Shorebirds are shrinking and shape-shifting: declining body size and lengthening bills in the past half-century

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ABSTRACT

Animals are predicted to shrink and shape-shift as the climate warms; declining in size, while their appendages lengthen. Determining which types of species are undergoing these morphological changes, and why, is critical to understanding species responses to global change, including potential adaptation to climate warming. We examine body size and bill length changes in 25 shorebird species using extensive field data (>200,000 observations) collected over 46 years (1975-2021) by community scientists. We show widespread body size declines over time, and after short-term exposure to warmer summers. Meanwhile, shorebird bills are lengthening over time but shorten after hot summers. Shrinking and shape-shifting patterns are consistent across ecologically diverse shorebirds from tropical and temperate Australia, are more pronounced in smaller species, and vary according to migration behaviour. These widespread morphological changes could be explained by multiple drivers, including adaptive and maladaptive responses to nutritional stress, or by thermal adaptation to climate warming.

INTRODUCTION

The impacts of climate change on animals are profound (Scheffers *et al.* 2016; Hoffmann *et al.* 2019). Species' geographic ranges are shifting (MacLean & Beissinger 2017), the timing of life-history events is changing (Visser *et al.* 2004; Jonzén *et al.* 2006), and climate-linked extinction has been documented (Waller *et al.* 2017). Evidence is also accumulating that animal body size is declining ('shrinking') (Gardner *et al.* 2011; Sheridan & Bickford 2011) while appendages – for example, limbs, ears, tails, and bills – are lengthening, causing changes in body shape ('shape-shifting') (Ryding *et al.* 2021). These changes may result from thermal adaptations to climate warming – because smaller bodies and longer appendages increase the relative surface area available for heat loss (Allen 1877; Salewski & Watt 2017) – or other drivers, including increased nutritional stress (Rode *et al.* 2010; Van Gils *et al.* 2016). Evidence for shrinking comes from studies showing widespread body size declines in birds (Van Buskirk *et al.* 2010; Weeks *et al.* 2020; Jirinec *et al.* 2021; Dubiner & Meiri 2022; Youngflesh *et al.* 2022). However, others report inconsistent changes (Salewski *et al.* 2010, 2014) and even increasing size through time (Yom-Tov & Yom-Tov 2005; Goodman *et al.* 2012; Warrington & Waterman 2023; Neate-Clegg *et al.* 2024), while predicted changes in appendage size are less well explored (Ryding *et al.* 2021). Inconsistent results across studies might be explained by animals changing size or shape as alternate strategies for increasing their relative surface area as the climate warms, necessitating further research investigating both shrinking and shape-shifting phenomena (Baldwin *et al.* 2023; Fröhlich *et al.* 2023). Variation in morphological trends may be further explained by drivers of morphological change impacting some species more than others. To better understand global climate change implications for species survival, we need better knowledge of the prevalence of morphological change across diverse species worldwide, including which types of species are shrinking and shape-shifting and why.

Empirical evidence for shrinking and shape-shifting trends is biased to temperate regions of the northern hemisphere (but see Jirinec et al. 2021), and it is unknown whether morphological changes differ for tropical and temperate populations. Temperate regions have been subject to more rapid warming than the tropics (IPCC 2021), which may entail greater disruption of food supply or phenological mismatch between breeding and peak food abundance, leading to smaller size due to reduced energy stores (Lameris *et al.* 2022) and negative impacts on growth during early development (Van Gils *et al.* 2016). Warming winters in temperate regions could reduce the energetic costs of thermoregulation, enabling smaller animals to persist over time (Zheng *et al.* 2023). Meanwhile, warming temperate summers might select for morphological change to improve heat loss in animals that are otherwise less well adapted to mitigate heat stress (Oswald & Arnold 2012). Conversely, in the tropics, slight warming may push animals closer to their physiological limits (Oswald & Arnold 2012), leading to stronger selection for reduced size and longer appendages to maximise heat loss, or size declines due to heat stress impacts on foraging.

Species size may influence morphological change; larger species are predicted to show stronger shrinking and shape-shifting trends because their low relative surface area makes them more vulnerable to heat stress (Geiser & Turbill 2009; McCain & King 2014). Alternatively, smaller species could show greater rates of morphological change due to inherent characteristics that facilitate rapid evolution (Zimova *et al.* 2023).

