

Research



**Cite this article:** Beausoleil M-O *et al.* 2019 Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*).

*Proc. R. Soc. B* **286**: 20192290.

<http://dx.doi.org/10.1098/rspb.2019.2290>

Received: 2 October 2019

Accepted: 6 November 2019

**Subject Category:**

Evolution

**Subject Areas:**

evolution, ecology

**Keywords:**

Darwin's finches, ecological speciation, fitness function, selection, Galápagos

**Author for correspondence:**

Marc-Olivier Beausoleil

e-mail: [marc-olivier.beausoleil@mail.mcgill.ca](mailto:marc-olivier.beausoleil@mail.mcgill.ca)

†These authors contributed equally to this article.

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4738814>.

# Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*)

Marc-Olivier Beausoleil<sup>1</sup>, Luke O. Frishkoff<sup>2</sup>, Leithen K. M'Gonigle<sup>3</sup>, Joost A. M. Raeymaekers<sup>4</sup>, Sarah A. Knutie<sup>5</sup>, Luis F. De León<sup>6,7</sup>, Sarah K. Huber<sup>8</sup>, Jaime A. Chaves<sup>9,10</sup>, Dale H. Clayton<sup>11</sup>, Jennifer A. H. Koop<sup>12</sup>, Jeffrey Podos<sup>13</sup>, Diana M. T. Sharpe<sup>6</sup>, Andrew P. Hendry<sup>1,†</sup> and Rowan D. H. Barrett<sup>1,†</sup>

<sup>1</sup>Department of Biology and Redpath Museum, McGill University, 859 Rue Sherbrooke Ouest, Montréal, Québec, Canada H3A 0C4

<sup>2</sup>Department of Biology, University of Texas at Arlington, Arlington, TX, USA

<sup>3</sup>Department of Biological Sciences, Simon Fraser University, Burnaby BC V5A 1S6, Canada

<sup>4</sup>Faculty of Biosciences and Aquaculture, Nord University, Bodø, Norway

<sup>5</sup>Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA

<sup>6</sup>Department of Biology, University of Massachusetts Boston, Boston, MA, USA

<sup>7</sup>Centro de Biodiversidad y Descubrimiento de Drogas, Instituto de Investigaciones Científicas y Servicios de Alta Tecnología, Panama

<sup>8</sup>Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA, USA

<sup>9</sup>Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Quito, Pichincha, Ecuador

<sup>10</sup>Galápagos Science Center, Puerto Baquerizo Moreno, Galápagos, Ecuador

<sup>11</sup>School of Biological Sciences, University of Utah, 257 South 1400 East, Salt Lake City, 84112 UT, USA

<sup>12</sup>Department of Biological Sciences, Northern Illinois University, 1425 W. Lincoln Hwy., DeKalb, IL 60115, USA

<sup>13</sup>Department of Biology, University of Massachusetts, 221 Morrill Science Center, Amherst, MA, USA

**id** M-OB, 0000-0003-3717-3223; LOF, 0000-0001-5738-2140; LKM, 0000-0002-6015-9748; JAMR, 0000-0003-2732-7495; SAK, 0000-0001-6423-9561; LFDL, 0000-0001-9317-420X; JAC, 0000-0003-0679-2603; DHC, 0000-0003-1698-3542; JAHK, 0000-0002-5332-3618; JP, 0000-0002-2546-7999; DMTS, 0000-0002-3986-4725; APH, 0000-0002-4807-6667; RDHB, 0000-0003-3044-2531

Disruptive natural selection within populations exploiting different resources is considered to be a major driver of adaptive radiation and the production of biodiversity. Fitness functions, which describe the relationships between trait variation and fitness, can help to illuminate how this disruptive selection leads to population differentiation. However, a single fitness function represents only a particular selection regime over a single specified time period (often a single season or a year), and therefore might not capture longer-term dynamics. Here, we build a series of annual fitness functions that quantify the relationships between phenotype and apparent survival. These functions are based on a 9-year mark-recapture dataset of over 600 medium ground finches (*Geospiza fortis*) within a population bimodal for beak size. We then relate changes in the shape of these functions to climate variables. We find that disruptive selection between small and large beak morphotypes, as reported previously for 2 years, is present throughout the study period, but that the intensity of this selection varies in association with the harshness of environment. In particular, we find that disruptive selection was strongest when precipitation was high during the dry season of the previous year. Our results shed light on climatic factors associated with disruptive selection in Darwin's finches, and highlight the role of temporally varying fitness functions in modulating the extent of population differentiation.

## 1. Introduction

Adaptive radiation can be envisioned as occurring on phenotypic fitness functions or surfaces that have multiple high-fitness peaks separated by low-fitness valleys [1,2]. While there are numerous studies of natural populations that

infer such peaks and valleys [3], few consider the effects of temporal variation [4]. In birds, for example, the classic representations of fitness functions for Darwin's finches [5], African seed crackers [6] and crossbills [7] do not provide estimates of disruptive selection across multiple years. Yet, temporal variation in fitness functions is very likely, which could facilitate or impede the process of adaptive radiation [8]. For instance, the presence of two discrete fitness peaks in one year might favour divergence; whereas a subsequent disappearance of those peaks might reverse any incipient divergence [9]. Temporal variation in fitness functions might be common given that (i) estimates of directional selection can vary widely through time [10], (ii) many populations show substantial phenotypic changes on short time scales [11] and (iii) several studies have documented speciation reversals, where formerly diverging species merge together again following environmental change [9,12]. However, direct assessments of temporal variation in fitness functions are generally lacking [4].

Temporal variation in fitness functions could be driven by many factors including intrinsic dynamics, such as density or frequency dependence [13], or extrinsic factors, such as biotic or abiotic environmental change [4]. Hinting at the importance of one particular factor, Siepielski *et al.* [10] found in a meta-analysis that 20–40% of temporal variation in directional selection could be explained by variation in precipitation. One context where variation in precipitation is expected to be particularly important is in neotropical environments with wet and dry seasons. These ecosystems can be subject to substantial interannual variation, most dramatically due to El Niño and La Niña events [14]. In such environments, many plants grow and reproduce predominantly during wet seasons; and so limited rainfall within those seasons—as well as severe dry seasons—can lead to extended droughts that limit primary productivity and cause high mortality for primary consumers [15].

Two alternative predictions can be advanced for how the variation in precipitation could influence selection between alternative fitness peaks. On the one hand, harsh conditions strengthen selection against maladapted individuals; hence increasing the strength of disruptive selection between alternative peaks. This prediction infers that niche differentiation between competing species should be greater when resources are more limited [16,17]. On the other hand, harsh conditions could increase competition among common phenotypes; hence lowering the heights of the fitness peaks—perhaps to the point that formerly discrete peaks are no longer separated by valleys. Indeed, many theoretical models [18,19] and some empirical studies [20] show that intense competition can reduce the heights of fitness peaks. To identify how variation in precipitation shapes evolutionary dynamics, we construct temporally variable fitness functions for a natural population of Darwin's finches.

