

# 4000 YEARS OF PHENOTYPIC CHANGE IN AN ISLAND BIRD: HETEROGENEITY OF SELECTION OVER THREE MICROEVOLUTIONARY TIMESCALES

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Received August 30, 2007

Accepted May 15, 2008

Pronounced phenotypic shifts in island populations are typically attributed to natural selection, but reconstructing heterogeneity in long-term selective regimes remains a challenge. We examined a scenario of divergence proposed for species colonizing a new environment, involving directional selection with a rapid shift to a new optimum and subsequent stabilization. We provide some of the first empirical evidence for this model of evolution using morphological data from three timescales in an island bird, *Zosterops lateralis chlorocephalus*. In less than four millennia since separation from its mainland counterpart, a substantial increase in body size has occurred and was probably achieved in fewer than 500 generations after colonization. Over four recent decades, morphological traits have fluctuated in size but showed no significant directional trends, suggesting maintenance of a relatively stable phenotype. Finally, estimates of contemporary selection gradients indicated generally weak directional selection. These results provide a rare description of heterogeneity in long-term natural regimes, and caution that observations of current selection may be of limited value in inferring mechanisms of past adaptation due to a lack of constancy even over short time-frames.

**KEY WORDS:** Directional selection, displaced optimum, mark-recapture, microevolutionary rates, survival, *Zosterops*.

Natural selection is commonly invoked to explain a wide spectrum of patterns of biological variation (reviews in Kinnison and Hendry 2001; Reiseberg et al. 2002), from those seen at small temporal and spatial scales, such as variation in survival across seasons (Grant 1985; Brown and Brown 1998; Badyaev et al. 2000), through to macroevolutionary patterns, such as the ten-

dency for species within a lineage to evolve toward larger body size (Kingsolver and Pfennig 2004). It is, however, recognized that the tempo of selection is likely to be heterogeneous during the development of adaptive divergence with the strength and form of selection, and the ability of a population to respond to selection, varying over time (Kinnison and Hendry 2001). This

heterogeneity is suggested to account for the frequent observation that evolutionary rates measured over long timescales are substantially less than those measured over short timescales (Reznick et al. 1997; Kinnison and Hendry 2001). Heterogeneity in selection strength has implications both for predicting the evolutionary trajectory of a population (Merilä et al. 2001b; Grant and Grant 2002) and for extrapolating from the current form of selection to study historical patterns of adaptation and divergence, because applying an assumption of constancy of selection becomes increasingly unrealistic as the time frame under consideration lengthens.

In a situation in which a species experiences a new or substantially altered environment, such as colonizing an island, the opportunity for strong directional selection is likely to be greatest in the early stages of divergence (Reznick et al. 1997; Hendry et al. 2000; Reznick and Ghalambor 2001). It is suggested that following an initially rapid directional change, the rate of divergence slows as a new optimum is approached or additive genetic variation is exhausted. Subsequently small shifts around this optimum may occur due to the action of stabilizing selection, directional selection in opposite directions as relatively small environmental fluctuations ensue, or random fluctuations due to drift (Lande 1976; Reznick et al. 1997; Hendry et al. 2000; Kinnison and Hendry 2001; Estes and Arnold 2007). An analysis of phenotypic divergence over a broad range of study species suggests that this model, referred to as the displaced optimum model, is generally appropriate across different timescales (Estes and Arnold 2007). Also, studies of historically introduced species and those subject to anthropogenic alterations show that rapid phenotypic evolution frequently follows exposure to a new environment (Kinnison and Hendry 2001; Hendry et al. 2008). Beyond such historical timeframes, it becomes increasingly difficult to reconstruct the temporal dynamics of divergence (but see Hunt et al. 2008). However, it is possible to draw inferences about evolutionary history over long timescales given a predivergence reference point, an estimate of divergence time, information on temporal patterns of morphological shifts over some historical timeframe, and knowledge of current microevolutionary processes operating in a population. This set of circumstances is rarely seen in natural systems because of the short timescales of most studies (but see Kruuk et al. 2001; Grant and Grant 2002; Coulson et al. 2003; Garant et al. 2004). Even for those populations where there is long-term data on the form of selection, the ancestral state is often not obvious, such that recent selection cannot be set in the context of broader scale patterns of historical isolation.

Here, we study evolutionary divergence in a population of island land bird for which we have multiple sources of information on the pattern of morphological adaptation and selection. The Capricorn silvereeye, *Zosterops lateralis chlorocephalus*, on Heron Island, Australia, is a relatively young form that is characterized by pronounced phenotypic size changes compared to

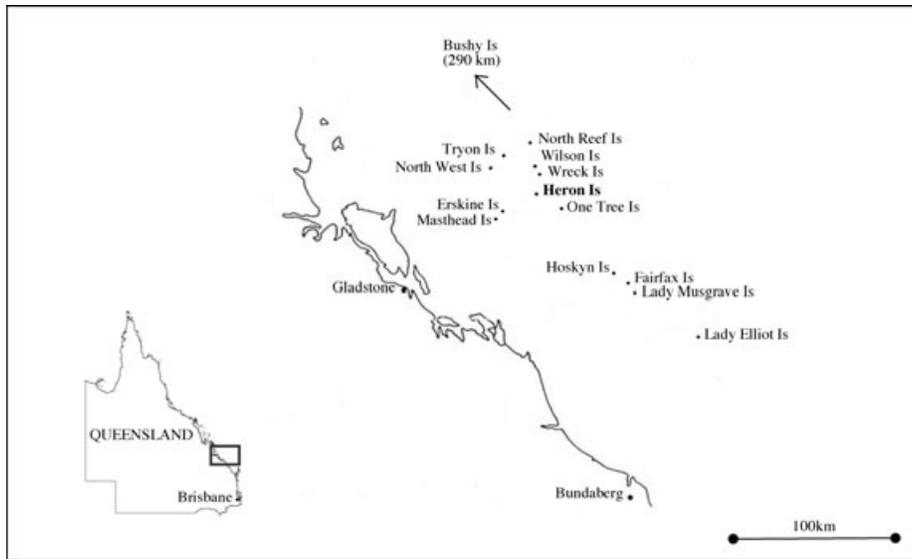
its mainland ancestor (Kikkawa 1976; Higgins et al. 2006). The islands inhabited by this subspecies have been formed no earlier than 4400 years ago and vegetated for 4000 years at most (Hopley 1982). This combined with mitochondrial DNA evidence supporting the recent origin of the population (Degnan and Moritz 1992) places an upper limit to the age of the population. Population age limits, combined with other evidence, have previously been used to suggest that the form of morphological divergence in this and related species is more consistent with natural selection than it is with either short-term founder effects or long-term genetic drift (Clegg et al. 2002a,b).

In this study, we examine patterns of morphological change in the Capricorn silvereeye across three microevolutionary timescales, providing a rare insight into the temporal dynamics of evolutionary change in a natural system. First, we compared morphological measurements between Heron Island and mainland *Zosterops* to quantify the long-term microevolutionary change that represents a shift to, or toward, the new optimum phenotype. Second, we compared morphological trends across four decades within the Heron Island population to examine temporal trends in morphology. In particular, we tested for the existence of directional trends that would suggest the action of continuing directional selection consistent with the long-term morphological divergence pattern, or a lack of trends, that would indicate that the population has reached a new optimum. Third, we used three years of recent census data from the Heron Island population to construct an individual-level model that best described survival in terms of individual phenotype in combination with age, time, and seasonal effects. To determine the type and strength of selection currently operating in this system, we estimate univariate and multivariate selection gradients for time periods identified from the survival analysis as being important predictors of variation in survival. Generally weak current directional selection would be expected for traits that reached the new optimum at some time in the past. We reconcile information on selective patterns over the three timescales to determine if the combined evidence is consistent with the expectations of divergence in a population subject to a novel selective regime, that is rapid evolution toward a displaced optimum, followed by stasis or oscillation around the new optimum.

## Methods

### HERON ISLAND STUDY POPULATION

The Capricorn silvereeye is restricted to island cays of the southern Great Barrier Reef (the Capricorn-Bunker Group) and Bushy Island 290 km to the north (Fig. 1). On Heron Island (23°26' S, 151°57' E), the silvereeye is the predominant breeding passerine (Kikkawa 1976) and the population size varies between 225 and 500 individuals (McCallum et al. 2000). There is very little



**Figure 1.** Map showing the position of Heron Island (in bold) in the Capricorn Bunker Group of the southern Great Barrier Reef of Australia. *Z. l. chlorocephalus* occurs on all named islands. Inset shows the mainland sample site of Brisbane and the relative location of the Capricorn Bunker Group (boxed region).

movement among the islands of the Capricorn-Bunker Group (<1% per generation) and therefore the population on Heron is effectively closed from a demographic viewpoint (Brook and Kikkawa 1998; McCallum et al. 2000). In population genetic terms, the Heron Island population is part of a metapopulation comprising the other Capricorn Bunker islands (Degnan 1993), and there is no observational or genetic data to suggest that gene flow between the island and mainland currently occurs (Kikkawa 1970; Degnan and Moritz 1992).