Morphological change is expected to vary with species' movement behaviour. If morphological changes are adaptive, long-distance migratory species may show weaker changes because their size and shape are constrained by their need to carry and conserve energy during long-distance travel, and thermoregulate in contrasting conditions at distant breeding and non-breeding grounds (Battley *et al.* 2003; Winkler & Leisler 2005; Zimova *et al.* 2021). Conversely, if morphological changes are driven by increasing nutritional stress, migratory species could show stronger size declines because they are more vulnerable to habitat degradation and phenological mismatch (Both *et al.* 2010; Klaassen *et al.* 2012) than non-migrants. Nomadic and partly-migratory species may be less vulnerable to climate warming and habitat degradation if they can flexibly re-locate to find food and seek thermally benign conditions (Dean 2004; Alonso *et al.* 2009; Nilsson *et al.* 2011; Teitelbaum & Mueller 2019), or perhaps face similar challenges to migratory species if conditions at distant foraging grounds are difficult to predict, costly to reach, and deteriorating over time (Runge *et al.* 2015; Pedler *et al.* 2018).

Australian shorebirds reside in habitats subject to high temperatures and intense solar radiation (Fig. 1), and perform behaviours indicative of heat stress (Battley *et al.* 2003). Longer bird bills are advantageous in hot conditions because bills dissipate heat (Tattersall *et al.* 2009, 2017), and small increases in bill length can substantially improve heat loss (Greenberg *et al.* 2012). Longer bills are also likely advantageous under nutritionally stressful conditions, as longer bills enable shorebirds to probe for a wider variety of benthic invertebrates (Mathot *et al.* 2007; Duijns *et al.* 2014). Shorebirds from hot, tropical northern Australia are smaller and have longer bills than conspecifics from temperate southern Australia, consistent with Bergmann's and Allen's Rules (McQueen *et al.* 2022). Consistent geographic patterns across ecologically diverse species suggest shorebird morphology is adapted to facilitate heat loss in hot environments (McQueen *et al.* 2022), and further suggests shorebirds will undergo morphological change as the climate warms.

Here we examine changes in the size and shape of Australian shorebirds over time, and in response to recent summer conditions. We use extensive field data (> 200,000 observations) collected from 25 species over 46 years (1975-2021) by community scientists of the Victorian Wader Study Group and Australasian Wader Studies Group. Community scientists have been studying shorebirds in hot, tropical north-western Australia ('northern' sites), where temperatures regularly exceed 35˚C, and temperate, south-eastern Australia ('southern' sites), where summers are subject to transient hot weather and heat wave events (Fig. 1A-C). Both regions have undergone climate warming since the 1970s, with greater warming in south-eastern Australia (Fig. 1D). Our study species span five taxonomic families, with diverse body sizes (mean species mass: 30-840 g) and movement behaviours, including long-distance migratory, nomadic or partly-migratory, and resident species.

We explore long-term shrinking and shape-shifting trends over time, and short-term responses to recent summer conditions. We assess whether morphological changes differ according to population location, species size, and movement behaviour.

METHODS

Community scientists of the Victorian Wader Study Group (VWSG) and Australasian Wader Studies Group (AWSG) typically catch shorebirds using cannon nets. Shorebirds are assigned unique leg bands enabling individual identification (mean captures per individual = 1.12, SD = 0.42, range = 1-15).

Our analyses include 25 species, comprising 12 sandpipers (Scolopacidae), six plovers (Charadriidae), three terns (Laridae), two stilts and avocets (Recurvirostridae) and two oystercatchers (Haematopodidae) (Table S1). We selected species from a larger dataset if they had samples spanning at least 30 years and at least ten mass, wing length and bill length measurements per decade from 1980 in either northern or southern Australia. The final dataset spans 46 years (mass: N = 203,444 observations from 1975-2021; wing length: N = 117,570, 1978-2021; bill length: N = 97,756, 1978-2021).

