



Beak of the pinch: anti-parasite traits are similar among Darwin's finch species

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Abstract

Darwin's finches are an iconic example of adaptive radiation. The size and shape of the beaks of different finch species are diversified for feeding on different size seeds and other food resources. However, beaks also serve other functions, such as preening for the control of ectoparasites. In diverse groups of birds, the effectiveness of preening is governed by the length of the overhanging tip of the upper mandible of the beak. This overhang functions as a template against which the tip of the lower mandible generates a pinching force sufficient to damage or kill ectoparasites. Here we compare feeding versus preening components of the beak morphology of small, medium, and large ground finches that share a single parasite community. Despite adaptive divergence in beak morphology related to feeding, the three species have nearly identical relative mandibular overhang lengths. Moreover, birds with intermediate length overhangs have the lowest feather mite loads. These results suggest that Darwin's finches maintain an optimal beak morphology to effectively control their ectoparasites.

Keywords Preening · Feather mites · *Geospiza* · Principal component analysis · Overhang

Introduction

In his Pulitzer Prize-winning book “Beak of the Finch”, Jonathan Weiner (1994) features Peter and Rosemary Grant's classic work on the adaptive radiation of Darwin's finches in the Galápagos Islands (Grant and Grant 2014). As carefully documented by the Grants,

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the beaks of Darwin's finches are adapted for feeding on different sized seeds and other food resources. For example, large ground finches (*Geospiza magnirostris*) have large, deep beaks capable of crushing large, tough seeds. Medium ground finches (*G. fortis*) have intermediate beaks for feeding on smaller seeds. Small ground finches (*G. fuliginosa*) have small, nimble beaks for feeding on the smallest seeds (Grant and Grant 2014). This diversification of foraging-related beak morphology is a hallmark of adaptive radiation in Darwin's finches, as well as other groups of birds (Cooney et al. 2017; Olsen 2017).

Although beaks are first and foremost adapted for feeding, they have other functions, such as preening. Preening serves to straighten and oil feathers and combat ectoparasites. Indeed, preening is the first line of defense against several groups of ectoparasites (Clayton et al. 2016; Bush and Clayton 2018). Among diverse groups of birds, such as North American scrub-jays, Hawaiian honeycreepers, and Peruvian songbirds, the effectiveness of preening is governed by the overhanging tip of the upper mandible of the beak (Clayton and Walther 2001; Moyer et al. 2002a; Freed et al. 2008). Removal of the overhang in rock pigeons (*Columba livia*) triggers a dramatic increase in populations of feather lice (Clayton et al. 2005). When the overhang is allowed to grow back, birds regain their ability to control lice. In pigeons, the overhang functions as a template against which the tip of the lower mandible generates a pinching force sufficient to crush lice. Remarkably, removal of the overhang has no effect on the feeding efficiency of pigeons, suggesting that it is a specific adaptation for ectoparasite control (Clayton et al. 2005).

Overhangs that are too long can incur a cost. For example, when overhangs grow too long, they are more susceptible to breakage (Clayton et al. 2005). Broken overhangs can have severe consequences for wild birds; rock pigeons with broken overhangs have thousands of lice and extensive feather damage (Clayton et al. 1999). Moreover, long overhangs may also impair feeding ability (Clayton et al. 2005). Thus, overhangs need to be short enough for birds to feed effectively, but long enough to control ectoparasites.

Effective preening for controlling feather lice is important because lice are known to have direct negative effects on host fitness (Clayton et al. 2008; Hoi et al. 2012; Clayton et al. 2016). Large populations of lice on birds with impaired preening cause feather damage that reduces host mating success and survival (Clayton 1990; Booth et al. 1993; Clayton et al. 1999). Preening also controls feather mite populations, such that birds with impaired preening experience dramatic increases in mites (Barlow 1967; Clayton 1991; Handel et al. 2010). The effect of such mites on host fitness has not been tested experimentally; however, feather mite increases are sometimes correlated with poor host condition, feather quality, and reduced plumage brightness (Thompson et al. 1997; Harper 1999). Some feather mites may be commensals, with little or no effect on host fitness (Blanco et al. 1997; Proctor and Owens 2010; Galván et al. 2012; Doña et al. 2018). Moreover, effects of mites may transition between parasitism and commensalism (Bronstein 1994; Jovani et al. 2017; Matthews et al. 2017). Regardless of their precise effect on the host, feather mites—like feather lice—appear to be controlled by preening.

