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MORPHOLOGICAL HERITABILITY IN A HYBRID BUNTING COMPLEX: *NEOSPIZA* AT INACCESSIBLE ISLAND

PETER G. RYAN¹

Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa

Abstract. Juvenile *Nesospiza* buntings measured 7–11 weeks after hatching were compared with the sizes of their parents to estimate the heritability (h^2) of six external morphological characters. There was no evidence of size selection before juveniles were seven weeks old, but some additional growth in bill size probably occurred after this age. All characters had significant heritabilities among Tristan Buntings (*N. acunhae*; $h^2 = 0.66$ – 0.95) and hybrids with Wilkins' Buntings (*N. wilkinsi*; $h^2 = 0.62$ – 0.93). Positive heritabilities also were found within color morphs of the Tristan Bunting, although not all regressions were significant. Hybrid offspring generally were intermediate in size between their parents' phenotypes, but one hybrid pair had an unusually small offspring, possibly the result of an extra-pair fertilization. Differences between h^2 estimates from sib-sib and parent-offspring regressions suggest that environmental factors contribute to morphological variability, but the large heritable component confirms the potential for rapid morphological evolution among the small *Nesospiza* populations. Calculation of the relative importance of genetic and environmental effects requires controlled breeding experiments, but cross-fostering between broods in the field should not be performed, to avoid disrupting the natural population structure.

Key words: color morphs, heritability, hybrids, islands, morphology, *Nesospiza* buntings, *Tristan da Cunha*.

Heredabilidad Morfológica en un Complejo Híbrido: *Nesospiza* en Isla Inaccessible

Resumen. Las dimensiones de juveniles de *Nesospiza* medidos 7–11 semanas después de eclosionar fueron comparadas con las de sus padres para estimar la heredabilidad (h^2) de seis caracteres morfológicos externos. No hubo evidencia de selección por tamaño antes de que los juveniles tuvieran siete semanas de edad, pero probablemente ocurrió un crecimiento adicional en el tamaño del pico luego de esta edad. Todos los caracteres tuvieron heredabilidades significativas entre *N. acunhae* ($h^2 = 0.66$ – 0.95) y entre híbridos con *N. wilkinsi* ($h^2 = 0.62$ – 0.93). También se encontraron heredabilidades positivas dentro de morfos de color de *N. acunhae*, aunque no todas las regresiones fueron significativas. Las crías híbridas generalmente tuvieron un tamaño intermedio entre el fenotipo de los padres, pero una pareja híbrida tuvo crías inusualmente pequeñas, posiblemente como resultado de una fertilización extra-pareja. Diferencias entre los estimativos de h^2 calculados mediante regresiones hermano-hermano y padres-crías sugieren que factores ambientales contribuyen a la variabilidad morfológica, pero el fuerte componente heredable confirma el potencial para evolución morfológica rápida entre las pequeñas poblaciones de *Nesospiza*. Los cálculos de la importancia relativa de factores genéticos y ambientales requieren experimentos con apareamientos controlados. Sin embargo, para evitar perturbar la estructura poblacional natural no deberían realizarse trasplantes de crías entre nidadas en el campo.

INTRODUCTION

Morphological variation among bird populations typically is assumed to be under genetic control,

but in at least some cases environmental factors are more important (James 1983). Given that the magnitude of an adaptive response is a function of the selection pressure and heritability (Falconer 1981), estimation of morphological heritability is essential before invoking evolutionary processes to explain morphological differences

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¹ E-mail: pryan@botzoo.uct.ac.za

among populations. Formally, the heritability of a trait (h^2) is the proportion of phenotypic variance (V_p) attributable to additive genetic variance (V_A , where $h^2 = V_A/V_p$). Assuming that selection acts solely on the trait in question, the evolutionary response (R) is the product of selection pressure (S) and heritability: $R = h^2S$ (Falconer 1981, Lynch and Walsh 1998).

