Wing shape variation in the medium ground finch (*Geospiza fortis*): an ecomorphological approach

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Wing design in birds is subject to a suite of interacting selective pressures. As different performance traits are favoured in different ecological settings, a tight link is generally expected between variation in wing morphology and variation in ecological parameters. In the present study, we document aspects of variation in wing morphology in the medium ground finch (*Geospiza fortis*) on Isla Santa Cruz in the Galápagos. We compare variation in body size, simple morphometric traits (body mass, last primary length, wing length, wing chord, and wing area) and functional traits (wing loading, aspect ratio and wing pointedness) across years, among populations, and between sexes. Functional traits are found to covary across years with differences in climatic conditions, and to covary among populations with differences in habitat structure. In dry years and arid locations, wing aspect ratios are highest and wings are more pointed, consistent with a need for a low cost of transport. In wet years and cluttered habitats, wing loading is lowest and wings are more rounded, suggesting enhanced capabilities for manoeuvrability. Sexes differ in wing loading, with males having lower wing loadings than females. Superior manoeverability might be favoured in males for efficient territory maintenance. Lastly, in contrast to functional traits, we found little consistent inter-annual or inter-site variation in simple morphometric traits. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **98**, 129–138.

ADDITIONAL KEYWORDS: climate – ecomorphology – habitat use – inter-annual – inter-population – sexual differences.

INTRODUCTION

Because the ability to move is of crucial importance in many different ecological contexts, the locomotor apparatus of many organisms is subject to suites of interacting selective pressures. Adaptations to ecological contexts have been noted in the morphology and function of bird wings, which may be shaped in part by natural or sexual selection. For example, in birds that migrate or that forage over great distances, low energetic costs of flight are desirable (Rayner, 1988). Energy-efficiency and enhanced speed in long-distance flight can be achieved by long and pointed wings (i.e. high aspect ratio), which are more

characteristic of migratory than sedentary birds (Mönkkönen, 1995; Lockwood, Swaddle & Rayner, 1998; Fernández & Lank, 2007). Manoeuvrability, on the other hand, appears to be the determinant performance trait for birds living and foraging in cluttered habitats, or in birds that perform acrobatic aerial mating displays (Rayner, 1988; Hedenström & Møller, 1992). Manoeuvrability is largely determined by a bird's wing loading (i.e. ratio of body weight to wing area) because the minimum turning radius is proportional to body mass and wing area (Norberg, 2002). Also, having short, rounder wings appears to enhance manoeuvrability (Kaboli *et al.*, 2007). In many species, manoevrability and wing loading have been found to correspond with microhabitat use, foraging behaviour, and sexual displays (Hedenström & Møller, 1992; Gamauf, Preleuthner & Winkler, 1998;

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Kaboli *et al.*, 2007). Lastly, speed and acceleration capacity are likely important for take-off (e.g. during predatory attacks). Because high take-off performance is associated with low aspect ratios and with low wing loadings, birds susceptible to high ground-predation rates tend to have less pointed and more rounded wings (Burns & Ydenberg, 2002; Swaddle & Lockwood, 2003).

In the present study, we document aspects of variation in wing morphology in the medium ground finch (*Geospiza fortis*) on Isla Santa Cruz, Galápagos, Ecuador, at three levels. First, we compare the wing morphology in a single population across three successive years. Second, we test whether wing morphology varies among different populations. Finally, we question whether sexes differ with respect to wing morphology.

The environmental conditions on the Galápagos Islands can be considered unpredictable and harsh in many ways. One of the most striking features of the Galápagos environment is the extraordinary annual variation in rainfall. Some years are characterized by extensive, heavy rains, whereas, in other years, hardly any rain falls. During dry years, food supplies are scarce and mortality in Galapagos finches is very high (Grant & Grant, 1989; Grant, 1999). In the present study, we compare wing morphology of one population of *G. fortis* across three consecutive years (2005, 2006, and 2007). The amount of rainfall on Santa Cruz varied greatly during these years, with hardly any rain in 2005, more typical rainfall in 2006, and heavy rains in 2007 (Grant & Grant, 2006; Huber *et al.*, 2007; Hendry *et al.*, 2009). Food supplies were limited in 2005, whereas, in 2007, seeds and caterpillars were very abundant. Food abundance in 2006 was intermediate compared to 2005 and 2007 (A.H. & B.V., pers. observ.). We hypothesize that, during dry years, such as 2005, birds with energetically efficient flight should be favoured. Because efficient flight is associated with high aspect ratios and wing pointedness, birds with more pointed wings should be favoured during dry periods. By contrast, the lush vegetation and the presence of insects during wet years should favour enhanced manoeuvrability and thus favour lower wing loadings and more rounded wings. Notably, interannual variation in wing aspect ratio, wing pointedness, and wing loading may be influenced not only by selection, but also by habitat choice (see below) and by variation in individual birds'condition, especially with regard to body mass, feather growth, and moult.

