










RESEARCH ARTICLE

Functional traits and foraging behaviour: Avian vampire fly larvae change the beak and fitness of their Darwin's finch hosts

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Abstract

1. The avian beak is a key morphological trait used for foraging. If parasites alter beak shape, we may expect changes in host foraging behaviour. Larvae of the avian vampire fly *Philornis downsi* cause naris enlargement in Darwin's finch nestlings when first and second instar larvae consume keratin, blood and tissue from inside the beak of the developing host. This naris malformation persists into adulthood, where nares that are >15% of total beak length are considered enlarged.
2. We measured effects of parasite-induced naris enlargement on foraging behaviour, foraging niche overlap and body condition in Darwin's finches on Floreana Island. Foraging behaviour was ranked by the stress per foraging technique exerted on the beak and ranged from least stress for 'gleaning' to most stress for 'chip off bark'.
3. Naris enlargement occurred in 34% of adult birds. The most common foraging technique differed among species: medium tree finches (*Camarhynchus pauper*) often chipped off bark to extract subsurface prey, small tree finches (*C. parvulus*) often gleaned surface prey from foliage, hybrids gleaned prey from bark and foliage, and small ground finches (*Geospiza fuliginosa*) mostly foraged on the ground. In *C. pauper*, birds with naris enlargement did more gleaning and less subsurface prey excavation. Foraging niche across species was most similar in birds with naris enlargement. Finally, body condition was lower in insectivorous tree finches with malformed beaks.
4. A novel aspect of this study is the idea that parasite-induced alterations to phenotype affect ecological processes and interspecific interactions at large temporal and spatial scales. The parasitism occurs early in life but the ecological effects of this parasitism, if causative, are happening later.

KEYWORDS

Camarhynchus, functional morphology, Galápagos Islands, *Geospiza*, host–parasite biology, niche partitioning, *Philornis downsi*

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1 | INTRODUCTION

Parasitism is the most common feeding mode on earth, far out-ranking herbivore, nectivore, insectivore or carnivore prevalence (Dobson et al., 2008; Poulin, 2011b). Almost half of all known species are parasitic and have co-evolved in diverse ways with hosts across evolutionary history (Hughes & Libersat, 2019; Marcogliese, 2005; Weinstein & Kuris, 2016). Parasitic taxa are tightly enmeshed in food webs (Lafferty et al., 2006). Yet, despite their prevalence and diverse biotic interactions, we still know remarkably little about how parasites affect the foraging behaviour of hosts (Anaya-Rojas et al., 2016). For example, parasites could contribute to population divergence if hosts have altered phenotypes either during or after infection, and if hosts change their foraging niche as the result of novel phenotype-habitat matching (Camacho et al., 2020; Jacobson et al., 2017; Schluter, 2000). When parasites physically alter functional morphological traits used by their hosts during foraging, they may inadvertently drive evolutionary niche divergence (Brunner et al., 2017; Miura et al., 2006).

Across taxa, there is evidence that foraging behaviour is tightly associated with the size and shape of functional morphological traits (Andersson, 2004; Friedman et al., 2019; Takahashi et al., 2007; Yamada & Boulding, 1998). Comparative studies have found that morphological traits can predict both foraging niche breadth and prey size (Yamada & Boulding, 1998), and can be

stronger predictors of foraging behaviour than phylogeny (Fenton & Bogdanowicz, 2002). Bird beaks are a classic example of a multifunctional trait (Friedman et al., 2019), and there is consistent evidence that foraging ecology and climate are significant drivers of phenotypic variation in beak morphology (Friedman et al., 2017; Olsen, 2017). Darwin's finches are a textbook example of an adaptive radiation that generated 17 species within about 1.5 million years (Grant & Grant, 2014a) (Figure 1). Each Darwin's finch species has a different beak size and shape, adapted to different forms of resource extraction, with long-term field research showing that change in resource availability is a strong selective force leading to change in beak morphology (Grant & Grant, 1989; Grant & Grant, 2002; Grant & Grant, 2014a; Kleindorfer et al., 2006; Petren et al., 2005; Schluter & Grant, 1984b; Sulloway & Kleindorfer, 2013). Beak forms predict feeding behaviour in birds (Boag & Grant, 1981; Cattau et al., 2018; Friedman et al., 2019), so if parasites alter avian beak shape (e.g. by causing malformation) then we may predict that parasites could also influence host foraging behaviour.

During the current Anthropocene era, human activities are rapidly changing biodiversity patterns across the globe, with accelerated rates of introduced species, including parasites (Bowman et al., 2017; Keys et al., 2019; Toral-Granda et al., 2017). Novel parasites can wreak havoc on naïve populations, causing high mortality rates, rapid population declines and species extinctions (Koop et al., 2016; McClure et al., 2020; Van Riper III et al., 1986). In general, fitness