### (a) Study system

The adaptive radiation of Darwin's finches is thought to have been driven largely by the availability of different food types, which is in turn influenced by spatial and temporal variation in climatic conditions [21,22]. Accordingly, beak sizes of finches on different islands match the food types most readily available on those islands [5]. Moreover, closely related species show exaggerated beak size divergence when inhabiting the same island, suggesting that competition enhances divergence through character displacement [5,23]. Thus, different finch species are thought to have evolved

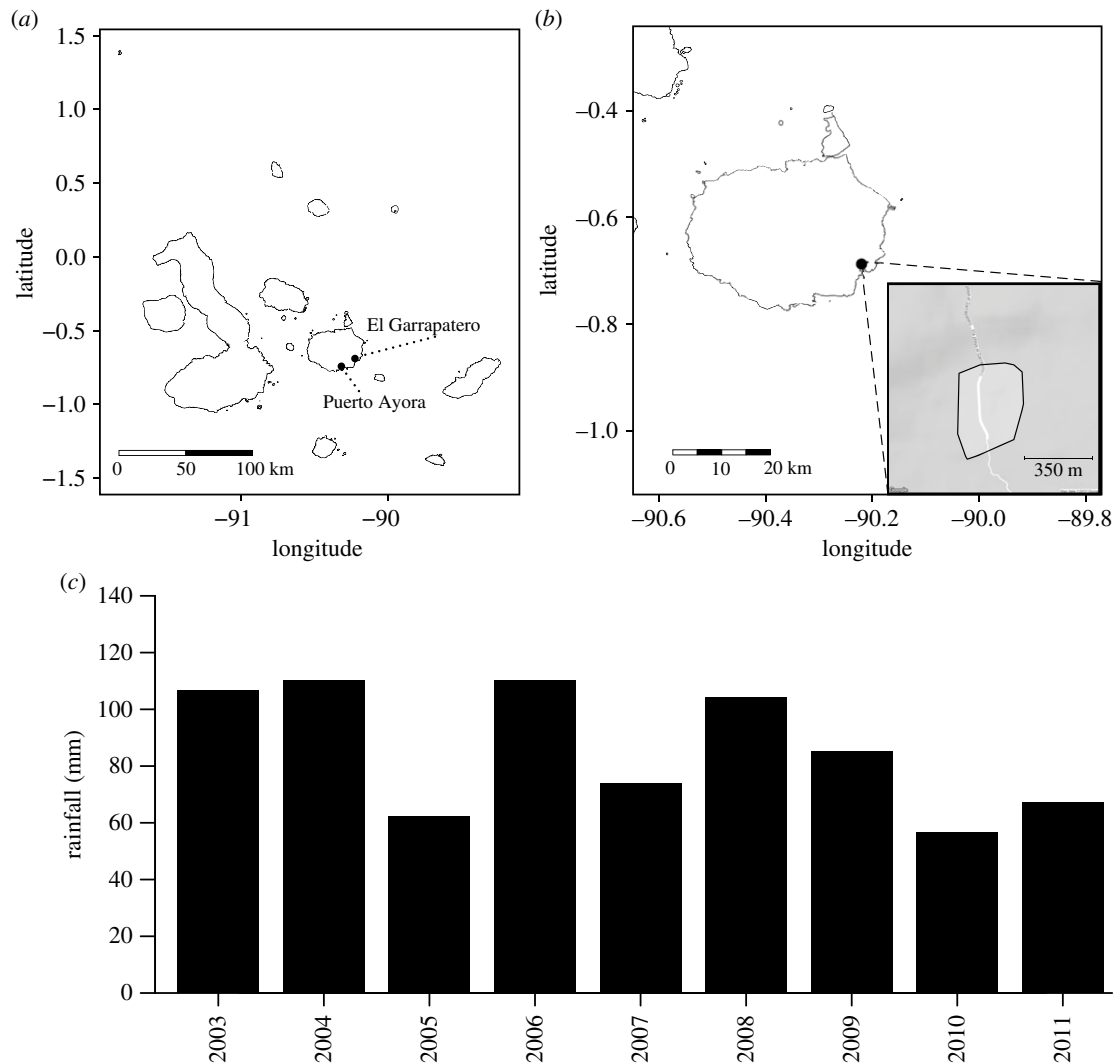
phenotypes that correspond to different fitness peaks separated by fitness valleys that are jointly shaped by local resource distributions and local interspecific competition.

Several observations suggest that Darwin's finches' fitness functions could be highly variable through time, potentially influencing their adaptive radiation. In particular, stochastic climatic events—especially El Niño and La Niña—that shape rainfall in the Galápagos are known to strongly modify plant reproduction, and hence, the abundance and distribution of seeds available for granivorous ground finches [24,25]. In drought years, with little rainfall during the wet season, the production of seeds is very low; whereas in wet years, with high rainfall during the wet season, seeds are usually produced in abundance [26,27]. Additionally, the dry seasons can vary from moderate amounts of rain to severe droughts with severe effects on the seed production. Inter-annual differences in seed production are known to have large effects on ground finches, which—during droughts—show high mortality [28], greater niche differentiation [25] and larger estimated directional coefficients [29,30]. Hence, estimating selection from fitness functions in multiple years could be used to explore how temporal environmental variation shapes disruptive selection and, thus, acts to drive or impede adaptive radiation.

Although natural selection in Darwin's finches surely influences multiple traits [21], much of the focus has been—for the seed-eating ground finches (*Geospiza* spp.)—on beak size and shape. Beak size (usually indexed as a linear combination of length, depth and width measurements) is highly heritable [21,30–33] and is clearly polygenic, including associations with several candidate genes [34,35]. Beak size functions in both food processing and species recognition [33,36], and hence represents a putative magic trait [19] that is under disruptive selection and influences reproductive isolation. Beak size correlates with diet [24], bite force [37], song features [38], mate choice [39] and selection [21]. Importantly, all of these effects and patterns are evident not only between species but also in the earliest stages of diversification within species [40].

Of particular interest are sympatric beak size morphotypes within the medium ground finch (*Geospiza fortis*), observed currently at El Garrapatero and formerly at Academy Bay on Santa Cruz Island [41]. The smaller morph is similar in size to *G. fortis* on many other islands [22], including Daphne Major [23]. The larger morph is not found in many other locations and, in fact, verges on the size of the large ground finch (*Geospiza magnirostris*) on at least some other islands; whereas *G. magnirostris* on Santa Cruz Island are larger still [22]. Overall, the differences between sympatric morphotypes of *G. fortis* on Santa Cruz mirror among-species differences in diet, bite force, song features, mate choice, allelic variants in candidate beak genes [35] and selection [23,36,41,42]. Thus, the two *G. fortis* beak size morphotypes provide an excellent system for studying how selection can shape the early stages of diversification.

We used a 9-year dataset to identify associations among beak size, fitness and climate. Our primary focus was on the putative selective disadvantage of birds with beak sizes that are intermediate between the small and large morphotypes in the well-studied bimodal population of *G. fortis* at El Garrapatero [16,22,23,42]. Our first objective was to identify whether observable disruptive selection between the small and large morphotypes was evident across the 9 years—as was the case in an earlier study [42] of a 2-year period in the same population.



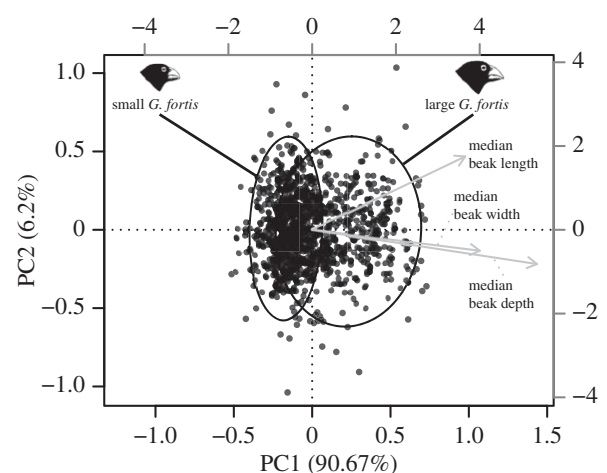
**Figure 1.** Map of the major Galápagos Islands. (a) Puerto Ayora, Santa Cruz Island and El Garrapatero (black dots). (b) Santa Cruz island (black dot is El Garrapatero). Inset: the polygon includes the sampling site at El Garrapatero. Maps from Google Maps (2017; Web Mercator projection, datum WGS84). (c) Climatic data from Puerto Ayora, located 10 km from El Garrapatero [43]. The y-axis corresponds to the cumulative dry season rainfall per year (June through December). Data from OpenStreetMap, [http://osm2.carto.com/viz/feaae54-9e89-11e4-ba3a-0e853d047bba/public\\_map](http://osm2.carto.com/viz/feaae54-9e89-11e4-ba3a-0e853d047bba/public_map) (accessed 8 October 2019).