#### DIVERGENCE FROM MAINLAND ANCESTOR

The island form examined here is larger than any of the Australian mainland *Zosterops* (Higgins et al. 2006) and is also different in shape, having a relatively broader, deeper bill and longer wings for their size (see Clegg et al. 2002b for multivariate comparisons). To quantify the form of size divergence between the island population and its ancestor, we compared a sample of 29 *Z. l. cornwalli* from the mainland (Brisbane, Australia, 27°17'S, 153°2'E, measured in 1998) with 103 adult *Z. l. chlorocephalus* caught on Heron Island (all measured by SMC between 2002 and 2003). The mainland individuals represent a typical sample of the presumed mainland ancestor, with mean morphological values comparable to ranges reported from museum specimens and live-caught birds measured by other people (wing: SMC mean = 59.5, reported ranges 55–61, 56–66 and 56–63; tail: SMC mean = 42.1, reported ranges 40–47, 38–49 and 37–45; tarsus: SMC mean = 16.3, reported ranges 16.4–18.5, 15.1–20.1 and 15.3–18.6) (reported ranges from Higgins et al. 2006). Likewise, the Heron Island sample is representative of the adult morphology of that

population (wing: SMC mean = 64.1, range of adult measurements [measured 1966 to 1998] by JK 59–69; tail: SMC mean = 47.7, JK range 43.5–54; tarsus: SMC mean = 19.11, JK range 17.6–24). In this comparison, we assume that the morphology of the current mainland population is approximately the same as the mainland ancestor of the Heron Island form. If the mainland form has since decreased in body size, then we will overestimate the amount of divergence that has occurred and if the mainland ancestor was larger than both the current mainland and island forms, then we will also misconstrue the direction of change. As the mainland form represented in this study is typical of other mainland *Zosterops* forms (Mees 1969; Higgins et al. 2006), it is extremely unlikely that the mainland form has decreased in body size since separation of the island form. Morphological shifts in the island form for each trait were calculated in standard deviation units (henceforth referred to as sdu), using log-transformed data and pooled standard deviation estimates. Net selection intensities, which estimate the amount of constant directional selection per generation required to explain observed morphological shifts, were estimated following Kinnison and Hendry (2001). First, the rate of evolution in Haldanes (sdu per generation) was calculated for each trait. Generation time of Heron Island silvereyes is between 2 and 3 years (mean breeding age over a 15 year period was 2.8 years). Separation ages of 3000 or 4000 years (the maximum time the island has been vegetated, (Hopley 1982)) were considered, resulting in minimum evolutionary rate estimates made across 2000 generations (2 year generation time, 4000 years of separation) and maximum rates across 1000 generations (3 year generation time, 3000 years of separation). To convert to net

selection intensity we used two estimates of heritability ( $h^2$ ), the first based on a current estimate for adult culmen traits ( $h^2 = 0.2$ ) (SMC, unpublished data), and the second using a typical value for avian morphology ( $h^2 = 0.5$ ) (Lynch and Walsh 1998), as the current estimate may not reflect long-term heritability.

As an alternative to assuming a steady rate of change, we examined evolution toward the new optimum following colonization of the new environment using a displaced optimum model of phenotypic evolution (Lande 1976; Estes and Arnold 2007). Calculations were made with a spreadsheet provided by Estes and Arnold (2007). The variables required to apply this model are the shift in phenotypic sdu, the effective population size ( $N_e$ ), trait heritability ( $h^2$ ), and the width of the fitness function ( $\omega^2$ ) that describes the strength of stabilizing selection (Estes and Arnold 2007). The shift in sdu for each trait was calculated as above, using log-transformed data and pooled standard deviation estimates. The long-term  $N_e$  of the Heron Island population is between 103 and 182 (Kikkawa and Degnan 1998). However, we used a lower, more conservative estimate ( $N_e = 50$ ), as divergence following founding would likely have occurred at lower  $N_e$  values. The use of a higher value for  $N_e$  resulted in narrower confidence intervals (not shown). Two measures of heritability ( $h^2 = 0.2$  and  $h^2 = 0.5$ ) were assumed as before. The approach to the optimum (assumed to be the current island phenotype), was modeled across three values of  $\omega^2$  (5, 10, and 50). These values correspond to a range from strong (5) to weak (50) stabilizing selection and are within a range of reasonable values identified by Estes and Arnold (2007).

### TRACKING MORPHOLOGY OVER FOUR DECADES

Morphological measures of wing, tail, tarsus and culmen lengths, and weight, taken between the years of 1966 to 1999, were examined for consistent, directional size shifts that would indicate continuity of directional selection. All measurements in this historical dataset were made by the same person (JK). The first four measures are the same traits measured for the survival analysis described below. However culmen length was originally measured from the tip of the culmen to the point where feathering begins, and therefore cannot be directly compared to the culmen length measure reported in the survival study described below. Also, culmen depth and width were not measured in this 34-year period. Despite these differences, relative size shifts of culmen length are useful in assessing the occurrence of consistent and sustained shifts. Adults and juveniles were analyzed separately and individuals of unknown age were excluded, as were any measures of wing or tail taken from molting individuals. The smallest sample size for juveniles was 8 and largest was 334, and for adults, 5 and 59, respectively. Unless otherwise specified, all statistical tests were conducted in the R statistical framework (R Development Core Team 2004). Means and 95% confidence intervals of measures were estimated over 10,000 bootstrap replicates. Directional

trends were assessed using Spearman's rank correlation, and the means for starting (1966) and end (1999) values compared with a  $t$ -test. Additionally, a Wilcoxon test was used to determine if there was any association between direction and magnitude of shift from year to year, specifically to determine if size increases or decreases were gradual or abrupt. This was limited to juveniles, and only from 1975 to 1999 (1979 to 1999 for weight), where gaps in years were minimal. Analyses of variance (ANOVAs) and post hoc Tukey's HSD tests were used to evaluate the significance of year-to-year shifts in means.

### MODELING RECENT SURVIVAL AND ESTIMATING SELECTION

Survival probabilities were estimated from individual capture histories using capture–recapture statistical analysis (Lebreton et al. 1992). The capture–recapture analysis is a standard statistical framework for the analysis of longitudinal presence–absence data in which survival and detection probabilities are modeled simultaneously through logistic regressions, and is the only analytical method available to obtain robust estimates of survival probability from presence–absence data (see Burnham et al. (1987); Lebreton et al. (1992) and Williams et al. (2002) for a detailed description of the methodology). Moreover, the flexible analytical framework allows an extensive modeling of the factors influencing survival and detection probabilities. It therefore allows us to fully appreciate the variables contributing to variation in survival, controlling for any bias in detection probabilities.

To estimate survival we used the capture history of juvenile and adult birds captured and resighted from the period of September 1999 to April 2003. Captured birds were marked with a unique combination of color bands (modified from Kikkawa 1997). At banding, six morphological measurements were taken: wing, tail and tarsus length, culmen length, depth, and width. Weight was not included in this analysis due to the large daily and seasonal variation typical of this measure (Kikkawa 1980). Resightings were made twice per year, during April at feeding stations, and in September in conjunction with mapping of territories in the breeding season (see also Kikkawa 1987; Robinson-Wolrath and Owens 2003), to distinguish summer versus winter survival. Birds were categorized into three age groups based on leg color and plumage condition (Kikkawa 2003): juvenile, first year adult, and adults of two years and over (referred to as 2+ year adults). The vast majority of newly marked individuals in the population were nestlings or juveniles, although survival from nestling to juvenile age was not included in this analysis. Rarely, an individual was banded as an adult of unknown age and these were included in the 2+ year adult category. Most of the birds were measured only once, either as a juvenile or an adult. However the measurement of 103 individuals at both life stages indicated that all traits in juveniles, except tarsus, had not reached full adult size

(results not shown). As time-varying individual covariates cannot be directly included in classical capture–recapture models, we conducted separate analyses for birds measured as juveniles and birds measured as adults. All individuals with juvenile measurements that entered the capture history while at the juvenile stage were included in the juvenile dataset. To ensure independence of the datasets, each individual was only used once, and therefore 41 individuals were excluded from the adult dataset due to their inclusion in the juvenile dataset. Although the sample size is smaller, their exclusion does not introduce any systematic bias in terms of adult survival.

Survival and detection probabilities were modeled simultaneously from capture–resighting data using a logit-link function and estimates derived by maximum likelihood using program MARK (White and Burnham 1999). The goodness-of-fit (GOF) of a model assuming time-dependent parameters was tested using the program U-CARE (Choquet et al. 2003). A more complex model structure, with extra parameters such as age, was considered when the GOF test was significant (see Tavecchia et al. 2007). A correction factor (*c-hat*) was applied where necessary to account for any extra binomial noise (Anderson et al. 1994).

We chose a number of a priori models for comparison to establish the most parsimonious base model to which individual covariates could be added. Previous studies have shown that population size fluctuates over years and that overwinter mortality may be particularly high for juveniles (Kikkawa 1980; Catterall et al. 1989). Therefore, we considered the possible influence of year (4 levels: 1999–2003), of age (3 levels: juveniles, first-year adults and 2+ year adults), of season (2 levels: winter and summer), and their interaction. Reduction of survival and recapture parameters were initially conducted in turn, keeping the most general structure for survival parameters when modeling recapture, and vice versa (see Grosbois and Tavecchia (2003) for rationale of model construction). Once the most parsimonious structure for both survival and recapture parameters was selected, we tested for an influence of individual morphometric traits, as studies in this and other populations of silvereyes have suggested that natural selection favors larger body size in island forms (Clegg et al. 2002b; Robinson-Wolrath and Owens 2003; Frentiu et al. 2007). A full model with all morphological traits and their quadratic terms was not tested due to sample size limitations. The selection analysis described below tests the same morphological covariates included in the survival model, however including them in the mark–recapture framework allows us to verify which traits are important predictors of survival while accounting for variation in recapture probabilities.