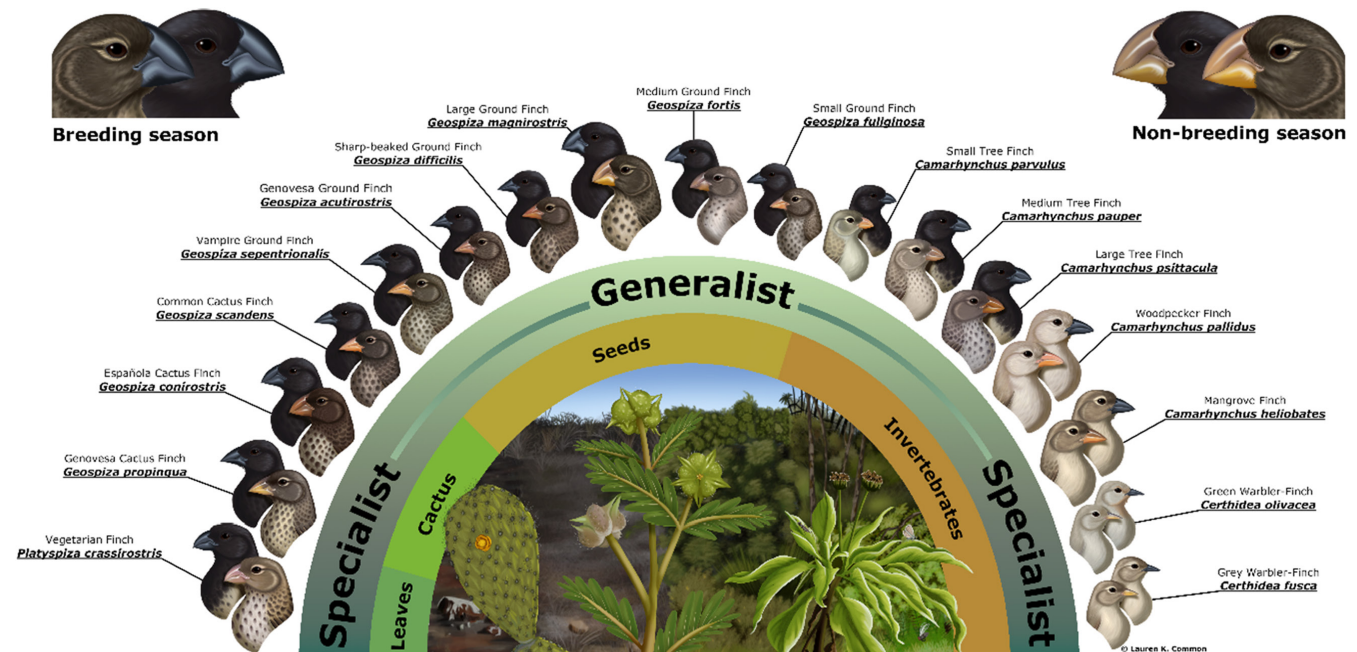


FIGURE 1 Foraging generalism and specialisation in the intact adaptive radiation of 17 Darwin's finch species on the Galápagos archipelago. The species assemblage evolved from a shared common ancestor ~1.5 million years ago. Male and female finches have pale beaks outside the breeding season (upper right) and dark beaks during the breeding season (upper left). Floreana Island once had 10 Darwin's finch species, but five species are now considered locally extinct (*Platyspiza crassirostris*, *Geospiza magnirostris*, *G. difficilis*, *Camarhynchus psittacula* and *Certhidea fusca*) and five species are extant (*C. pauper*, *C. parvulus*, *G. fuliginosa*, *G. fortis* and *G. scandens*). The *Camarhynchus* tree finches primarily occur in the forest highlands; there is also a hybrid group of tree finches that result from pairing between *C. pauper* and *C. parvulus*. Darwin's tree finches mostly consume invertebrates and Darwin's ground finches mostly consume seeds. Image credit and copyright: Lauren K. Common

disequilibria are predicted to occur during recent and novel parasite introductions (Schulte et al., 2010), with lower body condition or reduction in signal quality in hosts less able to withstand novel parasites (Britton et al., 2011). Condition-dependent signals are relevant to a range of biological questions. In the context of mate choice, for example, females can quickly scan for males in good body condition, as positive body condition score has been shown to correlate with immunocompetence genes that confer high parasite resistance, for example in the zebra finch *Taeniopygia guttata* (Gleeson et al., 2005). In general, birds in better body condition can be expected to have higher survival (Bowers et al., 2014).

Biological invasion is considered the greatest threat to biodiversity in the Galápagos Islands (Causton & Sevilla, 2006; Toral-Granda et al., 2017). Of the archipelago's six damaging invasive invertebrate species, the dipteran parasite *Philornis downsi* (hereafter avian vampire fly) is considered the greatest threat to the survival of all Galápagos land birds (Causton et al., 2006). In the Galápagos, the avian vampire fly is currently known to parasitise 22 of 28 terrestrial land bird species, including at least 11 of the 17 Darwin's finch species, and occurs on 15 of the 17 major islands sampled within the archipelago (Fessl et al., 2018; Wiedenfeld et al., 2007). Its blood-sucking larvae were first discovered in the nests of Darwin's finches on Santa Cruz Island in 1997 (Fessl et al., 2001), and on Floreana Island in 2004 (Kleindorfer, Peters, et al., 2014; Wiedenfeld et al., 2007). The adult fly is vegetarian and feeds on decaying plant matter (Fessl et al., 2001), but females oviposit into bird nests, where the eggs hatch into larvae that feed on the blood and tissue of developing nestlings (Fessl et al., 2006; O'Connor, Robertson, & Kleindorfer, 2010). The first instar larvae reside in the nares of the developing birds, and some second and third instars may also pass through the nares to feed internally on nestlings (O'Connor, Robertson, & Kleindorfer, 2010) (Figure 2a), causing enlarged naris size in the birds that survive to adulthood (Kleindorfer & Sulloway, 2016; Figure 2b).

Most studies have focused on the immediate impacts of acute avian vampire fly infections during the nestling phase, including severe blood loss, reduced haemoglobin concentration (Dudaniec et al., 2006) and a mean in-nest mortality of 55% (Addesso et al., 2020; Fessl et al., 2006; Kleindorfer & Dudaniec, 2016). Recent studies exploring the host and parasite microbiome found that the avian vampire fly microbiome differs across both parasite life stage (Jose et al., 2021) and the dietary niche of host species from which the parasite was sampled (Ben-Yosef et al., 2017), but host microbiome did not differ in relation to the presence/absence of avian vampire flies in the nest (Addesso et al., 2020). Darwin's finches with enlarged naris size have altered song that is associated with lower pairing success (Kleindorfer et al., 2019) and altered patterns of gene flow, including hybridisation (Kleindorfer, O'Connor, et al., 2014; Peters et al., 2019). Aside from altered song, we know very little about the long-term consequences of avian vampire fly parasitism for nestlings that survive to adulthood.