I studied *Nesospiza* buntings at Inaccessible Island, one of three main islands in the Tristan da Cunha archipelago, central South Atlantic Ocean. As with the more acclaimed Darwin's finches of the Galápagos (Lack 1947, Grant 1986), *Nesospiza* are one of the few examples of an emberizine adaptive radiation at an oceanic archipelago (Abbott 1978). The radiation among *Nesospiza* has been limited to two main forms: the abundant, small-billed Tristan Bunting (*N. acunhae*) and the scarce, large-billed Wilkins' Bunting (*N. wilkinsi*). At Inaccessible Island, there are two color morphs of Tristan Bunting as well as hybrids between Wilkins' and Tristan Buntings (Ryan et al. 1994). This diversity is remarkable because the ranges of the bunting taxa are correlated with different vegetation types on an island of only 15 km². The differences between taxa are most pronounced in bill size (Ryan 1992), suggesting that the morphological differences may be related to differences in the food spectrum in various habitats. In this paper I use parent-offspring regressions to estimate the heritability of *Nesospiza* morphology.

METHODS

I visited Inaccessible Island (37°18'S, 12°41'W) during October 1989–March 1990. Observations centered on three main study areas: Blenden Hall, Ringeye Valley, and Denstone Hill (Ryan et al. 1994). Blenden Hall is characterized by *Spartina arundinacea* tussock grassland and copses of *Phylica arborea* trees. It supports sympatric populations of Wilkins' Buntings and drab-colored, lowland Tristan Buntings. At the time of the study there was no hybridization between the two species at this site. Ringeye Valley on the western plateau has a mixture of *Blechnum palmiforme* and wet heath vegetation that supports primarily bright-colored, upland Tristan Buntings. Denstone Hill on the eastern plateau supports a range of hybrids at the ecotone between *Phylica* woodland and *Blechnum palmiforme* heath. Roux et al. (1992) describes the island and its vegetation types.

Buntings caught at all three study sites were aged and sexed using plumage characters (Ryan et al. 1994), measured, and individually color-marked. Six measurements were taken from each bird: wing length (flattened chord to the nearest 1 mm), tarsus length, total head length, culmen (from the ridge proximal to the nares to the bill tip, after Grant et al. 1985), total bill depth (measured vertically at the proximal edge of the nares), and lower bill width (the widest point of the lower mandible; all to the nearest 0.1 mm). Head length was calculated by subtracting culmen from total head length. All measurements were made by the author, and repeatabilities (Lessels and Boag 1987) were high for all characters ($r = 0.75$ – 0.91).

Birds were assigned to taxa based on their plumage and morphology (Ryan 1992, Ryan et al. 1994). "Hybrid" pairs were either mixed-species pairs (one Wilkins' and one Tristan Bunting) or pairs with at least one hybrid, identified by their intermediate morphology. Hybrids were identified as birds that were outside the 95% confidence interval for bill measures of 'pure' Tristan and Wilkins' Buntings, basing the limits for 'pure' Tristan and Wilkins' Buntings on breeding birds away from the hybrid area.

Searches were made for nests within the study areas, and any unbanded parents were targeted for capture. *Nesospiza* are strongly territorial, and almost all breeding is by monogamous pairs, making the identification of parents straightforward. Nestlings were banded with individually numbered bands when they were approximately ten days old. Where there were two chicks in the same nest they were banded on different legs, so they could be distinguished after fledging (clutch size is 1–2 eggs). Juveniles were recaptured once they were at least seven weeks old, by which time they had attained adult dimensions in all characters except bill length and depth (see below). A large proportion of juveniles could be recaptured because they remained on the natal territory, receiving food from their parents until 8–11 weeks after hatching. Although strictly speaking, heritabilities should be estimated by comparing parent-offspring measures at the same age, this technique is frequently used for estimates of morphological heritability among wild bird populations (e.g., Lynch and Walsh 1998).

STATISTICAL ANALYSES

Heritability estimates were derived by regressing offspring on parental (mother, father, and mid-parent) measurements. Midparent values are the arithmetic mean of parental measurements. The heritability of a character is equivalent to the slope of the midparent regression, and twice the slope of the single-parent regressions (Falconer 1981). Upper limits of heritability were estimated from full sib-sib intraclass correlations (t , after Lessels and Boag 1987), such that $h^2 \leq 2t$ (Falconer 1981), with the inequality emphasizing the possible influence of shared environmental conditions during growth on the resemblance between siblings. Genetic correlations between characters, and their standard errors, were calculated following Falconer (1981), using Statgraphics (STSC 1986) to calculate covariance matrices. Heritabilities were estimated for upland and lowland morphs of Tristan Buntings separately, as well as for the two taxa combined. Included in the combined sample were two "mixed" families comprising upland males mated with lowland females at the interface of the two morphs (Ryan et al. 1994).

