parasitized, research has found inconsistent patterns across species in the impact of parasite burden × chick begging on parental food delivery [10–12]. There are also gaps in knowledge because of missing information about the relative value of current versus future broods infested with ectoparasites,

which further hampers interpretation of adjustments in food delivery to parasitized offspring [13,14]. In this study, we take a different approach and ask a more fundamental question: can parental care at the nest act as a physical deterrent that prevents ectoparasites from entering the nest to oviposit? If longer in-nest attendance by parents deters ectoparasite oviposition, then factors that promote longer in-nest attendance such as brooding duration could be targets of selection when parasites impose strong fitness costs.

Most studies on host parental care in response to ectoparasites have tested the food compensation hypothesis, which predicts that parents will increase food delivery to offspring at parasitized nests to compensate for the nutritional and energetic costs of parasitism [15,16]. Evidence for the food compensation hypothesis has been mixed [17–21], perhaps due to sex differences in the value of current versus future broods [20]. Parental care can reduce the number of ectoparasites when parents consume or remove parasites during nest sanitation [22–24] or use aromatic plants with volatile chemical compounds during nest building or applied to themselves, which can deter ectoparasites [25–27] (but see [28]). However, no studies we are aware of have measured the role of parental in-nest attendance, a possible form of nest guarding, to reduce parasite burden, or the effect of behavioural conspicuousness of the attending birds, measured as parental activity at the nest, to deter or attract ectoparasites.

The offspring of Darwin's finches on the Galápagos Islands are currently being parasitized by the accidentally introduced avian vampire fly (*Philornis downsi*), a myiasis-causing ectoparasite [29]. Adult *P. downsi* were first collected from traps on Santa Cruz Island in 1964 [30]. The adult fly is vegetarian and feeds on decaying plant matter [31], but the developing fly larvae are parasitic and feed on the blood and tissue of avian chicks. These chicks suffer, by far, the most extreme costs of *P. downsi* parasitism, including blood loss, naris deformation, infected body wounds, and mortality [32]. On average, 55% of chicks die in the nest due to parasitism, with annual variation in mortality ranging from 20% to 100% per year [32]. Effects of *P. downsi* larvae on adult birds are considered indirect. For example, *P. downsi*-specific antibodies have been detected in some, but not all, adult finches [12,24], and adult finches that survived parasitism as chicks often sustain enlarged or malformed nares (nasal openings) as adults [33,34]. *Philornis downsi* females oviposit eggs onto nesting material [23] and perhaps onto chicks; after hatching, larvae crawl inside the nares of the chicks to consume blood or keratin [11]. Increasingly over the past decade, larvae on Santa Cruz Island are suspected to consume the blood of incubating females [35], with observations of temporal and island differences in *P. downsi* behaviour. For example, during 2000 to 2004 on Santa Cruz Island, *P. downsi* were only found in Darwin's finch nests with chicks (100% prevalence), but, since 2012 on Santa Cruz Island, *P. downsi* have regularly been found in Darwin's finch nests with eggs (80% prevalence in some species and some years) and in most nests with chicks (83% to 100% prevalence) [35], indicating adult *P. downsi* are ovipositing earlier in the nesting cycle. By contrast, on Floreana Island, during 2004 to 2016, *P. downsi* larvae and pupae were uncommon in nests with eggs (2% prevalence) but were found in all highland nests with chicks (100% prevalence) [36].

Currently, *P. downsi* is considered the biggest risk factor to the survival of all Galápagos land birds, and researchers are

urgently interested in identifying causative factors that explain *P. downsi* oviposition behaviour in host nests, which could be used to inform both mechanical removal and bio-control approaches [31,37]. Two main hypotheses have been proposed for how *P. downsi* locate host nests: (i) olfactory cues from the host and/or (ii) visual cues from host behaviour [37]. One observation at one Galápagos flycatcher (*Myiarchus magnirostris*) nest provides a clue that parental presence at, or near, a nest entrance may deter an ectoparasite from entering the nest [38]. In this detailed observation, two adult *P. downsi* females were observed resting approximately 50 cm from the nest entrance for approximately 40 min [38]. During a second observation period later in the day, after the attending female flycatcher had left the nest, one of the two *P. downsi* females entered the nest [38]. The flycatcher returned shortly thereafter; both fly and flycatcher remained in the nest for 8 min, then the flycatcher emerged and so did *P. downsi*, flying over the head of the flycatcher [38]. From in-nest video material in Darwin's small ground finch (*Geospiza fuliginosa*), *P. downsi* females were observed to enter and oviposit on the nesting material when the attending female was out of the nest [23]. Fly visitation length at the nest averaged 1.3–1.5 min and was terminated if the adult host returned [23].

We are interested in whether parental care in Darwin's finch hosts could attract or deter *P. downsi* from ovipositing in nests. We do not measure oviposition behaviour directly but use total number of *P. downsi* (larvae, pupae and puparia) per nest as a proxy for total oviposition behaviour. We test the following ideas. (i) If parental activity attracts *P. downsi* via visual cues, then we predict more *P. downsi* in nests with high levels of parental activity (many incubation events, many male and female visits with food delivery to chicks). (ii) If parental attendance at the nest attracts *P. downsi* via other cues, perhaps olfactory cues, then we predict more *P. downsi* in nests with greater parental nest attendance (longer incubation duration of eggs, longer brooding duration of hatchlings, interaction effect between food delivery by male and time inside nest by female). (iii) If parental attendance at the nest deters *P. downsi* from entering the nest, then we predict fewer *P. downsi* in nests with greater parental in-nest attendance (longer incubation duration of eggs, longer brooding duration of hatchlings). As a corollary of this prediction, we explore factors that may be associated with longer female nest attendance (male feeds to female, male feeds to chicks, chick age). Finally, we consider an alternative explanation, namely that the date of nesting explains variation in parental care, given changes in timing of activity associated with ambient temperature [39,40], invertebrate abundance [41] or other factors we did not measure. We also analysed nesting date in relation to number of *P. downsi* per nest, as the number of parasites may increase across the host nesting season [42].

## 2. Methods

### (a) Study site and species

Our study was conducted on two islands in the Galápagos archipelago from January to March during 2000 to 2020. On Santa Cruz Island (−0.624192, −90.384808), we observed Darwin's finch nesting behaviour in 2000, 2001, 2002 and 2004, and on Floreana Island (−1.299829, −90.455674) we observed nesting

behaviour in 2006, 2010, 2012, 2013, 2014, 2016 and 2020 (11 years of sampling spanning 21 years). The two focal species on Santa Cruz Island were small ground finch (*G. fuliginosa*) and small tree finch (*Camarhynchus parvulus*) and the four focal taxonomic groups on Floreana Island were small ground finch, small tree finch, medium tree finch (*C. pauper*) and the recently discovered hybrid *Camarhynchus* group that arises mostly from pairings between *C. pauper* females and *C. parvulus* males [43–45]. Male and female ground finches (*Geospiza* spp.) are easily distinguished once males are 1+ years old, as they become progressively black-bodied with age until attaining a fully black body around 5+ years old whereas females remain olive grey with streaked plumage [46]. In tree finches (*Camarhynchus* spp.), males become progressively black-headed until attaining a fully black crown and hood from around 5+ years old whereas females remain olive green [47,48]. We only consider the effects of male age on parental care because male age can be inferred from plumage colour, whereas female age cannot be inferred from plumage colour. In both ground and tree finches, only females incubate eggs and brood hatchlings [49]. Thus, one can easily discern the sexes of nesting Darwin's finches. Minimum longevity (calculated as the age at first capture plus the number of years until the last recapture) in these finches is 12–17 years [48].