We tested for size declines by examining changes in mass and wing length. Mass and wing length are strongly correlated (r = 0.82) and provide complementary means of assessing body size. Mass provides combined information on the size and nutritional status of the bird (Piersma & Davidson 1991), while wing length is a well-established proxy for structural size that is less influenced by recent foraging success (Gosler *et al.* 1998; Sullivan *et al.* 2019). Using an indicator of structural size is particularly important for determining size changes in shorebirds, where food intake varies substantially according to tidal conditions and migration timing (Marchant & Higgins 1993; Higgins & Davies 1996).

Mass was measured to the nearest 1 g (larger species) or 0.1 g (smaller species) using scales. Wing (maximum chord) length was measured from the shoulder to the tip of the longest, straightened primary feather to the nearest 1 mm (larger species) or 0.1 mm (smaller species) using a butt-ended ruler. Bill length was measured as the exposed culmen (tip of bill to base of feathers) to the nearest 0.1 mm using callipers. For sexually dimorphic species, sex was assigned by visual differentiation in the field, or subsequently, according to sex differences in morphology, based on information in Marchant and Higgins (1993) and Higgins and Davies (1996) and patterns in our data (McQueen *et al.* 2022). Age (first-year juveniles vs. adults ≥2 years) was determined in the field according to feather characteristics. Because age was not always recorded in the field, we also estimated age from repeat captures of individuals. We assumed birds that were not aged in the field or by recaptures (3,079 of 203,444 observations; 1.5%) were adults since adults comprise the majority of known-age observations (79%) (McQueen *et al.* 2022).

Research was carried out with animal ethics approval and approved by relevant jurisdictions, including jurisdictions currently known as the Department of Primary Industries and Regional Development; Department of Biodiversity Conservation and Attractions (Western Australia); Department of Environment and Water; Zoos South Australia; South Australian Museum (South Australia); Department of Environment, Land, Water and Planning; Parks Victoria; Philip Island Nature Parks (Victoria); Department of Primary Industries, Parks, Water and Environment (Tasmania). Bird banding was registered with the Australian Bird and Bat Banding Scheme.

Community scientists of the VWSG and AWSG have expert knowledge of shorebirds and data collection. Nevertheless, extensive data amassed over decades will inevitably have errors. We removed likely errors before analyses using standard procedures while blind to measurement date (McQueen *et al.* 2022). We excluded wing length measurements from birds moulting their ninth or tenth primary wing feather.

Climate data

We used mean maximum summer temperature to test for morphological changes in response to recent climate conditions because it encompasses a single, broad estimate of exposure to high temperatures and the frequency of high temperatures during an Australian summer. Australian winters are mild, and, in Australia, shorebirds likely experience the strongest climate-related stress during summer. We obtained mean monthly maximum temperature data from Australian Bureau of Meteorology weather stations close to shorebird study sites with complete or near-complete records from 1969 to 2021 (Fig. 1A-C; three stations were missing data from one summer). We calculated the 'mean maximum summer temperature' of a given year as the average mean maximum monthly temperature in December, January and February for each weather station. These months correspond with summer in southern Australia and approximately mid-wet season in tropical northern Australia (hence 'summer'). Mean maximum summer temperatures are highly correlated across the seven weather stations in south-eastern ($r > 0.7$) and four stations in north-western Australia ($r \geq 0.7$). We averaged mean maximum summer temperatures across stations within north-western and south-eastern Australia, and then over five years before a given shorebird sampling date to obtain an 'average mean maximum summer temperature' for the two regions. As a general trend, mean maximum summer temperatures at the field sites have increased over time (estimate from linear mixed model, including year as fixed effect and weather station as random term: northern Australia $\beta = 0.059$°C 10 years^{-1}, SE = 0.038, $P = 0.122$; southern Australia $\beta = 0.152$°C 10 years^{-1}, SE = 0.037, $P < 0.001$), corresponding with regional trends in north-western and south-eastern Australia (Fig. 1D) and warming trends estimated across the wet season (October-April) in northern Australia ($\beta = 0.163$°C 10 years^{-1}, SE = 0.033, $P < 0.001$).