The aim of this study is to measure the effects of naris malformation caused by avian vampire fly larvae on foraging behaviour

and body condition in adult Darwin's finches. Because naris malformation from avian vampire fly larvae can result in a beak with a large hole and, therefore, a beak with less structural support, we predict that beaks of birds with enlarged nares will be less capable of sustaining pressure during beak use (Abbott et al., 1975; Herrel et al., 2005; Soons et al., 2015). Soons et al. (2015) used micro-CT scans and dissections to measure feeding forces in 13 Darwin's finch species. The location of the von Mises (vM) beak stress correlated with beak shape and foraging mode, with lower stress measured during tip loading in species that use the tips of the beaks to glean invertebrates (e.g. 20MPa in *Camarhynchus parvulus* during gleaning). Somewhat higher stresses occurred for species that crush seeds and fruit using base biting (e.g. 30MPa in *Geospiza fuliginosa*). Even higher stresses were experienced by tip-biting species that probe and pry (e.g. 31–39MPa in *C. psittacula*). The highest recorded stresses were found in the grub-excavating woodpecker finch *Cactospiza pallida* under different loading regimes (base or tip biting, 80MPa; Soons et al., 2015). *Cactospiza pallida* often use their beak to chip off bark in the arid zone on Santa Cruz Island (Tebich et al., 2004). Similar foraging techniques are used by *C. pauper*, as both species mostly forage for invertebrates on bark and foliage and commonly use the foraging techniques of probe, pry and chip off. Tebich et al. (2004) measured invertebrate abundance on Santa Cruz Island in relation to *C. pallida* foraging, and (in some instances) found that bark could only be removed with a machete, reflecting the considerable force that is sometimes required to engage in this foraging behaviour.

In this study: (1) We predict that Darwin's finch beaks with enlarged nares will be used more often to glean and pick prey exposed on the surface, and less often for techniques that require high pressure on the beak, such as chipping, prying and probing for prey hidden beneath bark; (2) If birds with malformed beaks have convergent foraging behaviour, there may be shifts in foraging overlap between previously diverged species. We predict greater interspecific foraging niche overlap in birds across species with extreme naris size enlargement; (3) We expect to find a smaller coefficient of variation in naris size in beaks used for subsurface prey extraction than surface prey removal; and (4) Although we do not measure prey size or items consumed, we predict that birds with malformed beaks will have lower body condition, not least because of known associations between foraging efficiency and beak size and shape in Darwin's finches (Grant & Grant, 2014a), as well as lower body condition in other avian species with malformed beaks (Hodges et al., 2019).

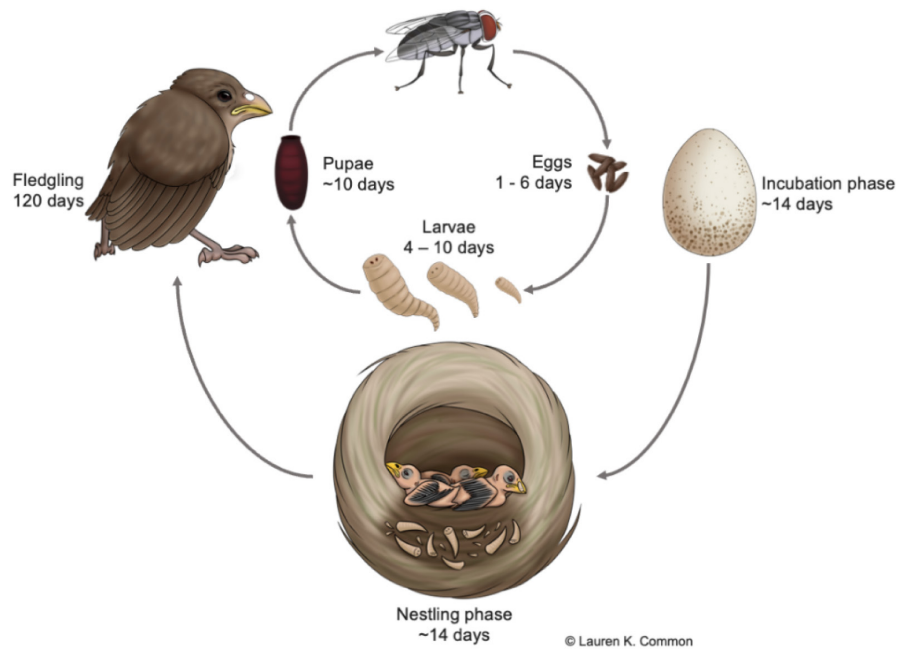
2 | MATERIALS AND METHODS

2.1 | Study site and species

We collected data on foraging behaviour and body condition from four genetic groups of Darwin's finches on Floreana Island in the Galápagos Archipelago. Birds were captured using mist-nets, scored for body condition, and colour banded (allowing for morphologically

FIGURE 2 The life cycle of the avian vampire fly *Philornis downsi* and its impacts on naris size in its Darwin's finch hosts. (a) Schemata of the life cycle of the avian vampire fly. Adult females oviposit into Darwin's finch nests during late incubation and/or early brooding. The first and second instar larvae feed on the nestlings' soft beak tissue for ~3 days before moving to the nest base, from where second and third instar larvae feed on the blood and tissue of developing nestlings for 4–10 days. Adult flies emerge from the pupae ~10 days later. The nestlings that survive often have enlarged nares. (b) Schemata of naris enlargement in (left) developing Darwin's finch nestling and (right) adult Darwin's finch. Previous experimental research showed that host naris enlargement is caused by avian vampire fly larvae inside the beak during development, and recapture data across years showed that the naris malformation persists in adults (Langton & Kleindorfer, 2019). Image credit and copyright: Lauren K. Common

(a) Life cycle of the avian vampire fly (*Philornis downsi*)



(b) Naris enlargement caused by avian vampire fly larvae



referenced foraging observations in the field). Birds were mist-netted during the breeding season across 10 different years of sampling: 2004–2006, 2008, 2012–2014, 2016 and 2020. Most (96%) foraging observations were recorded during February, but 2.3% and 1.9% of foraging observations were recorded during January and March, respectively. Tree finches were observed foraging in the forested highlands (−1.299829, −90.455674) and ground finches were observed in both the forested highlands and arid lowlands around Puerto Velasco Ibarra (−1.274444, −90.486944). The data are available on Dryad (Kleindorfer, 2021).