No attempt was made to weight families according to the number of offspring (cf. Bohren et al. 1961, Boag 1983), because this has little influence on heritability estimates unless there is considerable variance in family size (Falconer 1981); *Nesospiza* invariably had either one or two offspring. When two offspring were captured from the same family, their measurements were averaged for regression on parental values. All samples were from a single breeding season; thus there is no interannual variation (Boag and van Noordwijk 1987). *Nesospiza* are sexually dimorphic (males 1–5% larger than females in linear characters), but samples were too small to standardize for the sex of offspring (cf. Smith and Zach 1979). Juveniles cannot be readily sexed in the field; using a discriminant function derived from adult birds, the sex ratio of Tristan Bunting offspring was approximately equal (39 males, 35 females).

RESULTS

A total of 85 fully grown juvenile buntings from 60 families in which both parents had been measured was caught. An additional 12 juveniles from 10 families in which only one parent was measured also were caught. Too few Wilkins' Bunting juveniles of known parentage ($n = 3$)

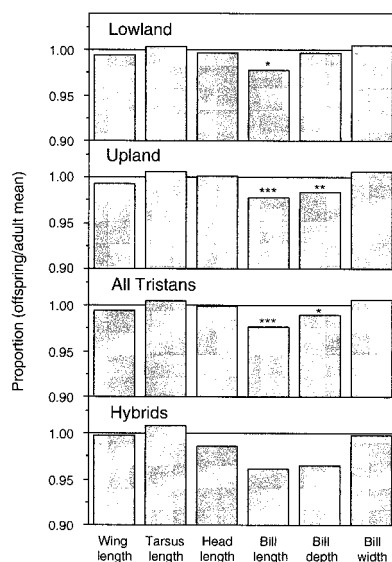


FIGURE 1. Comparison of mean offspring phenotypes with those of their parents among *Nesospiza* at Inaccessible Island. The 1.0-line indicates the mean parental phenotype. Significant differences (t -tests) depicted: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

were caught to estimate heritabilities; they are not considered further.

All juveniles measured were 7–11 weeks old, and thus age-related variance in offspring size is unlikely to have influenced the results. However, there may be some subsequent growth, particularly of bill characters (Grant 1983). Among Tristan Buntings, mean offspring bill lengths and, to a lesser extent, bill depths, were smaller than those of their parents (Fig. 1). These differences were greater among hybrids, but were not significant because of the large variances in hybrid means. Heritability estimates also could be biased by selection occurring before juveniles were measured. Comparisons of nestling sizes shortly before fledging found no significant differences between nestlings that were recovered after fledging and those that disappeared (Table 1). Nestlings that were not subsequently recaptured averaged smaller in all dimensions (Table 1), but this was influenced by a few stunted chicks. Their smaller size almost certainly resulted from nutritional deficiency (i.e., environmental rather than genetic causes, Ricklefs 1976).

SIBLING-SIBLING CORRELATIONS

Intraclass correlations between the morphological characters of siblings tend to overestimate h^2

TABLE 1. The mean size of 16-day-old nestling Tristan Buntings, comparing birds that were subsequently recaptured as juveniles (seven weeks or older) with birds that were not recaptured, and presumably died. Sizes of birds recaptured were not significantly different from those that disappeared (*t*-tests, all *P* > 0.1).

Character	Survived mean ± SD	Disappeared mean ± SD
Lowland morph	<i>n</i> = 22	<i>n</i> = 18
wing length	53.6 ± 1.7	52.0 ± 4.0
tarsus length	24.8 ± 0.7	24.4 ± 1.1
head length	31.9 ± 0.6	31.5 ± 0.8
bill length	9.6 ± 0.3	9.4 ± 0.4
bill depth	7.6 ± 0.2	7.5 ± 0.4
bill width	7.2 ± 0.2	7.0 ± 0.3
Upland morph	<i>n</i> = 28	<i>n</i> = 8
wing length	53.4 ± 2.7	53.0 ± 2.8
tarsus length	25.0 ± 0.7	24.6 ± 0.8
head length	31.5 ± 0.5	31.2 ± 0.7
bill length	9.1 ± 0.3	9.1 ± 0.4
bill depth	7.2 ± 0.3	7.2 ± 0.2
bill width	7.0 ± 0.2	6.9 ± 0.3