Confirming that disruptive selection is indeed present, we determined the intensity of disruptive selection across years. Finding that the pattern of selection was variable, we next asked whether temporal variation in rainfall in dry or wet seasons predicted temporal variation in disruptive selection. Finally, we used this analysis to evaluate alternative ideas for how variation in precipitation might influence fitness functions.

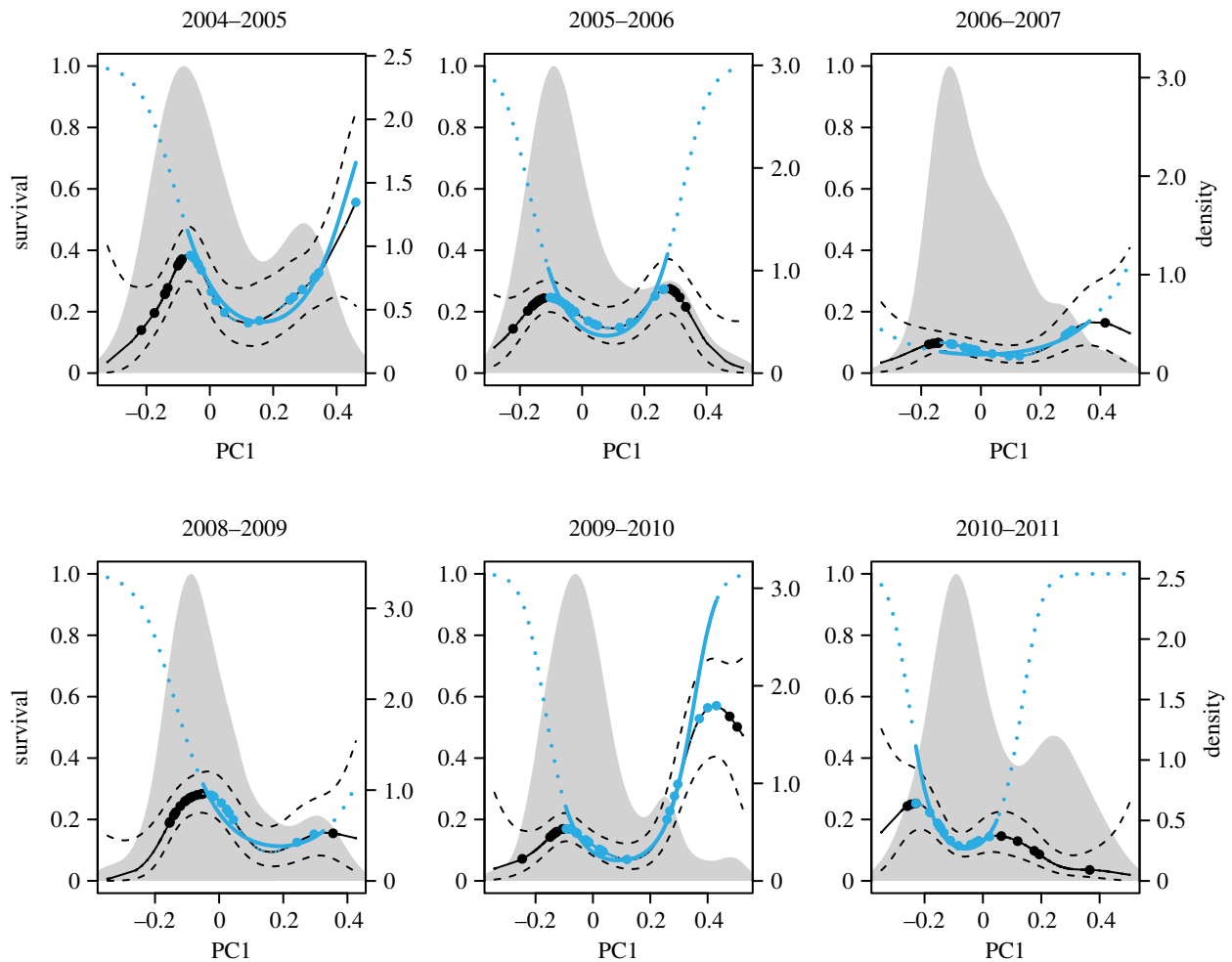
## 2. Material and methods

### (a) Data collection and field study site

We captured individual birds of the medium ground finch (*G. fortis*) annually between 2003 and 2011 at El Garrapatero ( $0^{\circ}41'22.9''$  S,  $90^{\circ}13'19.7''$  W), an arid zone site on Santa Cruz Island in Galápagos, Ecuador (figure 1a,b). Captures took place between January and April, which generally corresponds to the wet season—although the amount of rainfall during this season varied among years (dry season rainfall showing in figure 1c). The birds were captured in mist-nets placed across an area of about 20 hectares (figure 1b), with specific net locations determined by logistics and bird abundance. Captured birds were processed according to standard protocols (see electronic supplementary material; [23,40]). We then measured, with digital callipers (precision  $\pm 0.02$  mm), each bird's beak length, depth and width. Three separate measurements



**Figure 2.** Correlation biplot of the PCA based on beak dimensions (length, width and depth) for *G. fortis* (B). The first axis of variation (PC1) represents variation in beak size (bigger beaks have higher scores) and PC2 represents variation in beak shape (pointer beaks have higher scores). The grey axes (top and right) are scaled for the trait vectors (light grey), whereas the black axes (bottom and left) are scaled for the points. The black ellipses refer to the 95% expectation-maximization algorithm for mixtures of univariate normal [45]. Illustrations of heads of finches are reproduced from [3].



**Figure 3.** Fitness functions for *G. fortis* at El Garrapatero across 6 years of data (larger-beaked birds have  $PC1 \geq 0.2$ ). Solid black lines show the generalized additive model (GAM) results (dashed black line represents 1 s.e.). Solid blue lines (and dotted blue lines, quadratic functions that open upward) show quadratic logistic models (GLM) computed between the fitness function's peaks. Black and blue dots represent individual birds. Solid grey shades (right y-axes) represent the density distribution of phenotypes. The blue dotted line is the GLM function beyond the data used to run the models. (Online version in colour.)

were taken for each dimension on each bird and repeatability from our data, estimated with a type II ANOVA, has a mean of 92.8% (trait repeatability is as follows: width 96.5%, length 89.5% and depth 92.4%) [44]. We further increased precision and accuracy by using the median of the three measurements for subsequent analyses [40].

We first pooled *G. fortis* across all years (electronic supplementary material, table SI) for principal component analysis (PCA) of the three beak traits (length, depth and width; figure 2; electronic supplementary material, figure SA1) based on the covariance matrix because all beak traits were on the same scale (mm) and this ordination technique is consistent with previous work on Darwin's finches [23]. A correlation biplot is represented in figure 2. The first axis of variation (PC1) reflected overall beak size, as in previous work (see electronic supplementary material) [40,42]. Subsequent analyses focused on this axis as our research questions were specifically related to beak size (see Introduction).

We estimated annual dry-season rainfall (total amount of rain in millimetres from June through December; figure 1c) and wet-season rainfall (from January to May) at El Garrapatero using data from rain gauges at the town of Puerto Ayora 11 km to the southwest [43]. Rainfall was our focal climate variable because it is the main factor that affects plant reproduction and, hence, the abundance of food resources for ground finches [23]. Over the time frame of our study, the mean rainfall was 185.4 mm during the wet season (January through May) versus 96.37 mm during the dry season (June through December), with El Niño conditions present in 2004–2005, 2006–2007 and 2009–2010.