When estimating selection, we focused on categories identified as important predictors of survival in the capture–recapture

analysis to ensure that the analysis was conducted at the appropriate timescale and age class categories. For juveniles, each of the three overwinter periods were considered separately (sample sizes (survived/total) for winter 2000: 127/216; winter 2001: 25/71; winter 2002: 57/90) and then combined into a single analysis (across three winters 209/377). For adults, selection in each year from September to the following September (September to the following April for the last interval) was calculated separately (1999 to 2000: 111/154; 2000 to 2001: 99/137; 2001 to 2002: 85/144; 2002 to 2003: 76/109). Because a number of adult individuals were represented in multiple years, the datasets were not pooled, however selection gradients across the four years (from September 1999 to April 2003: 33/154) were calculated to give an indication of total selective effect across this time period. Within each dataset, traits were standardized to mean of 0 and unit variance. Relative fitness was measured by dividing individual survival scored as 1 = survived or 0 = died, by mean survival in each period. Univariate and multiple regression models were used to estimate linear ( $\beta$ ) and nonlinear ( $\gamma$ ) selection on body traits. Univariate regression provides estimates of total (direct and indirect) selection acting on a trait whereas multivariate regression provides estimates of the direct component only (Arnold and Wade 1984). Linear selection gradients were taken from models without quadratic terms, with the regression slope giving a direct estimate of the gradient. Nonlinear gradients were estimated from full models, with regression slopes and standard errors from quadratic terms doubled to give nonlinear selection gradients (Fairbairn and Preziosi 1996). Where sufficient data were available (across all winters for juveniles, and across the entire time period for adults), cross-product terms were included in regression models and the slopes were used as a direct estimate of correlational selection gradients. Significance of selection gradients was assessed using logistic regression models (Fairbairn and Preziosi 1996). Selection gradients were also calculated for principal components (PC) with PC extracted from log-transformed values of wing, tail, tarsus, culmen length, culmen depth, and culmen width.

## Results

### DIVERGENCE FROM MAINLAND ANCESTOR

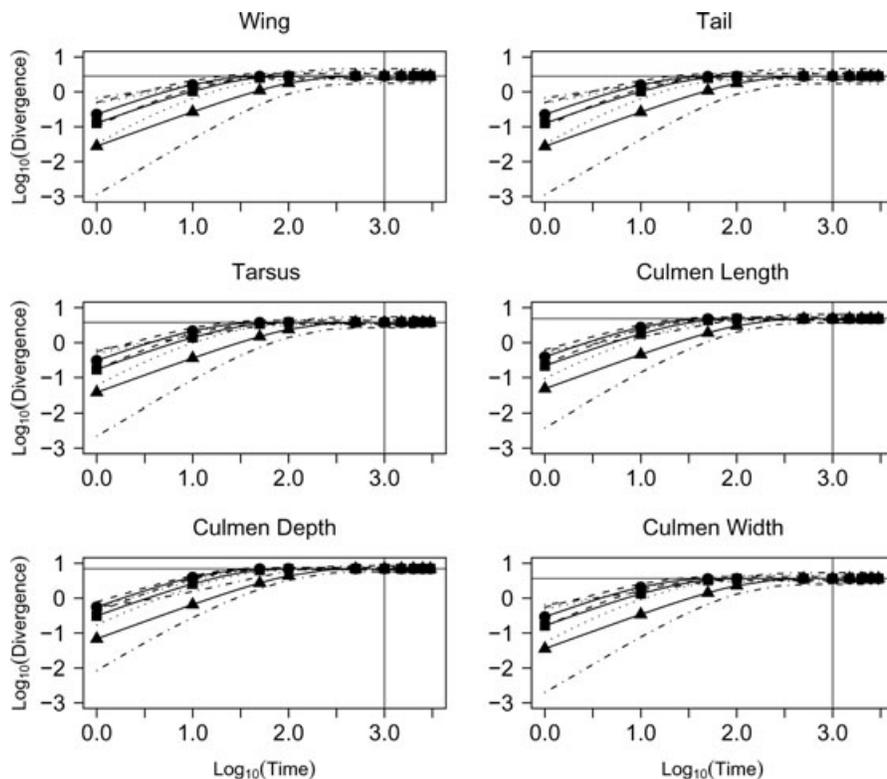
Comparison between mainland and Heron Island individuals indicated morphological trait shifts between 2.81 and 6.99 sdu (Table 1). Net selection intensities required to explain these shifts if they had occurred in a constant manner, ranged from 0.003 (for wing and tail) under the assumptions of the highest number of generations and higher heritability conditions, to an order of magnitude higher (e.g., 0.035 for culmen depth) when fewer generations and lower heritabilities were assumed (Table 1).

**Table 1.** Morphological shift in Heron Island silvereyes (standard deviation units, sdu) compared to a mainland sample. Maximum and minimum values for evolutionary rates (Haldanes) assume 1000 and 2000 generations of separation, respectively. Net selection intensities required to explain these rates, assuming constant selection, are calculated for two estimates of heritability ( $h^2=0.2$  and  $h^2=0.5$ ). CulL, culmen length to posterior nostril opening; CulD, culmen depth at anterior nostril opening; CulW, culmen width at anterior nostril opening.

Trait	Shift (sdu)	Evolutionary rate (Haldanes)		Net selection intensity			
		$t=1000$	$t=2000$	$h^2=0.2$		$h^2=0.5$	
				$t=1000$	$t=2000$	$t=1000$	$t=2000$
Wing	2.85	0.0028	0.0014	0.014	0.007	0.006	0.003
Tail	2.81	0.0028	0.0014	0.014	0.007	0.006	0.003
Tarsus	3.85	0.0039	0.0019	0.019	0.010	0.008	0.004
CulL	4.90	0.0049	0.0023	0.026	0.012	0.010	0.005
CulD	6.99	0.0070	0.0035	0.035	0.018	0.014	0.007
CulW	3.65	0.0037	0.0018	0.018	0.009	0.007	0.004
Weight	3.77	0.0038	0.0019	0.019	0.009	0.008	0.004

Application of the displaced optimum model to our data demonstrated that shifts are likely to have occurred very quickly, followed by many generations of relative stasis (Fig. 2). For all traits the approach to the optimum plateaued after only 100 generations had passed when the two stronger selection pressures were assumed ( $\omega^2 = 5$  or 10). Even under a more conservative scenario

of weak selection, the optimum was reached by 500 generations, well below the 1000 generation minimum we estimate has occurred since the establishment of the island silvereye population. The optimum was also reached before this minimum divergence time when lower trait heritability ( $h^2 = 0.2$ ) was assumed (results not shown).

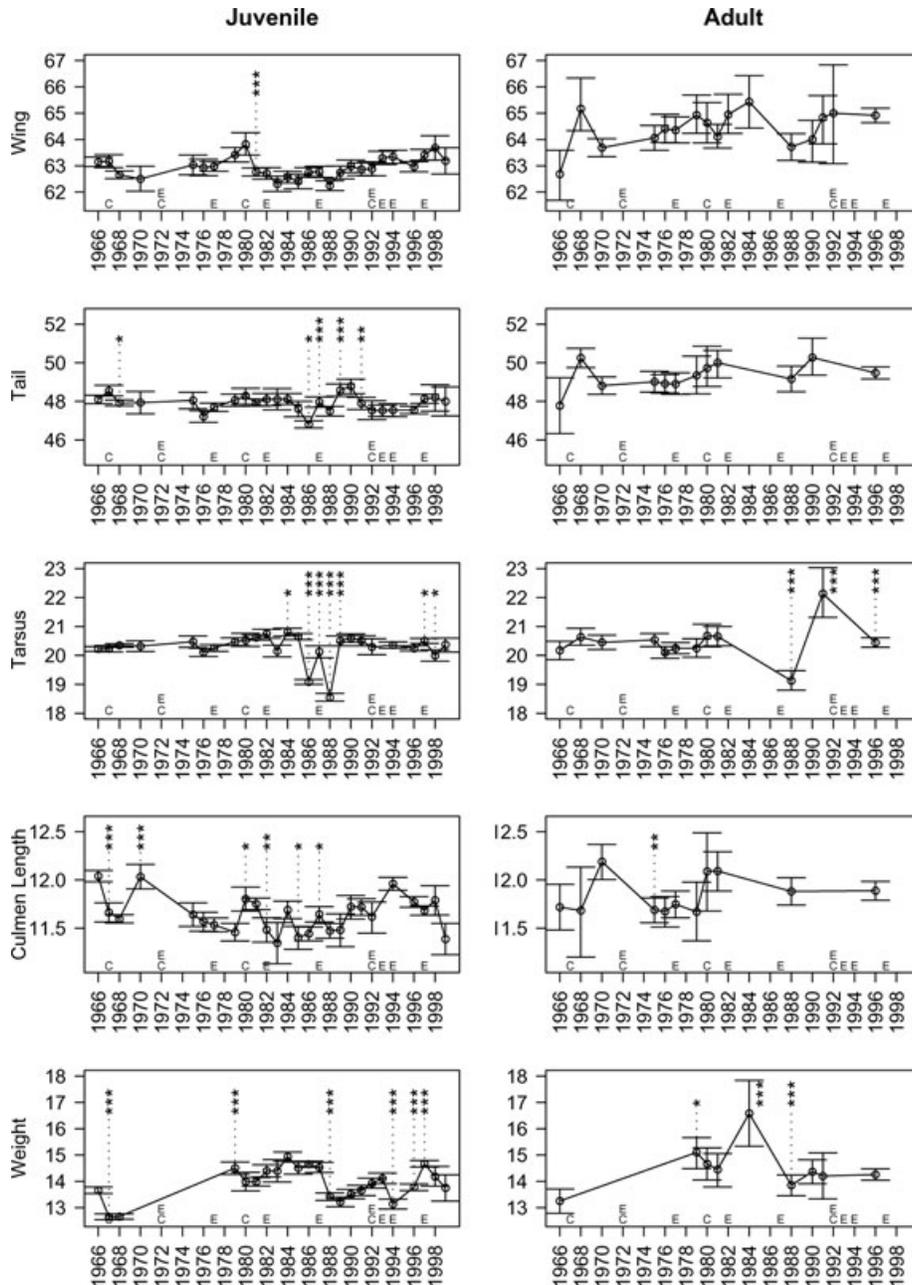


**Figure 2.** Displaced optimum models of divergence showing time of approach to the optimum (indicated by horizontal line) for three levels of selection:  $\omega^2 = 5$  (circles, 5% and 95% confidence intervals = dashed line;  $\omega^2 = 10$  (squares, confidence intervals = dotted line);  $\omega^2 = 50$  (triangles, confidence intervals = dash-dotted line). Trait heritability  $h^2 = 0.5$ . Vertical line indicates 1000 generations, a minimum estimate of divergence time for the island population. Time refers to the number of elapsed generations and divergence is measured in standard deviation units.