The four genetic groups of Darwin's finches included in this study are: medium tree finch *Camarhynchus pauper*, small tree finch (*C. parvulus*), the hybrid genetic group that arises from pairings between *C. pauper* females and *C. parvulus* males (Kleindorfer & Dudaniec, 2020; Peters et al., 2017, 2019; Peters & Kleindorfer, 2018), and small ground finch *Geospiza fuliginosa*. For the colour-banded tree finches, we assigned genetic population retrospectively based on previous genetic analysis using microsatellite markers (Kleindorfer & Dudaniec, 2020; Kleindorfer, O'Connor, et al., 2014). All four genetic groups occur in sympatry in the highlands of Floreana Island. *Geospiza fuliginosa* also commonly occurs in the lowlands. At the time of noting each foraging observation, we recorded the sex and age

of the individual, using established methods (Grant & Grant, 2014a; Kleindorfer, 2007; Langton & Kleindorfer, 2019). Male and female ground finches are easily distinguished once males are 1+ years old. Male ground finches become progressively black-bodied with age until attaining a fully black body around 5+ years old, while females remain olive grey with streaked plumage (Grant & Grant, 2014a). In tree finches, males become progressively black-headed until attaining a fully black crown and chin from around 5+ years old, while females remain olive green (Kleindorfer, 2007). Current longevity estimates from recaptured (wild) Darwin's finches are between 12 and 17 years (Langton & Kleindorfer, 2019).

2.2 | Avian vampire fly *Philornis downsi* prevalence and effects on naris size

Avian vampire fly larvae have been found in all Darwin's finch nests with nestlings in the Floreana Island highlands since 2004 (100% prevalence; Common et al., 2019, 2020; Kleindorfer et al., 2021; Kleindorfer & Dudaniec, 2016; Kleindorfer, Peters, et al., 2014). Highland nests had four times more avian vampire fly larvae per nest than lowland nests, which we measured in *G. fuliginosa* (O'Connor,

Dudaniec, & Kleindorfer, 2010). Nestling naris size is larger in nests with more avian vampire fly larvae per nestling (Katsis et al., 2021).

2.3 | Mist-netting, body condition and naris size

We mist-netted, measured and colour-banded 1435 birds, including 191 *C. pauper*, 351 *C. parvulus*, 149 *Camarhynchus* hybrids and 744 *G. fuliginosa*. During February of each year, for 2 weeks, we placed 6 × 12 m mist-nets in the study sites to capture and measure Darwin's finches. At the time of banding, each bird received a uniquely numbered aluminium band and colour-band combination. We measured culmen length (mm), beak length naris (length of the culmen to the anterior edge of the naris) (mm), beak depth (mm), beak width (mm), tarsus length (mm), flattened tail length (mm), naris size (mm) and body mass (g). We measured only the right naris from 2004 to 2012 and measured both the right and left nares from 2013 onwards; there was a strong positive correlation between the size of the right and left naris ($r = 0.71$, $p < 0.001$). From historical specimens collected during 1899 and 1962 (prior to confirmed avian vampire fly presence on the Galápagos), mean naris size in non-parasitised Darwin's finches was $1.75 \text{ mm} \pm 0.24 \text{ SD}$ and 12% of beak length (Kleindorfer & Sulloway, 2016). Here, we calculated naris size as percentage naris size relative to culmen length, and classed birds with naris size <15% as 'normal' and birds with naris size >15% as 'enlarged'; we used this approach to determine the percentage of birds with enlarged naris size relative to culmen length. We used naris size as a continuous variable to examine effects of naris size on body mass, a proxy for the birds' condition (hereafter 'body condition'). Body mass is frequently correlated with fat mass (i.e. ideal measure of body condition/energy reserves) in birds, explaining more than 50% of variation in fat mass in many species (reviewed in Labocha & Hayes, 2012). However, a necessary premise for the validity of this extrapolation is the absence of a correlation between body mass and other structural measures (Labocha & Hayes, 2012). In the case of a correlation between structural and body mass measures, it would be impossible to disentangle if body mass is a real indicator of body condition, size or the relationship between both (Labocha & Hayes, 2012). In the species studied here, body mass was only loosely correlated with the morphological traits 'tarsus length' and 'tail length' (Table S1).

2.4 | Foraging behaviour

We collected 1886 first foraging observations, including observations from 499 colour-banded birds (57 *C. pauper*, 195 *C. parvulus*, 89 *Camarhynchus* hybrids and 158 *G. fuliginosa*). As *C. parvulus* and hybrid birds cannot be distinguished in the field (Peters & Kleindorfer, 2018), we initially assigned all foraging records of un-banded smaller-bodied tree finches to *C. parvulus*, and later assigned ~30% of these observations to hybrid birds based on microsatellite

scoring. We collected most (96%) first foraging observations of birds along one 200 m transect per study plot ($N = 8$) on two separate days during February (generally the onset month for egg-laying in nesting Darwin's finches on Floreana Island), as well as ~4% ad hoc observations of colour-banded birds during January and March. We recorded one observation per bird to avoid pseudo-replication of individual foraging behaviour. For each bird encountered along the transect, we noted its foraging substrate (ground, foliage, bark, flower, fruit, moss), foraging technique (glean, pick, bite, probe, pry, chip off), and major dietary category (plant, seed, invertebrate, unknown; see Table S2 for definitions and, Myers et al., 2010; Schlotfeldt & Kleindorfer, 2006). We used the first foraging observation, as Darwin's finches do not alter their behaviour in the presence of human observers, and the first observation can be considered an independent observation.

2.5 | Ethical statement

This study was supported by ethics permits issued by the Flinders University Animal Welfare Committee (E270, E393, E480), occurred in accordance with the Austrian Animal Experiments Act (§ 2. Federal Law Gazette No. 501/1989), and research permission was granted by the Galápagos National Park (PC-021-99, PC-19-07, PC-39-09, PC-58-11, PC-38-12, PC-15-14, PC-23-16, PC-02-20).

2.6 | Statistical analysis

Data were analysed using SPSS 24.0 and R 3.6.1 (R Core Team, 2019). We used a generalised linear model to test the expected effects of species and naris size (continuous variable) on % subsurface prey extraction; we included foraging substrate, beak length, year and 'species × naris size interaction' in the model. We used ordinal regression with a six-step scale for foraging beak stress as the dependent variable and species category, maximum naris size and three other beak measurements (length, depth and width) as independent variables. Based on Soons et al.'s 2015 findings, we assigned a scale of maximum beak loading stress from lowest to highest: (1) glean and (2) pick, (3) biting and grasping, (4) probing, (5) prying and (6) chip off. If one assumes that birds more often use the least energetically expensive foraging technique, then we are led to predict a correlation between these techniques and their observed frequency, which we tested with correlation analysis.