Ecological variation occurs not only over time, but also across localities. On Santa Cruz Island, there is an approximately three-fold difference in rainfall between coastal and inland higher elevation sites (Grant, 1999). Associated with the local differences in precipitation are distinct vegetation zones. In the present study, we compare the wing morphology of three different populations of *G. fortis* that occur at elevations ranging from sea-level to high altitude (600 m a.s.l.), and in microhabitats ranging from open and dry, to densely vegetated, humid forest. For example, in the cluttered, humid upland forest, medium ground finches can be expected to benefit from enhanced manoeuvrability (Rayner, 1988; Norberg, 2002). We thus hypothesize that birds with high manoeuvrability and low wing loadings will be favoured in upland forest. As demonstrated by the negative correlation between wing loading and elevation among 43 species of hummingbirds (Altshuler & Dudley, 2002), wing loading at the highland site can also be expected to be lower than at the coastal sites. By contrast, dry, open sites with sparse vegetation and food, should favour birds with a low cost of transport, having high aspect ratio and highly pointed wings.

Our analyses also address the question of whether wing morphology and function differs between males and females, due to sexual differences in behaviour and ecology (Burns & Ydenberg, 2002; Fernández & Lank, 2007) or sexual selection on wing shape. As demonstrated in other bird species, males performing acrobatic aerial displays need to be agile and manoeuvrable, and tend to express comparatively small sizes and low wing loadings (Hedenström & Møller, 1992; Székely, Reynolds & Figuerola, 2000; Fernández & Lank, 2007). Whereas male birds constantly patrol their territory and actively chase other (male and female) birds, females do not defend territories and fly mostly in foraging related contexts. Comparison of male versus female wing aspect ratios and wing loadings may provide insight into the balance between manoeuvrability or energetic efficiency in territorial defense.

MATERIAL AND METHODS
FIELDWORK

We conducted fieldwork on the island of Santa Cruz, Galápagos, during the month of February of three consecutive years (2005–07). In 2005, we mist-netted ten individuals ($N_\male = 6$, $N_\female = 4$) at Academy Bay, near the *Iguana* pens at the Charles Darwin Research Station (CDRS), and four individuals ($N_\male = 3$, $N_\female = 1$) in the highlands at Los Gemelos. In 2006, we used mist nets to capture 44 birds ($N_\male = 24$, $N_\female = 20$) at the CDRS. In 2007, we captured 57 birds at the CDRS ($N_\male = 26$, $N_\female = 31$) and 59 birds at El Garrapatero ($N_\male = 32$, $N_\female = 26$) using mist nets. All birds were banded upon capture. In general, recapturing rates were low, but, if the same individual was captured

multiple times, only one set of measurements was used in the analyses. The Los Gemelos site consists of moist forest, dominated by *Scalesia* trees, and has a closed canopy (Grant, 1999). El Garrapatero represents the other extreme as it is a typical arid zone dry forest, with scattered *Bursera* trees, cacti, shrubs and small trees (Grant, 1999). The CDRS location is a more densely vegetated coastal site with more undergrowth and shrubs compared to El Garrapatero.

MEASUREMENTS

We weighed all birds to the nearest 0.1 g on an electronic balance (Scout Pro) and measured tarsus length to the nearest 0.01 mm using digital calipers (Mitutoyo) and last primary length to the nearest 0.1 mm using an aluminum ruler. Last primary length is measured as the distance between the wrist joint and the tip of the longest primary, which corresponds to the traditional museum measurement formerly called (flat) wing chord. For each bird, we took one digital picture (Nikon Coolpix 4500) of its fully extended right wing. For each individual, all measurements were performed on the same picture. A grid was placed in the background to provide a scale. Based on the digital pictures, we subsequently quantified ten additional morphological traits (i.e. wing length, wing chord, wing area, and the length of the first seven primaries). Wing length is defined as the distance between the shoulder joint and the tip of the outstretched wing. Wing chord is defined as the perpendicular distance from the base of the secondaries to the tip of the first secondary (i.e. to the line connecting the shoulder to the tip of the wing). Wing area was quantified by digitizing the outer edge of the wing (Fig. 1). The length of each primary was measured as the distance between the shoulder joint and the tip of the respective primary. We used the factor scores on the first two axes (PC1 and PC2) of a principal component analysis (PCA) in which the lengths of the seven primaries were entered, to obtain an estimate of wing pointedness (Mönkkönen, 1995; see also below). Finally, we calculated aspect ratio and wing loading for each bird based on those morphological measurements. Aspect ratio is defined as the ratio of four times wing length squared to total wing area (i.e. wing area × 2) (Rayner, 1988). Wing loading is defined as body mass divided by total wing area.

We refer to body mass, last primary length, wing length, wing chord and wing area as morphometric traits and to aspect ratio, wing loading and wing pointedness (PC1 and PC2) as functional traits.

STATISTICAL ANALYSIS

Only data for adult birds were included in the statistical analyses. Prior to the analyses all traits were logarithmically ($\log_{10}$) transformed.

We performed a PCA (varimax rotation) on the lengths of the first seven primaries and extracted two components (further referred to as PC1 and PC2) as an estimate of wing pointedness (Mönkkönen, 1995).