In this paper we explore the relationship between the beak morphology and ectoparasite loads of Darwin's ground finches. We compared beak size and shape to the abundance of ectoparasites among three species of ground finches, all of which have both feather mites and feather lice (Bulgarella and Palma 2017). Large, medium, and small ground finches have virtually identical mite and lice communities at our study site on Santa Cruz Island (Villa et al. 2013). We tested the prediction that, in contrast to the diversifying effect of feeding on beak morphology, Darwin's finches maintain similar preening-related beak morphology. Specifically, we predicted that the relative length of the upper mandibular overhang would not differ significantly among the three species of ground finches.

Materials and methods

We did field work from January to April 2009 at two locations on Santa Cruz Island (Galápagos archipelago, Ecuador): a highland site near Los Gemelos (0°37'50.95"S, 90°23'26.54"W), and a lowland site at the Charles Darwin Research Station on Academy Bay, Puerto Ayora (0°44'27.55"S, 90°18'10.10"W). Finches were captured with mist-nets between 0600 and 1100 h, and between 1600 and 1800 h. Each bird was placed in a single-use paper bag to avoid mixing parasites between birds. For each bird, we quantified body mass and beak length, width, and depth, as described in Grant et al. (1985) and illustrated in Grant (1986). We also quantified upper mandibular overhang length, as illustrated in Fig. 1b. We dust-ruffed each bird to quantify the diversity (number of taxa) and abundance of ectoparasites, as described in Villa et al. (2013). Abundance was the number of ectoparasites per individual bird (Bush et al. 1997). Birds were banded with numbered metal bands and released.

We analyzed variation in beak morphology among small, medium, and large ground finches using principal component analysis (PCA) in JMP v12. Beak length, width, depth, and overhang length were loaded into a PCA to provide four synthetic measurements of beak morphology (PC1-4) (Grant and Grant 2014). We tested for differences in each component of beak morphology among the three species using one-way ANOVAs with Tukey–Kramer post hoc tests.

We also examined the relationship between beak morphology and ectoparasite abundance. Because abundance is strongly influenced by host body size (Clayton and Walther 2001; Poulin 2007), we first removed the influence of body size by regressing each of the four beak measurements against host body mass to calculate residuals. The residuals of beak length, width, depth, and overhang length were then loaded into a PCA to provide four mass-corrected PCs of beak morphology.

We used linear mixed models (LMMs) to explore the relationship between the mass-corrected PCs and ectoparasite abundance among the three species of finches. For each LMM, we combined small, medium, and large finches for analysis. For all models, ectoparasite abundance was log transformed ($\log [n + 1]$) to achieve normality (Bush et al. 1997). We predicted ectoparasite abundance among all finches by modeling each PC as a fixed effect and included finch species as a random effect. An additional LMM was performed using relative overhang length, instead of PCs, as the fixed effect. Relative overhang length is the raw overhang length divided by the total length of the upper mandible. LMMs were fit in R v3.3.1 using the “lme4” library (Bates et al. 2015; R Core Team 2016). Degrees of freedom and resulting p-values were estimated with the Satterwaite approximation using the lmerTest library (Kuznetsova et al. 2016).

Results

We processed 90 finches, including 41 small ground finches, 39 medium ground finches, and 10 large ground finches (large ground finches are much less common than small and medium ground finches on Santa Cruz Island). We overlooked one or more measurements for two of the medium ground finch individuals, leaving a total of 88 finches with complete data. Feather mites were found on 61 of the 88 finches (69%) (Villa et al. 2013). We recovered a mean (\pm SE) of 12.4 ± 3.6 mites from small ground