### (b) Parental care behaviour

We analysed 541 1 h nest observations at 208 Darwin's finch nests during the incubation ( $n = 305$ ) or chick feeding ( $n = 236$ ) phase. The number of nests monitored per species was 59 *G. fuliginosa*, 79 *C. parvulus*, 58 *C. pauper* and 12 nests of hybrid *Camarhynchus* finches. We regularly mist-netted birds in the study area during the first two weeks of every field season and then subsequently located nests with colour-banded birds. At 149 nests, at least one bird per pair had unique colour bands, and, at 74 nests, both the male and female were colour-banded. In total, 110 males and 113 females were uniquely colour-banded (26 male and 25 female *G. fuliginosa*; 57 male and 67 female *C. parvulus*; 18 male and 11 female *C. pauper*; 9 male and 12 female hybrid finches).

Nests were monitored using our standardized protocol developed in 2000 and maintained throughout the study [39,43]. To confirm nesting activity, nests were routinely inspected (with binoculars and ladder from 2000 to 2006 and using a borescope since 2008) every 3 days during incubation and every 2 days during the nesting phase. During 1–2 days per phase (incubation, chick feeding), we made a 1 h focal sample observation (between 7:00 and 11:00), noting every behaviour with a time stamp. In about 15% of observations, the observation time was slightly shorter or longer than 60 min. This was accounted for in our analyses by applying the offset function within our statistical models [50]. The observer was seated on the ground, about approximately 20 m from the nest, with binoculars focused on the nest entrance. As Darwin's finches do not noticeably alter their behaviour in the presence of a human observer within 5 m [51], this observer distance was unlikely to disturb parental feeding. During the incubation phase, we recorded the following behaviours: (i) time female spends inside the nest during incubation; (ii) number of incubation events (number of bouts of incubation per hour of observation); (iii) incubation bout duration (min); and (iv) number of male food deliveries to the incubating female at or near the nest entrance. Behaviours recorded during the chick feeding phase (eggs hatched into chicks) were: (v) time female spends inside the nest sitting on hatchlings to provide warmth during the chick phase (brooding duration,  $\text{min h}^{-1}$ ); (vi) number of male visits per hour to the nest with food delivery to chicks; and (vii) number of female visits per hour to the nest with food delivery to chicks. We noted clutch size, brood size

and chick age at the time of behavioural observations for all nests from routine nest inspections.

### (c) Number of *Philornis downsi* per nest

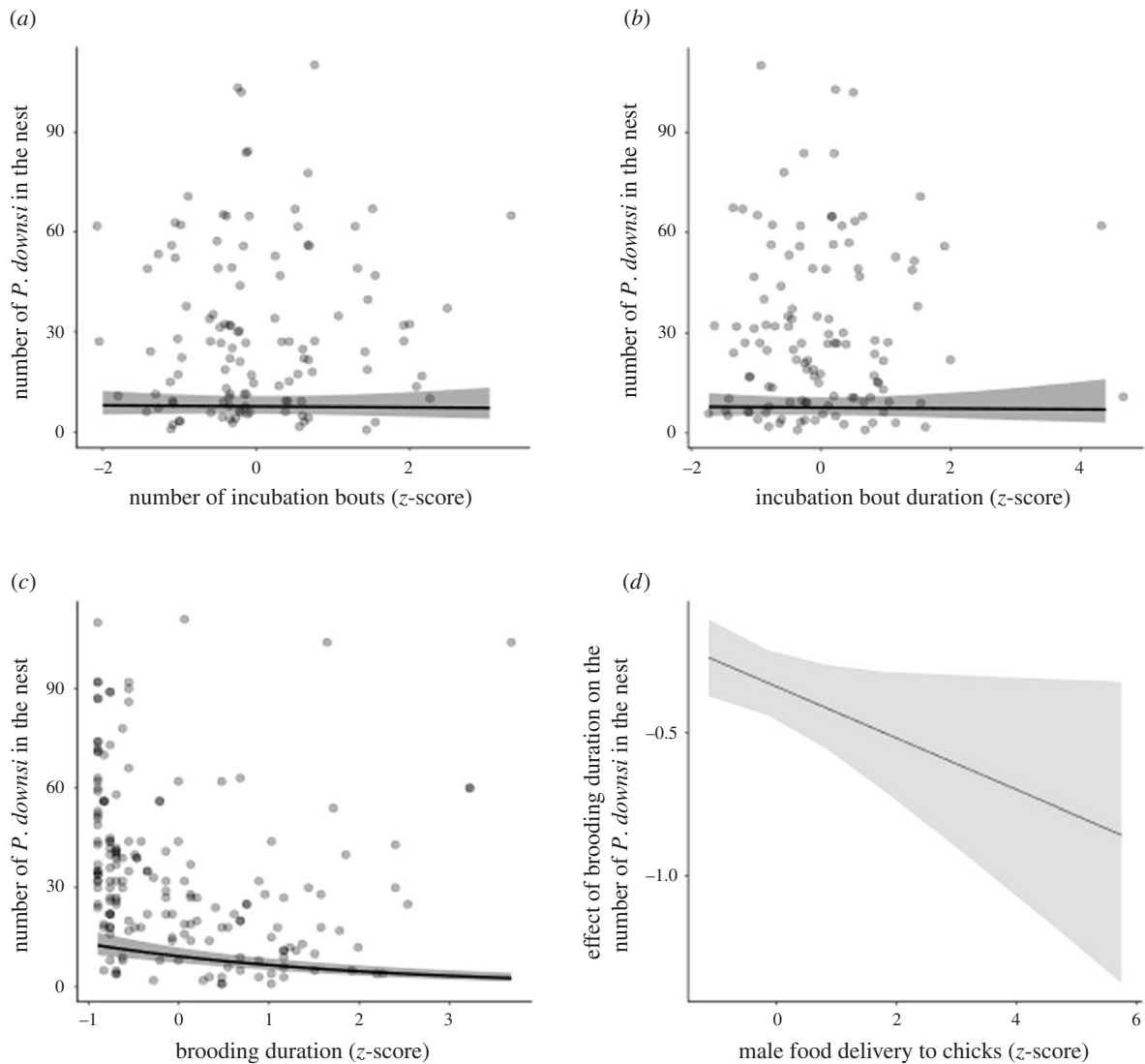
Once the nesting event had finished (i.e. the offspring had died or fledged), as confirmed by our routine nest monitoring, the nest was immediately collected from the field, stored in a plastic bag and transported to our on-site laboratory later in the day to count the number of *P. downsi* larvae, pupae and puparia [52]. Generally, all *P. downsi* were counted within 6 h and a maximum of 24 h post-nest collection. The *P. downsi* specimens from each nest were preserved in separate tubes containing 70% ethanol. We recorded the number of *P. downsi* per instar phase, though first and second instar were confirmed later with a microscope [52,53]. Here, we analysed the total number of *P. downsi* per nest as our main variable of interest and in relation to chick age at the time of nesting termination.