Migration behaviour

We classified species movement behaviour using information in Marchant and Higgins (1993) and Higgins and Davies (1996), following methods described by McQueen et al. (2022): Resident species are described as 'resident', 'mostly resident', 'sedentary' or 'mostly sedentary' and typically remain in the same region year-round (N = 4 species). Nomadic species are described as ‘nomadic’ or as making ‘opportunistic’ or ‘dispersive’ movements in response to rainfall. Partly-migratory species are described as ‘partly’ or ‘mostly’ migratory and have migratory and non-migratory groups within our study sites. We combined nomadic and partly-migratory species in the same category for comparative analyses (N = 5 species; see below). Long-distance ‘migratory’ species regularly travel between Australian non-breeding grounds and Arctic or Northern and Central Asian breeding grounds (N = 16 species).

Analyses

We analysed changes in shorebird size and bill length using linear mixed models for each species and across 25 species using phylogenetic mixed models. Analyses were conducted in R version 4.0.4 (R Core Team 2023).

Within-species analyses

We examined changes in body size and bill length over time using separate linear mixed models for three response variables (mass, wing length and bill length) for each of the 25 species using the package ‘lme4’ (Bates *et al.* 2015). We log-10 transformed mass to improve normality of residuals, and bill length to account for potential scaling effects. We scaled and centred log-10 mass, wing length and log-10 bill length to facilitate comparison of effect sizes across species. We tested for changes in bill length relative to body size by including scaled and centred log-10 wing length as a fixed effect. We included ‘year’, ‘age’ (adult vs juvenile) and – for species sampled in two regions of Australia – ‘sample location’ (north vs south Australia) as fixed effects. For four species, we ran additional analyses with ‘sex’ as a fixed effect and unsexed individuals excluded; these models yield similar results to those without sex (Fig. S1), so we present results from the simpler models.

We included ‘month’ (12 categories) as a random effect to control for seasonal variation in mass, wing length and bill length (Greenberg *et al.* 2013). We included the random slope age|month in mass and wing length models because age differences in migration and moult can affect seasonal variation in mass and wing length (Marchant & Higgins 1993; Higgins & Davies 1996). We compared models with and without the random slope and selected models with lower Akaike Information Criterion (Anderson & Burnham 2004). The random slope model was preferred for 20 out of 25 mass models and 18 out of 25 wing length models.

Community scientists of the VWSG and AWSG used separate datasheets for each capture event and data collection team. We therefore included 'datasheet ID' as a random effect to control for sampling effects. We included individual ID ('band number') as a random effect to control for repeated samples of the same individual; band number was excluded from analyses when recaptures comprised < 3% of the total sample.

Cross-species analyses

Changes over time

We tested for morphological change over time across 25 species using Bayesian phylogenetic linear mixed models run with the R packages 'INLA' (Rue *et al.* 2017) and 'phyr' (Li *et al.* 2020), using the 'automatic prior' included in 'phyr,' described by Simpson et al. (2017). We ran separate models for the response variables 'mass', 'wing length' and 'bill length'. All three morphological variables were log-10 transformed to improve normality of residuals. We included 'year', 'age' and 'sample location' as fixed effects. We tested for changes in bill length relative to body size by including log-10 wing length as a fixed effect ('relative bill length') and for changes in bill length irrespective of changes in body size by excluding wing length as a covariate ('absolute bill length'). Analysis of relative bill length using log-10 mass as a covariate yields similar results, suggesting results for relative bill length are robust to different measures of body size (Tables S5-6). We analysed changes in wing length relative to mass by including log-10 mass as a fixed effect ('relative wing length') to determine whether the structural size of birds is declining relative to an indicator of size and energetic resources. We included 'month' as a random intercept for wing length and mass models to control for seasonal effects. We included 'species' as a random intercept to account for repeated samples from the same species and phylogeny to account for species relatedness using a 'maximum clade credibility tree' made with 1000 phylogenetic trees from Jetz et al. (2012) and the R package 'phangorn' (Schliep 2011).

The models described above were used to obtain an overall estimate of morphological change; we further investigated whether changes in size and bill length varied according to population location (northern vs southern Australia), species mass, and migration behaviour (migratory, nomadic or partly-migratory, and resident). We ran separate interaction models for mass, wing length and bill length using the models described above and three two-way interactions: year × log-10 mean species mass, year × population location and year × migration behaviour. We calculated mean species mass to the nearest 10 g using VWSG and AWSG data.