Fig. 1 Comparisons of feeding and preening-related beak morphology among Darwin's ground finches on Santa Cruz Island, Galápagos. **a** Medium ground finch with **b** enlarged view of an average upper mandibular overhang (scale bar=0.45 mm); Medium ground finches with **c** small and **d** unusually large overhangs. **e** Distribution of PC1 across three species of Darwin's ground finches. PC1, which accounts for 78.2% of variation, is comprised predominantly of beak length, width, and depth (Table 1). PC1 can be interpreted as a synthetic measure of feeding morphology. Small, medium, and large ground finches differ significantly in PC1 (ANOVA with Tukey–Kramer post hoc tests; $df=2$, $F=404.34$, $P<0.001$ for all comparisons). **f** Distribution of PC2 across the same three species of Darwin's ground finches. PC2, which accounts for 20.6% of variation, is comprised almost exclusively of beak overhang length (Table 1). PC2 can be interpreted as a synthetic measure of preening morphology. Small, medium, and large ground finches do not differ significantly in PC2 (ANOVA with Tukey–Kramer post hoc tests; $df=2$, $F=2.76$, $P>0.05$ for all comparisons). **g** After correcting for differences in body mass among the finch species (Supplemental Table 1), feather mite abundance is not significantly associated with PC1 (LMM; $t=1.69$, $P>0.05$). **h** In contrast, feather mite abundance is highly significantly associated with PC2 (LMM; $t=3.76$, $P=0.0003$). Finches with intermediate PC2 scores had the fewest feather mites. Photographs courtesy of Kiyoko Gotanda (**a**) and Jeffery Podos (**c**, **d**)

finches, 37.6 ± 11.5 mites from medium ground finches, and 107.5 ± 36.2 mites from large ground finches. We also quantified the abundance of lice from each finch. Louse prevalence was extremely low, with only 5 of the 90 finches infested by lice. We therefore focused on the relationship between beak morphology and feather mites.

The principal component analysis provided four synthetic measures of beak morphology (PC1-4; Table 1). The first two principal components accounted for 98.8% of variation in beak morphology. Beak length, width, and depth all contributed approximately equally to PC1, which accounted for 78.2% of overall variation in beak morphology. PC1 was significantly different among the three finch species (Fig. 1e; ANOVA with Tukey–Kramer post hoc tests; $df=2$, $F=404.34$, $P<0.001$ for all comparisons). In contrast, PC2 accounted for 20.6% of overall beak variation and was made up almost entirely of overhang length (Table 1). Indeed, PC2 and raw overhang length were highly correlated (linear regression; $n=88$, $r=0.87$, $F=262.22$, $P<0.0001$). PC2 did not differ among the three finch species (Fig. 1f; ANOVA with Tukey–Kramer post hoc tests; $df=2$, $F=2.76$, $P>0.05$ for all comparisons).

To explore the relationship between beak morphology and mite abundance, we used a mass-corrected PCA (Supplemental Table 1). The first two mass-corrected principal components accounted for 78.5% of variation. Residual beak length, width, and depth all contributed approximately equally to PC1, which accounted for 53.1% of overall variation in beak morphology. There was no significant relationship between PC1 and mite abundance among finch species (Fig. 1g; Supplemental Table 2).

Mass-corrected PC2 accounted for 25.4% of overall beak variation and was made up almost entirely of residual overhang length (Supplemental Table 1). There was a highly significant quadratic relationship between mass-corrected PC2 and mite abundance among the three finch species (Fig. 1h; Supplemental Table 3).

Analysis of relative overhang length, instead of PC2, showed similar results. PC2 and relative overhang length were highly correlated (Fig. 2a; linear regression; $n=88$, $r=0.92$, $F=496.73$, $P<0.0001$). There was no significant difference in relative overhang length among the three finch species (Fig. 2b; ANOVA with Tukey–Kramer post hoc tests; $df=2$, $F=2.26$, $P>0.05$ for all comparisons). There was a significant quadratic relationship between relative overhang length and mite abundance among the three species (Fig. 2c; Supplemental Table 4).