### (d) Statistical analysis

All statistical analyses were performed in R v. 3.6.1 [54] under a pseudo-Bayesian framework with non-informative priors using the packages 'arm' [55] and 'lme4' [50]. For every statistical model (package 'lme4'), the restricted maximum-likelihood estimation method was applied, and all the assumptions were checked by visual inspection of the residual plots. In each model, we applied the function 'sim' and carried out 10 000 simulations to obtain the posterior distribution of every estimate, the mean value and the 95% credible interval (CrI) [55]. CrIs provide information about uncertainty around the estimates. We defined a difference between species (and hybrid birds) to be statistically meaningful when the posterior probability of the CrI difference (termed ' $p(\text{dif})$ ') was higher than 95%, and an effect to be statistically meaningful when the 95% CrI did not overlap with zero. A threshold of 5% is equivalent to the significance level in a frequentist framework (i.e.  $p$ -value of 0.05) [56].

#### (i) Effect of incubation and brooding behaviour on number of *Philornis downsi* per nest

To examine the effect of incubation and brooding behaviour on the number of *P. downsi*, we fitted separate Poisson generalized linear mixed effects models. The dependent variable was the number of *P. downsi* in the nest at the time of the nesting outcome. We included observation duration as an offset in the model. To measure the effect of incubation behaviour, the explanatory variables were number of incubation events, incubation bout duration, the interaction between these two variables and number of male food deliveries to the female. To measure the effect of brooding duration, the explanatory variables were female brooding duration percentage, number of female food deliveries to the chicks and number of male food deliveries to the chicks. For better model stability and to obtain standardized effect sizes (i.e. comparable estimates), every dependent variable and covariate was transformed into z-scores. We included the interaction terms between (i) brooding duration  $\times$  male food delivery to chicks, (ii) brooding duration  $\times$  female food delivery to chicks and (iii) male food delivery  $\times$  female food delivery to the chicks. Year, time of observation and nest ID nested within species were included as random factors to account for among-year variation, short-term environmental variation, among-species variation, and repeated measures, respectively. We are aware that parental age and breeding experience could influence brooding and incubation behaviours [57], though this is not always the case [58]. However, our sample size did not allow for including additional covariates in our models. To account for this, we carried out a separate analysis quantifying the effect of male age on the different parental care behaviours



**Figure 1.** Female incubation and brooding behaviour, number of *Philornis downsi* in Darwin's finch nests and male food delivery to chicks. (a) Relationship between number of female incubation bouts (per hour) and number of *P. downsi* in the nest. (b) Relationship between female incubation bout duration (min) and number of *P. downsi* in the nest. (c) Relationship between female brooding duration (min) and number of *P. downsi* in the nest. Longer female brooding duration is associated with fewer *P. downsi* per nest but depends on male provisioning behaviour. (d) Interaction between number of male food deliveries to the chicks and female brooding duration. Males that provided more food deliveries to the chicks enhanced the negative association between female brooding duration and number of *P. downsi* in the nest. Black lines represent the mean estimate, grey ribbons the 95% Crls and grey dots the raw data.

across species and found that this effect was, if any, very small (see electronic supplementary material, figure S1 and table S1 for details). Further, for a descriptive purpose and presentation of the raw data, variation in the parental care parameters for each species were quantified in separate models (see electronic supplementary material, figure S2 and table S2 for details).

To explore possible differences across islands, we ran the same models with the addition of island as covariate. For the model of brooding duration, species was removed as a random factor because it explained very little variance, and with it the complete model including island would not converge. The reason for running these models separately was because the addition of island as a covariate pushed the number of explanatory variables, covariates and interactions to the maximum limit allowed by our sample size.

In a separate model, we explored the effects of chick age and brooding duration on the number of *P. downsi*. Here, we carried out a Poisson generalized linear mixed effects model with number of *P. downsi* as the dependent variable. The explanatory variables were brooding duration percentage, chick age, the interaction between brooding duration  $\times$  chick age and island. As with the previous models, (i) numerical dependent variables

and covariates were converted to z-scores, and (ii) year, time of observation and nest ID nested within species were included as random factors.

### 3. Results

#### (a) Parental care and *Philornis downsi* parasitism

Within the incubation phase, there was no evidence that the number of female incubation events (figure 1a and table 1), number of male food deliveries to the incubating female (table 1), or female incubation bout duration (figure 1b and table 1) affected the number of *P. downsi* in the nest (electronic supplementary material, table S3). These results during the incubation phase were consistent across both islands (electronic supplementary material, table S4).

During the chick feeding phase, female food delivery to chicks was not associated with the number of *P. downsi* in the nest (table 2). Brooding duration had a negative effect on the number of *P. downsi* when all covariates are at their

**Table 1.** Effect of incubation behaviours on *P. downsi* parasitism. The response variable number of *P. downsi* was modelled with a Poisson error distribution. Estimates of fixed ( $\beta$ ) and random ( $\sigma^2$ ) effects with their 95% CrIs are shown in brackets. Values of '0.00' represent values smaller than 0.001. We found no statistically meaningful effects (i.e. all the CrI overlap zero) of any incubation behaviour on the number of parasites in the nest.

fixed effects	no. of <i>P. downsi</i> $\beta$ (95% CrI)
intercept	2.03 (1.78; 2.38)
no. of incubation events	-0.02 (-0.17; 0.13)
incubation bout duration	-0.02 (-0.18; 0.14)
no. of male food delivery to female	-0.06 (-0.14; 0.02)
no. of incubation events $\times$ incubation bout duration	-0.001 (-0.07; 0.06)
random effect	$\sigma^2$ (95%CrI)
year	0.14 (0.05; 0.32)
species	0.006 (0.001; 0.02)
nest ID	1.1 (0.83; 1.43)
time of observation	0.008 (0.005; 0.01)

mean (figure 1a and table 2), but this effect depended on male provisioning to chicks (interaction term in table 2). Specifically, when males delivered more food, the effect of brooding duration on number of *P. downsi* was stronger (figure 1b). Also, this effect was attenuated with increasing age of the chicks and disappeared after the chicks were older than 6 days (figure 2; interaction term, electronic supplementary material, table S4), a period in which females brooded less (electronic supplementary material, figure S3). We found the same relationship between brooding duration and *P. downsi* on both islands (electronic supplementary material, table S5, and figure S4).

The effect of brooding on the number of *P. downsi* remained statistically meaningful while accounting for the date of nesting onset (electronic supplementary material, table S6) and the date of nesting onset was not associated with female brooding duration and/or the number of parasites in the nest (electronic supplementary material, table S7). Finally, we found no evidence for shifts in parental behaviour (i.e. female brooding duration, male food deliveries, female food deliveries) across the years (electronic supplementary material, table S8).