as a result of common environmental influences during the nestling period (Falconer 1981, Alatalo and Lundberg 1986). Full-sibling correlations were positive (Table 2; ANOVA *F* > 1), with the exception of wing length, which presumably reflects the masking influence of sex on wing length variation (wing length exhibits greater sexual dimorphism than other characters, Ryan 1992). Sample sizes were small, with few significant differences between families of lowland and upland Tristan Buntings when treated separately (Table 2). Among the combined set of Tristan Buntings, where bill characters differed significantly between families, *h*² estimates from sib-sib correlations (2*t*) were 30–60% greater than those estimated from parent-offspring regressions (see below). Among hybrids, sib-sib *h*² estimates were up to twice those estimated from parent-offspring regressions.

PARENT-OFFSPRING REGRESSIONS

Significant positive regressions were detected between all midparent-offspring measurements of morphological characters for the combined set of Tristan Buntings (Table 3). Heritability estimates were high (0.66–0.95), suggesting that a large proportion of size variation is genetically determined. Separate regressions of lowland and upland morph Tristan Buntings also gave positive *h*² estimates, although not all regressions

TABLE 2. Intraclass correlations (*t*) between measurements of siblings in *Nesospiza* broods at Inaccessible Island. Twice the correlation values provide an upper estimate of character heritability (*h*² ≤ 2*t*). All families comprise two offspring.

Character	All Tristan Buntings <i>n</i> = 17	Lowland <i>n</i> = 6	Upland <i>n</i> = 11	Hybrids <i>n</i> = 8
Wing length	−0.39	−0.48	−0.50	−0.21
Tarsus length	0.33	0.31	0.36	0.81**
Head length	0.44 ⁺	0.39	0.46	0.62 ⁺
Bill length	0.67**	0.64 ⁺	0.44	0.64 ⁺
Bill depth	0.64**	0.42	0.30	0.70*
Bill width	0.49*	0.06	0.52 ⁺	0.69*

** *P* < 0.01, * *P* < 0.05, ⁺1-tailed *P* < 0.05 (ANOVAs).

were significant (Table 3). The large standard errors reflect the considerable scatter about the regression lines, and outliers frequently influenced the *h*² estimates (Fig. 2). Lowland heritabilities averaged larger than those of upland families, partly as a result of the greater morphological range expressed by lowland buntings (Fig. 2). There was no consistent difference in heritabilities of bill characters relative to those of body characters, nor was there concordance in the magnitude of character heritabilities between taxa.

Single parent-offspring regressions also gave *h*² estimates significantly greater than zero for the combined set of Tristan Buntings (Table 3). Heritability estimates from father-offspring regressions were similar to or greater than those from mother-offspring regressions, suggesting that non-genetic maternal effects have a negligible influence on *h*² estimates (Boag and van Noordwijk 1987), and that cuckoldry is relatively uncommon (cf. Boag 1983, Alatalo et al. 1984). The greater values for father-offspring regressions were influenced by a few outlying lowland Tristan Bunting families. Treating upland and lowland buntings separately, single parent-offspring regressions seldom were significant, with the exception of lowland father-offspring regressions (where outliers had a disproportionate influence). However, *h*² estimates were positive, and generally were similar to those estimated from midparent-offspring regressions (Table 3).

Offspring of hybrid pairs typically were intermediate between parental phenotypes, partic-

TABLE 3. Heritabilities ($h^2 \pm \text{SE}$) among *Nesospiza* at Inaccessible Island estimated by parent-offspring regressions. Sample sizes (n) are numbers of family units, followed by the total number of offspring.