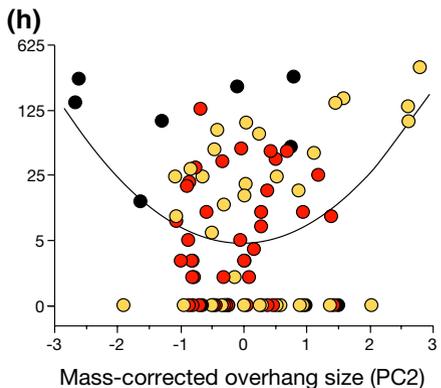
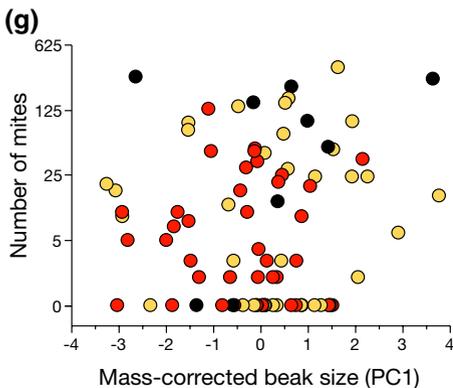
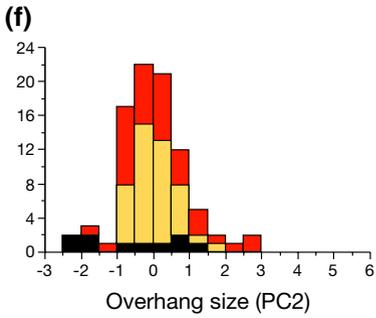
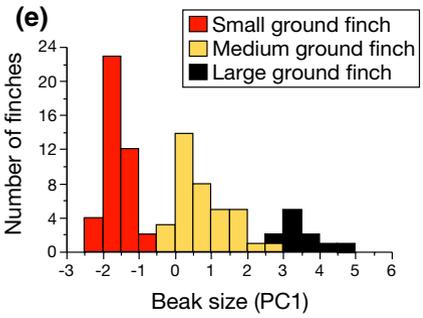
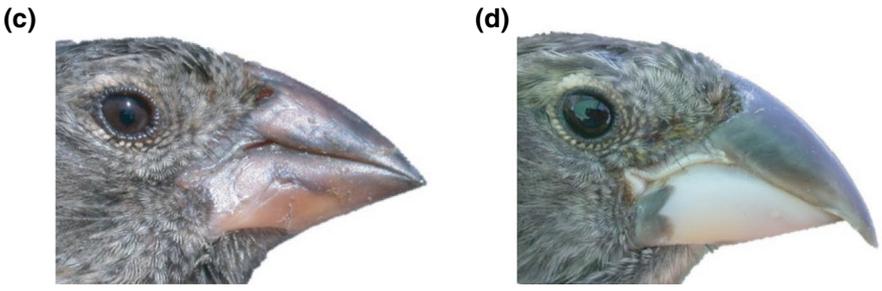
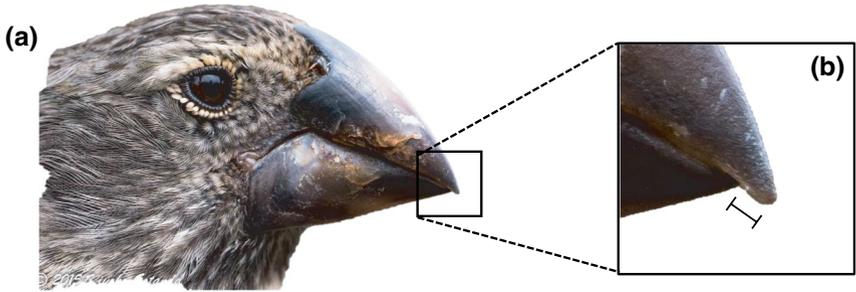


Table 1 Principal component analysis of beak morphology across Darwin's small medium and large ground finches

Beak dimension	Principal components			
	PC1	PC2	PC3	PC4
Eigenvalues				
	3.126	0.826	0.037	0.011
% Variation				
	78.2%	20.6%	0.9%	0.3%
Eigenvectors				
Length	0.555	-0.131	-0.778	-0.263
Depth	0.554	-0.170	0.607	-0.544
Width	0.556	-0.176	0.157	0.797
Overhang	0.276	0.961	0.030	0.014
Loadings				
Length	0.981	-0.119	-0.149	-0.028
Depth	0.979	-0.155	0.116	-0.057
Width	0.983	-0.160	0.030	0.084
Overhang	0.488	0.873	0.006	0.001