### (b) Statistical model to estimate selection coefficients

We calculated apparent survival [46] for individual birds between pairs of years, assuming perfect detection [47]. We did not account for variation in recapture rates [47] because we did not want to overfit our models. Apparent survival between two specific years was specified as a bird being recaptured in the latter or any subsequent year. Thus, some of the birds inferred to have died might simply have remained uncaptured or might have emigrated [48,49]. Although mortality and emigration are different biological processes, emigrating birds are nevertheless permanent losses to the local population and, hence, have the same consequences for selection within a generation. As with most other such studies, we also assume that recapture probability is constant and not affected by the phenotypes in question, and that prior-capture history does not affect survival and recapture probabilities.

To describe the overall primary contributors to variation in fitness (apparent fitness, as above), we first calculated a generalized linear model (GLM) with apparent fitness as a function of the explanatory variables beak size (PC1) and dry season rainfall across all years. The model included both linear and quadratic terms for beak size (PC1), as well as an interaction between these terms and total rainfall in the previous year (electronic supplementary material, tables SII and SIII). To capture flexible shapes in the fitness function, we next characterized the fitness function in each year individually without imposing an *a priori* mode of selection. Hence, we used a generalized additive model (*gam* in the *MGCV* R package), which is a generalized linear

model with the addition of smoothing functions of covariates (using a penalized smoothing of a thin plate regression spline; figure 3; [42,50–52]). The GAM is here intended as a heuristic (we do not focus on  $p$ -values) for inferring whether the fitness function has a convex shape consistent with disruptive selection against intermediate phenotypes. Details about the choice of smoothing parameter of the GAM can be found in the electronic supplementary material, figure SA2 and table SIV.

The fitness functions estimated from splines revealed at least two peaks in each year, consistent with an ongoing process of disruptive selection (figure 3). We next used a custom script (available on GitHub: [https://github.com/beausoleilmo/temporal\\_fitness\\_landscape](https://github.com/beausoleilmo/temporal_fitness_landscape) [53]) to extract the phenotypic values between the two maxima identified in each year. Using these between-peak trait values, we calculated nonlinear selection coefficients in order to estimate statistical significance specifically for the putative disruptive part of the fitness function (as in Hendry *et al.* [42]). Note that these selection estimates potentially include indirect selection caused by correlated traits; especially body size, given its high correlation with beak size (in our data, the Pearson correlation of mass (g) versus PC1 was  $r=0.789$ ). Fortunately, our hypotheses relate to total selection acting on beak size, which includes any indirect selection. The resulting estimates of disruptive selection were obtained via logistic regression (GLM) with a linear and a quadratic term to model both linear and nonlinear selection in each year [49,54]. In these logistic regressions, the subset (between-peak) of PC1 values used was first standardized to a mean of 0 and standard deviation of 1. The selection coefficient was standardized by dividing absolute fitness by mean fitness as in Janzen & Stern [54].

Because the logistic models represent only a subset of the phenotypic distribution, whereas the GAM represents a more comprehensive fitness function across morphospace, we kept only the logistic models that showed similar fits to the functions obtained from the spline models (this criterion led to the exclusion of the logistic coefficient for 2007). A Wald test was used to assess the significance of the raw logistic regression parameters. Given that we expected the quadratic term to be positive (meaning that the curve deflects upward, which is the pattern expected for disruptive selection), we halved the  $p$ -value to get a one-tailed test [42]. Our focal interest is the association between environmental variation and the effect size of the selection coefficient; these coefficients are generally weak and often non-significant for disruptive selection [55]. Quadratic coefficients from the logistic model were then converted to their linear equivalents according to Janzen & Stern [54] and were then doubled [56,57]. To assess logistic model fits, we report the pseudo- $R^2$  (table 1) and the goodness of fit results from the Hosmer–Lemeshow tests [58].

Finally, we related the between-peak quadratic coefficients to climate data, and thereby tested for correlations between environmental variation and disruptive selection between the peaks. Here, we modelled a weighted ( $1/s.e.^2$ ) linear regression between peak quadratic coefficients as predicted by the standardized mean = 0 and standard deviation = 1 across years. We identified three non-exclusive hypotheses regarding which period of rainfall would be most relevant to disruptive selection in a given year. First, wet season rainfall might be most important because low precipitation in the wet season would mean a protracted period of drought when combined with the dry season, thus potentially amplifying the strength of disruptive selection. Second, dry season rainfall might be most important if particularly severe dry seasons exacerbate fitness differences during the most strenuous time of year, again amplifying disruptive selection. Third, dry or wet season rainfall during the previous year might better predict the strength of selection than rainfall during the focal year, as rainfall in the previous year might influence the number of seeds in the seed bank during the subsequent year, as well as the number of birds competing for those seeds [30]. Hence, we performed four separate

**Table 1.** Estimates from the logistic models and Hosmer–Lemeshow goodness-of-fit tests (HL GOF). The estimates correspond to the GLM models in figure 3. The numbers in square brackets are the confidence interval calculated for 1 s.d. The *range data* PC1 column refers to the interval of the PC1 scores between the two fitness peaks. Asterisk indicates significance at  $p < 0.05$ .

year	HL GOF			estimates			deviance			range data PC1	
	$\chi^2$	$p$ -value	intercept	linear term ( $x$ )	$p$ -value	nonlinear term ( $x^2$ )	$p$ -value	model deviance	null deviance		pseudo- $R^2$
2004–2005	8.17	0.42	−1.59 [−2.39; −0.80]	−0.22 [−0.68; 0.23]	<0.05*	0.64 [0.05; 1.24]	0.42	80.39	83.76	0.04	[0.19; 1.95]
2005–2006	3.83	0.87	−1.83 [−2.48; −1.18]	−0.51 [−1.07; 0.04]	<0.05*	0.44 [0.01; 0.87]	0.13	110.15	113.27	0.03	[0.06; 1.33]
2006–2007	16.44	0.04	−2.74 [−3.42; −2.05]	0.07 [−0.53; 0.67]	<0.05*	0.15 [−0.29; 0.58]	0.85	92.82	93.66	0.01	[−0.04; 1.62]
2008–2009	11.81	0.16	−1.83 [−2.82; −0.85]	−0.51 [−1.27; 0.25]	<0.05*	0.29 [−0.44; 1.01]	0.27	50.92	52.16	0.02	[0.25; 1.51]
2009–2010	4.45	0.81	−2.57 [−3.26; −1.88]	−0.42 [−1.00; 0.15]	<0.05*	0.70 [0.28; 1.12]	0.23	100.09	112.29	0.11	[0.10; 1.85]
2010–2011	8.60	0.38	−2.09 [−2.74; −1.45]	−0.23 [−0.66; 0.21]	<0.05*	0.25 [−0.09; 0.59]	0.39	78.13	80.38	0.03	[−0.35; 0.57]

**Table 2.** Yearly between peak quadratic coefficients (GLM) estimated for birds between the two fitness peaks previously estimated by the GAM (figure 3).  $\beta$  and  $\gamma$  are the linear and quadratic standardized between peak quadratic coefficients. The 95% confidence interval (CI) is calculated for a one-tailed test ( $p$ -values were divided in two).  $N_0$  and  $N_1$  are the sample sizes for apparent mortality (0) and apparent survival (1).  $N$  is the total sample size. Asterisk indicates significance at  $p < 0.05$ .