We calculated the coefficient of variation in naris size between surface and subsurface prey removal per species. To compare possible changes in foraging niche overlap in birds with normal or enlarged naris size, we used Bray–Curtis dissimilarity and multidimensional scaling (PAST; Hammer et al., 2001). A Bray–Curtis dissimilarity score ranges from 0 (entirely different) to 1 (entirely similar) and a Bray–Curtis index of similarity is calculated as $(1 - \text{Bray Curtis score}) \times 100$.

To analyse morphological traits associated with body condition, we use the package `LME4` (Bates et al., 2007) to fit a linear mixed effect model under a pseudo-Bayesian framework using flat priors. For statistical interpretation, we used the function 'sim' from the package `ARM` (Gelman et al., 2020). From 10,000 simulations, we obtained the mean and the 95% credible intervals (CrI) of each model estimate. We considered an effect to be statistically meaningful if the 95% CrI did not overlap with zero or if the posterior probability (termed *Posterior[p]*) was higher than 95%. For details on this approach, see Schielzeth (2010).

To investigate whether naris size is related to adult body condition, we constructed a multivariate linear mixed effect model with body mass as the dependent variable (Labocha & Hayes, 2012). We used species, naris size, beak width, beak length, beak depth, tail length and tarsus length as explanatory variables. We included the interaction of each morphological trait with the genetically assigned species (or hybrid) grouping. Mean rainfall and temperature for the reproductive period were included as covariates. Year was included as a random factor. All the numerical explanatory variables and covariates were z-transformed using the function 'scale' from the package `BASE` (Korner-Nievergelt et al., 2015) to obtain standardised effect sizes (Schielzeth et al., 2020). Correlations between the variables of our model were low on average (0.2 to 0.37 for non-beak associations; see the correlation matrix in Table S3 and sources of variation Table S4).

3 | RESULTS

Naris size (mm, mean \pm SE) in birds for which we also have foraging observations was 2.2 ± 0.07 in *C. pauper* ($N = 57$), 2.0 ± 0.04 in *C. parvulus* ($N = 193$), 2.1 ± 0.05 in hybrid birds ($N = 94$) and 1.9 ± 0.03 in *G. fuliginosa* ($N = 135$). Culmen length (mm, mean \pm SE) was 13.3 ± 0.1 in *C. parvulus*, 14.0 ± 0.1 in hybrid birds, 15.2 ± 0.1 in *C. pauper* and 14.7 ± 0.01 in *G. fuliginosa*. For naris size as a percentage of culmen length, 314 (66%) birds had naris sizes that were $\leq 15\%$ of culmen length (normal naris size)

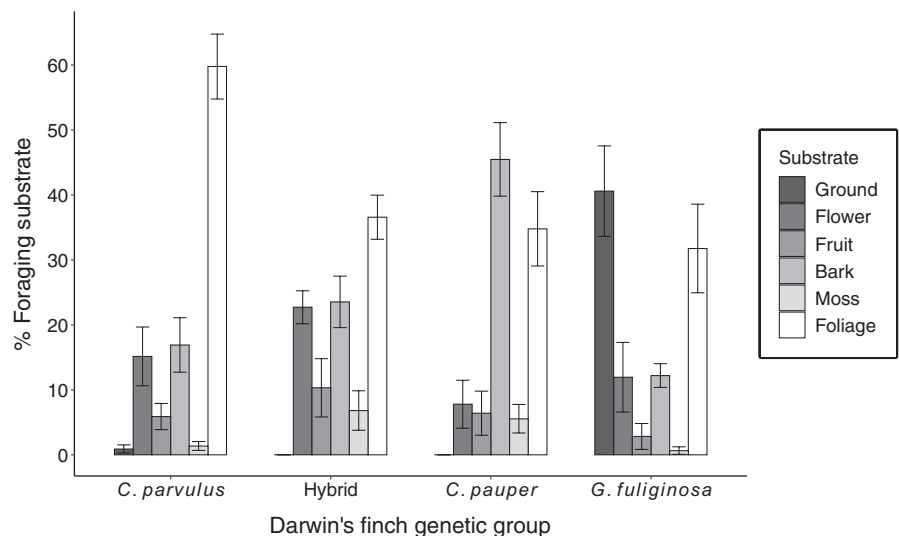
and 162 (34%) birds had naris sizes $>15\%$ of culmen length (enlarged naris size). Per genetic group, the percentage of birds with enlarged naris size was 37% in *C. parvulus*, 47% in hybrid birds, 35% in *C. pauper*, and 21% in *G. fuliginosa*.

3.1 | Foraging behaviour

Darwin's finches differed in their use of foraging substrate (GLM: $N = 1885$, $df = 3$, $F = 19.93$, $p = 0.001$; Partial Eta = 0.18). *Camarhynchus pauper* mostly foraged on bark, *C. parvulus* mostly foraged on foliage, hybrid finches mostly foraged on foliage and bark, and *G. fuliginosa* mostly foraged on the ground (Figure 3, Table S5). We compared foraging technique among species and in relation to naris size, foraging substrate, year and the interaction term species \times naris size. *Camarhynchus parvulus* (80%) and *G. fuliginosa* (75%) had the most surface prey removal, followed by hybrid birds (58%) and *C. pauper* (42%). There was a statistically significant effect for the interaction term species \times naris size in relation to subsurface foraging (GLM: $F = 3.76$, $df = 3457$, $p = 0.011$), as well as significant effects for year ($F = 2.72$, $df = 5457$, $p = 0.020$), and foraging substrate ($F = 26.92$, $df = 5457$, $p < 0.001$; Figure 4). The annual percentage difference in subsurface prey extraction was $40\% \pm 7$ in all Darwin's finches with normal naris size and $19\% \pm 6$ in all Darwin's finches with enlarged naris size. We see a similar pattern when comparing all foraging observations: in birds with normal naris size, *C. pauper* (58%) and hybrid birds (40%) more often used 'probe, pry or chip off' foraging techniques to extract hidden prey from beneath the surface compared with *C. parvulus* (12%) and *G. fuliginosa* (13%). But in birds with enlarged naris size, subsurface prey extraction was used less frequently in *C. pauper* (27%), hybrid (30%) and *G. fuliginosa* (5%) but remained at 13% in *C. parvulus* (Table S6).

