

# Hybridization fluctuates with rainfall in Darwin's tree finches

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Hybridization in natural populations may be an adaptive response to shifting climatic regimes, but understanding this can be limited by the timing of sampling effort and confident identification of hybrids. On the Galapagos Islands, Darwin's finches regularly hybridize; the islands also show extreme annual variation in rainfall, but the effect of annual rainfall on the frequency of finch hybridization is little known. Across a 20-year period on Floreana Island, we compare patterns of hybridization in sympatric Darwin's tree finches ( $N = 425$ ; *Camarhynchus* spp.) and test for an effect of annual rainfall on (1) the frequency of hybrids (*C. pauper* × *C. parvulus*) and (2) the percentage of male hybrid birds produced per year (hybrid recruitment). Annual rainfall correlated with recruitment positively for hybrids, negatively for *C. parvulus* and not at all for *C. pauper*. Furthermore, the percentage of hybrids (range: 12–56%) and *C. parvulus* did not change with sampling year, but the critically endangered *C. pauper* declined. Our findings indicate that hybrid recruitment is recurring and variable according to annual rainfall in *Camarhynchus* Darwin's finches.

ADDITIONAL KEYWORDS: annual rainfall – *Camarhynchus* – climate change – Darwin's finches – Galapagos Islands – hybridization – microsatellites.

## INTRODUCTION

Hybridization in natural populations is increasingly observed as a beneficial evolutionary process, despite examples of deleterious outcomes (Richards & Hobbs, 2015; Gramlich & Hörandl, 2016; Thompson *et al.*, 2018; Chan *et al.*, 2019). For example, there is evidence that the frequency of hybridization is increasing and may have fitness benefits for species threatened by climate change (Mallet *et al.*, 2011; Thomasset *et al.*, 2011; Canestrelli *et al.*, 2017). This increased frequency may be due to novel biotic interactions that occur during climate-mediated range shifts, or as a result of local species' declines (Peters *et al.*, 2019; Zhang *et al.*, 2020), and may be beneficial for increasing adaptive genetic variation in novel environmental conditions (Meier *et al.*, 2017; Pierce *et al.*, 2017; Bay *et al.*, 2019).

Many animals respond to climate change with a shift in geographical range that brings formerly

allopatric populations into sympatric or parapatric contact (Sánchez-Guillén *et al.*, 2013; Slender *et al.*, 2017; Joseph, 2018; Slender *et al.*, 2018a, b). The loss of environmental heterogeneity between populations as the result of range overlap could relax divergent selection, remove ecological barriers to gene flow and increase the probability of introgressive hybridization (Seehausen *et al.*, 2008). For sympatric species (e.g. such as those on islands), abiotic variables may drive changes in niche breadth and/or selection pressures on phenotypes that affect resource availability, and promote hybridization (Grant & Grant, 2014).

High rainfall has been associated with increases in species abundances (Holmgren *et al.*, 2001; Stevens & Watson, 2013) and, in some cases, an increased frequency of hybridization (Gee, 2004). Greater hybridization under high rainfall conditions may be the consequence of increased reproductive activity in general (Marchant *et al.*, 2016; Brooke, 2019), changes in the heterospecific encounter rate under higher community diversity and species densities

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(Willis *et al.*, 2011), or facultative mate choice change when environmental conditions are ephemeral (Pfennig, 2007). Teasing apart the ecological and environmental factors that influence hybridization is often limited by the timing of sampling effort and the confident assignment of hybrids in the absence of genetic data, or is confused by multiple agents of selection that are difficult to measure (Shipham *et al.*, 2019). In addition, quantifying interannual changes in hybridization frequency in long-lived, annually breeding populations is faced with the challenge of multiple cohorts of individuals that are the result of past hybridization events. This can prevent a fine temporal understanding of the environmental factors that may drive interannual hybridization rates (but see Jahner *et al.*, 2012).