To test for annual variation in body size and wing morphology, we compared tarsus length, morphometric traits, and functional traits for the population at the CDRS across the three consecutive years. To test for body size differences, we performed a two-way analysis of variance (ANOVA) with tarsus length as dependent variable and year and sex as factors. Subsequently, we performed a multivariate analysis of covariance (MANCOVA) with all morphometric traits as dependent variables, tarsus length as covariate, and year and sex as factors. Finally, we performed a
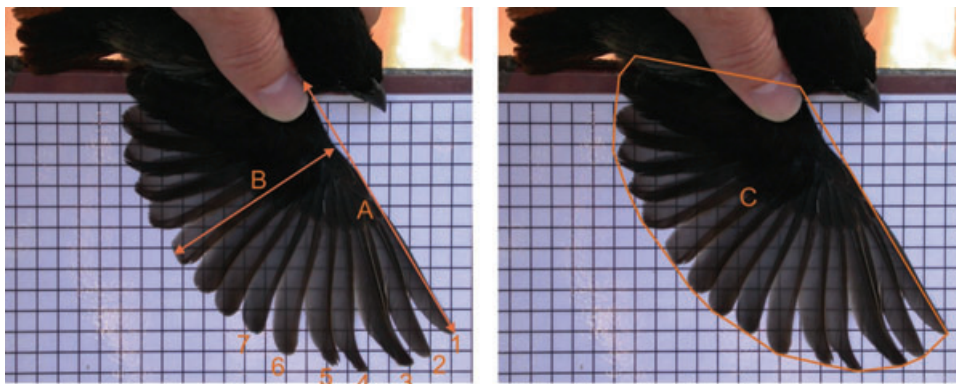

Figure 1. Photograph of an outstretched wing against a scaling grid (one square = 6.3 mm × 6.3 mm). A, wing length or the distance between the shoulder joint and the wing tip. B, wing chord or the perpendicular distance from the base of the secondaries to the tip of the first secondary. C, wing area. The tips of the first seven primaries are numbered from 1 to 7.

MANCOVA with aspect ratio, wing loading and wing pointedness (PC1, PC2) as dependent variables, tarsus length as covariate, and year and sex as factors to test whether the functional traits differ among years and between sexes. Nonsignificant interaction effects were removed from the ultimate model in all cases.

To compare body size and wing morphology among the different populations, we performed analyses similar to those described above. However, because most traits varied significantly among years (see Results), we needed to perform the analyses for each year separately and thus were only able to compare the populations on a two by two basis (i.e. Los Gemelos versus CDRS in 2005; El Garrapatero versus CDRS in 2007).

RESULTS

PCA

The first two components of the PCA explained 97% of the total variation in primary lengths. PC1 was positively correlated with the lengths of primary 1–4, whereas PC2 was positively correlated with the lengths of primary 5–7 (Table 1).

COMPARISON AMONG YEARS

Descriptive statistics for all measurements are presented in tables two and three. A two-way ANOVA with tarsus length as the dependent variable, and with year and sex as factors, did not show a significant year–sex interaction effect ($F_{2,105} = 1.61$,

Table 1. Factor loadings, eigenvalues and percentages of variance explained for the first two axes of the principal component analysis on the lengths of the seven first primaries

Variable	PC1	PC2
Primary 1	**0.886**	0.425
Primary 2	**0.852**	0.500
Primary 3	**0.809**	0.569
Primary 4	**0.778**	0.585
Primary 5	0.648	**0.733**
Primary 6	0.510	**0.846**
Primary 7	0.443	**0.879**
Eigenvalue	3.647	3.122
% Variance explained	52.10	44.60

The first four primaries are positively correlated with PC1; primaries 5–7 are positively correlated with PC2 (shown in bold). The factor scores of PC1 and PC2 are used as an estimate of wing pointedness.

$P = 0.20$). Tarsus length, however, did differ significantly between sexes and among years ($F_{1,107} = 14.93$, $P < 0.0001$ and $F_{2,107} = 11.93$, $P < 0.0001$, respectively). Males had longer tarsi, suggesting they are larger than females, and tarsus length was smallest in 2006 and largest in 2007 (Fig. 2A; Table 2).

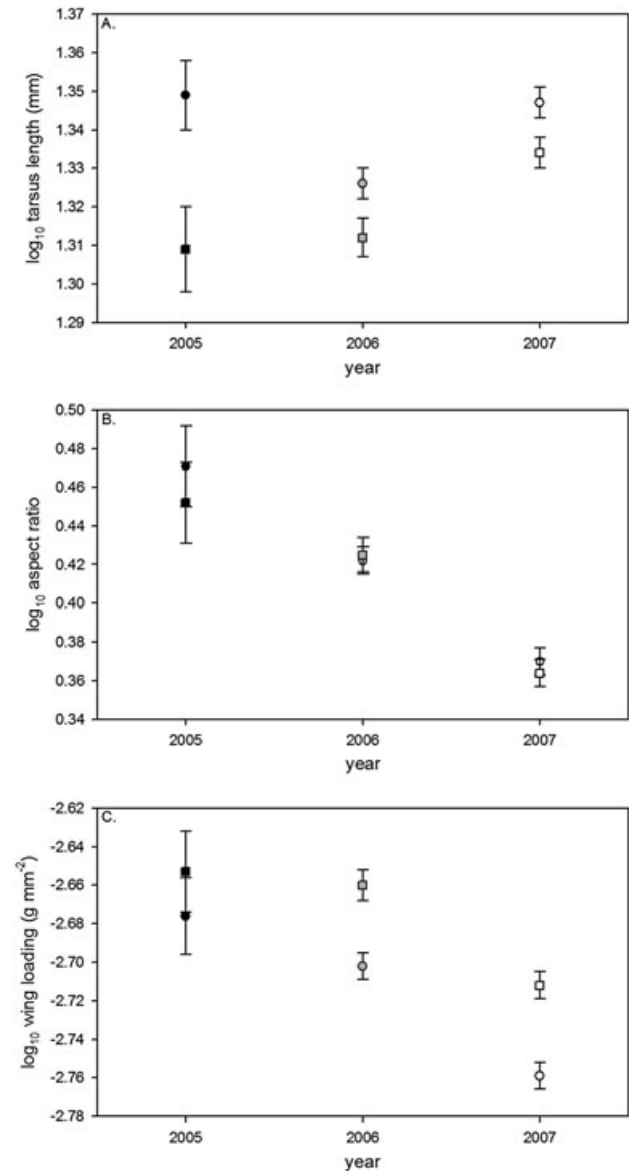In a MANCOVA with all morphometric traits as dependent variables, with tarsus length as covariate