year	$\beta$ average [95% CI]	$\beta$ s.e.	$\beta$ $p$ -value	$\gamma$ average [95% CI]	$\gamma$ s.e.	$\gamma$ $p$ -value	$N_0$	$N_1$	$N^a$
2004–2005	−0.15 [−0.46; 0.16]	0.19	0.21	0.87 [0.07; 1.68]	0.49	0.04*	50	20	70
2005–2006	−0.39 [−0.82; 0.03]	0.26	0.07	0.68 [0.02; 1.34]	0.40	0.05*	88	23	111
2006–2007	0.06 [−0.49; 0.62]	0.34	0.43	0.27 [−0.54; 1.08]	0.49	0.29	172	13	185
2008–2009	−0.41 [−1.02; 0.20]	0.37	0.14	0.46 [−0.70; 1.62]	0.70	0.26	44	11	55
2009–2010	−0.32 [−0.75; 0.11]	0.26	0.12	1.04 [0.42; 1.67]	0.38	0.01*	114	20	134
2010–2011	−0.19 [−0.55; 0.17]	0.22	0.20	0.42 [−0.14; 0.99]	0.34	0.11	84	14	98

<sup>a</sup>Sample size of individuals between the fitness peaks from figure 3 (blue points only).

analyses, relating disruptive selection in a given year to wet season or dry season rainfall in that year (no lag) or in the previous year (1-year lag). We assessed the significance of each regression at  $\alpha = 0.05$ ; however, we emphasize that this climate association analysis is exploratory and hence our primary objective was to generate hypotheses for future formal testing as opposed to performing definitive tests of these hypotheses.

### 3. Results

We captured and measured 1073 *G. fortis* from 2003 to 2011 at El Garrapatero (electronic supplementary material, table S1). The first principal component (PC1) explained 90.67% of the total variation (figure 2) and represented variation in beak size—as in previous analyses [23,59]. A consistent feature of the fitness functions inferred from the splines was the presence of two fitness peaks for *G. fortis* beak size (figure 3; solid black lines)—a pattern strongly implying disruptive selection between the peaks. The fitness maxima generally corresponded to peaks of the phenotypic distributions of the two beak size morphotypes—a finding also consistent with a hypothesis of disruptive selection (figure 3 and tables 2 and 3). However, the strength of disruptive selection between the peaks varied considerably among years (figure 3). We therefore next focused on birds with beak sizes between the two fitness maxima in each year. One year (2007–2008) was excluded owing to a low sample size for these intermediate birds ( $n = 13$ , with only four surviving individuals) that also led to inconsistency between the splines and the logistic estimates. The Hosmer–Lemeshow goodness of fit tests indicated that the GLM model was a good fit for the data in years except 2006–2007 (table 1). The quadratic term from the GLM was strong and significant in three years (2004–2005, 2005–2006 and 2009–2010; tables 1 and 2), but weak and not significant in the other three years. Similar results were obtained based on classic logistic regression approaches (table 2).

We detected an association between disruptive selection and climate (figure 4). A GLM including all years with sufficient data (2005, 2006, 2008, 2009, 2010, 2011) revealed a negative relationship between overall survival and cumulative dry-season rainfall the year before selection occurred ( $z$ -value =  $-1.97$ ,  $p$ -value =  $0.049$ ; electronic supplementary material, table SIII). That is, greater dry season rainfall led to higher overall finch mortality. The weighted linear regression revealed a positive association between quadratic selection coefficients and cumulative rainfall over the previous dry season. Thus, we can infer that greater dry season rainfall

generated stronger disruptive selection between the beak size morphotypes, although the association is weak and only marginally significant (slope =  $0.27$ ,  $R^2 = 0.67$ ,  $p$ -value =  $0.048$ ; figure 4b and table 3). No other periods of rainfall were predictive of disruptive selection (figure 4a,c,d).

### 4. Discussion

High variability in beak size for *G. fortis* on Santa Cruz Island has been repeatedly noted by researchers for nearly a century [22], with recent investigators specifically noting bimodal distributions of beak size measures [41]. A persistent question is how the two beak morphotypes have been maintained without having either fused back together or diverged into distinct species. Our approach here was to use a long-term mark–recapture dataset to investigate how changes in the consistency of disruptive selection might influence the degree of divergence at El Garrapatero, a relatively undisturbed site on Santa Cruz Island. We also explored one possible mechanism for changes in the strength of disruptive selection over time: variation in rainfall. Our analysis revealed temporally variable disruptive selection, with half of the years showing significant disruptive selection between fitness peaks (reduced fitness of birds with intermediate beak size) and half of the years showing non-significant disruptive selection. Additionally, inter-annual variation in selection was partly associated with the extent of rainfall in the previous year's dry season, with increased rainfall leading to greater overall finch mortality and stronger disruptive selection.

#### (a) Temporal variation and its causes

Many studies have reported inter-annual variation in selection, especially for directional selection [60]. By contrast, few have investigated temporal variation in disruptive selection between fitness peaks in natural populations (but see [61]). Variation in this form of selection is expected to be crucial in the early stages of adaptive divergence, ecological speciation and adaptive radiation [3,62]. To gain some additional insight into the importance of disruptive selection between fitness peaks, we calculated the lowest predicted fitness (apparent survival) between peaks in relation to the predicted fitness of birds on the two phenotypic optima. From this estimate, the depth of the fitness valley was greatest between years 2009–2010, where fitness in the valley bottom was 10.0% lower than fitness of the small-morph peak and 50.0% lower than fitness of the large-morph peak, as inferred from the splines in figure 3. This pattern differs most markedly from the fitness estimates

**Table 3.** Coefficients of linear regressions of the amount of rain and between peak quadratic coefficients for the same years as the between peak quadratic coefficients (2004, 2005, 2006, 2008, 2009 and 2010) and with a 1-year lag (2003, 2004, 2005, 2007, 2008 and 2009). The regressions are shown in figure 4. Asterisk indicates significance at  $p < 0.05$ .

	intercept [95% CI]		quadratic coefficients [95% CI]		s.e.	p-value	R <sup>2</sup>	n	degrees of freedom	
	s.e.	p-value	s.e.	p-value						
dry season	same year	0.66 [0.39; 0.93]	0.14	0.01*	0.04 [−0.25; 0.33]	0.15	0.792	0.02	6	4
	1-year lag	0.61 [0.45; 0.77]	0.08	<0.05*	0.27 [0.09; 0.44]	0.09	0.048*	0.67		
wet season	same year	0.64 [0.40; 0.88]	0.12	0.01*	−0.16 [−0.47; 0.15]	0.16	0.370	0.20		
	1-year lag	0.63 [0.43; 0.83]	0.10	<0.05*	0.19 [−0.01; 0.39]	0.10	0.132	0.47		