Darwin's finches have several features that make them especially useful for the study of hybridization. First, this young lineage formed about 1.5 Mya and the descendant finches frequently hybridize, with evidence from *Geospiza* and *Camarhynchus* on different islands (Grant & Grant, 1996a, 1997, 2014, 2016; Kleindorfer *et al.*, 2014; McKay & Zink, 2015). Second, the Galápagos is known for its oscillating climate and high variation in rainfall patterns (Wiedenfeld & Jiménez-Uzcátegui, 2008) that can influence the survival (Boag & Grant, 1981) and breeding success (Cimadom *et al.*, 2014) of Darwin's finches. Third, adult male finches become increasingly black-bodied (*Geospiza*) or black-headed (*Camarhynchus*) with every year of moult until reaching their final adult plumage at 4–5+ years of age (Grant, 1990; Kleindorfer, 2007; Langton & Kleindorfer, 2019). Therefore, Darwin's finch cohorts can be confidently aged in the field as yearlings up to 3+ years of age, enabling male birth year to be retrospectively calculated.

On Floreana Island, hybridization among Darwin's tree finches (*Camarhynchus* spp.) was suggested to be the result of species collapse (Kleindorfer *et al.*, 2014; Peters *et al.*, 2017) in the face of environmental change, including impacts from the introduced myiasis-causing fly *Philornis downsi* (Kleindorfer & Dudaniec, 2016; Common *et al.*, 2019). In 2005, the large tree finch (*Camarhynchus psittacula*) was considered rare and possibly absent on Floreana Island (Grant *et al.*, 2005), and we could no longer confirm its presence in 2010 (Kleindorfer *et al.*, 2014). Instead, we found evidence for one-way genetic introgression from the extant larger-bodied finches (*C. pauper*) to smaller-bodied finches (*C. parvulus*) (Peters *et al.*, 2017). The resulting hybrid birds were of intermediate body size, their song was indistinguishable from that of the male parental species (*C. parvulus*) (Peters & Kleindorfer, 2018; Kleindorfer *et al.*, 2019), and hybrid males had fewer *P. downsi* parasites in their nest compared with either of the parental species (Peters *et al.*, 2019).

Finally, Kleindorfer *et al.* (2014) found a 73% increase in the percentage of *Camarhynchus* hybrids between 2005 and 2010.

Here, with eight years of sampling data spanning approximately two decades, we investigate the role of annual rainfall in driving hybridization frequency between Darwin's tree finches (*C. pauper* and *C. parvulus*) on Floreana Island. We quantify the percentage and number of hybrid birds captured per sampling year, and we quantify hybrid recruitment per year via the percentage of hybrid male births per year, back-calculated using male age data from plumage coloration. Under conditions of increasing hybridization among *C. pauper* and *C. parvulus* on Floreana Island (Kleindorfer *et al.*, 2014), we test the predictions that (1) the year of sampling will be correlated with the number and percentage of hybrids and not annual rainfall, and (2) if rainfall (a correlate of resource abundance) influences avian productivity and annual recruitment in particular, we expect to find a positive effect of rainfall in all *Camarhynchus* finches (both the parental and the hybrid birds). Finally, (3) if rainfall has hybrid-specific effects on recruitment and survival, we predict to find a positive effect of annual rainfall on the percentage of hybrid birds captured per year and hybrid annual recruitment that differs from each of the *Camarhynchus* parental species.

## MATERIAL AND METHODS

### SPECIES SAMPLING AND STUDY SITE

Our study was conducted in the highlands of Floreana Island, Galápagos Archipelago, during February and in some cases March/April of 1997, 2005, 2006, 2010, 2012, 2013, 2014 and 2016 (eight years of sampling spanning 20 years). The focal tree finch species were small tree finch (*Camarhynchus parvulus*), medium tree finch (*C. pauper*), and the recently discovered hybrid group arising from pairings between *C. pauper* females and *C. parvulus* males (Kleindorfer *et al.*, 2014; Peters *et al.*, 2017), which all occur in sympatry in the highland habitat. Darwin's finches were captured in mist-nets and subsequently banded with a numbered aluminium band and a unique combination of colour bands at the base of Cerro Pajas Volcano (site area 2.4 km<sup>2</sup>; 1°17'43"S, 90°27'23"W) (described in Kleindorfer *et al.*, 2014). In 1997, mist-netting was conducted by P. R. and B. R. Grant opportunistically within the study area and these birds were not colour banded.