Character	Midparent-offspring $h^2 \pm \text{SE}$	Father-offspring $h^2 \pm \text{SE}$	Mother-offspring $h^2 \pm \text{SE}$
All Tristan Buntings (n)	(45, 62)	(49, 66)	(51, 68)
wing length	$0.93 \pm 0.22^{***}$	$1.51 \pm 0.35^{***}$	$0.79 \pm 0.35^*$
tarsus length	$0.75 \pm 0.21^{***}$	$0.90 \pm 0.35^*$	$0.92 \pm 0.26^{***}$
head length	$0.66 \pm 0.19^{**}$	$0.74 \pm 0.25^{**}$	$0.55 \pm 0.30^+$
bill length	$0.85 \pm 0.13^{***}$	$1.11 \pm 0.23^{***}$	$0.89 \pm 0.22^{***}$
bill depth	$0.95 \pm 0.20^{***}$	$1.46 \pm 0.28^{***}$	$0.90 \pm 0.32^{**}$
bill width	$0.69 \pm 0.17^{***}$	$0.97 \pm 0.29^{**}$	$0.79 \pm 0.21^{***}$
Lowland morph (n)	(20, 26)	(23, 29)	(22, 28)
wing length	0.86 ± 0.65	0.99 ± 0.79	0.17 ± 0.60
tarsus length	$0.95 \pm 0.24^{***}$	$1.52 \pm 0.47^{**}$	$0.90 \pm 0.26^{**}$
head length	$0.66 \pm 0.32^+$	$0.94 \pm 0.38^*$	0.30 ± 0.43
bill length	$0.89 \pm 0.28^{**}$	$1.28 \pm 0.39^{**}$	$0.74 \pm 0.35^*$
bill depth	$0.97 \pm 0.38^*$	$1.58 \pm 0.41^{***}$	$0.88 \pm 0.50^+$
bill width	0.55 ± 0.35	$1.06 \pm 0.46^*$	0.35 ± 0.27
Upland morph (n)	(23, 34)	(24, 35)	(27, 38)
wing length	$0.69 \pm 0.35^+$	$1.32 \pm 0.52^*$	0.50 ± 0.54
tarsus length	0.47 ± 0.37	0.21 ± 0.53	1.03 ± 0.61
head length	$0.88 \pm 0.28^{**}$	0.76 ± 0.52	$1.03 \pm 0.46^*$
bill length	$0.73 \pm 0.19^{**}$	$0.71 \pm 0.35^+$	$0.72 \pm 0.34^*$
bill depth	$0.55 \pm 0.31^+$	0.50 ± 0.52	0.51 ± 0.41
bill width	$0.81 \pm 0.22^{**}$	0.78 ± 0.46	$1.13 \pm 0.26^{***}$
Hybrids (n)	12, 20	12, 20	12, 20
wing length	$0.77 \pm 0.35^+$	0.45 ± 0.50	$1.15 \pm 0.57^+$
tarsus length	$0.93 \pm 0.19^{***}$	$1.18 \pm 0.33^{**}$	0.85 ± 0.47
head length	$0.90 \pm 0.14^{***}$	$0.71 \pm 0.34^+$	$0.84 \pm 0.33^*$
bill length	$0.62 \pm 0.14^{**}$	$0.54 \pm 0.30^+$	$0.59 \pm 0.25^*$
bill depth	$0.81 \pm 0.15^{***}$	$0.69 \pm 0.35^+$	$0.91 \pm 0.31^*$
bill width	$0.93 \pm 0.17^{***}$	$0.83 \pm 0.38^+$	$1.28 \pm 0.39^{**}$

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, +1-tailed $P < 0.05$.

ularly where there was a great size difference between mates (Fig. 3). There was one exception to this pattern, where a small female mated to a large male produced a single, small juvenile. Given the intermediate nature of most other hybrid offspring, this suggests the possibility of an extra-pair fertilization by a smaller male. Midparent-offspring regressions were all highly significant (Table 3), with the exception of wing length, which is the least variable character among hybrids (Fig. 4). Compared with Tristan Buntings, there was no concordance between characters in the magnitude of h^2 estimates ($r_s = 0.38$, $P > 0.5$). The midparent-offspring regression of tarsus length is unusual in appearing to be curvilinear (Fig. 4). Intermediate-sized hybrid offspring were characterized by relatively long tarsi, possibly as a result of a non-additive genetic effect. The relatively low heritability of bill length, and to a lesser extent bill depth, contrasts with the high heritabilities of other characters except wing length (Fig. 4, Table 3). The low

bill length and depth heritabilities occur despite close phenotypic correlation between these and other characters (Table 4), and may be influenced by these characters not being fully grown; small regression slopes would arise if larger birds grew more slowly (cf. Fig. 1). However, they could also result from non-additive genetic interactions associated with hybridization. Single parent-offspring regressions for hybrids were less significant than were those of Tristan Buntings as a result of the large size differences between parents in many hybrid pairs (Fig. 3).