The correlation between the six foraging behaviours (1—glean, 2—pick, 3—biting and grasping, 4—probing, 5—prying and 6—chip off) and their observed frequency was substantial ($r_{\text{alerting}} = 0.88$, $p = 0.01$, one-tailed test).

FIGURE 3 Foraging substrate ($N = 1886$ observations) shown as mean annual percentage (\pm SE) used by four Darwin's finch genetic groups on Floreana Island. The genetic groups differed significantly in foraging substrate: Small tree finches (*Camarhynchus parvulus*) foraged mostly on foliage; hybrid tree finches (*C. pauper* \times *C. parvulus*) foraged mostly on foliage, bark and flowers; medium tree finches (*C. pauper*) foraged mostly on bark; small ground finches (*Geospiza fuliginosa*) foraged mostly on the ground



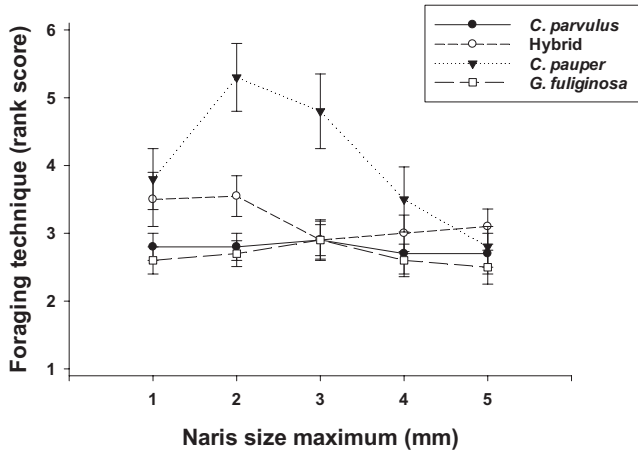


FIGURE 4 Naris size (mm) (maximum per bird) in relation to mean foraging technique rank (1 = glean, 2 = pick, 3 = bite, 4 = probe, 5 = pry, 6 = chip off) whereby categories 1–3 involve surface prey removal and categories 4–6 involve subsurface prey extraction. Statistical analyses were performed using naris size as a continuous variable; for graphical purposes, we created a binned naris size variable to show the effects visually. In the entire sample, the species × naris size interaction term predicted subsurface prey extraction. When examining patterns per species, the mostly bark-feeding medium tree finch *Camarhynchus pauper* experienced the greatest impact of naris deformation on altered foraging behaviour. Medium tree finches with enlarged nares had less subsurface prey extraction and more surface prey removal

To assess whether beak malformation is associated with foraging strategies in Darwin's finches, we used ordinal regression with a six-step scale for foraging beak stress as the dependent variable and species category, maximum naris size and three other beak measurements (culmen length, beak depth and width) as independent

variables. The association between enlarged nares and using beaks in a high-stress manner was not significant, although beak depth did predict high-stress beak use (Wald $\chi^2 = 5.32$, $df = 1$, 474 $p = 0.021$). Hybrids, and especially *C. pauper*, were more likely to use such stressful foraging techniques (hybrids: Wald $\chi^2 = 4.08$, $df = 1$, 474 $p = 0.043$, and *C. pauper*: Wald $\chi^2 = 8.09$, $df = 1$, 474 $p = 0.004$). We also found a significant interaction between species type and enlarged naris size, but only for *C. pauper*, which showed a marked reduction in high-stress foraging strategies among birds with enlarged nares (Wald $\chi^2 = 5.89$, $df = 1$, 474 $p = 0.015$).

3.2 | Coefficient of variation and niche overlap

In all genetic groups except the hybrid finches, the coefficient of variation in naris size was lower in birds using subsurface prey extraction than surface prey removal (coefficient of variation per species shown as subsurface extraction vs. surface prey removal respectively; *C. pauper*: 21.5 vs. 25.8, *C. parvulus*: 23.8 vs. 27.9; *G. fuliginosa*: 16.2 vs. 20.7; hybrids: 23.8 vs. 22.6). In birds with normal naris size, the Bray–Curtis foraging similarity score was lower and, hence, less similar between species (0.78) than when birds had enlarged naris size and foraging similarity score was higher (0.95). The increase in foraging similarity across species in birds with malformed beaks is shown in the Paired Group (UPGMA) Bray–Curtis similarity plot (Figure 5).

3.3 | Body condition

From the six morphological traits measured, large naris size was the only trait that was negatively associated with body

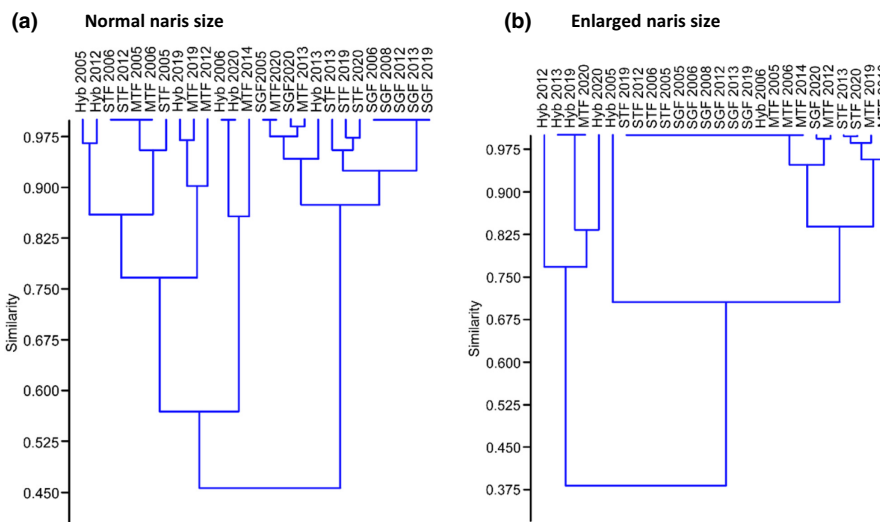


FIGURE 5 Results of paired group (UPGMA) Bray–Curtis similarity index using percentage foraging behaviour (surface prey removal vs. subsurface prey extraction) per species and year (2005–2020). Species are abbreviated (*Camarhynchus parvulus* = STF, hybrid = Hyb, *C. pauper* = MTF, *Geospiza fuliginosa* = SGF) followed by year; for example, STF 2005, Hyb 2005, MTF 2005 and SGF 2005. The data are shown for (a) birds with normal naris size ($\leq 15\%$ of culmen length), and (b) birds with enlarged naris size ($> 15\%$ of culmen length). The coefficient of similarity was lower (0.78) when birds had normal naris size, and higher (0.95) when birds had enlarged naris size