### GENOTYPING AND IDENTIFICATION OF HYBRIDS

DNA was extracted and genotyped using nine microsatellite loci designed for Darwin's medium ground finch (*Geospiza fortis*: GF01, GF03, GF04,

GF05, GF06, GF07, GF11, GF12, GF13; [Petren, 1998](#)), with the protocols described by [Kleindorfer \*et al.\* \(2014\)](#) and [Peters \*et al.\* \(2017\)](#). Genotyping was conducted at the same sequencing facility for all years except 1997 ( $N = 41$ ) and 2016 ( $N = 26$ ). Allele size ranges for 1997 data were made consistent and comparable across all datasets using microsatellite scoring protocols developed for the remainder of the dataset. Previous analyses found that none of the loci showed significant linkage disequilibrium or deviation from Hardy–Weinberg equilibrium ([Kleindorfer \*et al.\*, 2014](#); [Peters \*et al.\*, 2017](#)).

To verify morphologically assigned individuals as parental species or hybrids, we used the Bayesian clustering method implemented in STRUCTURE v.2.3.2 ([Pritchard \*et al.\*, 2000](#)). The number of genetic clusters ( $K$ ) was determined using the method of [Evanno \*et al.\* \(2005\)](#) and using the  $\ln K$  method. Due to the high admixture between the *C. parvulus* and hybrid birds resulting from female-driven asymmetrical introgression and the relative genetic isolation of *C. pauper* ([Peters \*et al.\*, 2017](#)), all field-assigned *C. parvulus* and hybrid birds were assigned to population 1 and all *C. pauper* birds were assigned to population 2. For hybrid detection, STRUCTURE was run with  $K = 2$  for 10 iterations with a 100 000 burn-in followed by a run length of 500 000 Markov chain Monte Carlo (MCMC) replications. As performed and evaluated by [Kleindorfer \*et al.\* \(2014\)](#), individuals with assignment probabilities to each cluster  $< 0.75$  were considered of hybrid origin. We calculated mean assignment probabilities and the percentage of assignments to each cluster and of hybrid origin ( $\pm$ SE) as an average across all runs. Observed heterozygosity ( $H_o$ ) and allele richness ( $A_r$ ) were calculated for each species per year in GENALEX v.6.1 ([Peakall & Smouse, 2006](#)).

#### IDENTIFYING BIRTH YEAR

The birth year of Darwin's finch males was calculated based on the proportion of black plumage on the chin or crown (calculated for males sampled in each year except 1997). Male *Camarhynchus* finches have brown plumage as yearlings and increase the proportion of black on the chin and crown (scored B0–B5) ([Kleindorfer, 2007](#)) with each annual moult until attaining a fully black chin and crown at ~6 years old (B5) ([Langton & Kleindorfer, 2019](#)). Because females remain olive grey throughout their lives, their birth year cannot be reliably calculated ([Langton & Kleindorfer, 2019](#)). We retrospectively assigned birth year for males based on their plumage at the time of capture. We only assigned year of birth to males that were first captured between B0 and B3 given that B4 males may sustain B4 plumage for several years

and B5 males sustain B5 plumage for the rest of their lives and minimum longevity has been calculated as 12–15 years ([Langton & Kleindorfer, 2019](#)). We use the short-hand terms 'birth year' and 'number of births' to refer to males assigned to a birth year from their plumage at the time of capture; we do not analyse data on clutch size, fledging success or recruitment more generally. Unequal sex ratios have been associated with extreme weather conditions in Darwin's ground finches (Geospizidae), which tend to result in male-biased sex ratios ([Grant & Grant, 2019](#)). We analysed data for male hybrids only and did not assume equal hybrid frequencies of females because of possible sex-differences in survival (e.g. due to female predation during incubation), and therefore in recruitment.