Figure 2. Mean tarsus length (A), aspect ratio (B), and wing loading (C) for male (●) and female (■) *Geospiza fortis* at the Charles Darwin Research Station (Academy Bay, Santa Cruz, Galápagos Islands) over a period of 3 years. Colours refer to the different years (black, 2005; grey, 2006; white, 2007). Error bars represent one standard error. Mean aspect ratio and wing loading are estimated marginal means at a tarsus length of 1.33.

Table 2. Raw data on tarsus length and linear wing traits of the medium ground finch (*Geospiza fortis*) on the island of Santa Cruz

Location	Year	Sex	N_t	Tarsus length (mm)	N_l	Mass (g)	Last primary length (mm)	Wing length (mm)	Wing chord (mm)	Wing area (mm²)
CDRS	2005	1	6	22.37 ± 0.53	3	23.60 ± 1.89	72.50 ± 3.06	90.23 ± 3.61	62.13 ± 1.44	5480.67 ± 189.54
	2005	2	4	20.38 ± 0.53	3	20.87 ± 1.16	66.99 ± 2.76	82.73 ± 2.54	58.07 ± 1.24	4851.67 ± 155.57
	2006	1	24	21.22 ± 0.21	23	23.51 ± 0.55	71.98 ± 0.90	88.47 ± 1.16	61.61 ± 0.72	5954.91 ± 153.88
	2006	2	20	20.52 ± 0.25	18	22.82 ± 0.65	69.39 ± 0.54	84.04 ± 0.91	58.16 ± 0.55	5294.78 ± 77.07
	2007	1	26	22.26 ± 0.24	26	22.20 ± 0.54	71.81 ± 0.69	85.64 ± 0.96	60.99 ± 0.53	6243.19 ± 101.14
	2007	2	31	21.58 ± 0.17	28	22.51 ± 0.44	67.57 ± 0.55	81.68 ± 0.80	58.03 ± 0.50	5770.29 ± 91.69
Gem	2005	1	3	22.07 ± 0.70	2	23.50 ± 2.50	69.90 ± 1.35	88.98 ± 0.88	61.00 ± 0.80	6053.50 ± 162.50
	2005	2	1	20.85	1	20.00	64.10	78.30	54.40	4910.00
Gar	2007	1	32	21.84 ± 0.23	32	21.76 ± 0.52	69.36 ± 0.69	84.42 ± 0.81	57.49 ± 0.48	5587.56 ± 105.64
	2007	2	26	21.61 ± 0.19	25	23.21 ± 0.59	68.24 ± 0.75	82.16 ± 1.09	55.81 ± 0.45	5400.72 ± 92.48

Data are the mean ± SE for both sexes (1, males; 2, females) for three populations (CDRS, Charles Darwin Research Station headquarters; Gem, Los Gemelos; Gar, El Garrapatero), and for three consecutive years at CDRS. Sample sizes are given for measurements of tarsus length (N_t) and the linear traits (N_l).
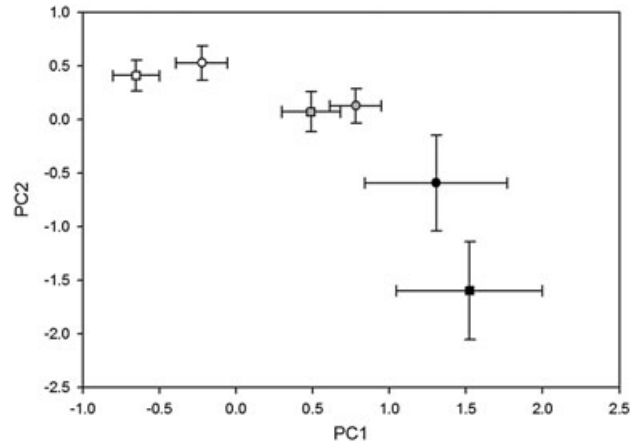

Figure 3. Mean principal component (PC)2 against mean PC1 for male (●) and female (■) *Geospiza fortis* at the Charles Darwin Research Station over a period of 3 years. Colours refer to the different years (black, 2005; grey, 2006; white, 2007). Error bars represent one standard error. Means are estimated marginal means at a tarsus length of 1.33.

and with year and sex as factors, no interaction effects were significant (all $P > 0.22$). Year, sex, and tarsus length all had significant effects on the morphometric traits as a whole ($F_{10,186} = 9.45$, $P < 0.0001$; $F_{5,92} = 11.81$, $P < 0.0001$ and $F_{5,92} = 17.71$, $P < 0.0001$, respectively). Subsequent two-way ANCOVAs, on each morphometric trait separately, revealed that all morphometric traits differed significantly among years (all $P < 0.012$), between the sexes (all $P < 0.023$) and covaried with tarsus length (all $P < 0.0001$). Whereas wing chord and wing length were similar in 2005 and 2006, and smallest in 2007, wing area showed the opposite pattern. Last primary length and body mass were largest in 2005 and smallest in 2007. In addition, males had longer, wider and larger wings than females, but females appeared to be heavier.