## 4. Discussion

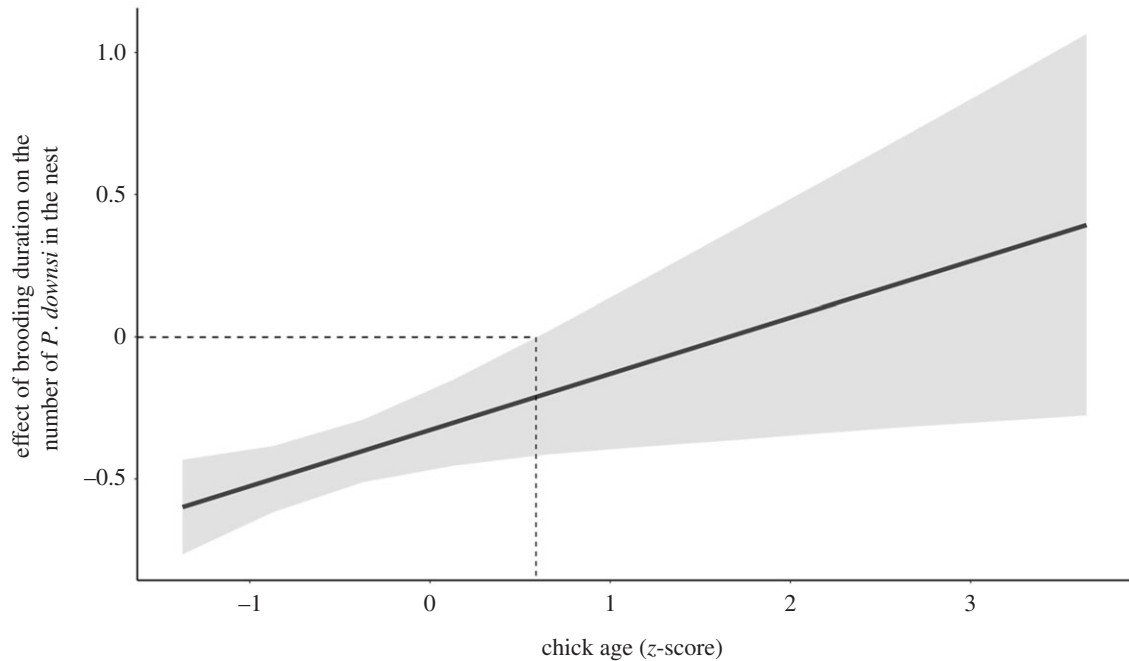
The temporal window for ectoparasite oviposition behaviour can be influenced by parental care, which may alter the course of age-specific costs to offspring survival from ectoparasites. If temporal patterns of host parental care differ across the sexes—for example, in systems with uniparental male or female in-nest attendance—the threat of parasite oviposition may increase sex-specific costs of parental care to the attending parent [59,60]. In this study on Darwin's finches parasitized by *P. downsi* (Diptera: Muscidae), longer female brooding duration during the first days post-hatch was associated with fewer *P. downsi*. Increased male food delivery

to chicks strengthened the effect of longer brooding duration on fewer *P. downsi*, irrespective of male age or species. There was no effect of nesting date on patterns of parental care or number of *P. downsi*, and no effect of parental care during the incubation phase on number of *P. downsi*.

We found no effect of year on parental care variables in this study, which is perhaps surprising given strong natural selection by *P. downsi*. There are several possible reasons why female brooding duration did not lengthen over time due to directional selection. Opposing environmental factors such as resource quality and abundance, thermal risk and predation risk, which we did not measure, can potentially impact parental care decisions in a given year [3]. Further, there is no evidence in birds that brooding duration or food delivery are heritable traits [61,62]. Finally, given that Darwin's finches can live to approximately 17 years, our generational sampling time window may be too shallow to detect such an evolutionary change should it occur, as the parents survive *P. downsi* but the offspring die [63].

Understanding mechanisms related to the timing of parental care and temporal windows of costs and benefits from parental care that increase or reduce parasite burden will shed light on evolutionary pressures that favour parental care traits. For example, in non-social *Ammophila* wasps, larvae may be parasitized by cuckoo flies (Diptera: Miltogramminae) that gain access to the wasp larvae when females open the nest to tend the larvae [64]. Female wasps that progressively provision offspring and abandon parasitized offspring lose less investment than females that mass provision each larva at oviposition [64]. The *Ammophila* wasp study provides experimental evidence for an adaptive value of progressive provisioning across the nesting cycle, as well as benefits of nest guarding to avoid costs of parasitism in a uniparental carer. Our study provides evidence in some songbirds that coordinated female and male parental care may be favoured when longer in-nest attendance by females and increased food provisioning by males deters ectoparasites from entering the nest.

We acknowledge that longer in-nest attendance could have many functions, including thermal insulation of chicks [65], defence against nest predators [66] and removal of ectoparasites via nest sanitation [23,24]. We consider female nest sanitation an unlikely explanation for our consistent finding of fewer *P. downsi* in nests with longer female brooding duration, for two reasons. Firstly, the 1st instar *P. downsi* larvae reside inside the nares of chicks and emerge to feed externally on the chicks from d2 to d4 onwards [53]. We may expect an increase in brooding (and nest sanitation) later in the nesting cycle (i) after *P. downsi* have emerged from the chicks' nares around d3 and (ii) when there are more *P. downsi* in the nest from d3 onwards (electronic supplementary material, figure S3). However, rather than finding an increase in female brooding duration after d3 as the number of *P. downsi* increased, we found a stronger impact of early female brooding duration on fewer *P. downsi* (figure 2), and as observed generally in songbirds, a decrease in female brooding duration with chick age (electronic supplementary material, figure S3). We suggest that female presence at the nest early post-hatch deters *P. downsi* from entering the nest to oviposit. Further, we predict that the fitness benefit should be maximized when females prevent parasites from ovipositing on the youngest chicks, which are small, defenceless, and still unable to self-preen. Our statistical analysis,



**Figure 2.** Interaction between chick age (z-score) and brooding. The effect of brooding on the number of *Philornis downsi* was attenuated with increasing age. When the 95% CrI overlaps zero, there is no effect of brooding duration on the number of *P. downsi*, and this is the case for chicks older than 6 days (dashed line). Black lines represent the mean estimate and grey ribbons the 95% CrIs. Details on this model's estimates can be found in the electronic supplementary material, table S4.