## TRACKING MORPHOLOGY ACROSS FOUR DECADES

Our examination of morphological measurements revealed no consistent trends across any trait in the 34-year period from 1966 to 1999 (for adult tail, Spearman's rank correlation,  $\rho = 0.55$ ,  $P > 0.065$ ; for all other traits,  $\rho < 0.33$ ,  $P > 0.2$ ), with fluctuations in direction of shifts for both juvenile and adult traits. For juvenile and adult wing length, and juvenile weight, short time se-

ries (6–10 years) of gradual trait size increases were interrupted, with a more abrupt decrease in average trait size noted across one or two years. These abrupt changes were sometimes followed by the resumption of the gradual pattern of change seen beforehand (Fig. 3). Overall, however, there was no statistical indication that size increases for juveniles were either more gradual or more abrupt than size decreases ( $P > 0.34$ , Wilcoxon tests for all traits).



**Figure 3.** Morphological measurements for juvenile and adult individuals from 1966 to 1999. All measurements are in millimeters, except weight, in grams. Error bars are 95% bootstrapped confidence intervals. Dotted vertical lines indicate years where measurements are significantly different from the previous measured year, according to a post hoc Tukey's HSD test. Significance: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Timing of cyclones (C) that directly hit or came close to Heron Island, and El Niño events (E) of moderate to severe impact are indicated.

Posthoc Tukeys HSD tests show years where mean values were significantly different from the previous year or the last available datapoint (Fig. 3). There were no obvious patterns across all traits, however significant year-to-year shifts in juvenile tail, tarsus, and culmen length clustered in the 1980s. The perturbation of juvenile tarsus in the mid to late 1980s was particularly conspicuous in comparison to the stability of this measure observed at other times. No significant net size shift was observed from the beginning to the end of the time-series for juvenile wing ( $t$ -test,  $t = -0.08$ ,  $P > 0.9$ ), tail ( $t = 0.18$ ,  $P > 0.8$ ), tarsus ( $t = -0.7$ ,  $P > 0.4$ ) and weight ( $t = -0.3$ ,  $P > 0.7$ ), and adult tarsus ( $t = -1.3$ ,  $P > 0.1$ ) and culmen length ( $t = -1.3$ ,  $P > 0.1$ ). Juvenile culmen length decreased significantly from 1966 to 1999 ( $t = 4.3$ ,  $P < 0.0005$ ). Adult traits that displayed a significant increase were wing ( $t = -5.7$ ,  $P < 0.0005$ ), tail ( $t = -3.4$ ,  $P < 0.01$ ), and weight ( $t = -3.6$ ,  $P < 0.005$ ).

Overall, net shifts were observed in some traits, but trends were very variable and appeared episodic in nature. We examined the possibility that either cyclones or El Niño events coincided with morphological fluctuations. Four major cyclones hit or came in close proximity to Heron Island, in 1967, 1972, 1980, and 1992 (McCallum et al. 2000). An inspection of Figure 3 shows no consistent phenotypic impacts associated with cyclones in the data series. A significant decrease in juvenile tail and culmen length followed the 1967 cyclone, but in 1980, juvenile culmen length increased following the cyclone. Decreased juvenile weight was noted in the same or following year for two cyclones. Apart from these few associations, cyclones did not coincide with abrupt trait size changes. Likewise, there was limited evidence that El Niño events influenced the phenotype of the population. During the 34-year period, eight El Niño events occurred (one consisting of multiple years 1992 to 1994), of which six had a moderate to very strong impact in the region (marked in Fig. 3; Australian Bureau of Meteorology). Fluctuations in wing, tail, tarsus, and culmen lengths were not obviously associated with El Niño cycles. Abrupt decreases in average juvenile weight did coincide with El Niño years (1987, 1994, and 1997), although no such decrease was seen in 1982.

## MODELING RECENT SURVIVAL AND ESTIMATING SELECTION

### *Juvenile traits and survival probability*

Juvenile parameters were estimated from the capture histories of 510 birds that were measured and entered the encounter history as a juvenile (Table 2A). Model assessment preceding the inclusion of individual covariates is shown in Appendix 1A. A significantly large portion of variance remained unexplained under the simplest model of time variation in survival and recapture (Model 0, Appendix 1A) (GOF:  $\chi^2_{19} = 43.51$ ,  $P = 0.001$ ) and a more general model including specific parameters for juvenile, first-year

adults, and 2+ year adults (Model 1) provided a better description of the data ( $\chi^2_9 = 13.52$ ,  $P = 0.14$ ). The correction factor calculated from Model 1 was 1.503 (13.52/9), and was used to scale the deviance of subsequent models to correct for possible individual heterogeneity due to differences in covariate values. Note that when individual covariates were later included in models, the scale parameter was not used as these models already account for individual heterogeneity. In the most parsimonious model without individual covariates (Model 12, Appendix 1A) juvenile survival was season dependent and additionally showed variation across each of the three winters, as illustrated in Figure 4. Recapture estimates for the seven occasions in order were: 0.82, 0.82, 0.32, 0.85, 0.95, 0.92, and 0.83. Models were simplified by considering constant recapture across the last three capture occasions.

The addition of individual covariates to the base model (Model 12) improved the survival models tested (Table 2A). The best model that included individual covariates indicated that culmen width is the crucial trait influencing juvenile overwinter survival. There was only a marginal difference, as indicated by the AIC weight, between the two best models. The best model (Model 23, Table 2A) included a quadratic term for culmen width and the next best model (Model 18, Table 2A) included only the univariate term for culmen width. When other morphometric traits were considered separately (Models 13 to 17) or when combinations of body traits (Model 19) or culmen traits (Models 20 to 22 and 24) were included, models had lower support (Table 2A). Note that the link between survival and individual traits was considered only for the juvenile stage as trait value changes with individual age and adult values were unknown for most of these birds (see Methods).

### *Adult traits and survival probability*

We analyzed 248 capture histories of birds measured as adults. Model assessment preceding the inclusion of individual covariates is shown in Appendix 1B. The simplest model in which all parameters were time dependent (Model 25; Appendix 1B) provided a good fit of the data ( $\chi^2_{16} = 6.07$ ,  $P = 0.98$ ) and no correction factor was necessary. Recapture estimates for the seven occasions were 0.56, 0.98, 0.30, 0.97, 0.86, 0.97, and 0.83, respectively. The most parsimonious model without covariates showed yearly variation in survival (Model 32, Appendix 1B). Unlike juveniles, there was no strong seasonal effect on adult survival (Models 30 and 31), and particularly no specific effect of winter (Model 34). Yearly survival was generally high for adults (average = 0.81 calculated from Model 32), although some variation was evident (Fig. 4).

The addition of individual covariates to Model 32 revealed that, similar to juvenile survival, adult survival is influenced by a culmen trait, but in this case it is culmen length rather than

**Table 2.** Modeling survival and recapture probability including individual covariates for (A) birds measured as juveniles, and (B) birds measured as adults. For birds measured as juveniles, individual covariates were added to a base model (Model 12 Appendix 1A) of survival:  $2age.seas.yr^{\dagger}$  and recapture:  $2age.seas.yr^{\ddagger}$ . For birds measured as adults, individual covariates were added to a base model (Model 32, Appendix 1B) of survival:  $yr$  and recapture:  $seas.yr$ . (See Appendix 1 for model notation.) AICc, Akaike's Information Criterion; Np, number of estimable parameters; Weight, Akaike weights; DEV, model deviance. Individual covariate labels as in Table 1. Squared values refer to quadratic effects. For juveniles, individual covariate effects were applied to winter time-periods only, except Model 24, where the individual covariates were modeled across all time periods. The best model in each case is shown in bold.