GENETIC CORRELATIONS

Genetic correlations provide an estimate of the proportion of phenotypic correlation between morphological characters attributable to genetic rather than environmental variation (Falconer 1981). This is an important measure because it determines the extent to which selection acting on a specific character also influences other, related characters through pleiotropy or linkage

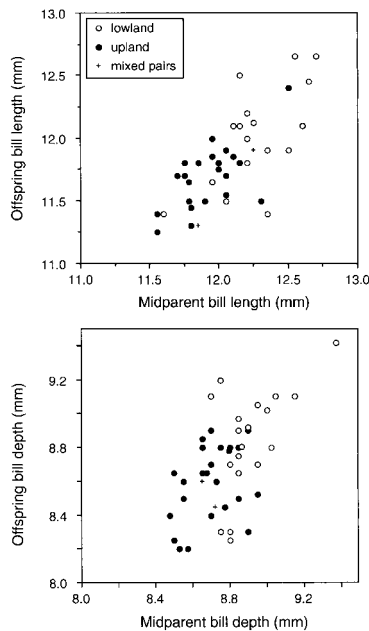


FIGURE 2. Midparent-offspring biplot of bill length among Tristan Buntings breeding at Inaccessible Island. Midparent values are the arithmetic mean of parental measurements.

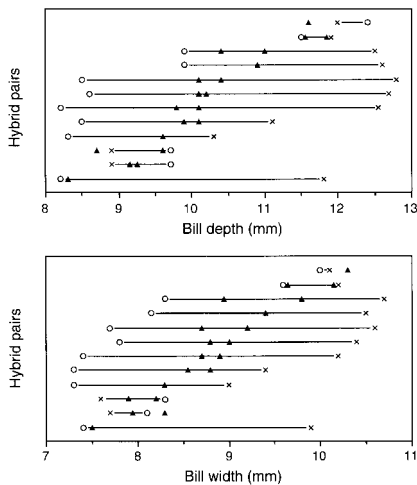


FIGURE 3. Bill sizes of *Nesospiza* hybrid juveniles at Inaccessible Island, in relation to the bill sizes of their parents. Paired males (crosses) and females (circles) are linked by lines, with offspring phenotypes depicted by triangles. Families are arranged in descending mean parental bill size (same order for both figures), with the exception of the pair that may have had an extra-pair fertilization, which is the bottom family in both figures.

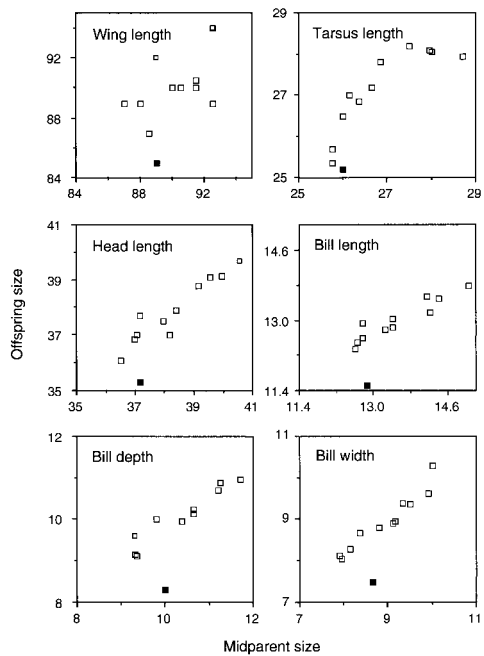


FIGURE 4. Midparent-offspring regressions of six morphological characters among *Nesospiza* hybrids (midparent values are the arithmetic mean of parental measurements). The solid point in each case depicts the family with doubtful male parentage. Regression lines not shown; all except wing length are highly significant (see Table 3).

disequilibrium. In general, external morphological measures of *Nesospiza* buntings covary positively (Ryan 1992). Particularly strong positive correlations were found among hybrids (Table 4), which is to be expected given the large size range within this group. Coupled with high heritabilities, this resulted in strong genetic correlations (Table 5).