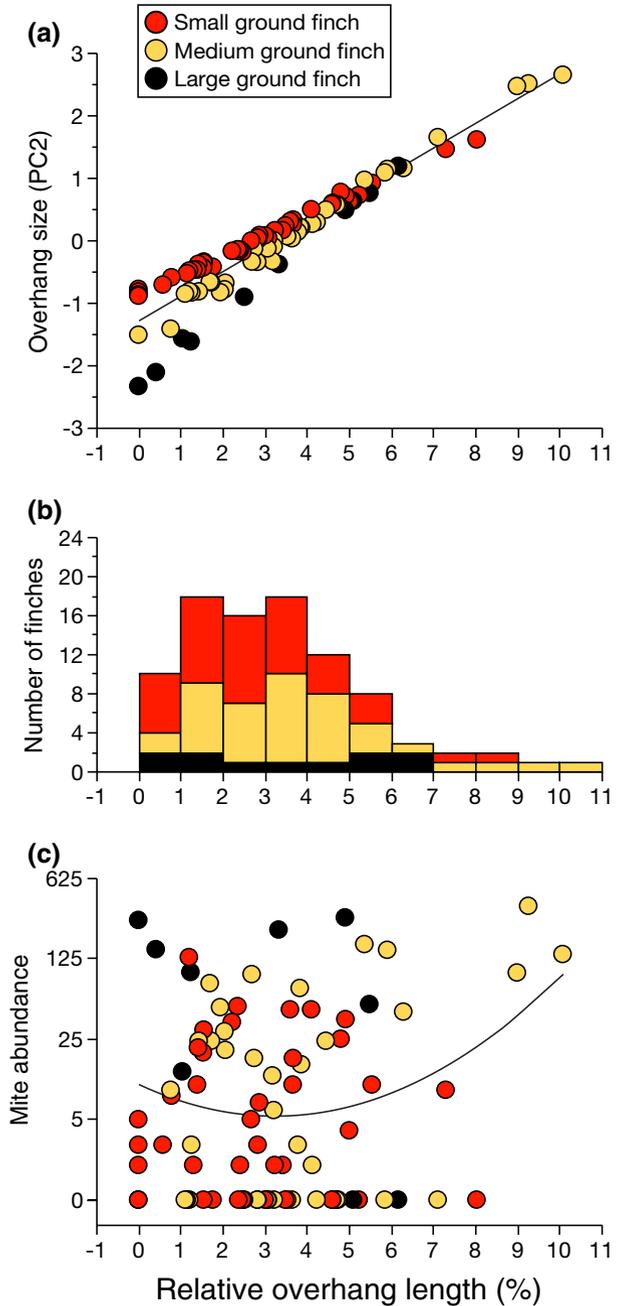
Discussion

Although Darwin's finch beak morphology has been studied extensively in relation to foraging ecology, it has not been studied in relation to preening ecology. We explored variation in beak morphological traits related to both feeding and preening in small, medium, and large ground finches on Santa Cruz Island, Galápagos. Although foraging-related components of beak morphology differed among the three species (Fig. 1e), preening-related morphology did not differ among species (Fig. 1f). Despite adaptive divergence in overall beak size, the three species had very similar relative mandibular overhang lengths (Fig. 2b). Moreover, across the three species, birds with intermediate length overhangs had the lowest feather mite loads (Fig. 1h). These results suggest that, in contrast to foraging-related beak morphology, Darwin's finches maintain similar preening-related beak morphology.

Ectoparasites collected from birds in this study were similar to those reported from previous surveys of ectoparasites of Darwin's ground finches (Palma and Price 2010; Palma and Peck 2013; Bulgarella and Palma 2017). Although lice on ground finches are often relatively common, the prevalence of lice on birds in our study was low (<6%). A possible explanation is that feather lice are more susceptible than feather mites to abiotic factors, such as low humidity (Moyer et al. 2002b). Thus, the low prevalence of lice in our study may have reflected climatic conditions during our field season in 2009. In contrast, the prevalence of feather mites in our study (69%) was much higher than that of lice.