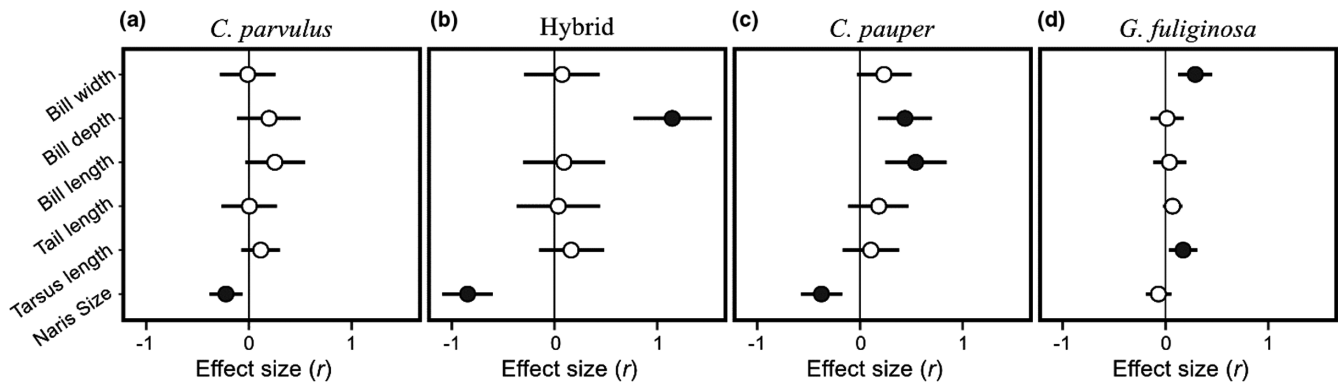


FIGURE 6 Effect of morphological traits on body mass in different Darwin's tree finch (*Camarhynchus*) and ground finch (*Geospiza*) groups: (a) *C. parvulus* ($N = 240$), (b) hybrid *C. parvulus* \times *C. pauper* ($N = 104$), (c) *C. pauper* ($N = 136$), and (d) *G. fuliginosa* ($N = 410$). Circles and horizontal bars represent the standardised effect size (r) and the 95% credible interval, respectively, for each morphological trait. Open circles represent effect sizes with no statistical support and filled circles represent statistically meaningful effect sizes (i.e. $\text{Posterior}(p) > 95\%$).

condition (Figure 6). This effect was large in *C. parvulus* (Figure 6a; $\text{Posterior}[p] = 99.6\%$), *C. pauper* (Figure 6c; $\text{Posterior}[p] = 99.9\%$) and hybrids (Figure 6b; $\text{Posterior}[p] > 99.9\%$) and followed a similar trend in *G. fuliginosa* but with a smaller effect size (Figure 6d; $\text{Posterior}[p] = 85.5\%$). Depending on the genetic group, different beak properties were positively associated with body condition. In *C. pauper*, beak depth and beak length were positively associated with body condition (Figure 6b; $\text{Posterior}(p) = 99.9\%$ for beak depth and $\text{Posterior}(p) > 99.9\%$). In hybrid birds, beak depth was associated with better body condition (Figure 6c; $\text{Posterior}(p) > 99.9\%$). In *G. fuliginosa*, beak width had a positive association with body condition (Figure 6d; $\text{Posterior}(p) > 99.9\%$). For additional details on the model estimates, see Table S4.

4 | DISCUSSION

We document potential ecological and fitness consequences from a change in an animal functional trait caused by a dipteran parasite feeding on the beak of its avian host. Between 21% and 47% of adult Darwin's finches had malformed beaks caused by early-life parasitism from avian vampire fly *P. downsi* larvae. Malformed beaks were used less often for subsurface prey extraction, and beaks used for subsurface prey extraction had less variation in naris size compared with beaks used for surface prey extraction. The relationship between naris enlargement and foraging behaviour was strongest in the critically endangered *C. pauper*, a species that most commonly extracted prey from beneath bark using chip off movements of the beak. There are potentially biologically important implications of this species-dependent association between naris size and foraging, considering that *C. pauper* could provide key ecosystem services such as subsurface prey removal of grubs from bark. Foraging niche similarity across species increased when birds had naris enlargement, as birds with enlarged nares more commonly gleaned prey from foliage surfaces. While not causative, this potential increase in interspecific competition for surface invertebrates could explain our observation that birds with naris enlargement

had lower body mass, although other explanations for this pattern of association are possible. Future experimental approaches could aim to disentangle the role of early-life naris enlargement on foraging technique and body condition across life stages.

Darwin's finches, described by some as 'the crown jewels of ornithology' (Kricher, 1999) for their remarkable and rapid divergence in beak size and shape and associated foraging divergence, are now increasingly an example of 'reverse speciation' (Grant & Grant, 2014b; Kleindorfer, O'Connor, et al., 2014). Across the last two decades, for example, we have been documenting an increase in the percentage of hybrid crossings between *C. pauper* and *C. parvulus* (Kleindorfer & Dudaniec, 2020). Here, we show rapid shifts in foraging behaviour associated with normal versus enlarged naris size. The 73% of malformed *C. pauper* that engaged in surface prey removal were more likely to overlap in their foraging habits with *C. parvulus*, which also engage mostly in surface prey removal irrespective of their naris size. In addition to increased overlap in foraging behaviour, such changes may be associated with potential shifts in mating opportunity and other forms of competition that we did not measure.