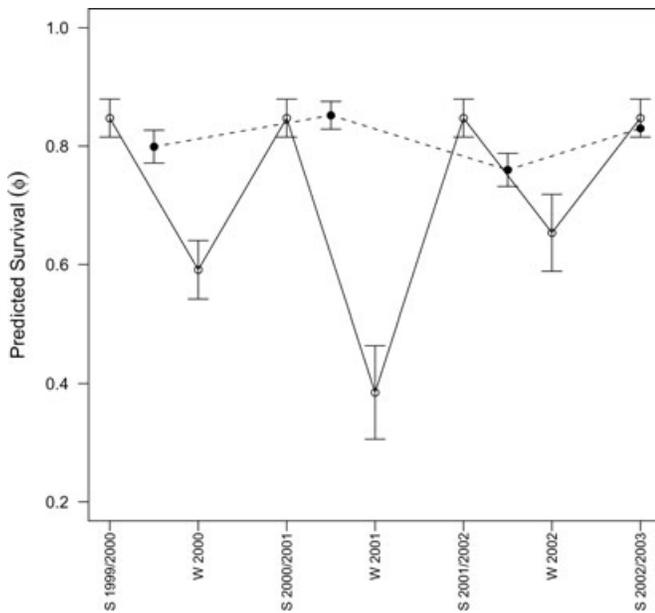
Model	Covariate	AICc	Np	$\Delta AICc$	Weight	DEV
(A)						
13	wing	1926.62	13	6.48	0.015	1900.29
14	tail	1926.72	13	6.58	0.015	1900.34
15	tarsus	1925.59	13	5.45	0.026	1899.27
16	culL	1926.81	13	6.67	0.014	1900.49
17	culD	1926.75	13	6.61	0.014	1900.43
18	culW	1920.30	13	0.16	0.363	1893.97
19	wing+tail+tarsus	1928.97	15	8.84	0.005	1898.55
20	culL+culD+culW	1922.86	15	2.72	0.101	1892.43
21	culL+culL <sup>2</sup>	1926.88	14	6.74	0.014	1898.50
22	culD+culD <sup>2</sup>	1928.78	14	8.64	0.005	1900.40
<b>23</b>	<b>culW+culW<sup>2</sup></b>	<b>1920.14</b>	<b>14</b>	<b>0</b>	<b>0.393</b>	<b>1891.76</b>
24	culW+culW <sup>2</sup>	1924.95	14	4.81	0.035	1896.58
(B)						
36	wing	1135.21	11	9.36	0.006	1112.81
37	tail	1133.97	11	8.13	0.011	1111.58
38	tarsus	1133.51	11	7.67	0.014	1111.12
39	culL	1128.12	11	2.28	0.198	1105.73
40	culD	1137.33	11	11.48	0.002	1112.86
41	culW	1131.45	11	5.6	0.038	1109.05
42	wing+tail+tarsus	1136.92	13	11.08	0.002	1110.37
43	culL+culD+culW	1133.79	14	7.94	0.012	1105.15
<b>44</b>	<b>culL+culL<sup>2</sup></b>	<b>1125.85</b>	<b>12</b>	<b>0</b>	<b>0.619</b>	<b>1101.38</b>
45	culD+culD <sup>2</sup>	1133.60	12	7.75	0.013	1109.13
46	culW+culW <sup>2</sup>	1129.76	12	3.92	0.087	1105.29

width (Model 44, Table 2B). In contrast to the juvenile analysis in which the difference between the two best models was marginal, including a quadratic effect for adult culmen length improved the fit of the model more than threefold according to the AIC weights. The inclusion of other traits, either considered separately (Models 36 to 41) or as suites of body and bill traits (Models 42, 43, 45, and 46), resulted in less well-supported models of adult survival (Table 2B). Note that PC rather than single traits were also used as individual covariates in juvenile and adult survival models. However these resulted in less well-supported models than those based on single traits (results not shown).

### Selection gradients

Selection gradients are given in Tables 3 and 4 for juveniles and adults, respectively. In juveniles, significant selection gradients were detected for one trait only, culmen width (Table 3A,B). The total (direct plus indirect) effect of selection on juvenile culmen

width was positive and highly significant in the first winter and when all winters were considered together (Table 3A). Analysis using multivariate selection gradients indicated that selection on culmen width was not influenced by indirect effects from other traits in the model (Table 3B). Significant negative  $\gamma$  values additionally indicate a net stabilizing effect on juvenile culmen width (Table 3A), again not influenced by other traits included in the model (Table 3B). Across all winters, significant correlational selection gradients were detected for tail and culmen width (gradient =  $0.18 \pm 0.07$ ,  $P < 0.05$ ). A negative correlational gradient between tarsus and culmen length was marginally nonsignificant (gradient =  $-0.14 \pm 0.07$ ,  $P = 0.052$ ). Selection gradients calculated for PC were not significant, although positive directional selection on PC1 (overall body size) in the first winter, and stabilizing selection on PC2 (body shape: longer wing and tail contrasted with narrower culmen width) across all winters, approached significance (Appendix 2A,B).



**Figure 4.** Predicted survival for juveniles (open circle, solid line), and adults (solid circle, dotted line). Average survival for juveniles is given each season and for adults each year. S, summer season, representing survival between September and April each year; W, winter season, survival between April and September. Yearly survival for adults is given from September to the following September.

In adults, total positive directional selection was detected for culmen length in Year 1 and across the entire four-year period (Table 3A). After accounting for the influence of other measured traits, significant selection coefficients for culmen length remained at these two time periods as well as in Year 4 (Table 4B). However total selection on culmen length in Year 4 was not significant (Table 4A). Direct negative selection on tarsus length in Years 1 and 4 and across all four years, likewise did not result in a net selective outcome. Significant total nonlinear selection was found for tail length and culmen width (stabilizing selection), and culmen depth (disruptive selection) in Year 1, and tail length (stabilizing selection) for all four years (Table 4A), and could be attributed to direct selection on these traits at these times (Table 4B). Across the four-year period, significant correlational selection was seen for one trait combination only, tarsus and culmen width (gradient =  $-0.47 \pm 0.20$ ,  $P < 0.01$ ). Selection gradients calculated for PC showed significant stabilizing selection on PC1 (body size) in Year 3 and across all four years (Appendix 2C,D). Stabilizing selection on PC2 (body shape: longer wing and tail contrasted with shorter tarsus) was evident in Year 2 and across all years (Appendix 2C,D). There was a suggestion of directional selection on overall body size in Year 1, but the gradient was marginally nonsignificant.

**Table 3.** Selection gradients ( $\pm$ standard error) for juveniles over winter. (A) Univariate linear ( $\beta_1$ ) and nonlinear ( $\gamma_1$ ) selection gradients and (B) multivariate linear ( $\beta_3$ ) and nonlinear ( $\gamma_2$ ) selection gradients. Significance: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . Subscript notation for  $\beta$  and  $\gamma$  follows Fairbairn and Preziosi (1996).

(A)								
Trait	Winter 2000		Winter 2001		Winter 2002		All winters	
	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$
Wing	$-0.01 \pm 0.06$	$0.12 \pm 0.08$	$0.14 \pm 0.16$	$0.11 \pm 0.22$	$-0.09 \pm 0.08$	$0.01 \pm 0.06$	$-0.02 \pm 0.05$	$0.07 \pm 0.04$
Tail	$0.06 \pm 0.06$	$< -0.01 \pm 0.08$	$-0.18 \pm 0.16$	$0.14 \pm 0.13$	$0.03 \pm 0.08$	$0.06 \pm 0.11$	$0.01 \pm 0.05$	$0.04 \pm 0.05$
Tarsus	$0.08 \pm 0.06$	$-0.02 \pm 0.09$	$-0.14 \pm 0.16$	$0.05 \pm 0.24$	$0.04 \pm 0.08$	$0.17 \pm 0.11$	$0.08 \pm 0.05$	$0.07 \pm 0.07$
CulL	$0.05 \pm 0.06$	$0.16 \pm 0.10$	$-0.18 \pm 0.16$	$0.08 \pm 0.15$	$-0.08 \pm 0.08$	$-0.14 \pm 0.11$	$< -0.01 \pm 0.05$	$0.11 \pm 0.07$
CulD	$0.06 \pm 0.06$	$0.03 \pm 0.07$	$-0.17 \pm 0.16$	$0.34 \pm 0.21$	$-0.08 \pm 0.09$	$-0.06 \pm 0.09$	$0.03 \pm 0.05$	$0.02 \pm 0.05$
CulW	$0.13 \pm 0.06^*$	$-0.18 \pm 0.09^*$	$0.06 \pm 0.16$	$-0.09 \pm 0.23$	$0.13 \pm 0.10$	$0.10 \pm 0.20$	$0.17 \pm 0.05^{***}$	$-0.12 \pm 0.07$

(B)								
Trait	Winter 2000		Winter 2001		Winter 2002		All winters	
	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$
Wing	$-0.06 \pm 0.06$	$0.12 \pm 0.08$	$0.32 \pm 0.20$	$0.06 \pm 0.23$	$-0.10 \pm 0.10$	$0.03 \pm 0.07$	$-0.05 \pm 0.05$	$0.05 \pm 0.04$
Tail	$0.07 \pm 0.06$	$-0.05 \pm 0.08$	$-0.32 \pm 0.20$	$< -0.01 \pm 0.16$	$0.11 \pm 0.10$	$0.02 \pm 0.11$	$0.03 \pm 0.05$	$< -0.01 \pm 0.06$
Tarsus	$0.03 \pm 0.07$	$-0.05 \pm 0.09$	$-0.09 \pm 0.17$	$0.03 \pm 0.27$	$0.08 \pm 0.09$	$0.19 \pm 0.12$	$0.06 \pm 0.05$	$0.04 \pm 0.07$
CulL	$-0.07 \pm 0.09$	$0.21 \pm 0.11$	$-0.14 \pm 0.19$	$0.15 \pm 0.16$	$-0.11 \pm 0.10$	$-0.15 \pm 0.13$	$-0.11 \pm 0.06$	$0.12 \pm 0.07$
CulD	$-0.01 \pm 0.08$	$0.08 \pm 0.08$	$-0.14 \pm 0.20$	$0.39 \pm 0.25$	$-0.10 \pm 0.10$	$-0.07 \pm 0.10$	$-0.04 \pm 0.06$	$0.04 \pm 0.06$
CulW	$0.16 \pm 0.08^*$	$-0.22 \pm 0.10^*$	$0.15 \pm 0.19$	$-0.28 \pm 0.25$	$0.11 \pm 0.11$	$0.01 \pm 0.23$	$0.22 \pm 0.06^{***}$	$-0.16 \pm 0.07^*$

**Table 4.** Selection gradients ( $\pm$ standard error) for adults. (A) Univariate linear ( $\beta_1$ ) and nonlinear ( $\gamma_1$ ) selection gradients and (B) multivariate linear ( $\beta_3$ ) and nonlinear ( $\gamma_2$ ) selection gradients. Significance: \*  $P < 0.05$ , \*\*  $P < 0.01$ . Year 1, Sept 1999 to Sept 2000; Year 2, Sept 2000 to Sept 2001; Year 3, Sept 2001 to Sept 2002; Year 4, Sept 2002 to April 2003; All Years, Sept 1999 to April 2003. Subscript notation for  $\beta$  and  $\gamma$  follows Fairbairn and Preziosi (1996).