A MANCOVA with the four functional traits (i.e. wing loading, aspect ratio, PC1 and PC2, as dependent variables, tarsus length as covariate, and year and sex as factors) did not reveal any significant interaction effect (all $P > 0.28$). By contrast, all main effects were significant (year: $F_{8,192} = 12.17$, $P < 0.0001$; sex: $F_{4,95} = 9.81$, $P < 0.0001$; tarsus length: $F_{4,95} = 13.64$, $P < 0.0001$). Subsequent two-way ANCOVAs revealed that all four functional traits differed among years (all $P < 0.0001$), whereas males and females only differed with regard to wing loading and PC1 (both $P < 0.043$). Wing loading, PC1 and PC2 covaried with tarsus length ($P < 0.003$). Wing loading, aspect ratio, and PC1 were smallest in 2007 and largest in 2005 (Figs 2B, C, 3). PC2 showed the opposite pattern, suggesting that average wing pointed-

Table 3. Raw data on the functional wing traits of the medium ground finch (*Geospiza fortis*) on the island of Santa Cruz

Location	Year	Sex	N_f	Aspect ratio	Wing loading (g mm^{-2})	Score PC1	Score PC2
CDRS	2005	1	3	2.97 ± 0.15	0.0022 ± 0.0001	1.54 ± 0.71	−0.50 ± 0.37
		2	3	2.82 ± 0.10	0.0021 ± 0.0001	1.00 ± 0.21	−1.91 ± 1.28
	2006	1	23	2.65 ± 0.05	0.0020 ± 0.00001	0.72 ± 0.20	0.09 ± 0.18
		2	20	2.66 ± 0.04	0.0021 ± 0.0001	0.18 ± 0.17	−0.15 ± 0.12
	2007	1	26	2.36 ± 0.04	0.0018 ± 0.00001	0.05 ± 0.18	0.69 ± 0.14
		2	28	2.32 ± 0.04	0.0020 ± 0.00001	−0.60 ± 0.16	0.44 ± 0.14
Gem	2005	1	2	2.62 ± 0.02	0.0019 ± 0.0002	0.35 ± 0.04	−0.36 ± 0.52
		2	1	2.50	0.0020	−1.23	−0.19
Gar	2007	1	32	2.57 ± 0.04	0.0020 ± 0.00001	0.08 ± 0.15	−0.35 ± 0.18
		2	25	2.51 ± 0.05	0.0021 ± 0.00001	−0.64 ± 0.18	−0.41 ± 0.23

Data are the mean ± SE for both sexes (1, males; 2, females) for three populations (CDRS, Charles Darwin Research Station headquarters; Gem, Los Gemelos; Gar, El Garrapatero), and for three consecutive years at CDRS. Sample sizes are given (N_f).

ness decreased from 2005 to 2007 (Fig. 3). Also, males had lower wing loadings and longer wings than females (Fig. 2B, C; Table 3).

COMPARISON AMONG LOCATIONS

In neither of the two-way ANOVAs comparing tarsus length between sexes and locations was there a significant sex–location interaction effect (both $P > 0.29$). Tarsus length differed significantly between the sexes in both pairwise locality comparisons (CDRS-Los Gemelos: $F_{1,11} = 7.82$, $P = 0.02$; CDRS-El Garrapatero: $F_{1,112} = 4.41$, $P = 0.04$), but did not differ significantly among locations (both $P > 0.34$; Fig. 4A). Across all localities, males have longer tarsi than females.

The two-way MANCOVAs comparing morphometric traits (tarsus length entered as covariate) of birds captured at the CDRS to those of birds from Los Gemelos and El Garrapatero did not reveal any significant interaction effect (all $P > 0.36$). In the CDRS–Los Gemelos comparison, morphometric traits did not differ between locations ($F_{5,1} = 9.01$, $P = 0.25$) or between sexes ($F_{5,1} = 2.18$, $P = 0.47$) and did not covary with tarsus length ($F_{5,1} = 2.78$, $P = 0.43$). In the CDRS–El Garrapatero comparison, sex, location and tarsus length had a significant effect on the morphometric traits ($F_{5,103} = 14.93$, $P < 0.0001$; $F_{5,103} = 15.98$, $P < 0.0001$ and $F_{5,103} = 24.88$, $P < 0.0001$, respectively). Subsequent ANOVAs on each trait separately showed that all traits differed between the sexes (all $P < 0.012$) and covaried with tarsus length (all $P < 0.0001$). Whereas males had longer and wider wings, females were heavier for a given body size. Wing chord and wing area differed significantly between locations (both $P < 0.0001$), with birds from the CDRS having wider and larger wings than birds from El Garrapatero. All other traits did not differ between locations (all $P > 0.26$).

The two-way MANCOVAs (i.e. both pairwise spatial comparisons) with all four functional traits entered as dependent variables, tarsus length as covariate, and sex and location as factors, did not reveal any significant interaction effects (all $P > 0.44$). In the CDRS–Los Gemelos comparison, none of the main effects was significant (all $P > 0.12$). Subsequent ANCOVAs on each trait seperately, however, revealed a significant difference in aspect ratio, wing loading, and PC1 between locations (all $P < 0.017$). Wing loading also differed between the sexes ($P = 0.03$) and covaried with tarsus length ($P = 0.02$). Aspect ratio, wing loading, and PC1 appeared to be smaller at Los Gemelos than at CDRS (Figs 4B, C, 5) and females appeared to have higher wing loadings than males.