Similar to previous studies (Grant and Grant 2014), our PCA showed that small, medium, and large ground finches differ significantly in PC1, which is a proxy for overall beak size (Fig. 1e). PC1 comprised roughly equal proportions of beak length, width, and depth, which are traits related to adaptive differences in foraging ecology (Grant and Grant 2014). By contrast, the three species of finches did not differ significantly in PC2 (Fig. 1f), which was comprised almost entirely of beak overhang length. Despite their differences in beak size, the three species of finches had nearly identical PC2 scores. Since the beak overhang is known to be critical for ectoparasite control, PC2 can be interpreted as an index of preening morphology.

Fig. 2 Comparisons of relative overhang lengths among Darwin’s ground finches on Santa Cruz Island, Galápagos. **a** PC2, which is a synthetic measure of overhang size, is highly correlated with relative overhang length (linear regression; $n = 88$, $r = 0.92$, $F = 496.73$, $P < 0.0001$). **b** Distribution of relative overhang length across three species of Darwin’s ground finches. Small, medium, and large ground finches do not differ significantly in relative overhang length (ANOVA with Tukey–Kramer post hoc tests; $df = 2$, $F = 2.26$, $P > 0.05$ for all comparisons). **c** Feather mite abundance is significantly associated with relative overhang length (LMM; $t = 2.09$, $P < 0.05$). Finches with intermediate relative overhang values had the fewest feather mites



After correcting for interspecific differences in finch body mass, we showed that PC2 is highly correlated with mite abundance (Fig. 1h). Across small, medium, and large ground finches, individuals with intermediate PC2 scores had the fewest mites. The ten birds with PC2 scores nearest the mean had an average of 18 mites. By contrast, the ten birds with

PC2 scores farthest from the mean (in either direction) had nearly seven-fold more mites, with an average of 118 mites. This pattern strongly suggests that finches with extreme overhangs (Fig. 1c, d) are not as effective at controlling ectoparasites.

The significant quadratic relationship between mass-corrected PC2 and mite load was not an artifact of contrasting linear relationships within the three finch species. While there was a weak positive relationship between PC2 and mite load in the medium ground finch (linear regression; $n=37$, $R^2=0.12$, $F=4.83$, $P=0.03$), there was no relationship between mite load and PC2 for either the small ($R^2=0.02$, $P=0.35$) or large ground finches ($R^2=0.20$, $P=0.19$).

To make our results easier to compare to other systems, we repeated the analysis using relative overhang length, instead of PC2. Across Darwin's finches, the overhang length was on average (\pm SE) $3.2 \pm 0.2\%$ of the total length of the upper mandible. We compared this relative overhang length to the number of mites on finches. This approach showed the same result as our first analysis using mass-corrected PC2. Together, these results indicate that adaptive diversification of finch beaks for feeding on different food resources has not "dragged" along morphological traits critical for preening. Instead, preening-related morphology appears to be conserved across species. Since small, medium, and large ground finches are infested by virtually identical ectoparasite communities, this result makes biological sense.

Our results suggest that individuals in a population that have an extreme beak overhang (very long or very short; Fig. 1c, d) are not as good at controlling ectoparasites. Assuming beak overhang length has a heritable component, selection may constrain overhang length to keep it within the optimal range, independent of feeding related beak morphology. However, we are aware of no evidence to suggest that overhang length is heritable. Indeed, overhang length appears to be a plastic trait in other groups of birds. Beak overhangs are formed from keratin and are analogous to human fingernails, which are subject to routine wear from the environment. For seed-eaters like Darwin's finches, most of the wear likely comes from feeding (Matthysen 1989). Filing down of the overhang opposes constant growth of the beak keratin. In seed-eating birds, keratin grows quickly; e.g. at a rate of 0.07 mm/day in Black-capped chickadees (*Poecile atricapillus*) (Van Hemert et al. 2012) and 0.085 mm/day in Nuthatches (*Sitta europaea*) (Matthysen 1989). Thus, optimal overhang length may reflect a balance between keratin growth and wear rates. Regardless of the precise underlying mechanism, our study indicates that small, medium, and large ground finches appear to converge on the same optimal relative overhang length for parasite control. The similarity in preening-related morphology suggests that, despite strong divergent selection for feeding, beaks do not diverge in preening related morphology.