**Table 2.** Effect of brooding behaviours on *P. downsi* parasitism. The response variable number of *P. downsi* was modelled with a Poisson error distribution. Estimates of fixed ( $\beta$ ) and random ( $\sigma^2$ ) parameters with their 95% CrIs are shown in brackets. Statistically meaningful effects are those where the CrI do not overlap zero (i.e. posterior  $p$  greater than 95%) and are marked in italics.

fixed effects	no. of <i>P. downsi</i> $\beta$ (95% CrI)
intercept	2.27 (1.98; 2.48)
brooding duration (%)	<i>-0.33 (-0.45; -0.22)</i>
no. of female food delivery to chicks	0.11 (-0.004; 0.21)
no. of male food delivery to chicks	-0.03 (-0.12; 0.06)
brooding duration (%) $\times$ no. of female food delivery	0.01 (-0.10; 0.08)
brooding duration (%) $\times$ no. of male food delivery	<i>-0.09 (-0.17; -0.01)</i>
no. of male food delivery $\times$ no. of female food delivery	0.003 (-0.08; 0.07)
random effect	$\sigma^2$ (95%CrI)
year	0.06 (0.03; 0.11)
species	0.00 (0.00; 0.00) <sup>a</sup>
nest ID	0.69 (0.57; 0.83)
time of observation	0.09 (0.06; 0.11)

<sup>a</sup>0.00 indicates value smaller than 0.0001.

which controlled for the potential confounding effect of chick age on brooding duration and number of *P. downsi*, supports this view.

If in-nest attendance buffers against ectoparasites entering the nest to oviposit, then we predict stronger selection on coordination of male and female behaviour to enhance nest guarding. The mechanism by which choosy females could

predict within-pair coordination is unknown, but future research could explore signals of male quality, such as rhythmicity of song or other pre-mating interactive behaviour between the male and female [67–71]. Across systems, females have been shown to increase parental care when paired with a high-quality male [72,73], whereby older males may signal quality because of experience and capacity

to survive [74]. The minimum longevity of 12–17 years in Darwin's finches [48] is rather long for small songbirds (13–18 g). Females paired with older males could receive direct benefits, including a safer nest site, increased male vigilance and/or increased food delivery to the female [47,75,76]. Females paired with older males may also receive indirect benefits, including good genes for their offspring or increased male provisioning of offspring [74,77]. In this study, there was a mix of results for direct and indirect benefits to females paired with older males. For example: (i) in hybrid nests, older males provided more food deliveries to the incubating female (direct benefit) and females paired with older males had longer brooding duration (indirect benefit; see electronic supplementary material, figure S2); (ii) in *C. parvulus* nests, females paired with older males had longer incubation duration (indirect benefit, see electronic supplementary material, figure S2) and (iii) in *G. fuliginosa* nests, older males provided more food deliveries to chicks (indirect benefit; see electronic supplementary material, figure S2).

Reduced ectoparasite burden from longer female in-nest attendance may create evolutionary incentives for males to provide more food deliveries to attending females, or for increased male incubation, brooding and/or helper care. For example, male Moustached Warblers (*Acrocephalus melanopogon*) contribute to incubation even though they do not possess fully developed brood patches; they prevent egg cooling and provide a form of nest guarding [66,78], and helper males provide extra incubation and supplemental feeds to chicks [79,80]. Helper behaviour was also observed at Darwin's finch nests during 1979 on Daphne Major Island. At 11 of 21 Cactus Finch (*G. scandens*) nests, chicks were fed 1–10 times per day by a visiting conspecific male; these helper males provided between 1.7% and 24.9% of all food regurgitations at a nest per day, had comparable feeding rates to the paternal male and, in four cases, also removed faecal sacs from the nest [81]. Thus, there exists behavioural plasticity in parental feeding care in some Darwin's finch groups that could be the target of selection should helper behaviour become advantageous.

Cooperative breeding in birds is widespread in systems that experience high levels of brood parasitism [82]. Helper birds in cooperatively breeding groups may provide additional nest guarding that deters brood parasites from entering the nest to oviposit [83], a form of frontline defence [84–86]. Future research could explore proximate and ultimate explanations for nest guarding against brood parasites and ectoparasites [87]. Since female *P. downsi* flies probably use visual or olfactory cues from the nest to locate and infect avian hosts, nest guarding has the potential to be an effective strategy to prevent infection by *P. downsi*, but experimental studies are required to unveil this causal relationship.

Although both islands showed the same relationship between female brooding duration and number of *P. downsi*, the Santa Cruz data were collected from 2000 to 2004 and the Floreana Island data were collected from 2004 to 2020. Since 2004, there have been measurable shifts in *P. downsi* and host behaviour on both islands. *Philornis downsi* oviposition and hatching have shifted towards earlier in the host incubation period on Santa Cruz Island, whereas *P. downsi* hatching (and perhaps oviposition) occurs during chick feeding on Floreana [35,52,88]. On Floreana Island, the

proportion of hybrid tree finches in the population increased to 55% in 2006 and has since remained at approximately 40% [43,45], and higher admixture (e.g. greater introgression among *C. parvulus* and *C. pauper*) was associated with fewer *P. downsi* per nest [44,89] and different patterns of parental care (this study). All *P. downsi* life stages measured on Santa Cruz and Floreana Island between the years 2004 and 2020 have become approximately 20–30% smaller [52], pointing to coevolutionary dynamics. This current study identifies effects of parental care that may be associated with changes in fly oviposition behaviour and success, which could produce new host and parasite equilibria across islands and time [90].

In conclusion, the results of this study show that the number of *P. downsi* in nests was not related to the number of host visits, but was negatively related to female in-nest attendance during the brooding period. This case study presents evidence that an introduced ectoparasite may select for longer in-nest attendance by host females to physically prevent parasites from ovipositing (with potentially higher costs to host females than males) and leads to the prediction that there may be selection for coordinated host male and female behaviour to guard the nest when presence at the nest safeguards the nesting contents. Using modelling approaches, studies have found evidence for cross-scale feedbacks between host resource abundance and parasite transmission [91] and shifts from fluctuating to directional selection dynamics that drive greater genetic divergence between host populations [92]. Our study highlights the role of host parental care behaviour as one factor that may affect the timing of parasite oviposition behaviour and may therefore play a role in shaping selection dynamics in an emerging host–parasite system.

**Ethics.** The work was approved by the Flinders University Animal Welfare Committee (E270, E393, E480-19).

**Data accessibility.** Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.mw6m905x6> [93].

**Authors' contributions.** S.K.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; L.K.C.: data curation, investigation, writing—review and editing; J.A.O.: data curation, investigation, writing—review and editing; J.G.-L.: investigation, writing—review and editing; A.C.K.: investigation, writing—review and editing; R.Y.D.: investigation, supervision, writing—review and editing; D.C.-N.: data curation, investigation, project administration, supervision, writing—review and editing; N.M.A.: formal analysis, methodology, software, validation, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for—work performed therein.