#### ANNUAL RAINFALL

Rainfall was collected daily in the highlands of Santa Cruz Island by the Charles Darwin Research Station Solanda Rea at Bella Vista (180 m asl) during January 1987 to March 2016, and by Charles Darwin Foundation Dr Heinke Jäger at El Carmen Rolf Seivers (~300 m asl) during April–December 2016. We have previously shown comparable rainfall patterns between the highlands of Santa Cruz and Floreana Islands, with a 7- to 13-mm difference between islands ([Ben-Yosef \*et al.\*, 2017](#)). The islands are ~60 km apart.

#### STATISTICAL ANALYSES

Data were analysed using SPSS Statistics 23.0 (IBM). Data were inspected for assumptions of normality and homogeneity of variance. To examine the effect of annual rainfall and year on the number of birds captured, we used multiple regression analysis. To account for interannual variation in capture effort and avian productivity on our estimates of hybridization frequency, we weighted our models by the number of birds captured per year, and used least squares regression to test the association between rainfall and the number and percentage of birds per genetic cluster (*C. parvulus*, *C. pauper*, hybrid birds).

## RESULTS

#### EFFECTS OF YEAR AND RAINFALL ON HYBRIDIZATION

We had similar capture effort across years, with no significant effects of rainfall or year on the number of birds captured in mist-nets (year:  $r_{\text{part}} = -0.09$ ,  $P = 0.845$ ; rainfall  $r_{\text{part}} = -0.19$ ,  $P = 0.691$ ). Genetic cluster analysis using STRUCTURE identified 180 *C. parvulus* (males = 114, females = 45, unknown = 21), 104 *C. pauper* (males = 64, females = 25, unknown = 15) and 141 hybrid birds (males = 87, females = 49,

unknown = 5) (note: P. R. Grant and B. R. Grant did not sex birds captured in 1997) with an assignment probability cut-off of < 0.75 for hybrid assignment (Supporting Information, Table S1; Fig. S1). The sample size of each parental species and hybrid bird as defined by genetic assignment probabilities is shown in Table 1. The percentage of birds with genetic admixture (i.e. with hybrid ancestry) was 12% in 1997, but varied between 38 and 56% from 2005 to 2016 (Table 1; Fig. S1).

However, the year of study ( $N = 8$ ) was not significantly correlated with the number of hybrids [ $r = 0.33$ ,  $P = 0.429$ , slope coefficient = 0.64, 95% confidence interval (CI) -1.22 to 2.51] or the percentage of hybrids ( $r = 0.50$ ,  $P = 0.208$ , slope coefficient = 1.07, 95% CI -0.79 to 2.92) caught in a given year (Table 1). The patterns were different in the two parental species: in *C. parvulus*, the year of study was not significantly correlated with the number ( $r = -0.04$ ,  $P = 0.925$ , slope coefficient = -0.09, 95% CI -2.31 to 2.13) or percentage ( $r = -0.121$ ,  $P = 0.776$ , slope coefficient = -0.18, 95% CI -1.65 to 1.29) of birds caught in a given year, whereas in the critically endangered *C. pauper*, the year of study was negatively correlated with the percentage of birds caught ( $r = -0.817$ ,  $P = 0.013$ , slope coefficient = -0.89, 95% CI -1.52 to -0.26) but not the number of birds

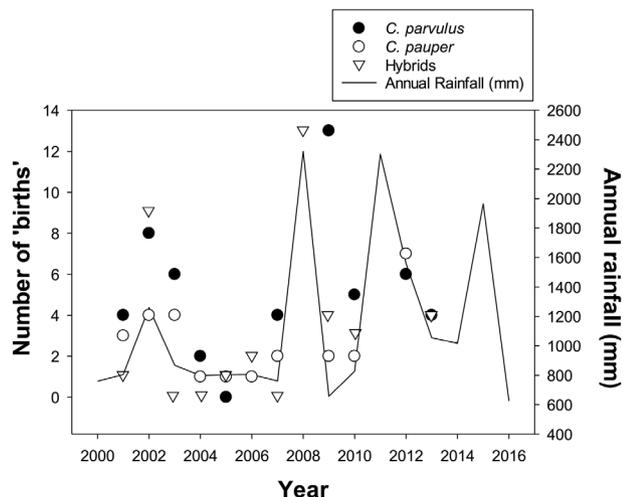
caught ( $r = -0.27$ ,  $P = 0.512$ , slope coefficient = -0.35, 95% CI -1.59 to 0.89) (Table 1).