Our results are consistent with previous studies showing the importance of an intermediate overhang length for controlling ectoparasites. Bush and Clayton (2018) reported that Western scrub-jays (*Aphelocoma californica*) with long or short overhangs have more lice than birds with intermediate overhangs. Reanalysis of the data in their paper shows that scrub-jays, which have very different beak shapes than Darwin's finches, have a mean (\pm SE) relative overhang length of $3.4 \pm 0.4\%$ ($n=20$), which is remarkably similar to that of Darwin's finches. It would be interesting to survey other groups of birds to determine their relative overhang lengths.

To our knowledge, this study is the first to provide evidence that Darwin's finches maintain similar preening-related components of beak morphology. While there is little doubt that beaks are first and foremost tools for feeding, our results suggest that beak morphology, even in well-known systems, should be evaluated with both feeding and preening in mind.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Barlow JC (1967) A bill deformity in a European tree sparrow, *Passer montanus* (Linnaeus). *Can J Zool* 456:889–890
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Blanco G, Tella JL, Potti J (1997) Feather mites on group-living red-billed choughs: a non-parasitic interaction? *J Avian Biol* 28:197–206
- Booth DT, Clayton DH, Block BA (1993) Experimental demonstration of the energetic cost of parasitism, in free-ranging hosts. *Proc R Soc Lond B* 253:125–129
- Bronstein JL (1994) Conditional outcomes in mutualistic interactions. *Trends Ecol Evol* 9:214–217
- Bulgarella M, Palma RL (2017) Coextinction dilemma in the Galapagos Islands: Can Darwin's finches and their native ectoparasites survive the control of the introduced fly *Philornis downsi*? *Insect Conserv Div*. <https://doi.org/10.1111/icad.12219>
- Bush SE, Clayton DH (2018) Anti-parasite behaviour of birds. *Philos Trans R Soc B*. <https://doi.org/10.1098/rstb.2017.0196>
- Bush AO, Lafferty KD, Lotz JM, Shostak AM et al (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. *J Parasitol* 83:575–583
- Clayton DH (1990) Mate choice in experimentally parasitized rock doves: Lousy males lose. *Am Zool* 30:251–262
- Clayton DH (1991) Coevolution of avian grooming and ectoparasite avoidance. In: Loye JE, Zuk M (eds) *Bird-parasite interactions: ecology, evolution, and behaviour*. Oxford University Press, Oxford, pp 258–289
- Clayton DH, Walther BA (2001) Influence of host ecology and morphology on the diversity of Neotropical bird lice. *Oikos* 94:455–467
- Clayton DH, Lee PLM, Tompkins DM, Brodie ED III (1999) Reciprocal natural selection on host-parasite phenotypes. *Am Nat* 154:261–270
- Clayton DH, Moyer BR, Bush SE, Jones TG, Gardiner DW, Rhodes BB, Goller F (2005) Adaptive significance of avian beak morphology for ectoparasite control. *Proc R Soc Lond B* 272:811–817
- Clayton DH, Adams RJ, Bush SE (2008) Phthiraptera, the Chewing Lice. In: Atkinson CT, Thomas NJ, Hunter DB (eds) *Parasitic diseases of wild birds*. Wiley, Ames, pp 515–526
- Clayton DH, Bush SE, Johnson KP (2016) *Coevolution of life on hosts: integrating ecology and history*. University of Chicago Press, Chicago
- Cooney CR, Bright JA, Capp EJR, Chira AM, Hughes EC, Moody CJA, Nouri LO, Varley ZK, Thomas GH (2017) Mega-evolutionary dynamics of the adaptive radiation of birds. *Nature* 542:344–347
- Doña J, Proctor H, Serrano D, Johnson KP, Oploo AO, Huguet-Tapia JC, Ascunce MS, Jovani R (2018) Feather mites play a role in cleaning host feathers: new insights from DNA metabarcoding and microscopy. *Mol Ecol*. <https://doi.org/10.1111/mec.14581>
- Freed LA, Cann C, Bodner GR (2008) Explosive increase in ectoparasites in Hawaiian forest birds. *J Parasitol* 94:1009–1021
- Galván I, Aguilera E, Atiénzar F, Barba E, Blanco G, Cantó JL, Cortés V, Frías Ó, Kovács I, Meléndez L, Møller AP, Monrós JS, Pap PL, Piculo R, Senar JC, Serrano D, Tella JL, Vágási CI, Vögeli M, Jovani R (2012) Feather mites (Acari: Astigmata) and body condition of their avian hosts: a large correlative study. *J Avian Biol* 43:001–007
- Grant PR (1986) *Ecology and evolution of Darwin's finches*. Princeton University Press, Princeton