**Competing interests.** We declare we have no competing interests.

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## References

- Trivers RL. 1974 Parent–offspring conflict. *Integr. Comp. Biol.* **14**, 249–264.
- Winkler DW. 1987 A general model for parental care. *Am. Nat.* **130**, 526–543. (doi:10.1086/284729)
- Clutton-Brock TH. 2019 *The evolution of parental care*. Princeton, NJ: Princeton University Press.
- Stearns SC. 1989 Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259–268. (doi:10.2307/2389364)
- Santos E, Nakagawa S. 2012 The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *J. Evol. Biol.* **25**, 1911–1917. (doi:10.1111/j.1420-9101.2012.02569.x)
- Briskie JV, Martin PR, Martin TE. 1999 Nest predation and the evolution of nestling begging calls. *Proc. R. Soc. Lond. B* **266**, 2153–2159. (doi:10.1098/rspb.1999.0902)
- Fontaine J, Martin T. 2006 Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecol. Lett.* **9**, 428–434. (doi:10.1111/j.1461-0248.2006.00892.x)
- Colombelli-Négrel D, Robertson J, Kleindorfer S, Sulloway F. 2010 Extended parental care of fledglings: parent birds adjust anti-predator response according to predator type and distance. *Behaviour* **147**, 853–870. (doi:10.1163/000579510X495771)
- Ghalambor CK, Peluc SI, Martin TE. 2013 Plasticity of parental care under the risk of predation: how much should parents reduce care? *Biol. Lett.* **9**, 20130154. (doi:10.1098/rsbl.2013.0154)
- Romano A, Rubolini D, Caprioli M, Boncoraglio G, Ambrosini R, Saino N. 2011 Sex-related effects of an immune challenge on growth and begging behavior of barn swallow nestlings. *PLoS ONE* **6**, e22805. (doi:10.1371/journal.pone.0022805)
- O'Connor JA, Robertson J, Kleindorfer S. 2014 Darwin's finch begging intensity does not honestly signal need in parasitised nests. *Ethology* **120**, 228–237. (doi:10.1111/eth.12196)
- Knutie SA *et al.* 2016 Galápagos mockingbirds tolerate introduced parasites that affect Darwin's finches. *Ecology* **97**, 940–950. (doi:10.1890/15-0119.1)
- Christe P, Richner H, Oppliger A. 1996 Begging, food provisioning, and nestling competition in great tit broods infested with ectoparasites. *Behav. Ecol.* **7**, 127–131. (doi:10.1093/beheco/7.2.127)
- Richner H, Tripet F. 1999 Ectoparasitism and the trade-off between current and future reproduction. *Oikos* **86**, 535–538. (doi:10.2307/3546657)
- Tripet F, Richner H. 1997 Host responses to ectoparasites: food compensation by parent blue tits. *Oikos* **78**, 557–561. (doi:10.2307/3545617)
- Morrison BL, Johnson LS. 2002 Feeding of house wren nestlings afflicted by hematophagous ectoparasites: a test of the parental compensation hypothesis. *Condor* **104**, 183–187. (doi:10.1093/condor/104.1.183)
- Møller AP. 1994 Parasite infestation and parental care in the barn swallow *Hirundo rusticala*: a test of the resource-provisioning model of parasite-mediated sexual selection. *Ethology* **97**, 215–225. (doi:10.1111/j.1439-0310.1994.tb01041.x)
- Darolova A, Hoi H, Schleicher B. 1997 The effect of ectoparasite nest load on the breeding biology of the Penduline Tit *Remiz pendulinus*. *Ibis* **139**, 115–120. (doi:10.1111/j.1474-919X.1997.tb04510.x)
- Bouslama Z, Lambrechts MM, Ziane N, Djenidi R, Chabi Y. 2002 The effect of nest ectoparasites on parental provisioning in a north-African population of the Blue Tit *Parus caeruleus*. *Ibis* **144**, E73–E78. (doi:10.1046/j.1474-919X.2002.00070\_5.x)
- Hund AK, Aberle MA, Safran RJ. 2015 Parents respond in sex-specific and dynamic ways to nestling ectoparasites. *Anim. Behav.* **110**, 187–196. (doi:10.1016/j.anbehav.2015.09.028)
- Heyer E, Cimadom A, Wappl C, Tebbich S. 2020 Parental care in the small tree finch *Camarhynchus parvulus* in relation to parasitism and environmental factors. *Ibis* **163**, 137–149.
- Clayton DH, Koop JA, Harbison CW, Moyer BR, Bush SE. 2010 How birds combat ectoparasites. *Open Ornithol. J.* **3**(10), 41–71. (doi:10.2174/1874453201003010041)
- O'Connor JA, Robertson J, Kleindorfer S. 2010 Video analysis of host-parasite interactions in nests of Darwin's finches. *Oryx* **44**, 588–594. (doi:10.1017/s0030605310000086)
- Koop JA, Owen JP, Knutie SA, Aguilar MA, Clayton DH. 2013 Experimental demonstration of a parasite-induced immune response in wild birds: Darwin's finches and introduced nest flies. *Ecol. Evol.* **3**, 2514–2523. (doi:10.1002/ece3.651)
- Clark L, Mason JR. 1985 Use of nest material as insecticidal and anti-pathogenic agents by the European starling. *Oecologia* **67**, 169–176. (doi:10.1007/BF00384280)
- Cimadom A *et al.* 2016 Darwin's finches treat their feathers with a natural repellent. *Sci. Rep.* **6**, 1–9. (doi:10.1038/srep34559)
- Quiroga MA, Beltzer AH. 2012 Host use by *Philornis* sp. in a passerine community in central Argentina. *Revista Mexicana de Biodiversidad* **83**, 110–116.
- Gwinner H, Oltrogge M, Trost L, Nienaber U. 2000 Green plants in starling nests: effects on nestlings. *Anim. Behav.* **59**, 301–309. (doi:10.1006/anbe.1999.1306)
- Fessl B, Couri MS, Tebbich S. 2001 *Philornis downsi* Dodge & Aitken, new to the Galapagos Islands (Diptera, Muscidae). *Studia Dipterol.* **8**, 317–322.
- Causton C *et al.* 2006 Alien insects: threats and implications for conservation of Galápagos Islands. *Ann. Entomol. Soc. Am.* **99**, 121–143. (doi:10.1603/0013-8746(2006)099[0121:AITAIF]2.0.CO;2)
- Fessl B, Heimpel GE, Causton CE. 2018 Invasion of an avian nest parasite, *Philornis downsi*, to the Galapagos Islands: colonization history, adaptations to novel ecosystems, and conservation challenges. In *Disease ecology, social and ecological interactions in the Galapagos Islands* (ed. P Parker), pp. 213–268. Cham, Switzerland: Springer. (doi:10.1007/978-3-319-65909-1\_9)
- Kleindorfer S, Dudaniec RY. 2016 Host-parasite ecology, behavior and genetics: a review of the introduced fly parasite *Philornis downsi* and its Darwin's finch hosts. *BMC Zool.* **1**, 1. (doi:10.1186/s40850-016-0003-9)
- Galligan TH, Kleindorfer S. 2009 Naris and beak malformation caused by the parasitic fly, *Philornis downsi* (Diptera: Muscidae), in Darwin's small ground finch, *Geospiza fuliginosa* (Passeriformes: Emberizidae). *Biol. J. Linn. Soc.* **98**, 577–585. (doi:10.1111/j.1095-8312.2009.01309.x)
- Kleindorfer S, Sulloway FJ. 2016 Naris deformation in Darwin's finches: experimental and historical evidence for a post-1960s arrival of the parasite *Philornis downsi*. *Glob. Ecol. Conserv.* **7**, 122–131. (doi:10.1016/j.gecco.2016.05.006)
- Cimadom A, Tebbich S. 2020 Timing of infestation influences virulence and parasite success in a dynamic multi-host–parasite interaction between the invasive parasite, *Philornis downsi*, and Darwin's finches. *Oecologia* **195**, 249–259.
- Common LK, Dudaniec RY, Colombelli-Négrel D, Kleindorfer S. 2019 Taxonomic shifts in *Philornis* larval behaviour and rapid changes in *Philornis downsi* Dodge & Aitken (Diptera: Muscidae): an invasive avian parasite on the Galápagos Islands. In *Life cycle and development of Diptera*. See <https://core.ac.uk/display/322444219>. (doi:10.5772/intechopen.88854)
- Causton C, Cunninghame F, Tapia W. 2011 Management of the avian parasite *Philornis downsi* in the Galapagos Islands: a collaborative and strategic action plan. *Galapagos Rep.* **2012**, 167–173.
- Lincango P *et al.* 2015 Interactions between the avian parasite, *Philornis downsi* (Diptera: Muscidae) and the Galapagos flycatcher, *Myiarchus magnirostris* Gould (Passeriformes: Tyrannidae). *J. Wildl. Dis.* **51**, 907–910. (doi:10.7589/2015-01-025)
- Hopkins K, Moss BR, Gill AB. 2011 Increased ambient temperature alters the parental care behaviour and reproductive success of the three-spined stickleback (*Gasterosteus aculeatus*). *Environ. Biol. Fishes* **90**, 121–129. (doi:10.1007/s10641-010-9724-8)
- Schlicht L, Kempnaers B. 2020 The effects of season, sex, age and weather on population-level variation in the timing of activity in Eurasian Blue Tits *Cyanistes caeruleus*. *Ibis* **162**, 1146–1162. (doi:10.1111/ibi.12818)
- Arnold KE, Ramsay SL, Henderson L, Larcombe SD. 2010 Seasonal variation in diet quality: antioxidants, invertebrates and blue tits *Cyanistes caeruleus*. *Biol. J. Linn. Soc.* **99**, 708–717. (doi:10.1111/j.1095-8312.2010.01377.x)