The sample size for mist-netted males captured as B0–B3, for which birth year could be calculated, was 71 *C. parvulus*, 41 *C. pauper* and 53 hybrid birds. Annual highland rainfall during 1997–2016 ranged from 584 to 2322 mm ( $N = 20$  years) and was positively associated with recruitment (number of births that survived at least one year and were mist-netted in subsequent years) in hybrids ( $N = 53$ ;  $r_{\text{part}} = 0.79$ ,  $P = 0.001$ , slope coefficient = 101.5, 95% CI 49.4 to 153.5) and *C. pauper* ( $N = 41$ ;  $r_{\text{part}} = 0.63$ ,  $P = 0.021$ , slope coefficient = 130.4, 95% CI 23.4 to 237.3) but was negatively associated with recruitment in *C. parvulus* ( $N = 71$ ;  $r_{\text{part}} = -0.61$ ,  $P = 0.026$ , slope coefficient = -77.1, 95% CI -142.8 to -11.4) (Fig. 1). The percentage of recruited males increased significantly with increasing annual rainfall in hybrids ( $r_{\text{part}} = 0.73$ ,  $P = 0.003$ , slope coefficient = 32.2, 95% CI 13.5 to 50.0,  $N = 20$  years), the percentage of *C. parvulus* recruits decreased significantly with annual rainfall ( $r_{\text{part}} = -0.75$ ,  $P = 0.003$ , slope coefficient = -32.2, 95% CI -50.9 to -13.5), and there was no significant effect of annual rainfall on the percentage of recruits in *C. pauper* ( $N = 41$ ;  $r_{\text{part}} = -0.12$ ,  $P = 0.690$ , slope coefficient = -4.8, 95% CI -30.1 to 20.6) (Fig. 2). There was no significant

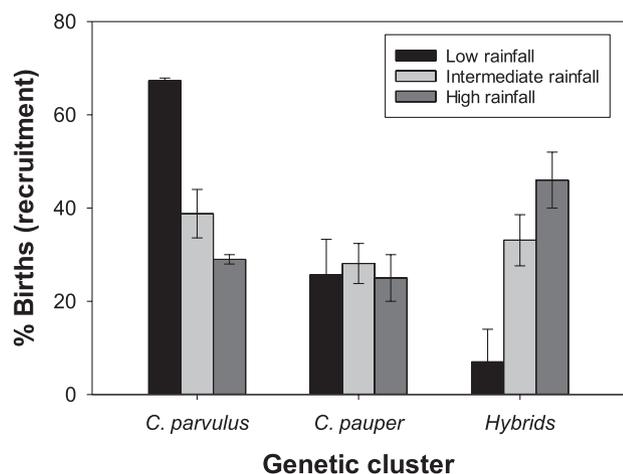
**Table 1.** Number ( $N$ ) of *Camarhynchus* tree finches and percentage (%) of *C. parvulus*, *C. pauper* and hybrid birds (*C. pauper* × *C. parvulus*) mist-netted on Floreana Island from 1997 to 2016

Year	Annual rainfall (mm)	No. of <i>Camarhynchus</i> mist-netted	% <i>C. parvulus</i> mist-netted	% <i>C. pauper</i> mist-netted	% Hybrids mist-netted
1997	2595.2				
1998	2044.7	41	51.2	36.6	12.2
1999	<b>583.9</b>				
2000	<b>760.0</b>				
2001	804.7				
2002	1258.8				
2003	868.0				
2004	800.0				
2005	803.7	88	44.3	27.3	28.4
2006	805.2	9	22.2	22.2	55.6
2007	<b>762.4</b>				
2008	2322.2				
2009	<b>657.0</b>				
2010	827.8	88	36.4	23.9	39.8
2011	2301.6				
2012	1559.4	33	45.5	27.3	27.3
2013	1054.6	83	45.8	18.1	36.1
2014	1015.5	57	38.6	24.6	36.8
2015	1963.8				
2016	<b>626.1</b>	26	42.3	15.4	42.3

Highland annual rainfall (mm) recorded on Santa Cruz Island is shown per year. Low rainfall years (<800 mm) are highlighted in bold and El Niño years with high rainfall (>2000 mm) in italics.