In the CDRS–El Garrapatero comparison, location ($F_{2,104} = 19.97$; $P < 0.0001$), sex ($F_{2, 104} = 12.84$; $P < 0.0001$), and tarsus length ($F_{2,104} = 17.65$; $P < 0.0001$) had signficant effects on the functional traits. Subsequent ANCOVAs on each trait separately revealed a significant difference in aspect ratio, wing loading, and PC2 (all $P < 0.0001$) between locations. Birds at El Garrapatero had greater aspect ratios and wing loadings, and more pointed wings (i.e. PC2 smaller) than birds at CDRS (Figs 4B, C, 5; Table 3). Additionally, sexes differed in wing loading and PC1 (both $P < 0.001$) with males having smaller wing loadings and longer wings (i.e. greater PC1) than females. Tarsus length covaried with wing loading, PC1 and PC2 (all $P < 0.001$) but not with aspect ratio ($P = 0.49$).

DISCUSSION
AMONG YEAR VARIATION

Size, wing loading, wing aspect ratio, and wing pointedness in *G. fortis* individuals from the CDRS differ
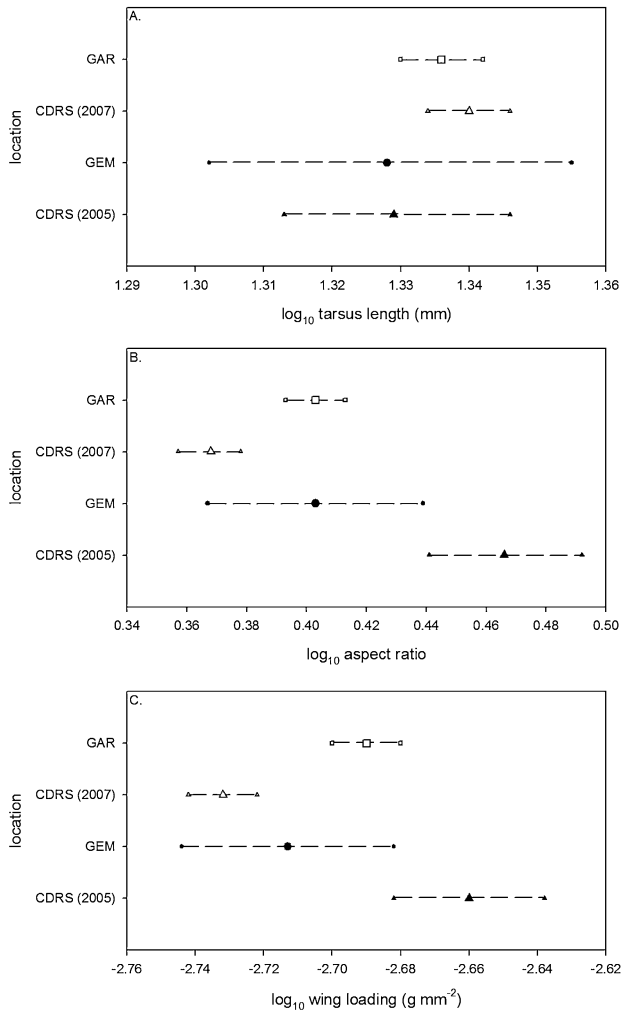
Figure 4. Mean and range (i.e. minimum and maximum) tarsus length (A), aspect ratio (B), and wing loading (C) of birds at CDRS in 2005 and 2007 (▲), at El Garrapatero (Gar; ■) and Los Gemelos (Gem; ●). Colours refer to the different years (black, 2005; white, 2007). El Garrapatero and Los Gemelos are compared separately and relative to the CDRS site in 2007 and 2005, respectively. Mean aspect ratio and wing loading in the Los Gemelos–CDRS comparison are estimated marginal means at a tarsus length of 1.33; in the El Garrapatero–CDRS comparison, means are estimated marginal means at a tarsus length of 1.34.

Figure 5. Mean principal component (PC)2 against mean PC1 of birds at CDRS in 2005 and 2007 (▲), at El Garrapatero (Gar; ■) and Los Gemelos (Gem; ●). Colours refer to the different years (black, 2005; white, 2007). Error bars represent one standard error. Means are estimated marginal means at a tarsus length of 1.33 and 1.34 in the Los Gemelos–CDRS and El Garrapatero–CDRS comparison, respectively. Comparisons are made separately and relatively to the CDRS site because this was the only site from which we gathered data for all 3 years.