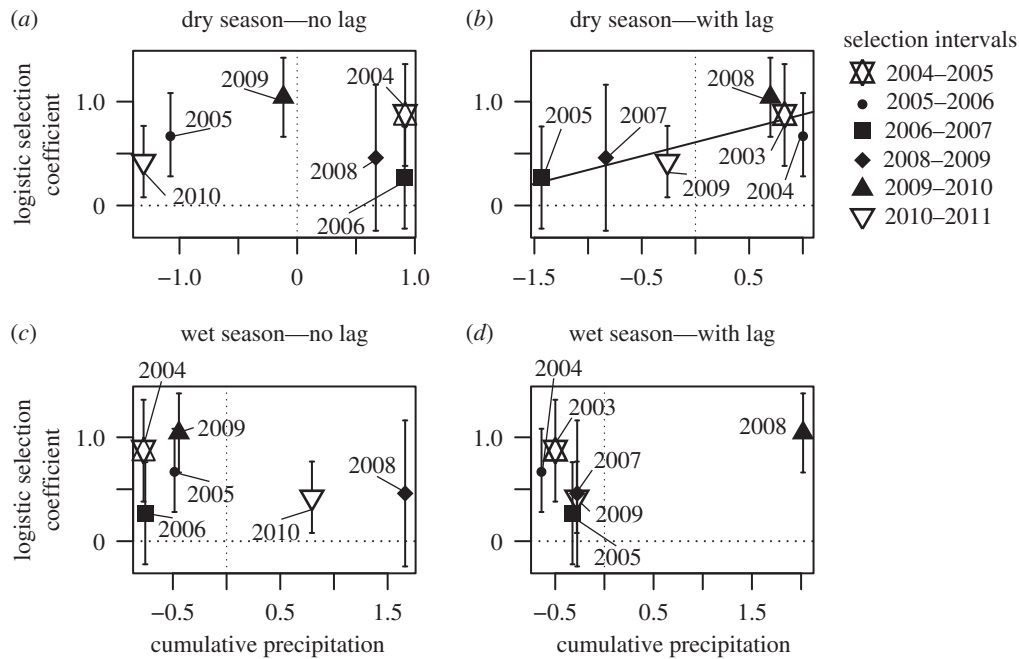
for 2006–2007, where fitness in the valley bottom was 4.4% lower than fitness on the small-morph peak and 11.3% lower than fitness on the large-morph peak. These extreme alternatives for valley depth exceed the range of the few estimates that have been recorded for other sympatric morphotypes (or young species) in natural settings. For instance, comparative values for other systems are 6.6–30.7% for pupfish (fig. 2, durophage-generalist major axis in [63]) and 8.3–44.1% and for juvenile African seedcrackers (fig. 1, lower mandible length (mm) in [6]).

Our exploratory analysis suggests that climate may be a possible driver of the pronounced temporal variation in selection on *G. fortis* at El Garrapatero, with disruptive selection strongest in years with relatively high rainfall during the previous dry season. At first glance, this might seem to contradict previous work showing that selection on Darwin's finches is strongest during drought periods—as documented on Daphne Major [21,30,64]. However, the previous work focused on directional selection in a unimodal population, whereas we focused on disruptive selection in a bimodal population; hence, the different outcomes are not necessarily contradictory. Yet, two aspects of this outcome remain unanswered: (i) why does higher (rather than lower) rainfall generate strong disruptive selection, and (ii) why is this effect delayed by a 1-year lag? For the first question, we hypothesize that drier conditions could increase intraspecific competition among similar phenotypes, and hence more dramatically reduce the survival of common phenotypes at the phenotypic modes [65]. That is, drier conditions could shrink the peaks more than the valleys, hence generating weaker disruptive selection. For the second question, we hypothesize that higher dry season rainfall in a given year will lead to higher reproduction and higher offspring survival in that year, hence making competition more severe during the next year's dry season [30]. These are hypotheses emerging after analysis; yet, they suggest the value of reconsidering several standard assumptions of the factors that favour diversification in this classic system for studying adaptive radiation.

We recognize that our results are particular to the specific range of climate conditions that took place during our study, and thus might not translate to even more extreme conditions. For instance, the maximum dry season rainfall at El Garrapatero during our study was 110.1 mm (2004) and the minimum was 56.6 mm (2010). These levels are far from the extremes observed at other time periods or at other locations. Dry-season rainfall at our study site has previously been as high as 968.0 mm (1983) and as low as 23.8 mm (1980). Similarly, dry season rainfall is estimated to have been near zero during the key periods of strong selection on Daphne Major [21,30,64]. Additional years of sampling that span such extremes will be needed to see if our main result, that disruptive selection is stronger when conditions are less harsh in the previous year, holds (or is perhaps amplified) under even more extreme conditions.

### (b) Consequences of temporal dynamics in disruptive selection

Disruptive selection is one mechanism that can maintain phenotypic and genetic variation [66–68]. Hence, persistent disruptive selection provides a reasonable hypothesis for the maintenance of divergent beak size in Santa Cruz *G. fortis*. Other mechanisms likely contributing to intraspecific variation



**Figure 4.** Between-peak quadratic coefficients as a function of cumulative rainfall. Valley quadratic coefficients obtained from fitness functions of the logistic regression. Rainfall is standardized across years to a mean = 0 and standard deviation = 1. (a,b) The weighted ( $1/s.e.^2$ ) linear relationship between dry season's precipitation and valley quadratic coefficients without a lag (a) and a 1-year lag (b), respectively. Weighted linear relationship between precipitation in the wet season and valley quadratic coefficients without a lag (c) and a 1-year lag (d), respectively. Each point is labelled with the year in which precipitation was calculated from, for a selection interval. The error bars are selection coefficient standard error in table 2. Line with a significant slope is shown.

for finches in general, and perhaps Santa Cruz *G. fortis* in particular, include hybridization between species and spatial variation in selection coupled with gene flow within species [69]. These processes have not been explicitly quantified for our study population but, overall, gene flow among islands is relatively low in relation to the size of resident populations [23,70] and movement within an island is also somewhat restricted. For instance, our long-term data include only one individual out of 8417 birds (0.01%) that moved between our two study sites separated by only 10 km. It has been argued that disruptive selection on a resource polymorphism is a key contributor to speciation and adaptive radiation [71]. It may be that El Garrapatero finches represents an ongoing analogue of this situation that likely drove the adaptive radiation of Darwin's finches in the first place [40].

What might be the influence of temporal variation in strength of disruptive selection? Generally, it has been argued that temporal variation in directional selection will maintain variation within populations [72]. However, the basic logic applied in studies of directional selection might not apply to temporal variation in disruptive selection. Instead, consistently strong disruptive selection would be expected to maintain variation more robustly than would a temporal mix of strong and weak disruptive selection, given that the latter would promote fusion. In the arid coastal zones of the Galápagos, the climate is typically harsh, with prolonged dry seasons resulting in strong selection. In an El Niño year, rain is expected to release disruptive selection in that year but perhaps, as shown here, enhance it in a subsequent year. Hence, temporal variation in selection could be a critical factor in the process of adaptive radiation.

We were interested not just in variation in selection but also in the degree to which it generates and maintains alternative morphs: reasonably discrete large and small beak size morphs with relatively few intermediates. To exemplify the difference in these two inferences, consider a comparison of two populations on Santa Cruz Island: the El Garrapatero

*G. fortis* population that is the focus of this study, and the Academy Bay *G. fortis* population located approximately 10 km to the southwest. Both are highly variable in beak size [41], but only the former is currently bimodal, meaning that it is characterized by a statistically defensible dip in the beak size frequency distribution between large and small beak size morphs [41]. The reason for this difference between sites seems to be that recent human influences at Academy Bay have modified what finches feed on [73]—and thereby reduced or eliminated disruptive selection. Available data do not allow estimates of disruptive selection for Academy Bay, but the present study shows that temporal variation in disruptive selection can be strong even at relatively undisturbed sites. Perhaps this variation, especially the periods of weak disruptive selection, explains the fact that the two morphs do not appear to be progressing towards the status of separate species—even at the relatively undisturbed El Garrapatero site.

## 5. Whither now?

Few studies have quantified temporal variation in disruptive selection in natural populations, and we are not aware of any that have done so for bimodal populations diverging intra-specifically on the same axes as the adaptive radiation of which they are a part. A main finding of our study is that such selection is, in fact, variable in strength—leading to questions about its influence on adaptive radiation. An important next stage seems to be a theoretical one. We need to determine how the mean strength of disruptive selection, as well as the effect of temporal variation in that selection, should shape adaptive radiations. Consistently strong disruptive selection is likely to promote divergence [3], but the influence of temporal variation around that mean is uncertain. A first question might be the extent to which symmetrical variation around that mean should enhance or degrade divergence. In short,



does a given high value contribute more or less to divergence than a correspondingly low value. Other important parameters might be the specific distribution of symmetrical variation around the mean (e.g. does a skewed distribution enhance or degrade divergence) and the nature of autocorrelation (do runs of similar deviations from the mean enhance or degrade divergence). Finally, asymmetry about the mean might be critical: that is, do extreme high levels of disruptive selection have a stronger effect on promoting divergence than similarly extreme low levels of disruptive selection on constraining divergence. Future studies that investigate temporal variation in fitness surfaces of multiple morphotypes or species will help to answer these questions, and thus improve our understanding of the potential for ecological speciation and adaptive radiation.