**Figure 1.** The association between annual rainfall (mm) and number of births per year that survived to be mist-netted in subsequent years (measure of recruitment success) in small tree finch (*Camarhynchus parvulus*), medium tree finch (*C. pauper*) and hybrid birds on Floreana Island. Annual rainfall correlated with recruitment positively for hybrids, negatively for *C. parvulus* and not at all for *C. pauper*. Birth year was calculated for male birds captured during mist-netting because age can be assessed from plumage coloration.



**Figure 2.** The percentage (mean  $\pm$  SE) of 'births' per genetic cluster in relation to annual rainfall (low rainfall, intermediate rainfall, high rainfall) on Floreana Island. Low rainfall years had <800 mm rainfall and high rainfall years had >2000 mm rainfall (Table 1). The 'percentage of births' per year, an indirect measure of recruitment, was retrospectively calculated for male birds captured during mist-netting in later years because age can be assessed from plumage coloration.

effect of sampling year on hybrid recruitment (i.e. the percentage of male 'births') for hybrids ( $r = -0.12$ ,  $P = 0.670$ , slope coefficient =  $-0.033$ , 95% CI  $-0.19$  to  $0.13$ ) or the parental species (*C. parvulus*:

$r = -0.160$ ,  $P = 0.570$ ; slope coefficient =  $-0.059$ , 95% CI  $-0.28$  to  $0.16$ ; *C. pauper*:  $r = 0.21$ ,  $P = 0.450$ , slope coefficient =  $0.051$ , 95% CI  $-0.09$  to  $0.19$ ).

## DISCUSSION

Understanding the effects of climatic factors on interannual patterns of hybridization is necessary to uncover the temporal and ecological factors that promote the formation of hybrids. This study reveals marked annual shifts in hybridization in Darwin's *Camarhynchus* tree finches on Floreana Island that were not correlated with year of sampling but were strongly positively correlated with rainfall. Specifically, with data for male birth year spanning a 20-year period, we found that the number and percentage of hybrid males recruited into the population increased with increasing annual rainfall, when finch productivity and food resources are high (Holmgren *et al.*, 2001). This positive relationship between annual rainfall and the percentage of hybrid recruits was not found in the parental species and was independent of the number or percentage of hybrids captured per sampling year (i.e. eight years of data). Considering effects of year, we mist-netted a lower proportion of critically endangered *C. pauper* compared with *C. parvulus* and hybrid birds across the decade (O'Connor *et al.*, 2010), underlining concern for monitoring the fate of *C. pauper* in the face of introduced threats from biotic and abiotic factors. The finding of a positive effect of rainfall on hybrid recruitment lends strong support for climate-associated selection for hybrid birds in years of high rainfall.

Indeed, the outcome of hybridization can be favoured by selection (Kagawa & Takimoto, 2018), as evidenced by its large role in the adaptive radiation of Darwin's finches (Palmer & Kronforst, 2015; Almén *et al.*, 2016), as found for other taxa such as cichlid fish (Meier *et al.*, 2017) and monkeyflowers (Rieseberg, 1997; Stankowski & Streisfeld, 2015). A recently documented evolutionary outcome of hybridization in Darwin's ground finches was speciation *in situ* (Grant & Grant, 2017), where on Daphne Major in 1981, a resident female *Geospiza fortis* paired with an immigrant male *G. conirostris* and produced a lineage of reproductively isolated birds within three generations (Lamichhaney *et al.*, 2018). On Floreana, we have documented the opposite phenomenon of 'species collapse' due to hybridization among *Camarhynchus* species (Kleindorfer *et al.*, 2014; Peters *et al.*, 2017, 2019), and the current study finds that high rainfall may be facilitating this process.