42. Young BE. 1993 Effects of the parasitic botfly *Philornis carinatus* on nestling house wrens, *Troglodytes aedon*, in Costa Rica. *Oecologia* **93**, 256–262. (doi:10.1007/BF00317679)
43. Kleindorfer S *et al.* 2014 Species collapse via hybridization in Darwin's tree finches. *Am. Nat.* **183**, 325–341. (doi:10.1086/674899)
44. Peters K, Myers S, Dudaniec R, O'Connor J, Kleindorfer S. 2017 Females drive asymmetrical introgression from rare to common species in Darwin's tree finches. *J. Evol. Biol.* **30**, 1940–1952. (doi:10.1111/jeb.13167)
45. Kleindorfer S, Dudaniec RY. 2020 Hybridization fluctuates with rainfall in Darwin's tree finches. *Biol. J. Linn. Soc.* **130**, 79–88. (doi:10.1093/biolinean/blaa029)
46. Price TD. 1984 Sexual selection on body size, territory and plumage variables in a population of Darwin's finches. *Evolution* **38**, 327–341. (doi:10.1111/j.1558-5646.1984.tb00291.x)
47. Kleindorfer S. 2007 Nesting success in Darwin's small tree finch, *Camarhynchus parvulus*: evidence of female preference for older males and more concealed nests. *Anim. Behav.* **74**, 795–804. (doi:10.1016/j.anbehav.2007.01.020)
48. Langton A, Kleindorfer S. 2019 Minimum longevity and age-related male plumage in Darwin's finches on Floreana Island. *J. Ornithol.* **160**, 351–361. (doi:10.1007/s10336-019-01626-1)
49. Dobrevá MP *et al.* 2021 Sex identification in embryos and adults of Darwin's finches. *PLoS ONE* **16**, e0237687. (doi:10.1371/journal.pone.0237687)
50. Bates D, Mächler M, Bolker B, Walker S. 2014 Fitting linear mixed-effects models using lme4. *arXiv:1406.5823v1*.
51. Goodale E, Podos J. 2010 Persistence of song types in Darwin's finches, *Geospiza fortis*, over four decades. *Biol. Lett.* **6**, 589–592. (doi:10.1098/rsbl.2010.0165)
52. Common LK, O'Connor JA, Dudaniec RY, Peters KJ, Kleindorfer S. 2020 Evidence for rapid downward fecundity selection in an ectoparasite (*Philornis downsi*) with earlier host mortality in Darwin's finches. *J. Evol. Biol.* **33**, 524–533. (doi:10.1111/jeb.13588)
53. Fessl B, Sinclair BJ, Kleindorfer S. 2006 The life-cycle of *Philornis downsi* (Diptera: Muscidae) parasitizing Darwin's finches and its impacts on nestling survival. *Parasitology* **133**, 739–747. (doi:10.1017/s0031182006001089)
54. Team, R. C. 2020 *RStudio: integrated development environment for R*. Boston, MA: RStudio, PBC. See <http://www.rstudio.com/>
55. Gelman A, Su YS, Yajima M, Hill J, Pittau MG, Kerman J. 2020 Arm: data analysis using regression and multilevel/hierarchical models. R package, version 9.01.
56. Korner-Nievergelt F *et al.* 2015 *Bayesian data analysis in ecology using linear models with R, BUGS, and Stan*. New York, NY: Academic Press.
57. Williams K, Sudnick M, Anderson R, Fitschen-Brown M. 2020 Experience counts: the role of female age in morning incubation and brooding behavior in relation to temperature. *J. Avian Biol.* **51**. (doi:10.1111/jav.02397)
58. Bambini G, Schlicht E, Kempnaers B. 2019 Patterns of female nest attendance and male feeding throughout the incubation period in Blue Tits *Cyanistes caeruleus*. *Ibis* **161**, 50–65. (doi:10.1111/ibi.12614)
59. Hurtrez-Boussès S, Renaud F, Blondel J, Perret P, Galan MJ. 2000 Effects of ectoparasites of young on parents' behaviour in a Mediterranean population of Blue Tits. *J. Avian Biol.* **31**, 266–269. (doi:10.1034/j.1600-048X.2000.310219.x)
60. Cheney KL, Côté IM. 2003 Indirect consequences of parental care: sex differences in ectoparasite burden and cleaner-seeking activity in longfin damselfish. *Mar. Ecol. Prog. Ser.* **262**, 267–275. (doi:10.3354/meps262267)
61. Sheldon B, Kruuk L, Merila J. 2003 Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* **57**, 406–420. (doi:10.1111/j.0014-3820.2003.tb00274.x)
62. Wetzel DP, Hatch MI, Westneat DF. 2015 Genetic sources of individual variation in parental care behavior. *Behav. Ecol. Sociobiol.* **69**, 1933–1943. (doi:10.1007/s00265-015-2006-x)
63. Merilä J, Sheldon B, Kruuk L. 2001 Explaining stasis: microevolutionary studies in natural populations. *Genetica* **112**, 199–222. (doi:10.1023/A:1013391806317)
64. Field J, Brace S. 2004 Pre-social benefits of extended parental care. *Nature* **428**, 650–652. (doi:10.1038/nature02427)
65. Bruzual J, Peak S, Brake J, Peebles E. 2000 Effects of relative humidity during the last five days of incubation and brooding temperature on performance of broiler chicks from young broiler breeders. *Poult. Sci.* **79**, 1385–1391. (doi:10.1093/ps/79.10.1385)
66. Kleindorfer S, Hoi H. 1997 Nest predation avoidance: an alternative explanation for male incubation in *Acrocephalus melanopogon*. *Ethology* **103**, 619–631. (doi:10.1111/j.1439-0310.1997.tb00173.x)
67. Logue DM, Chalmers C, Gowland AH. 2008 The behavioural mechanisms underlying temporal coordination in black-bellied wren duets. *Anim. Behav.* **75**, 1803–1808. (doi:10.1016/j.anbehav.2007.10.036)
68. Haunhorst CB, Fürtbauer I, Schülke O, Ostner J. 2020 Female macaques compete for 'power' and 'commitment' in their male partners. *Evol. Hum. Behav.* **41**, 117–125. (doi:10.1016/j.evolhumbehav.2019.11.001)
69. Moore BL, Connor RC, Allen SJ, Krützen M, King SL. 2020 Acoustic coordination by allied male dolphins in a cooperative context. *Proc. R. Soc. B* **287**, 20192944. (doi:10.1098/rspb.2019.2944)
70. Monari PK, Rieger NS, Hartfield K, Schefelker J, Marler CA. 2020 Oxytocin promotes convergence in personality between members of a monogamous pair. *bioRxiv*.
71. Pettitt BA, Bourne GR, Bee MA. 2020 Females prefer the calls of better fathers in a Neotropical frog with biparental care. *Behav. Ecol.* **31**, 152–163.
72. Horváthová T, Nakagawa S, Uller T. 2012 Strategic female reproductive investment in response to male attractiveness in birds. *Proc. R. Soc. B* **279**, 163–170. (doi:10.1098/rspb.2011.0663)
73. Robart AR, Sinervo B. 2019 Females increase parental care, but not fecundity, when mated to high-quality males in a biparental fish. *Anim. Behav.* **148**, 9–18. (doi:10.1016/j.anbehav.2018.11.012)
74. Brooks R, Kemp DJ. 2001 Can older males deliver the good genes? *Trends Ecol. Evol.* **16**, 308–313. (doi:10.1016/S0169-5347(01)02147-4)
75. Black JM, Owen M. 1995 Reproductive performance and assortative pairing in relation to age in barnacle geese. *J. Anim. Ecol.* **64**, 234–244. (doi:10.2307/5758)
76. Potti J. 2000 Causes and consequences of age-assortative pairing in pied flycatchers (*Ficedula hypoleuca*). *Etologia* **8**, 29–36.
77. Wappal C, Cimadam A, Filek N, Heyer E, Tebbich S. 2020 Under adverse conditions, older small tree finch males (*Camarhynchus parvulus*) produce more offspring than younger males. *Ethology* **126**, 966–975. (doi:10.1111/eth.13069)
78. Kleindorfer S, Fessl B, Hoi H. 1995 More is not always better: male incubation in two *Acrocephalus* warblers. *Behaviour* **132**, 607–625. (doi:10.1163/156853995X00234)
79. Fessl B, Kleindorfer S, Hoi H. 1996 Extra male parental behaviour: evidence for an alternative mating strategy in the moustached warbler *Acrocephalus melanopogon*. *J. Avian Biol.* **27**, 88–91. (doi:10.2307/3676965)
80. Kleindorfer S, Hoi H, Blomqvist D, Fessl B. 2005 High frequency of extra-pair fertilisations in the moustached warbler, a songbird with a variable breeding system. *Behaviour* **142**, 1133–1148. (doi:10.1163/156853905774405272)
81. Price T, Millington S, Grant P. 1983 Helping at the nest in Darwin's finches as misdirected parental care. *Auk* **100**, 192–194. (doi:10.1093/auk/100.1.192)
82. Feeney WE *et al.* 2013 Brood parasitism and the evolution of cooperative breeding in birds. *Science* **342**, 1506–1508. (doi:10.1126/science.12440039)
83. Canestrari D, Marcos JM, Baglione V. 2009 Cooperative breeding in carrion crows reduces the rate of brood parasitism by great spotted cuckoos. *Anim. Behav.* **77**, 1337–1344. (doi:10.1016/j.anbehav.2009.02.009)
84. Feeney WE, Welbergen JA, Langmore NE. 2012 The frontline of avian brood parasite–host coevolution. *Anim. Behav.* **84**, 3–12. (doi:10.1016/j.anbehav.2012.04.011)
85. Medina I, Langmore NE. 2016 Batten down the thatches: front-line defences in an apparently defenceless cuckoo host. *Anim. Behav.* **112**, 195–201. (doi:10.1016/j.anbehav.2015.12.006)
86. Noh H-J, Jacomb F, Gloag R, Langmore NE. 2021 Frontline defences against cuckoo parasitism