significantly among years. Whereas birds were smallest in 2006 and largest in 2007, wing loading, aspect ratio, and wing pointedness were greatest in 2005 and smallest in 2007. Although, all morphomotric traits appear to differ among years too, no clear patterns become apparent. Whereas last primary length and body mass are greatest in 2006, wing chord and length are similar in 2005 and 2006, but smallest in 2007, and area generally increases with year. Because aspect ratio and wing loading are
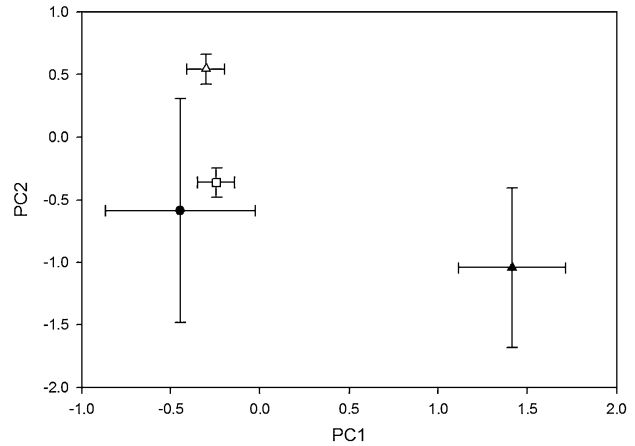
calculated based on different combinations of wing length, wing area, and body mass measurements, this suggests that the relationship among the different morphometric and functional traits is not linear.

During the three consecutive years of study, climatic conditions varied widely. After more than 1 year of virtually no rain, some heavy rains fell in March 2005, marking the end of the most prolonged drought on Santa Cruz in four decades (Grant & Grant, 2006; Hendry *et al.*, 2009). More typical rainfall prevailed in 2006 (Huber *et al.*, 2007), and 2007 was a very wet year, in which vegetation was lush and food abundant (A.H. & B.V., pers. observ.). The variation in precipitation across the 3 years of study appears to be reflected to some extent in the annual variation in wing morphology. Because of the drought in 2004 and the first 2 months of 2005, food supplies to finches were extremely scarce. It can thus be expected that birds needed to forage over greater distances to meet their nutritional requirements, and would thus benefit from energy-efficient flight. A low cost of transport appears to be associated with high aspect ratios and more pointed wings (Rayner, 1988; Norberg, 2002), which may help to explain why birds captured in the first year of study had comparatively more pointed wings.

Wing loading is predicted to be linked to manoeuvrability and birds with low wing loadings and rounder wings supposedly show greater manoeu-

vrability (Norberg, 1979, 2002; Brewer & Hertel, 2007; Fernández & Lank, 2007; Kaboli *et al.*, 2007). In wet periods in the Galapagos, vegetation tends to be lush and manoeuvrability for foraging efficiently in and between blooming trees and bushes may be advantageous. Indeed, wing loading was lowest for our 2007 sample. Manoeuvrability may also be favoured during wet years because of the presence of aerial prey (insects). Because food tends not to be limited in wetter years, animals could presumably sustain this energetically more expensive type of flight. Our data thus suggest, albeit in only a preliminary manner, that wing morphology and function may respond to changing ecological circumstances, alternatively emphasizing manoevrability and flight efficiency. Regardless, shifting values of wing loading, aspect ratio, and wing pointedness may arise from the combined effects of selection, active habitat choice (with birds choosing their most appropriate habitats), changing body masses, and variable patterns of feather growth and usage, which are influenced by condition, metabolic reserves, and nutrient availability, especially during moult.

The interpretation of the among-year variation in size (i.e. tarsus length) is less straightforward. In addition, year effects are different in males and females. Whereas female body size increases from 2005 to 2007, male birds captured in 2006 are of smaller body size than those captured in 2005 and 2007. It has been demonstrated previously that body size in *G. fortis* is under strong directional selection, favouring large birds during droughts because they are the only ones capable of cracking large, hard seeds (Grant, 1999; Grant & Grant, 2002). Selection, however, appears to act in the opposite direction in some dry years and small birds may survive better than large ones as they need less energy to sustain themselves (Grant, 1999). Our results, however, corroborate neither of these findings in male *G. fortis* because male body size is largest and similar in the driest and wettest year. The among year variation in female body size, however, appears to corroborate the hypothesis that selection is acting on small body size in dry years. However, because our sample sizes were low, especially in the extremely dry year (i.e. 2005), these results should be interpreted cautiously. Moreover, one might not necessarily expect responses to selection to be manifest within the space of single years, especially during droughts when breeding output is generally minimal.

AMONG LOCATION VARIATION

The results obtained in the present study demonstrate that aspect ratio and wing loading differ between birds captured at the three different sites.

PC1 differs significantly in the Los Gemelos–CDRS comparison, with birds at the first site having shorter wings, whereas PC2 differs significantly in the CDRS–El Garrapatero comparison, suggesting that birds captured at El Garrapatero had more pointed wings. As for the morphometric traits, few differed significantly among locations; only in the CDRS –El Garrapatero comparison, two out of the five morphometric traits differed significantly. Body size did not differ among the three sites.

Relative to the birds at the CDRS, birds at Los Gemelos had lower aspect ratios and wing loading, whereas birds at El Garrapatero had higher aspect ratios and wing loading, and more pointed wings. Los Gemelos is located at high altitude (around 600 m a.s.l.) and consists of a humid and dense *Scalesia* forest with closed canopy (Grant, 1999). For flying animals that live in cluttered habitats (Norberg, 1994, 2002; Gamauf *et al.*, 1998), manoeuvrability should be favoured. In addition, the elevational variation, although relatively small, may contribute to the variation in wing loading. For example, in hummingbirds, spanning an elevation gradient from 400–4300 m a.s.l., it has been shown that a low wing loading is advantageous in low-density air and that wing loading correlates inversely with elevation (Altshuler & Dudley, 2002, 2003). These observations are consistent with our observation that finches at Los Gemelos have the lowest wing loadings. The habitat at El Garrapatero is comparatively open and birds occurring at this site likely do not need to be as manoeuvrable, but rather may benefit from being relatively fast, consistent with their high wing loadings (Rayner, 1988; Norberg, 2002). The CDRS site can be regarded as intermediate with respect to habitat type. As expected, *G. fortis* occurring here are also intermediate with respect to wing loading.