Research increasingly documents the link between hybridization and climate change effects with studies of novel contact zones between previously allopatric

species (Hewitt, 2011; Mallet *et al.*, 2011; Ottenburghs *et al.*, 2015). Introgression or hybridization is often found in these zones, potentially due to the breakdown of reproductive barriers via niche modification or expansion (Wellenreuther *et al.*, 2010; Mallet *et al.*, 2011; Keller *et al.*, 2013; Gómez *et al.*, 2015). Such species 'mixing' can be an important source of new genetic variation that may allow adaptive traits to be introgressed into a population via alleles that increase a species' fitness (Lewontin & Birch, 1966; Arnold, 2004). Indeed, adaptive alleles with high fitness benefit may rapidly spread throughout a hybrid population when reproductive barriers are weak or absent (Brand *et al.*, 2013).

For Darwin's finches, rainfall is tightly linked to resource availability and, in turn, to survival of Darwin's ground finch hybrids (*Geospiza* spp.) (Grant & Grant, 1996a). Apart from the role of climate, anthropogenic selection pressures may be further driving the increased recruitment of *Camarhynchus* hybrids on Floreana. The endemic *Scalesia* forest present on a few of the Galapagos Islands is where *Camarhynchus* finches predominantly nest, and this habitat has been degrading across the archipelago (Rentería *et al.*, 2012; Gardener *et al.*, 2013; Cimadamor *et al.*, 2019), as well as in our study area (our personal observations) due to introduced weeds, pests and agricultural practices. This habitat degradation may reduce the abundance of native seeds and insects, leading to selection for a broader foraging niche breadth through hybridization via an intermediate bill size (Boag & Grant, 1981; Grant & Grant, 1996b; Langton & Kleindorfer, 2019).

A significant natural selection pressure on Darwin's finches is the introduced blood-feeding parasitic fly *Philornis downsi* (Kleindorfer & Dudaniec, 2016; Common *et al.*, 2019), which was first discovered in Darwin's finch nests in 1997 (Fessl *et al.*, 2018). We previously found that nests of hybrid birds possess fewer *P. downsi* than nests of parental species (Peters *et al.*, 2019), suggesting that hybridization confers some resistance to *P. downsi*. It is possible that selection resulting from *P. downsi* on Floreana Island favours greater genetic introgression between parental species (Peters & Kleindorfer, 2015, 2018; Peters *et al.*, 2019), and may help to explain why hybrid birds are much more common on Floreana than on Daphne Major where hybrids occurred in just 2–5% of breeding pairs (Grant & Grant, 2008). Overall, our analysis of increased hybrid recruitment relative to parental species suggests that hybrid offspring are at a selective advantage in years of high rainfall, with interacting factors that are acting in concert to sustain a growing hybrid swarm on Floreana Island, which may be better equipped under anthropogenic pressures.

A notable difference between patterns of hybridization in the tree finches on Floreana and the ground finches on Daphne Major is that on Floreana, there was some admixture (genetic assignment ranging between 0.75 and 0.96) between parental species detected in all individuals we sampled (Supporting Information, Fig. S1; see also Peters *et al.* 2017), whereas on Daphne Major, the majority of *G. fortis* were genetically assigned to *G. fortis* with a probability at or very close to 1.0 (Grant & Grant, 2010). These different patterns across islands are unlikely to be the result of poor marker resolution given that similar microsatellite datasets were used in both cases. Furthermore, preliminary analysis of the Floreana population using ~15 000 single nucleotide polymorphisms indicated some genetic admixture within the parental species (R. Y. Dudaniec *et al.*, unpublished data).