Changes in response to summer climate

Using similar Bayesian phylogenetic linear mixed models, we tested for changes in shorebird body size and bill length according to summer climate. We assessed changes in mass, wing length and bill length (response variables) according to the average mean maximum summer temperature over five years before sampling (see above). We ran separate models for northern and southern populations because climate conditions differ for north-western and south-eastern coastal Australia (Fig. 1B-C). We included species in the model provided they had at least ten samples per decade from 1980 spanning 30 years.

RESULTS

Changes over time

Across all species, shorebird mass and wing length has declined over time (decrease in mass = -0.62% per decade, 95% CI = -0.67, -0.56%, N = 203,444; decrease in wing length = -0.14% per decade, 95% CI = -0.16, -0.12%, N = 117,570; Tables S2-3). Mass and wing length declines are widespread: of

25 species sampled, 22 show mass declines (13 species with 95% confidence; one species shows increased mass with 95% confidence) and 18 show wing length declines (11 with 95% confidence; one species shows wing lengthening with 95% confidence) (Fig. 2). Shorebird wing length has also declined while controlling for mass (decrease in relative wing length = -0.12% per decade, 95% CI = -0.14, -0.10%, N = 116,203, Table S4). Shorebird bills have lengthened overall, both when controlling for wing length (increase in relative bill length = 0.07% per decade, 95% CI = 0.03, 0.11%, N = 97,756; Table S5) and independent of reductions in body size (increase in absolute bill length = 0.05% per decade, 95% CI = 0.01, 0.10%, N = 97,756; Table S7). However, bill length changes are highly variable among species: of the 25 species sampled, 14 show bill lengthening over time – five species with 95% confidence – while four species show bill shortening over time with 95% confidence (Fig. 3). Size declines do not appear to be traded off against bill lengthening; of five species with statistically significant increases in bill length, three show statistically significant reductions in mass (Figs 2, 3). Smaller species show steeper mass and wing length declines (Fig. 2; Tables S8-9), and greater bill lengthening over time (Fig. 3; Tables S10-11).

Shorebird size has declined in northern and southern Australia. Mass declines are more pronounced in northern populations (Fig. 4A), while wing length declines are more pronounced in southern populations (Fig. 4B). Bill lengthening is more pronounced in northern populations (Fig. 4C).

Migratory species show weaker mass and wing length declines than non-migratory species (Fig. 4A, B). Nomadic or partly-migratory species show steeper mass declines than resident and migratory species (Fig. 4A). Resident species show greater increases in bill length than non-resident species (Fig. 4C). Shorebird bills shortened in migratory species from southern Australia (Fig. 4C).

Correlation with summer climate

Shorebird mass generally decreased after warmer summers (mean maximum temperature during summer or mid-wet season over five years) in northern and southern Australia, although mass increased following warmer summers in southern Australian migrants (Fig. 5A-B). Mass declines following warmer summers were steeper in nomadic or partly-migratory species from northern Australia (Fig. 5A). Likewise, wing length generally decreased following warmer summers (Fig. 5C-D). In contrast to temporal trends, relative bill length decreased following warmer summers (Fig. 5E-F). Smaller species generally show steeper mass and wing length declines following hot summers (Tables S12-15). Smaller species show steeper bill length declines following hot summers in southern Australia (Table S16) but this is not the case for shorebirds in northern Australia (Table S17).

DISCUSSION

Shorebirds are shrinking, while their bills are lengthening (resulting in shape-shifting) over time. Mass and wing length declines are widespread across 25 species (Figs 2; 4A-B), while bill lengthening trends are highly variable among species (Figs 3, 4C). Shorebird bills are lengthening relative to their body size, and in the absolute sense, irrespective of body size declines (supplementary note 1). Shorebird wing length is also declining relative to mass, suggesting that the structural size of shorebirds is decreasing relative to a combined measure of body size and energetic resources. Consistent with temporal trends, shorebird size declined after warmer Australian summers (Fig. 5A-D). In contrast to bill lengthening over time, shorebird bills shortened after warmer Australian summers (Fig. 5E-F). Morphological changes are broadly consistent across tropical and temperate populations (Fig. 4A, C), smaller species exhibit steeper size declines and changes in bill length (Figs 2, 3), and morphological changes vary with movement behaviour (Fig.4).