Most phenotypic correlations between morphological characters of Tristan Buntings were significant (Table 4). Positive correlations were found between all lowland characters, and between most upland characters (Table 4). Among the combined Tristan Bunting data set, strong positive correlations were found within bill and body measures, but correlations generally were weak between bill and body measures (Table 4). This results from the relative differences in size between morphs, with upland buntings characterized by large bodies and small bills, whereas lowland buntings have small bodies and large bills (Ryan 1992). Genetic correlations between Tristan Bunting characters reflect this difference;

TABLE 4. Phenotypic correlations (r_p) between morphological characters of *Nesospiza* pairs and their offspring at Inaccessible Island, based on families with both parental sexes measured.

Character	Wing length	Tarsus length	Head length	Bill length	Bill depth	Bill width
All Tristan Buntings ($n = 152$)						
wing length		0.50	0.43	0.20	0.30	0.26
tarsus length	***		0.48	0.21	0.20	0.31
head length	***	***		0.74	0.59	0.61
bill length	*	**	***		0.67	0.50
bill depth	***	*	***	***		0.70
bill width	**	***	***	***	***	
Lowland morph ($n = 66$)						
wing length		0.39	0.55	0.49	0.54	0.41
tarsus length	**		0.63	0.58	0.44	0.42
head length	***	***		0.81	0.60	0.55
bill length	***	***	***		0.62	0.56
bill depth	***	***	***	***		0.76
bill width	***	***	***	***	***	
Upland morph ($n = 80$)						
wing length		0.53	0.58	0.36	0.56	0.44
tarsus length	***		0.52	0.16	0.24	0.39
head length	***	***		0.66	0.57	0.67
bill length	***	ns	***		0.60	0.31
bill depth	***	*	***	***		0.58
bill width	***	***	***	**	***	
Hybrids ($n = 44$)						
wing length		0.83	0.88	0.82	0.88	0.88
tarsus length	***		0.91	0.84	0.90	0.93
head length	***	***		0.97	0.98	0.96
bill length	***	***	***		0.96	0.92
bill depth	***	***	***	***		0.98
bill width	***	***	***	***	***	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns = not significant.

those for lowland and upland buntings treated separately were all positive, whereas several correlations between bill and body characters were negative for the combined data set (Table 5).

DISCUSSION

The heritabilities estimated for *Nesospiza* fall within the range of values typically obtained for morphological traits of passerine birds (0.5–1.1; Boag and van Noordwijk 1987, McKittrick 1990, Lynch and Walsh 1998, Grant and Grant 2000). This result suggests that *Nesospiza* external morphology has considerable additive genetic variance, and thus there is potential for rapid morphological evolution. Several factors influence heritability estimates, however, including assortative mating, low measurement repeatabilities, differences in male-female variances, and incomplete growth of juveniles (Falconer 1981, Boag and van Noordwijk 1987). In this case there is no evidence of assortative mating on the

basis of morphology (Ryan 1992), measurement repeatabilities are great, and there is little sex-related difference in morphological variances (Ryan 1992). Genotype-phenotype interactions also can affect h^2 estimates (Falconer 1981, Boag 1983). The greater h^2 estimates derived from sib-sib correlations compared with those from parent-offspring regressions suggest that there is a considerable element of non-genetic variability in offspring size. No attempt was made to correlate bird size with territory size, because there were no obvious differences between territories within study areas (Ryan 1992), and cross-fostering experiments in other studies have detected little evidence of post-hatching environmental effects on offspring phenotypes (Smith and Dhondt 1980, Dhondt 1982, Alatalo and Lundberg 1986). However, genotype-phenotype interactions could exert a significant influence on combined Tristan Bunting h^2 estimates.

The two morphs of Tristan Bunting occupy

TABLE 5. Genetic correlations (r_A) between morphological characters of *Nesospiza* breeding at Inaccessible Island, based on midparent-offspring regressions presented in Tables 3 and 4. r_A above diagonal, SE of r_A below diagonal (calculated after Falconer 1981). Bold values show where the 95% confidence interval exceeds 0.