- Grant PR, Grant BR (2014) 40 years of evolution: Darwin's finches on Daphne Major Island. Princeton University Press, Princeton
- Grant PR, Abbott I, Schluter D, Curry RL, Abbott LK (1985) Variation in the size and shape of Darwin's finches. *Biol J Linn Soc* 25:1–39
- Handel CM, Pajot LM, Matsuoka SM, Hemert CV, Terenzi J, Talbot SL, Mulcahy DM, Meteyer CU, Trust KA (2010) Epizootic of beak deformities among wild birds in Alaska: an emerging disease in North America? *Auk* 127:882–898
- Harper DGC (1999) Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Anim Behav* 58:553–562
- Hoi H, Kristofik J, Darolova A, Hoi C (2012) Experimental evidence for costs due to chewing lice in the European bee-eater (*Merops apiaster*). *Parasitology* 139:53–59
- Jovani R, Doña J, MdelM Labrador, Serrano D (2017) Opening the doors of parasitology journals to other symbionts. *Trends Parasitol* 33:578–579
- Kuznetsova A, Brockhoff PB, Haubo R, Christensen B (2016) lmerTest Package: tests in linear mixed effects models. R package version 2.0–30, <https://CRAN.Rproject.org/package=lmerTest>
- Matthews AE, Larking JL, Raybuck DW, Slevin MC, Stoleson SH, Boves TJ (2017) Feather mite abundance varies by symbiotic nature of mite-host relationship does not differ between two ecologically dissimilar warblers. *Ecol Evol*. <https://doi.org/10.1002/ece3.3738>
- Mathysen E (1989) Seasonal variation in bill morphology of nuthatches *Sitta europaea*: dietary adaptations or consequences? *ARDEA* 77:117–125
- Moyer BR, Peterson AT, Clayton DH (2002a) Influence of bill shape on ectoparasite load in Western scrub-jays. *Condor* 104:675–678
- Moyer BR, Drown DM, Clayton DH (2002b) Low humidity reduces ectoparasite pressure: implications for host life history evolution. *Oikos* 97:223–228
- Olsen AM (2017) Feeding ecology is the primary driver of beak shape diversification in waterfowl. *Funct Ecol*. <https://doi.org/10.1111/1365-2435.12890>
- Palma RL, Peck SB (2013) An annotated checklist of parasitic lice (Insecta: Phthiraptera) from the Galapagos Islands. *Zootaxa* 3627:001–087
- Palma RL, Price RD (2010) The species of Myrsidea Waterston (Insecta: Phthiraptera: Menoponidae) from the Galapagos Islands, with descriptions of new taxa. *Tuhinga* 21:135–146
- Poulin R (2007) Evolutionary ecology of parasites, 2nd edn. Princeton University Press, Princeton
- Proctor H, Owens I (2010) Mites and birds: diversity, parasitism and coevolution. *Trends Ecol Evol* 15:358–364
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org>
- Thompson CW, Hillgarth N, Leu M, McClure HE (1997) High parasite load in house finches (*Carpodacus mexicanus*) is correlated with reduced expression of a sexually selected trait. *Am Nat* 149:270–294
- Van Hemert C, Handel CM, O'Hara TM (2012) Evidence of accelerated beak growth associated with avian keratin disorder in black-capped chickadees (*Poecile atricapillus*). *J Wildl Dis* 48:686–694
- Villa SM, Le Bohec C, Koop JAH, Proctor HC, Clayton DH (2013) Diversity of feather mites (Acari: Astigmata) on Darwin's finches. *J Parasitol* 99:756–762
- Weiner J (1994) The beak of the finch. Cambridge University Press, Cambridge