The reasons for such marked differences between the two systems are not clear, but we propose the following. (1) *Camarhynchus pauper* and *C. parvulus* appear to have diverged from each other more recently than *G. fortis* and *G. scandens*, which may have facilitated low rates of hybridization and gene sharing. This is indicated by the phylogeny given by Lamichhaney *et al.* (2015), which shows that *C. pauper* and *C. parvulus* (from Santa Cruz) share their most common recent ancestor whereas relationships for *Geospiza* are variable and often not shared. (2) The documented loss of the large tree finch *C. psittacula* on Floreana may have promoted long-term, ongoing hybridization between 'larger and smaller birds', resulting in a hybrid swarm-like pattern on Floreana, with a gradient of genetic assignment probabilities from larger- to smaller-bodied birds (Kleindorfer *et al.*, 2014; Peters *et al.*, 2017). Finally, (3) selection pressures from habitat fragmentation in the Floreana highlands, which is severe and ongoing, combined with mortality impacts associated with *P. downsi*, may further promote hybridization. Indeed, we found that hybridization did increase after 1997, when *P. downsi* was first discovered in Darwin's finch nests (Fessl *et al.*, 2001).

Genetically distinguishing the occurrence and frequency of hybrids formed by sympatric and recently derived species can be challenging alongside the ecological and genetic processes that define species' boundaries (Gow *et al.*, 2006). Here, we partially overcome this difficulty with a validated hybrid genetic assignment test for the study system (Kleindorfer *et al.*, 2014; Peters *et al.*, 2017) and having the capacity to age males and ascertain hybrid birth rates, and therefore, annual hybrid recruitment. Most avian hybridization studies have been unable to quantify hybrid birth rate due to an inability to assign hybrid age (Jackson *et al.*, 1992; Ebels *et al.*, 2001),

and so potentially provide misleading estimates of hybrid recruitment and the drivers of hybridization. Notably, in the current study we do not assume an equal sex ratio of male to female hybrid birds and make conclusions for male hybrids only, due to the possibility of sex-specific fitness differences (Langton & Kleindorfer, 2019). Furthermore, we were only able to confidently assign male age up to ~4 years based on plumage coloration, and with an estimated longevity of 12–15 years (Langton & Kleindorfer, 2019), we could not assess hybrid recruitment for older males. Therefore, our estimated values for hybrid recruitment provide a relative rather than actual measure for the population.

### CONCLUSION

We found that rainfall shapes evolutionary trajectories in Darwin's finches via its association with hybridization, adding to evidence that rainfall also interacts with finch productivity (Grant *et al.*, 2000), resource availability (De León *et al.*, 2014; Grant & Grant, 1989) and parasite impact (Dudaniec *et al.*, 2007; Kleindorfer & Dudaniec, 2016; Peters *et al.*, 2019). Our findings suggest that the oscillatory dynamics of rainfall on the Galapagos Islands combined with climatic extremes due to El Niño events are likely to have a large impact on the evolutionary trajectory of the *Camarhynchus* population on Floreana Island. The medium tree finch, *C. pauper*, is already listed as Critically Endangered and is under increasing threat from weeds, agricultural impacts and the parasitic fly *P. downsi*, within its native *Scalesia* habitat (O'Connor *et al.*, 2010), which may be a precursor to increased hybridization with *C. parvulus* when conspecifics are rare and finch productivity is high (Kleindorfer *et al.*, 2014, 2019; Peters *et al.*, 2017). In conjunction with the results of previous studies, hybridization in Darwin's tree finches may increase genetic variation for greater adaptive capacity under habitat degradation and the novel biotic interactions and physiological challenges presented under climate change. Further tracking of interannual trends in hybridization, or exploring the functional and adaptive significance of introgressed hybrid alleles for hybrid fitness, will help to reveal the evolutionary benefit of hybridization.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

**Table S1.** Genetic data characteristics (number of alleles 'Na', observed heterozygosity 'Ho' and expected heterozygosity 'He') per microsatellite locus and per genetic cluster: *C. parvulus* ( $N = 180$ ), *C. pauper* ( $N = 104$ ) and the hybrid group ( $N = 141$ ).

**Figure S1.** Individual assignment probabilities ( $N = 425$ ) of *Camarhynchus* birds sampled from Floreana Island. Parental species were assigned based on a 0.75 assignment probability to a cluster.

## SHARED DATA

The microsatellite data and the master file used for analysis are available from the Dryad data repository (doi:[10.5061/dryad.ttdz08ktq](https://doi.org/10.5061/dryad.ttdz08ktq); Dudaniec, 2020).