There could be ecological consequences to changes in Darwin's finch foraging behaviour, which require further study. For example, we might expect an increase in heterospecific competition between *C. pauper* and *C. parvulus*, and a decline in *Scalesia* tree health and perhaps ecosystem function, given a reduction in tree-bark grub removal (Gregory & Van Strien, 2010).

Few studies have examined altered foraging behaviour in hosts as the consequence of non-manipulative prior parasite exposure (Møller & Rozsa, 2005; Price, 1980), even though host-parasite interactions are known to generate novel selection pathways and can be a source of evolutionary innovation (Duffy & Sivars-Becker, 2007; Poulin, 2011a). Parasites may alter host foraging behaviour for a variety of reasons. Potential hosts may avoid particular food items or foraging habitats to minimise their exposure to parasites (Koch et al., 2017; Lozano, 1991). Hosts may also seek out food items that reduce host palatability to parasites or that contain anti-parasitic or anti-disease compounds (Fouks & Lattorff, 2011; Richardson

et al., 2016). Parasitism may also result in pathology that, in turn, influences foraging behaviour. Altered foraging behaviour has been observed in birds with psittacine circoviral disease (PCD); for example, sulphur-crested cockatoos (*Cacatua galerita*) have impaired feeding ability due to beak malformation (McOrist et al., 1984) and infected budgerigars (*Melopsittacus undulates*) may lose their feathers and become 'runners' or 'hikers' that have to forage on the ground (Raidal et al., 2015; Raidal & Peters, 2018). Hence, foraging niche may be affected when pathogens (e.g. ectoparasites or viruses) alter avian functional traits used for foraging.

According to niche theory, species are functionally different and coexist when they are functionally adapted to different niches (Holt, 2009; Kearney et al., 2010). The niche concept has been defined in many ways, and, since Hutchinson and MacArthur (1959), is often considered as a multi-dimensional environmental space where stable populations can be maintained, either as 'realised niche' when biotic interactions such as predation and competition are included, or as 'physiological niche' when only abiotic factors are considered (Jeffries & Lawton, 1984; Schluter & Grant, 1984a). The axes of environmental niches can be constructed based on biotic and abiotic factors and used to predict biological and ecosystem-level outcomes, including survival, development, reproduction, population dynamics and species interactions (Jeffries & Lawton, 1984). Across different environments, variation in resource types and distribution can be a driver of phenotypic trait divergence (Benkman, 2003; Schluter, 2000). Because different phenotypes can exploit available resources differently, selection should favour phenotypes that are close to the adaptive fitness peak while phenotypes further away from the adaptive peak will experience reduced fitness (Schluter, 2000). In *The Origin of Species*, Darwin (1859) proposed his 'principle of divergence' to account for changes in traits that could promote speciation on the one hand and coexistence of diverse forms on the other, given reduced competitor overlap in the latter. In this study, our finding of increased niche similarity in birds with naris enlargement points to 'reverse niche specialisation' as one possible consequence of early-life parasitism. Avian hosts with naris enlargement were more likely to engage in potentially less profitable surface prey removal, and, hence, to converge on foraging technique. This change in foraging behaviour, should it be occurring, also entails moving away from a potential adaptive fitness peak that may have favoured beaks selected to sustain pressures for probing, prying and chipping off bark.

Birds with enlarged naris size had lower body mass in *Camarhynchus* tree finches but not in *G. fuliginosa*. Tree finches have a slightly curved beak and mostly forage in and on trees, removing prey from the surface of bark or leaves, probing into moss and leaves, and chipping and prying at bark to remove prey under the bark or within the tree trunk (Peters & Kleindorfer, 2015; Tebbich et al., 2004). Future work should address changes to load bearing when a curved beak has small versus large naris size, similar to approaches used to measure beak stress in Darwin's finches with normal naris size (Soons et al., 2015). Perhaps lower body condition in birds with naris enlargement is a by-product of increased foraging niche overlap and, hence, interspecific competition, although this possibility remains to be tested (Abbott et al., 1977; Price &

Kirkpatrick, 2009). In contrast to the pattern in tree finches, naris size in *G. fuliginosa* was not associated with lower body mass; this is consistent with previous findings on Santa Cruz Island (Galligan & Kleindorfer, 2009). *Geospiza fuliginosa* have conical beaks and consume smaller and softer seeds compared with larger-beaked ground finches (Abbott et al., 1975). Perhaps the required seed-crushing force of a straighter and smaller beak in ground finches is less affected by naris size differences than the tree finches' curved beak, which is used to consume a range of fruits and invertebrate prey. Nevertheless, we fully acknowledge there are many alternative explanations for how parasitism reduces host body condition (Bennett et al., 1988; Booth et al., 1993; Tschirren et al., 2007), which future study could address in adult Darwin's finches.

This study provides some evidence that parasite-induced alterations in phenotype separated in time and space can have potential downstream ecological effects. Perhaps naris enlargement caused by avian vampire fly larvae during early development increases interspecific competition via niche overlap, when host foraging specialisations are compromised in birds with malformed beaks. These altered host foraging specialisations could reduce potential ecosystem services, such as subsurface grub removal (e.g. Parasharya et al., 1994) from tree bark, to the detriment of ecosystem functioning and tree health, for example. Despite the challenges of basing conclusions on correlational data in natural systems, where experimentation is not always possible, our findings suggest that early-life experiences and phenotypic changes can generate measurable ecological shifts via changes in foraging behaviour and niche overlap. Few studies to date have examined how prior parasitism can cause life-long changes in ecological interactions for a host, which is one form of sublethal effects. In addition, the findings draw attention to ways that parasites can have long-lasting effects on communities far beyond the time period during which they are acutely infecting a host.

AUTHORS' CONTRIBUTIONS

S.K. designed the research and wrote the first draft of the paper; S.K., D.C.-N., L.K.C., J.A.O., K.J.P., A.C.K. and R.Y.D. collected the data; N.M.A., F.J.S. and S.K. analysed the data. All authors edited the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data for this manuscript are available on Dryad <https://doi.org/10.5061/dryad.2z34tmpk9>.

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