**Ethics.** Fieldwork was conducted under the University of Massachusetts Amherst Animal Use Protocols for 2003, 2004, 2005, 2006: #23-10-09; 2007, 2008, 2009: #26-10-16; 2010, 2011: #2009-0063; and the University of Utah for 2008 and 2009 IACUC #07-08004. The Galápagos National Park Service permit are as follows: 2003, 2004, 2005, 2006, 2007: #PC-009-98; 2008: #PC-01-08; 2009: #PC-21-07, Ext. 01-09; 2010 and 2011: #PC-58-10.

## References

- Simpson GG. 1944 *Tempo and mode in evolution*. New York, NY: Columbia University Press.
- Arnold SJ, Pfrender ME, Jones AG. 2001 The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* **112**, 9–32. (doi:10.1023/A:1013373907708)
- Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Calsbeek R, Gosden TP, Kuchta SR, Svensson EI. 2012 Fluctuating selection and dynamic adaptive landscapes. In *The adaptive landscape in evolutionary biology* (eds EI Svensson, R Calsbeek), pp. 89–109. Oxford, UK: Oxford University Press.
- Schluter D, Grant PR. 1984 Determinants of morphological patterns in communities of Darwin's finches. *Am. Nat.* **123**, 175–196. (doi:10.1086/284196)
- Smith TB. 1993 Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* **363**, 618–620. (doi:10.1038/363618a0)
- Benkman CW. 2003 Divergent selection drives the adaptive radiation of crossbills. *Evolution* **57**, 1176–1181. (doi:10.1111/j.0014-3820.2003.tb00326.x)
- Gosden TP, Svensson EI. 2008 Spatial and temporal dynamics in a sexual selection mosaic. *Evolution* **62**, 845–856. (doi:10.1111/j.1558-5646.2008.00323.x)
- Seehausen O, Takimoto G, Roy D, Jokela J. 2008 Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Mol. Ecol.* **17**, 30–44. (doi:10.1111/j.1365-294X.2007.03529.x)
- Siepielski AM *et al.* 2017 Precipitation drives global variation in natural selection. *Science* **355**, 959–962. (doi:10.1126/science.aag2773)
- Hendry AP, Farrugia TJ, Kinnison MT. 2008 Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* **17**, 20–29. (doi:10.1111/j.1365-294X.2007.03428.x)
- Kearns AM *et al.* 2018 Genomic evidence of speciation reversal in ravens. *Nat. Commun.* **9**, 1–13. (doi:10.1038/s41467-018-03294-w)
- Svensson E, Sinervo B. 2000 Experimental excursions on adaptive landscapes: density-dependent selection on egg size. *Evolution* **54**, 1396–1403. (doi:10.1554/0014-3820(2000)054[1396:EEOALD]2.0.CO;2)
- Palmer CE, Pyle RL. 1966 The climatological setting of the Galápagos. In *The Galápagos* (ed. RI Bowman), pp. 93–99. Berkeley, CA: University of California Press.
- Grant PR, Grant BR, Keller LF, Petren K. 2000 Effects of El Niño events on Darwin's finch productivity. *Ecology* **81**, 2442–2457. (doi:10.2307/177466)
- Grant PR, Grant BR, Smith JN, Abbott IJ, Abbott LK. 1976 Darwin's finches: population variation and natural selection. *Proc. Natl Acad. Sci. USA* **73**, 257–261. (doi:10.1073/pnas.73.1.257)
- Smith JNM, Grant PR, Grant BR, Abbott IJ, Abbott LK. 1978 Seasonal variation in feeding habits of Darwin's ground finches. *Ecology* **59**, 1137–1150. (doi:10.2307/1938228)
- Dieckmann U, Doebeli M, Metz JAJ, Tautz D. 2004 *Adaptive speciation*. Cambridge, UK: Cambridge University Press.
- Gavrilets S. 2004 *Fitness landscapes and the origin of species*. Princeton, NJ: Princeton University Press.
- Svensson EI, Calsbeek R. 2012 *The adaptive landscape in evolutionary biology*. Oxford, UK: Oxford University Press.
- Grant BR, Grant PR. 1993 Evolution of Darwin's finches caused by a rare climatic event. *Proc. R. Soc. Lond. B* **251**, 111–117. (doi:10.1098/rspb.1993.0016)
- Lack D. 1947 *Darwin's finches*. Cambridge, UK: Cambridge University Press.
- Grant PR. 1999 *Ecology and evolution of Darwin's finches*. Princeton, NJ: Princeton University Press.
- Abbott IJ, Abbott LK, Grant PR. 1977 Comparative ecology of Galápagos ground finches (*Geospiza* Gould): evaluation of the importance of floristic diversity and interspecific competition. *Ecol. Monogr.* **47**, 151–184. (doi:10.2307/1942615)
- De León LF, Podos J, Gardezi T, Herrel A, Hendry AP. 2014 Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists. *J. Evol. Biol.* **27**, 1093–1104. (doi:10.1111/jeb.12383)
- Grant BR, Grant PR. 1981 Exploitation of *Opuntia* cactus by birds on the Galápagos. *Oecologia* **49**, 179–187. (doi:10.1007/BF00349186)
- Grant BR, Grant PR. 1989 *Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos*. Chicago, IL: The University of Chicago Press.
- Grant PR, Grant BR. 2011 Causes of lifetime fitness of Darwin's finches in a fluctuating environment. *Proc. Natl Acad. Sci. USA* **108**, 674–679. (doi:10.1073/pnas.1018080108)
- Grant PR. 1985 Climatic fluctuations on the Galápagos Islands and their influence on Darwin's finches. *Ornithol. Monogr.* **36**, 471–483. (doi:10.2307/40168299)
- Grant PR, Grant BR. 2002 Unpredictable evolution in a 30-year study of Darwin's finches. *Science* **296**, 707–711. (doi:10.1126/science.1070315)
- Boag PT. 1983 The heritability of external morphology in Darwin's ground finches (*Geospiza*)