Trait	Year 1		Year 2		Year 3		Year 4		All years	
	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$
Wing	0.03 $\pm$ 0.05	-0.04 $\pm$ 0.07	-0.01 $\pm$ 0.05	0.02 $\pm$ 0.07	0.04 $\pm$ 0.07	-0.12 $\pm$ 0.09	-0.04 $\pm$ 0.06	-0.12 $\pm$ 0.07	<-0.01 $\pm$ 0.16	-0.31 $\pm$ 0.22
Tail	-0.05 $\pm$ 0.05	-0.29 $\pm$ 0.08**	-0.02 $\pm$ 0.05	-0.03 $\pm$ 0.09	-0.01 $\pm$ 0.07	0.01 $\pm$ 0.08	0.04 $\pm$ 0.06	-0.01 $\pm$ 0.06	-0.20 $\pm$ 0.16	-0.58 $\pm$ 0.24*
Tarsus	-0.03 $\pm$ 0.05	-0.03 $\pm$ 0.08	-0.04 $\pm$ 0.05	-0.10 $\pm$ 0.08	-0.03 $\pm$ 0.07	-0.07 $\pm$ 0.12	-0.09 $\pm$ 0.06	0.15 $\pm$ 0.10	-0.18 $\pm$ 0.16	-0.13 $\pm$ 0.24
CulL	0.15 $\pm$ 0.05**	-0.09 $\pm$ 0.07	0.04 $\pm$ 0.05	-0.05 $\pm$ 0.07	0.03 $\pm$ 0.07	-0.14 $\pm$ 0.09	0.09 $\pm$ 0.06	-0.04 $\pm$ 0.08	0.48 $\pm$ 0.15**	-0.26 $\pm$ 0.21
CulD	0.01 $\pm$ 0.05	0.12 $\pm$ 0.05*	-0.04 $\pm$ 0.05	0.05 $\pm$ 0.06	0.07 $\pm$ 0.07	0.06 $\pm$ 0.07	<-0.01 $\pm$ 0.06	-0.06 $\pm$ 0.06	0.20 $\pm$ 0.16	0.13 $\pm$ 0.17
CulW	0.10 $\pm$ 0.05	-0.18 $\pm$ 0.08*	0.05 $\pm$ 0.05	-0.08 $\pm$ 0.08	0.11 $\pm$ 0.07	-0.04 $\pm$ 0.09	-0.08 $\pm$ 0.06	0.01 $\pm$ 0.09	<0.01 $\pm$ 0.16	-0.45 $\pm$ 0.24

Trait	Year 1			Year 2			Year 3			Year 4			All years		
	$\beta_3$	$\gamma_2$	$\gamma_1$	$\beta_3$	$\gamma_2$	$\gamma_1$	$\beta_3$	$\gamma_2$	$\gamma_1$	$\beta_3$	$\gamma_2$	$\gamma_1$	$\beta_3$	$\gamma_2$	$\gamma_1$
Wing	<0.01 $\pm$ 0.05	<0.01 $\pm$ 0.07	-0.03 $\pm$ 0.06	0.04 $\pm$ 0.07	0.03 $\pm$ 0.07	-0.11 $\pm$ 0.09	-0.06 $\pm$ 0.07	-0.08 $\pm$ 0.07	-0.07 $\pm$ 0.16	-0.18 $\pm$ 0.21					
Tail	-0.06 $\pm$ 0.05	-0.27 $\pm$ 0.08**	<-0.01 $\pm$ 0.06	<0.01 $\pm$ 0.09	-0.04 $\pm$ 0.08	0.01 $\pm$ 0.08	0.08 $\pm$ 0.07	<0.01 $\pm$ 0.06	-0.24 $\pm$ 0.16	-0.53 $\pm$ 0.24*					
Tarsus	-0.11 $\pm$ 0.05*	-0.05 $\pm$ 0.07	-0.05 $\pm$ 0.06	-0.11 $\pm$ 0.09	-0.05 $\pm$ 0.08	-0.05 $\pm$ 0.12	-0.16 $\pm$ 0.07*	0.17 $\pm$ 0.10	-0.41 $\pm$ 0.16*	-0.11 $\pm$ 0.23					
CulL	0.18 $\pm$ 0.06**	-0.05 $\pm$ 0.07	0.06 $\pm$ 0.06	-0.02 $\pm$ 0.08	<0.01 $\pm$ 0.08	-0.10 $\pm$ 0.10	0.16 $\pm$ 0.07*	-0.06 $\pm$ 0.09	0.68 $\pm$ 0.17***	-0.13 $\pm$ 0.21					
CulD	-0.04 $\pm$ 0.05	0.09 $\pm$ 0.05*	-0.06 $\pm$ 0.06	0.05 $\pm$ 0.07	0.06 $\pm$ 0.08	0.04 $\pm$ 0.08	0.02 $\pm$ 0.07	-0.05 $\pm$ 0.07	0.18 $\pm$ 0.16	-0.13 $\pm$ 0.17					
CulW	0.07 $\pm$ 0.06	-0.20 $\pm$ 0.08*	0.06 $\pm$ 0.06	-0.08 $\pm$ 0.09	0.09 $\pm$ 0.08	<-0.01 $\pm$ 0.12	-0.12 $\pm$ 0.07	0.08 $\pm$ 0.10	-0.19 $\pm$ 0.19	-0.42 $\pm$ 0.24					

(B)

## Discussion

The examination of evolutionary divergence of a morphologically distinct island-dwelling bird population, considered over three microevolutionary timescales has provided a rare empirical insight into the tempo and mode of divergence in a natural system. The *Zosterops* population on Heron Island has undergone a substantial body size increase since colonization, a maximum of 4000 years ago. Theoretically, sustained directional selection can produce large-scale shifts, even with weak selection pressures (Kingsolver and Pfennig 2004). However, constancy of selection is likely to be an unrealistic assumption in most systems (Kinnison and Hendry 2001; Estes and Arnold 2007). In Heron Island *Zosterops*, this issue is highlighted when comparing current selection strengths with net selection intensities required to explain the long-term morphological shift. Current selection was higher, frequently an order of magnitude higher, than the net selection intensity required to explain long-term divergence for many traits, and was interpreted as evidence of heterogeneity in form and strength of selection over the divergence period (Kinnison and Hendry 2001).

### CHARACTERIZING HETEROGENEITY IN SELECTION

Establishing the presence of heterogeneity in selection operating in a system is a first step to understanding the divergence process. However, reconstructing that heterogeneity across evolutionary time is a difficult task. In the case presented here, three lines of evidence support a scenario of rapid evolution toward a new optimum followed by many generations of minimal change. First, the comparison of mainland and island phenotypes shows that a substantial shift in the optimum phenotype accompanied the colonization of the island environment. Second, tracking the morphology of the island population over a period of four decades demonstrates a lack of directional change that would be consistent with ongoing directional selection. Finally, recent estimates of selection gradients based on survival analysis show that current selection is relatively weak for most traits that have increased significantly in size in the island form.

The rate at which the silveryeye population shifted toward the new island optimum after colonization was explored using the displaced optimum model (Estes and Arnold 2007). Under a range of potential adaptive landscapes, the approach to the new optimum occurred in far fewer generations than even the lowest estimate of divergence time (1000 generations). This supports the hypothesis that under novel selective conditions on the island, the bulk of the evolutionary difference observed developed rapidly, possibly in the first couple of hundred generations after colonization. This would represent at least a doubling of the maximum evolutionary rate reported in Table 1, and even if we assume the shift occurred over a conservative 500 generations, all estimates of evolutionary rates would be above the median value ( $5.3 \times 10^{-3}$ ) reported

by Kinnison and Hendry (2001). Historically documented colonizations by *Zosterops lateralis* from Australia to New Zealand and outlying islands indicate that morphological shifts can occur quickly, too quickly to be accounted for by drift alone (Clegg et al. 2002b). We can only speculate on the proximate causes of selection during the period following colonization. However given that the newly established population was experiencing a novel environment in numerous aspects of ecology (e.g., changes in interspecific competition, predator and parasite pressures, and resource availability), physiology (e.g., changes in response to the new abiotic environment), and behavior (e.g., changes in dominance behavior associated with levels of intraspecific competition), it is likely that a complex and multifaceted selection regime was operating.

Following an initial phase of rapid divergence we suggest that the population has since remained relatively stable, with oscillations occurring around the optimum phenotype. In support of this, we find no consistent directional trends for any trait over a 34-year period. Fluctuations in the direction of change also resulted in a lack of net size shifts when comparing the beginning and end of the time period for most juvenile and some adult traits. Additionally, for traits in which a significant net shift was noted across decades, recent significant selection gradients were not directional (e.g., adult tail length increased significantly when comparing 1966 to 1999 measurements, whereas contemporary selection was stabilizing). Conversely, traits that have recently been subject to directional selection show no significant shift across decades (e.g., adult tarsus and culmen length) (Table 5). These results, describing temporal variation in direction and strength and targets of selection, support the view of a population tracking relatively small changes in the environment. A caveat of this interpretation is that we are assuming that the morphological fluctuations are the result of a selective response. Cases in which directional selection has been shown to be operating but the morphological response is in the opposite direction (e.g., Larsson et al. 1998; Garant et al. 2004) or there is no phenotypic response despite the selection pressure (Merilä et al. 2001b) caution that morphological shifts may not be accurately reflecting the underlying selective mechanism. However, detecting fluctuating and episodic selection and shifts in targets of selection is not uncommon in long-term studies (e.g., Grant 1985; Schluter et al. 1991; Grant and Grant 1995, 2002; Badyaev et al. 2000; Coulson et al. 2003). For instance, Grant (1985) showed that directional selection for longer and deeper bills in *Geospiza conirostris* was counteracted by selection in the opposite direction on correlated traits, on the same trait in the other sex, and at different life stages, thereby constraining evolutionary change. In *G. fortis* and *G. scandens* natural selection was also seen to vary between oscillating, directional, episodic, and gradual over a 30-year period due to environmental events that could not be predicted (Grant and Grant 2002).