Character	Wing length	Tarsus length	Head length	Bill length	Bill depth	Bill width
All Tristan Buntings ($n = 45$)						
wing length		0.46	0.43	−0.22	−0.07	0.44
tarsus length	0.14		0.67	0.52	−0.33	0.82
head length	0.15	0.10		0.62	0.64	0.68
bill length	0.08	0.11	0.13		0.64	0.76
bill depth	0.16	0.15	0.10	0.07		0.64
bill width	0.14	0.06	0.10	0.06	0.10	
Lowland morph ($n = 20$)						
wing length		0.41	0.03	0.32	0.37	0.41
tarsus length	0.26		0.56	0.62	0.69	0.64
head length	0.43	0.17		0.60	0.63	0.96
bill length	0.31	0.12	0.18		0.47	0.75
bill depth	0.33	0.12	0.19	0.19		0.53
bill width	0.41	0.17	0.03	0.19	0.25	
Upland morph ($n = 23$)						
wing length		0.45	0.49	0.44	0.63	0.69
tarsus length	0.35		0.81	0.55	0.52	0.66
head length	0.22	0.12		0.67	0.60	0.69
bill length	0.21	0.22	0.11		0.34	0.75
bill depth	0.23	0.34	0.19	0.24		0.60
bill width	0.19	0.19	0.11	0.08	0.18	
Hybrids ($n = 12$)						
wing length		0.90	0.87	0.91	0.85	0.85
tarsus length	0.04		0.93	0.92	0.91	0.91
head length	0.05	0.02		0.88	0.89	0.90
bill length	0.04	0.02	0.03		0.86	0.90
bill depth	0.06	0.02	0.03	0.04		0.87
bill width	0.06	0.02	0.02	0.03	0.03	

different habitats (Ryan et al. 1994) and have different diets (Ryan 1992); the subtle morphological differences between morphs could result from genetic differences, or from genotype-environment interactions (i.e., when gene expression is influenced by habitat), or from both factors (Via and Lande 1985). In the absence of cross-fostering experiments, it is not possible to estimate reliably the relative genetic and environmental contributions to morphological variation. Some studies that have switched eggs between habitats have detected a marked environmental influence on offspring size (James 1983), whereas others have found little environmental influence (Alatalo and Lundberg 1986). The similarity of heritability estimates from father-offspring and mother-offspring regressions suggests that extra-pair fertilizations are rare (Boag 1983), which accords with observations of strict mate-guarding among both sexes of *Nesospiza* (Ryan 1992).

There has been debate about the evolutionary

significance of high morphological heritabilities (Rose 1983, Arthur 1984, Gustafsson 1986, Mousseau and Roff 1987). The response of any trait to natural selection is proportional to the trait's heritability, but stabilizing selection should tend to reduce genetic variation, ultimately leading to fixation and zero heritabilities (Fisher 1930). The constant climate at the Tristan Islands (Wace and Holdgate 1976) is likely to promote stabilizing selection, but this need not lead to small heritabilities if there is disruptive selection on bill size due to habitat-specific differences in feeding conditions (Grant and Grant 1979, Grant 1983). Such conditions could account for the morphological differences between the two morphs of Tristan Buntings at Inaccessible Island, with selection counterbalancing introgression between the two morphs. Alternatively, the phenotypic differences between Tristan Bunting morphs in different habitats could be achieved given genotype-environment interaction and stabilizing selection over the en-

tire Tristan Bunting range (Via and Lande 1985). However, the significant heritabilities of many characters within Tristan Bunting morphs suggest that the size differences between morphs are at least partly determined by genetic differences. The tendency for negative genetic correlations between bill and body characters in the combined set of Tristan Buntings indicates that these characters can respond independently to selection pressures (Via and Lande 1985).

The intermediate sizes of hybrid offspring, their high morphological heritabilities, and strong genetic correlations between characters confirm the genetic basis of size differences between Tristan and Wilkins' Buntings. The generally close agreement between offspring and midparent sizes in families with highly disparate parental phenotypes suggests that virtually all genetic variation in size is additive. This result is similar to that found among Darwin's finches, where hybrid ground finches *Geospiza* are intermediate in size between parental phenotypes, and parent-offspring regressions yield significant heritability estimates (0.4–1.0; Grant and Grant 1994). Among *Nesospiza*, the only exception to hybrid intermediacy was the tendency for mid-sized hybrids to have relatively long tarsi, which might be related to the greater amount of time hybrids spend feeding in trees (Ryan 1992).

Experimental manipulations would help to resolve some of the unanswered questions raised by this study. In particular, cross-fostering of broods would allow accurate estimation of the relative importance of genetic and environmental effects during *Nesospiza* development (James 1983). However, such manipulations would alter the natural population structure, and perhaps the best approach would involve captive breeding experiments within and between taxa under controlled environmental conditions (Arthur 1984).

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