- in the large-billed gerygones. *Anim. Behav.* **174**, 51–61. (doi:10.1016/j.anbehav.2021.01.021)
87. Kleindorfer S, Evans C, Colombelli-Négrel D, Robertson J, Griggio M, Hoi H. 2013 Host response to cuckoo song is predicted by the future risk of brood parasitism. *Front. Zool.* **10**, 30. (doi:10.1186/1742-9994-10-30)
88. Causton CE *et al.* 2019 Population dynamics of an invasive bird parasite, *Philornis downsi* (Diptera: Muscidae), in the Galapagos Islands. *PLoS ONE* **14**, e0224125. (doi:10.1371/journal.pone.0224125)
89. Peters KJ, Evans C, Aguirre JD, Kleindorfer S. 2019 Genetic admixture predicts parasite intensity: evidence for increased hybrid performance in Darwin's tree finches. *R. Soc. Open Sci.* **6**, 181616. (doi:10.1098/rsos.181616)
90. Edessa GK, Koya PR. 2020 Modeling and stability analysis of host-parasite population dynamics. *Math. Model. Appl.* **5**, 28.
91. Laanto E, Hoikkala V, Ravantti J, Sundberg L-R. 2017 Long-term genomic coevolution of host-parasite interaction in the natural environment. *Nat. Commun.* **8**, 1–8. (doi:10.1038/s41467-017-00158-7)
92. Betts A, Gray C, Zelek M, MacLean R, King K. 2018 High parasite diversity accelerates host adaptation and diversification. *Science* **360**, 907–911. (doi:10.1126/science.aam9974)
93. Kleindorfer S. 2021 Parental care in Darwin's finches. Dryad Digital Repository. (doi:10.5061/dryad.mw6m905x6)