Body size declines across Australian shorebirds add to growing evidence of global shrinking trends, encompassing bird species from the Amazon (Jirinec *et al.* 2021), Middle East (Yom-Tov 2001; Dubiner & Meiri 2022), North America (Van Buskirk *et al.* 2010; Weeks *et al.* 2020; Youngflesh *et al.* 2022), and Australia (Gardner *et al.* 2009). These results suggest global environmental change is impacting fundamental aspects of avian biology. Body size declines in response to warmer summer conditions further suggest that morphological changes may be directly related to climate warming, where effects of repeated exposure to warmer temperatures build over time to explain long-term trends. There are multiple plausible explanations for size declines, and additional research is needed to formally assess the magnitude of increased heat transfer with reduced body size (Nord *et al.* 2024; but see Youngflesh *et al.* 2024). However, thermal adaptation to climate warming provides the most parsimonious explanation for consistent trends across Australian shorebirds, with smaller size enabling greater surface-area-to-volume ratios, and hence greater capacity to disperse body heat. Size declines in non-migratory species in tropical northern Australia further suggest size declines are at least partly explained by adaptation to facilitate heat loss, rather than increased survival of smaller individuals due to reduced energetic costs of keeping warm (Zheng *et al.* 2023), as these shorebirds rarely experience cold conditions.

Thermal adaptation to climate warming can further explain bill lengthening trends through time, as bird bills dissipate body heat, and longer bills improve heat loss (Tattersall *et al.* 2017). However, changes in bill length are highly variable, with bill shortening trends observed for individual species (Fig. 3) and across southern Australian migratory shorebirds (Fig. 4C). In contrast to temporal trends, shorebird bills also shortened following recent exposure to warmer summers (Fig. 5E-F). Bill shortening might occur if longer bills become a liability under extremely hot conditions, when bills become a source of heat gain (Ryeland *et al.* 2017; Mitchell *et al.* 2018). For example, heat gain via bills might explain bill shortening in oriental plovers, which forage on hot, arid plains (Fig. 3; Marchant & Higgins 1993), while widespread bill shortening following hot summers could occur through the loss of longer-billed individuals that are vulnerable to intense heat (Greenberg & Danner 2012; Probst *et al.* 2022). Contrasting selection, favouring longer bills as the climate warms but shorter bills under extremely hot conditions could explain more variable bill length changes among species; if bill length changes are adaptive, contrasting selection could impede long-term adaptation to climate warming.

An alternative explanation is that shorebirds are under increasing nutritional stress, leading to widespread mass and wing length declines, bill shortening following warmer summers (maladaptive response), and bill lengthening over time (adaptive response). Mass, wing and bill length declines could occur through lost energy stores (Teplitsky *et al.* 2008), nutritional strain during moult (Pehrsson 1987), stunted bill growth (Zuluaga & Danner 2023), and increased bill wear (Greenberg *et al.* 2013), potentially due to heat stress impacts on foraging, increased required foraging effort, and declining invertebrate prey (Fujii 2012; Aarif *et al.* 2021). Adaptation to more nutritionally stressful environments could also explain bill lengthening trends through time if longer bills allow shorebirds access more diverse prey, or reach invertebrates buried deeper beneath sand and mud in warmer conditions (Mathot *et al.* 2007; Duijns *et al.* 2014).

High temperatures impact early development, leading to smaller body size (Andrew *et al.* 2017) and longer bills in birds (Burness *et al.* 2013; Larson *et al.* 2018), while nutritional stress in early life can lead to stunted bill growth (Øyan & Anker-Nilssen 1996; Van Gils *et al.* 2016). These plastic effects could explain morphological changes over time and following warmer summers, when foraging capacity and parental provisioning may be affected by heat stress. However, developmental plasticity does not explain size declines in tree swallows (Shipley *et al.* 2022), and is unlikely to explain size declines and bill shortening following hot Australian summers in migratory shorebirds (Fig. 5) since their early development occurs in the northern hemisphere.