**Table 5.** Summary of directions of phenotypic shift and current selection for each trait over three timescales. Trait labels as in Table 1. J, juvenile; A, adult. Pop. Div. is the direction in change of the island compared to the mainland population. Net change indicates if a significant size shift in a positive (+) or negative direction (–) was observed from 1966 to 1999 or if no net shift (no  $\Delta$ ) occurred (but note that no consistent trends were observed for any trait across decades). Codes for total (univariate linear) and direct (multivariate linear) selection are: –ns, negative direction but nonsignificant; +ns, positive direction but nonsignificant; –, significant negative selection; +, significant positive selection; na=not assessed. Bold indicates significant results.

Trait	Pop. Div. (millennia)	Net change (decades)		Selection (years)			
		J	A	Indirect		Direct	
				J	A	J	A
Wing	+	no $\Delta$	+	–ns	–ns	–ns	–ns
Tail	+	no $\Delta$	+	+ns	–ns	+ns	–ns
Tarsus	+	no $\Delta$	no $\Delta$	+ns	–ns	+ns	–
CulL	+	–	no $\Delta$	–ns	+	–ns	+
CulD	+	na	na	+ns	+ns	–ns	+ns
CulW	+	na	na	+	+ns	+	–ns
Weight	+	no $\Delta$	+	na	na	na	na

Reviews of estimates of selection gradients and differentials across a range of studies indicate generally weak directional selection for morphological traits (median  $|\beta| = 0.17$ ) (Kingsolver et al. 2001), tending to be weaker still when calculated using viability (survival) analysis and conducted over a timescale of years, (median  $|\beta| = 0.07$ ) (Hoekstra et al. 2001). The estimates of selection presented here are therefore in line with other studies of this kind (morphological studies based on survival across a number of years), and with few exceptions discussed below, are consistent with a generally weak directional selection regime. The weak strength of recent directional selection on individual traits and cases of stabilizing selection on overall body size and some shape parameters during some years supports the idea of maintenance near an optimum as directional selection wanes and stabilizing selection becomes more prevalent (Hunt et al. 2008).

Significant directional selection was detected for culmen measurements and tarsus length from 1999 to 2003. This finding remains compatible with the maintenance of the population near some optimum according to a number of scenarios that have been invoked to explain the existence of stasis in systems that are subject to directional selection (see Merilä et al. 2001b). First, the current directional selection on culmen traits and tarsus length may be transient, and opposing selection at other times and life-history stages may negate any directional shifts (Schluter et al. 1991; Grant and Grant 2002). Second, the traits may appear to

be under direct selection due to selection on other traits that are highly genetically correlated. Shifts in direction of selection on any correlated traits could therefore limit change in the traits of interest. Third, selection can only produce a response if it acts on a heritable trait rather than one that is largely or entirely plastic (Falconer and Mackay 1996). Morphological traits such as those of interest here, culmen length and width, and tarsus length, generally have a significant additive genetic variation component in birds (Merilä and Sheldon 2001). For Heron Island silvereyes, analysis in progress indicates heritability estimates in the order of 0.7 for tarsus and 0.2 for culmen measures (S. M. Clegg, F. D. Frenitu, I. P. F. Owens, and M. Blows, unpubl. results). Therefore, for culmen measures at least, there is the possibility that the directional selection detected will not result in an evolutionary response. Finally, even if a trait is highly heritable, such as tarsus length, selection may act entirely or partly on the remaining environmental component of phenotypic variation rather than directly on the genetic component, limiting an evolutionary response (e.g., Alatalo et al. 1990). Long-term studies of wild bird populations have demonstrated selection acting on environmental deviations, however concurrent selection on genetic components were also evident (Merilä et al. 2001a; Garant et al. 2004).

We cannot fully assess which, if any, of these alternatives may limit evolutionary change despite directional selection on tarsus and culmen measures without a more complete understanding of the underlying quantitative genetic parameters in the population. However, morphological trends over the previous decades indicate that changes in the direction of selection at different times is a plausible mechanism to explain why traits under current directional selection have not exhibited an evolutionary shift over decades. Short series of trends in the data suggest that at times in previous years, larger bills in both juveniles and adults may have conferred a selective advantage, but reversals of direction of selection have resulted in no net change. Our selection study may have therefore coincided with a time period when having a larger bill directly improved chances of survival. There is also some indication that opposing selection directions at different life-history stages may operate. The multivariate selection coefficient for culmen width in juveniles is matched by a coefficient of similar magnitude, but opposite sign in adults, although the adult estimate is not significant due to small sample sizes. Selection on correlated traits is also possible in this system. Significant or near-significant correlational selection was noted for a limited set of traits, and depending on the genetic correlation between them, the response to selection may be limited.

#### ENVIRONMENTAL INFLUENCES ON MORPHOLOGY

The proximate environmental causes of morphological fluctuations across decades and years are not easily identified. Two types of large-scale recurring environmental disturbances that possibly

influence the pattern of morphological fluctuations are tropical cyclones and El Niño events. Tropical cyclones may act as a selective agent, with a particular phenotype gaining a selective advantage during and immediately after a cyclone, similar to what has previously been shown to occur in birds that experience extreme and abrupt environmental events (e.g., Bumpus 1899; Brown and Brown 1998). High mortality rates from cyclones (Brook and Kikkawa 1998; McCallum et al. 2000) could also provide conditions conducive to rapid, drift-mediated phenotypic shifts. El Niño events are less abrupt, lasting from months to years, and lead to lower than expected average rainfall with severe events characterized by extreme and extended drought conditions. However, despite the potential for either cyclones or El Niño events to affect morphological fluctuations in the population, we found little evidence that either type of event produced a consistent effect in the Heron Island silvereye population. Surviving a cyclone may simply be due to chance but drift may not have an opportunity to affect the phenotypic distribution due to rapid recovery from postcyclone population decreases (McCallum et al. 2000). El Niño events vary in their severity and therefore, it may be unreasonable to expect consistent impacts across separate events. A more detailed analysis of survival at these times would be required to fully assess the impact of these complex environmental events, as has been done for Darwin's finches on the Galápagos Islands where selective episodes were driven by El Niño cycles (Grant and Grant 1993).

Environmental fluctuations that result in an interplay of factors affecting food abundance and population density (Brook and Kikkawa 1998; McCallum et al. 2000) are a likely explanation for the variation in survival probability and selection for different ages, seasons and years seen across the survival study. The age-related differences in survival may reflect successful passage through earlier selection filters, or be due to increases in competence gained through experience throughout the lifetime of an individual (Forslund and Pärt 1995). The evidence that adult birds are not released from selection, despite having passed through previous selection filters, along with changes in aggressive behavior across the lifetime of individuals (Kikkawa 1987), and shifts in juvenile and adult foraging strategies (Catterall et al. 1989; Jansen 1989) implies an important role for experience gained with age in determining survival.

Previous studies of the population have noted that when population densities were very high, larger individuals had higher overwinter survival (Kikkawa 1980; Robinson-Wolrath and Owens 2003). Under high-density conditions, links between bill size and foraging ability or efficiency, such as that found in other avian species (e.g., Boag and Grant 1981; Grant 1986; Smith 1987; Benkman 1993) may be more pronounced. Alternatively, a less direct mechanism may be at play, where larger sized individuals have an advantage in aggressive interactions and thereby

control of food resources (Robinson-Wolrath and Owens 2003). In the Heron Island population, larger bill size and overall body size has been shown to be positively associated with the proportion of fights won (Kikkawa 1980), making this mechanism a contender for explaining the advantages of large bill over short timescales. However, whether fluctuations in these traits seen over decades and years represent a plastic or genetic response to selection requires additional quantitative treatment.

## Conclusions

Directional selection has been an important force in the divergence of the Capricorn silvereye from its mainland ancestor. However evidence from three microevolutionary timescales indicates that there has been temporal variation in the form and strength of selection in the 4000 years or less since colonization. A model of rapid directional evolution toward a new phenotypic optimum, followed by an extended time of proximity around the acquired optimum is consistent with the substantial phenotypic shift, relative phenotypic stability across four recent decades and generally weak current directional selection for morphological traits. Traits that are subject to contemporary directional selection may not have an evolutionary response if selection is reversed over time, is in opposing directions at different life-history stages, or if genetic correlations limit a response to selection. Additionally, there is a possibility that additive genetic variation in the direction of the observed morphological shift has been depleted via the action of directional selection. A full multivariate quantitative genetic approach is needed to assess how limited the population may be in terms of its ability to mount an evolutionary response to any further optimum shifts, particularly if the direction is an extension of the preceding trajectory.

## ACKNOWLEDGMENTS

We thank S. Arnold, M. Blows, T. Coulson, M. Crawley, S. Estes, H. Hollocher, R. Lande, D. Orme, A. Phillimore, and J. Worthington Wilmer for comments on the manuscript and suggestions or help with analyses; C. Catterall, P. Fisk, C. Edwards, M. Losiak, F. Manson, S. Robinson-Wolrath, S. Scott, and C. Wiley for contributions to field work; P. Douglas for early database management; Heron Island Research Station, P & O Heron Island Resort, Queensland Museum, and M. Blows for logistical support. Insightful comments from three anonymous referees greatly improved the manuscript. All work was conducted under permits from the Australian Bird and Bat Banding Scheme, Queensland Environmental Protection Agency and Animal Ethics Committee of The University of Queensland. Funding was provided by grants from Natural Environment Research Council (UK) and the Australian Research Council.