- on Isla Daphne Major, Galápagos. *Evolution* **37**, 877–894. (doi:10.2307/2408404)
32. Boag PT, Grant PR. 1978 Heritability of external morphology in Darwin's finches. *Nature* **274**, 793–794. (doi:10.1038/274793a0)
33. Grant PR, Grant BR. 1997 Genetics and the origin of bird species. *Proc. Natl Acad. Sci. USA* **94**, 7768–7775. (doi:10.1073/pnas.94.15.7768)
34. Lamichhane S, Han F, Berglund J, Wang C. 2016 A beak size locus in Darwin's finches facilitated character displacement during a drought. *Science* **352**, 470–474. (doi:10.1126/science.aad8786)
35. Chaves JA, Cooper EA, Hendry AP, Podos J, De León LF, Raeymaekers JAM, MacMillan WO, Uy JAC. 2016 Genomic variation at the tips of the adaptive radiation of Darwin's finches. *Mol. Ecol.* **25**, 5282–5295. (doi:10.1111/mec.13743)
36. Huber SK, De León LF, Hendry AP, Bermingham E, Podos J. 2007 Reproductive isolation of sympatric morphs in a population of Darwin's finches. *Proc. R. Soc. B* **274**, 1709–1714. (doi:10.1098/rspb.2007.0224)
37. Herrel A, Podos J, Huber SK, Hendry AP. 2005 Evolution of bite force in Darwin's finches: a key role for head width. *J. Evol. Biol.* **18**, 669–675. (doi:10.1111/j.1420-9101.2004.00857.x)
38. Podos J. 2001 Correlated evolution of morphology and vocal signal structure in Darwin's finches. *Nature* **409**, 185–188. (doi:10.1038/35051570)
39. Ratcliffe LM, Grant PR. 1983 Species recognition in Darwin's finches (*Geospiza*, Gould). II. Geographic-variation in mate preference. *Anim. Behav.* **31**, 1154–1165. (doi:10.1016/S0003-3472(83)80022-0)
40. De León LF, Rolshausen G, Bermingham E, Podos J, Hendry AP. 2012 Individual specialization and the seeds of adaptive radiation in Darwin's finches. *Evol. Ecol. Res.* **14**, 365–380.
41. Hendry AP, Grant PR, Grant BR, Ford HA, Brewer MJ, Podos J. 2006 Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proc. R. Soc. B* **273**, 1887–1894. (doi:10.1098/rspb.2006.3534)
42. Hendry AP, Huber SK, De León LF, Herrel A, Podos J. 2009 Disruptive selection in a bimodal population of Darwin's finches. *Proc. R. Soc. B* **276**, 753–759. (doi:10.1098/rspb.2008.1321)
43. Charles Darwin Foundation. 2019 DataZone: climatology database Puerto Ayora. See <https://www.darwinfoundation.org/en/datazone/climate/puerto-ayora> (accessed 7 June 2016).
44. Sokal RR, Rohlf FJ. 1995 *Biometry*, 3rd edn. New York, NY: WH Freeman and Company.
45. Benaglia T, Chauveau D, Hunter DR, Young D. 2009 MIXTOOLS: an R package for analyzing finite mixture models. *J. Stat. Softw.* **32**, 1–29. (doi:10.18637/jss.v032.i06)
46. Gilroy JJ, Virzi T, Boulton RL, Lockwood JL. 2012 A new approach to the 'apparent survival' problem: estimating true survival rates from mark-recapture studies. *Ecology* **93**, 1509–1516. (doi:10.1890/12-0124.1)
47. Kellner KF, Swihart RK. 2014 Accounting for imperfect detection in ecology: a quantitative review. *PLoS ONE* **9**, 1–8. (doi:10.1371/journal.pone.0111436)
48. Pradel R, Hines JE, Lebreton J.-D, Nichols JD. 1997 Capture-recapture survival models taking account of transients. *Auk* **53**, 60–72. (doi:10.2307/2533097)
49. Kingsolver JG, Smith SG. 1995 Estimating selection on quantitative traits using capture-recapture data. *Evolution* **49**, 384–388. (doi:10.1111/j.1558-5646.1995.tb02252.x)
50. Wood SN. 2017 *Generalized additive models: an introduction with R*, 2nd edn. Boca Raton, FL: Chapman & Hall/CRC Press.
51. R Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org>.
52. Schluter D. 1988 Estimating the form of natural selection on a quantitative trait. *Evolution* **42**, 849–861. (doi:10.1111/j.1558-5646.1988.tb02507.x)
53. Beausoleil M-O *et al.* 2019 Script available on GitHub: Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*). See [https://github.com/beausoleilmo/temporal\\_fitness\\_landscape/blob/master/scripts/Analysis\\_fit\\_land.R](https://github.com/beausoleilmo/temporal_fitness_landscape/blob/master/scripts/Analysis_fit_land.R).
54. Janzen FJ, Stern HS. 1998 Logistic regression for empirical studies of multivariate selection. *Evolution* **52**, 1564–1571. (doi:10.1111/j.1558-5646.1998.tb02237.x)
55. Kingsolver JG, Hoekstra HE, Hoekstra JM, Berrigan D, Vignieri SN, Hill CE, Hoang A, Gilbert P, Beerli P. 2001 The strength of phenotypic selection in natural populations. *Am. Nat.* **157**, 245–261. (doi:10.1086/319193)
56. Stinchcombe JR, Agrawal AF, Hohenlohe PA, Arnold SJ, Blows MW. 2008 Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution* **62**, 2435–2440. (doi:10.1111/j.1558-5646.2008.00449.x)
57. Lande R, Arnold SJ. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226. (doi:10.2307/2408842)
58. Hosmer Jr DW, Lemeshow S, Sturdivant RX. 2013 *Applied logistic regression*. Hoboken, NJ: John Wiley & Sons.
59. Huber SK, Podos J. 2006 Beak morphology and song features covary in a population of Darwin's finches (*Geospiza fortis*). *Biol. J. Linn. Soc.* **88**, 489–498. (doi:10.1111/j.1095-8312.2006.00638.x)
60. Siepielski AM, Dibattista JD, Carlson SM. 2009 It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecol. Lett.* **12**, 1261–1276. (doi:10.1111/j.1461-0248.2009.01381.x)
61. Morrissey MB, Hadfield JD. 2011 Directional selection in temporally replicated studies is remarkably consistent. *Evolution* **66**, 435–442. (doi:10.1111/j.1558-5646.2011.01444.x)
62. Nosil P. 2012 *Ecological speciation*. Oxford, UK: Oxford University Press.
63. Martin CH, Wainwright PC. 2013 Multiple fitness peaks on the adaptive landscape drive adaptive radiation in the wild. *Science* **339**, 208–211. (doi:10.1126/science.1227710)
64. Grant PR, Grant BR. 2014 *40 years of evolution*. Princeton, NJ: Princeton University Press.
65. Bolnick DI. 2004 Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* **58**, 608–618. (doi:10.1111/j.0014-3820.2004.tb01683.x)
66. Rueffler C, Van Dooren TJM, Leimar O, Abrams PA. 2006 Disruptive selection and then what? *Trends Ecol. Evol.* **21**, 238–245. (doi:10.1016/j.tree.2006.03.003)
67. Bolnick DI. 2004 Waiting for sympatric speciation. *Evolution* **58**, 895–899. (doi:10.1111/j.0014-3820.2004.tb00421.x)
68. Dieckmann U, Doebeli M. 1999 On the origin of species by sympatric speciation. *Nature* **400**, 354–357. (doi:10.1038/22521)
69. Vagvolgyi J, Vagvolgyi MW. 1990 Hybridization and evolution in Darwin's finches of the Galápagos Islands. *Accad. Naz. Linc. Atti Conv. Linc.* **85**, 749–772.
70. Lawson LP, John N, Kenneth P. 2019 Darwin's finches: a model of landscape effects on metacommunity dynamics in the Galápagos Archipelago. *Ecography* **42**, 1636–1647. (doi:10.1111/ecog.04511)
71. Skúlason S, Smith TB. 1995 Resource polymorphisms in vertebrates. *Trends Ecol. Evol.* **10**, 366–370. (doi:10.1016/S0169-5347(00)89135-1)
72. Sasaki A, Ellner S. 1997 Quantitative genetic variance maintained by fluctuating selection with overlapping generations: variance components and covariances. *Evolution* **51**, 682–696. (doi:10.1111/j.1558-5646.1997.tb03652.x)
73. De León LF, Sharpe DMT, Gotanda KM, Raeymaekers JAM, Chaves JA, Hendry AP, Podos J. 2018 Urbanization erodes niche segregation in Darwin's finches. *Evol. Appl.* **47**, 151–184. (doi:10.1111/eva.12721)
74. Beausoleil M-O *et al.* 2019 Data from: Temporally varying disruptive selection in the medium ground finch (*Geospiza fortis*). Dryad Digital Repository. (doi:10.5061/dryad.zcrjdfn6q)