As is the case with the yearly variation, among location variation in aspect ratio appears to be associated with differences in climatic conditions at the different sites. El Garrapatero is a typical arid zone with dry forest, with limited food supplies (A.H. & B.V., pers. observ.). Because birds occurring at this site may need to forage over greater distances to meet their daily nutritional requirements and because food is scarce, the energetic cost of flight may provide an important selective pressure and lead to high aspect ratio wings and more pointed wings (Rayner, 1988; Mönkkönen, 1995; Tellería & Carbonell, 1999; Norberg, 2002; Swaddle & Lockwood, 2003). Indeed, birds at El Garrapatero are sometimes observed flying relatively large distances (up to 0.5 km) towards possible coastal feeding sites (A.G. & J.P., pers. observ.). Food appears to be more abundant, however, in the moist and humid forest at Los Gemelos, relaxing selection for low energy flight and

the need for high aspect ratio wings. The fact that the aspect ratio and wing pointedness of birds at the CDRS is intermediate is not surprising because this site can be regarded as intermediate with respect to precipitation and food abundance (A.H. & B.V., pers. observ.).

SEXUAL DIFFERENCES

None of the year–sex interaction effects were significant when comparing birds at CDRS over a 3-year period, but tarsus length, all morphometric traits (i.e. body mass, last primary length, wing length, wing chord, and wing area), and wing loading and PC1 differed significantly between the sexes. Males are larger, have relatively longer, wider and larger wings, and lower wing loadings than females. Females are heavier than males. In addition, sexual differences appear to be similar at the different sites because the sex by location interaction effect was nonsignificant in all analyses. The larger body size in male *G. fortis* in the present study is in agreement with earlier reports that males are on average larger than females (Grant, 1999). Rather than resource partitioning by the sexes, sexual selection has been invoked to explain the sexual size dimorphism in *G. fortis* (Grant, 1999). Whereas in females, small body size appears to be selected for as small females breed earlier, larger males are preferred by females when the population sex ratio becomes male-biased during periods of drought (Grant, 1999).

In many bird species, sexual differences in body mass, wing span, area, and loading have been explained by sexual differences in ecology and/or behaviour (Burns & Ydenberg, 2002; Fernández & Lank, 2007). *Geospiza fortis* males actively chase other birds away from their territory. Although it is currently unclear which component of the flight is important during such chases, it is likely that the smaller wing loadings of males may make them comparatively manoeuvrable, although at the possible cost of flight efficiency and speed. Unlike wing loading, aspect ratio does not differ between males and females. This may not be surprising because both males and females need to fly similar distances when foraging (Grant, 1999). Thus, similar energetic costs of flight can be expected, resulting in similar aspect ratios.

DIFFERENTIAL EFFECT ON MORPHOMETRIC AND FUNCTIONAL TRAITS

When comparing results of our analyses on morphometric traits and functional traits, we find that the latter differ more among years and locations than the former. In addition, differences in wing loading, aspect ratio, and wing pointedness are associated with the environmental (i.e. climate and habitat) variation, and these ecomorphological associations are consistent with expected performance requirements under different ecological conditions. The among-year differences with respect to the morphometric traits, by contrast, cannot be interpreted unambiguously in light of environmental variation. The results obtained in the present study thus suggest that the functional traits can be regarded as putatively adaptive, whereas simple, morphometric traits do not appear to be selected for in either context. These findings illustrate the importance of investigating functionally relevant traits when studying variation within and across species.

CONCLUSIONS

Darwin's finches have served as a textbook example of an adaptive radiation because of the close association between the dietary variation and the variation in beak morphology. A plethora of studies exist demonstrating how beak morphology may vary across years, within and among populations, and among species (Grant *et al.*, 1976; Grant, 1999; Schluter, 2000; Grant & Grant, 2002, 2006; Hendry *et al.*, 2006). The results obtained in the present study clearly indicate that finches show a considerable amount of year to year and among-population variation in wing shape. In addition, among-year and among-location variation in wing morphology in *G. fortis* on Santa Cruz may be explained by variation in climatic conditions (i.e. amount of precipitation) and habitat use. The interpretation of body size differences, by contrast, appear to be less straight-forward. Sexual differences in body size and wing morphology are likely to be related to sexual differences in reproductive pressures, behaviour, and/or ecology. Lastly, the results obtained in the present study suggest that the functionality of traits appears to be of prime importance in explaining variation in wing morphology in *G. fortis*. However, we do not imply that the observed differences in wing morphology are solely the result of (genetic) adaptation to local conditions *per se*. The apparent correlation between wing morphology and environmental traits may also be attributed to non-inherited factors, such as body condition (note, however, that relative body mass did not differ among years and locations), molting, and feather condition, which are also known to vary with food availability. Studies over additional years and comparisons among additional localities would be needed to distinguish among these potential contributing factors. However, despite our uncertainty in pinpointing potential proximate causes for the observed differences in wing shape, the consequences of the observed differences in wing morphology on functional traits and the functional capacity of the birds remains.

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