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Associate Editor: H. Hollocher

**Appendix 1.** Comparison of models of survival and recapture prior to adding individual covariates for (A) birds measured as juveniles and (B) birds measured as adults. QAICc, corrected Akaike's Information Criterion; Np, number of estimable parameters; Weight, Akaike weights; DEV, model deviance. Model notation: 3age, different parameters for juvenile, first-year adults and 2+year adults; 2age, different parameters for juvenile and all adults; seas, different parameters for seasons of winter and summer; yr, different parameters for year. ', interaction between main effects; '+', only main effects (i.e., parallel regression), '-'=constant (i.e., no effects). ‡ season effect only in juveniles; † year dependent only in summer survival; \* year dependent only in winter survival; § equal recapture over last three occasions. The best model in each case is shown in bold.

Model	Survival	Recapture	QAICc	Np	ΔQAICc	Weight	DEV
(A)							
0	seas.yr	seas.yr	1312.15	13	23.34	<0.001	1285.82
1	3age.seas.yr	3age.seas.yr	1302.29	26	13.48	<0.001	1249.02
2	3age.seas.yr	2age.seas.yr <sup>§</sup>	1294.35	21	5.54	0.038	1251.52
3	3age+seas+yr	3age.seas.yr	1306.87	20	18.06	<0.001	1266.11
4	3age+seas	3age.seas.yr	1305.38	18	16.57	<0.001	1268.76
5	3age.seas	3age.seas.yr	1303.91	20	15.10	<0.001	1263.16
6	3age.yr	3age.seas.yr	1325.70	21	36.89	<0.001	1282.87
7	3age+seas	2age.seas.yr <sup>§</sup>	1300.28	11	11.48	0.002	1278.05
8	3age.seas	2age.seas.yr <sup>§</sup>	1293.42	13	4.61	0.061	1267.09
9	2age.seas	2age.seas.yr <sup>§</sup>	1292.82	11	4.01	0.082	1270.58
10	2age.seas <sup>†</sup>	2age.seas.yr <sup>§</sup>	1291.29	10	2.48	0.176	1271.09
11	2age.seas.yr <sup>††</sup>	2age.seas.yr <sup>§</sup>	1294.64	13	5.83	0.033	1268.31
12	<b>2age.seas.yr<sup>†</sup>*</b>	<b>2age.seas.yr<sup>§</sup></b>	<b>1288.81</b>	<b>12</b>	<b>0</b>	<b>0.608</b>	<b>1264.53</b>
(B)							
25	seas.yr	seas.yr	1137.51	13	4.28	0.041	1110.96
26	seas.yr	seas.yr <sup>§</sup>	1140.27	12	7.05	0.010	1115.80
27	seas.yr	seas+yr	1142.60	11	9.38	0.003	1120.20
28	seas.yr	seas	1200.97	9	67.75	<0.001	1182.70
29	seas.yr	yr	1241.94	11	108.72	<0.001	1219.54
30	yr+seas	seas.yr	1135.27	11	2.05	0.125	1112.87
31	seas	seas.yr	1137.51	9	4.29	0.041	1119.24
32	<b>yr</b>	<b>seas.yr</b>	<b>1133.22</b>	<b>10</b>	<b>0</b>	<b>0.348</b>	<b>1112.89</b>
33	-	seas.yr	1135.46	8	2.24	0.114	1119.25
34	seas.yr <sup>*</sup>	seas.yr	1139.39	11	6.17	0.016	1116.99
35	seas.yr <sup>††</sup>	seas.yr	1133.51	11	0.28	0.302	1111.12

**Appendix 2.** Selection gradients ( $\pm$ standard error) on principal components (PC). Univariate linear ( $\beta_1$ ) and nonlinear ( $\gamma_1$ ) selection gradients for (A) juveniles and (C) adults. Multivariate linear ( $\beta_3$ ) and nonlinear ( $\gamma_2$ ) selection gradients for (B) juveniles and (D) adults. Significance: # $P < 0.1$ , \*  $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . PC were calculated for each dataset separately. Proportion of variation described by each PC for juveniles: PC1 33% to 48%; PC2 17% to 20%; PC3 12% to 19%. In juveniles, PC1 represents overall body size, PC2 is a shape axis, contrasting longer wing and tail with shorter tarsus and/or smaller bill measures for different winters, and PC3 is a shape axis contrasting wing length with tail length and shifts in tarsus and culmen width. Proportion of variation for adults: PC1 31% to 34%; PC2 21% to 22%; PC3 14% to 15%. In adults, PC1 represents overall body size, PC2 is a shape axis with increased wing and tail length contrasted with decreased tarsus and/or culmen length, and PC3 is a shape axis but trait loadings and directions vary across years. Subscript notation for  $\beta$  and  $\gamma$  follows Fairbairn and Preziosi (1996).

Trait	Winter 2000		Winter 2001		Winter 2002		All winters	
	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$
PC1	0.09 $\pm$ 0.06#	<-0.01 $\pm$ 0.10	-0.13 $\pm$ 0.16	0.22 $\pm$ 0.21	-0.04 $\pm$ 0.08	-0.06 $\pm$ 0.14	0.07 $\pm$ 0.05	0.06 $\pm$ 0.07
PC2	-0.04 $\pm$ 0.06	-0.04 $\pm$ 0.08	0.15 $\pm$ 0.16	0.33 $\pm$ 0.22	-0.01 $\pm$ 0.08	0.06 $\pm$ 0.10	-0.08 $\pm$ 0.05#	0.02 $\pm$ 0.05
PC3	-0.03 $\pm$ 0.06	0.03 $\pm$ 0.09	-0.13 $\pm$ 0.16	-0.08 $\pm$ 0.27	-0.30 $\pm$ 0.25	<0.01 $\pm$ 0.07	0.02 $\pm$ 0.05	0.01 $\pm$ 0.07

Trait	Winter 2000		Winter 2001		Winter 2002		All winters	
	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$
PC1	0.09 $\pm$ 0.06#	<0.01 $\pm$ 0.10	-0.13 $\pm$ 0.16	0.18 $\pm$ 0.22	-0.04 $\pm$ 0.08	-0.04 $\pm$ 0.15	0.07 $\pm$ 0.05	0.06 $\pm$ 0.07
PC2	-0.04 $\pm$ 0.06	-0.05 $\pm$ 0.08	0.15 $\pm$ 0.16	0.31 $\pm$ 0.24	-0.01 $\pm$ 0.08	0.04 $\pm$ 0.10	-0.08 $\pm$ 0.05#	0.01 $\pm$ 0.05
PC3	-0.03 $\pm$ 0.07	0.02 $\pm$ 0.09	-0.13 $\pm$ 0.16	-0.12 $\pm$ 0.28	-0.10 $\pm$ 0.08	<0.01 $\pm$ 0.07	0.02 $\pm$ 0.05	<-0.01 $\pm$ 0.07

Trait	Year 1		Year 2		Year 3		Year 4		All years	
	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$	$\beta_1$	$\gamma_1$
PC1	0.09 $\pm$ 0.05#	-0.08 $\pm$ 0.07	<0.01 $\pm$ 0.05	0.02 $\pm$ 0.07	0.07 $\pm$ 0.07	-0.20 $\pm$ 0.08*	-0.02 $\pm$ 0.06	0.03 $\pm$ 0.08	0.18 $\pm$ 0.16	-0.42 $\pm$ 0.22#
PC2	-0.03 $\pm$ 0.05	-0.16 $\pm$ 0.08*	-0.01 $\pm$ 0.05	-0.12 $\pm$ 0.08	-0.01 $\pm$ 0.07	-0.01 $\pm$ 0.10	<-0.01 $\pm$ 0.06	0.09 $\pm$ 0.10	-0.09 $\pm$ 0.16	-0.45 $\pm$ 0.24#
PC3	<0.01 $\pm$ 0.05	0.12 $\pm$ 0.07	0.01 $\pm$ 0.05	-0.03 $\pm$ 0.07	-0.12 $\pm$ 0.07	0.06 $\pm$ 0.10	-0.01 $\pm$ 0.06	-0.09 $\pm$ 0.06	0.11 $\pm$ 0.16	0.21 $\pm$ 0.23

Trait	Year 1		Year 2		Year 3		Year 4		All years	
	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_3$	$\gamma_2$	$\beta_1$	$\gamma_1$
PC1	0.09 $\pm$ 0.05#	-0.10 $\pm$ 0.07	<0.01 $\pm$ 0.06	0.02 $\pm$ 0.07	0.07 $\pm$ 0.07	-0.20 $\pm$ 0.09*	-0.02 $\pm$ 0.06	0.03 $\pm$ 0.08	0.18 $\pm$ 0.16	-0.45 $\pm$ 0.22*
PC2	-0.03 $\pm$ 0.05	-0.18 $\pm$ 0.08*	-0.01 $\pm$ 0.05	-0.12 $\pm$ 0.08	-0.01 $\pm$ 0.07	0.01 $\pm$ 0.09	<-0.01 $\pm$ 0.06	0.13 $\pm$ 0.10	-0.09 $\pm$ 0.16	-0.52 $\pm$ 0.24*
PC3	<0.01 $\pm$ 0.05	0.12 $\pm$ 0.07	0.05 $\pm$ 0.05	-0.02 $\pm$ 0.07	-0.12 $\pm$ 0.07	0.09 $\pm$ 0.10	-0.01 $\pm$ 0.06	-0.12 $\pm$ 0.06#	0.11 $\pm$ 0.16	-0.25 $\pm$ 0.23