Smaller species show steeper size declines and bill length changes over time and after hot summers (Figs. 2, 3). Smaller shorebird species may be under stronger selection to adapt to climate warming because they forage and roost closer to the ground, where conditions are warmer due to reflected heat and boundary layer effects (Cartar & Morrison 2005; Mitchell *et al.* 2018). Smaller species also typically occupy warmer, shallow water and sandy habitats than larger species that wade in deeper water (Marchant & Higgins 1993; Higgins & Davies 1996). Alternatively, smaller shorebirds might have a greater capacity to undergo rapid morphological change because smaller body size is associated with traits thought to facilitate rapid adaptive evolution, including faster metabolic rates, larger effective population sizes, greater genetic variance, and shorter generation times (Martin & Palumbi 1993; Gillooly *et al.* 2005; Fontanillas *et al.* 2007; Etienne *et al.* 2012). However, recent research on birds found no relationship between rates of morphological change and species population size; that species size does not correlate with greater variation in morphological traits, and that body size better predicts rates of morphological change than indicators of generation length (Zimova *et al.* 2023). Faster morphological change in smaller species appears to be widespread, as it is now observed across birds from Australia (Figs 2, 3), tropical East Africa (Neate-Clegg *et al.* 2024), the Amazon, and North America (Zimova *et al.* 2023).

Migratory species show weaker size declines and inconsistent changes in bill length over time. Inconsistent bill length changes could be explained by the thermal costs of long bills at cold, northern hemisphere breeding grounds (McQueen *et al.* 2023). Weaker size declines may similarly reflect greater constraints on migrants due to minimum energy store and wing length requirements for efficient, long-distance flight (Winkler & Leisler 2005). Recent research demonstrates increasing wing length alongside mass declines in migratory and non-migratory birds, interpreted as a potential adaptation for improved flight efficiency since larger wings relative to mass reduces wing loading (Weeks *et al.* 2020; Jirinec *et al.* 2021). By contrast, we show decreases in absolute and relative wing length. However, the strength of wing length decline in Australian shorebirds approximately corresponds with flight distance – i.e. weakest in migratory, intermediate in nomadic or partly-migratory and strongest in resident species – suggesting that wing length declines might be constrained by competing selection for flight efficiency. Contrasting changes in wing length across studies could reflect differences in the relative strength of selection for flight efficiency or reduced body size, or variation in size-dependent mortality across populations (Bailey *et al.* 2020).

Nomadic or partly-migratory shorebirds show the steepest mass declines with time and in response to summer climate, especially in northern Australia (Figs 2A, 5A). These species differ in their foraging ecology, breeding grounds, and overall size and shape, making it difficult to speculate a single reason for steeper mass declines. However, three of four northern Australian nomadic or partly-migratory shorebirds travel to inland Australia in response to irregular flooding of salt lakes and ephemeral wetlands (whiskered tern, black-winged stilt, and red-necked avocet; Marchant & Higgins 1993; Higgins & Davies 1996). This region is hot and has undergone rapid climate warming (IPCC 2021) (Fig. 1D), as well as anthropogenic changes to river flows, leading to wetland degradation implicated in black-winged stilt and red-necked avocet population declines during the study period (1973-2014) (Nebel *et al.* 2008; Clemens *et al.* 2016). Steeper mass declines in these species may therefore be driven by thermal adaptation under strong selection pressure, or a rapid loss of energy stores under deteriorating conditions.

Conclusions

Shorebird mass and wing length have declined over time, and after warmer summers, with consistent trends across ecologically diverse species. Meanwhile, shorebird bills have lengthened over time, but shortened after warmer summers, with less consistent trends across species, suggestive of evolutionary constraints or conflicting selection pressure acting on bill lengths. Further research investigating the drivers of morphological change is a priority for predicting global change impacts on species survival: If body size declines indicate increasing nutritional stress, species showing steeper size declines should show rapid population declines to reflect the reduced carrying capacity of their local environment. If body size declines are an adaptive response to climate warming, species with steeper size declines may be responding to stronger selection pressure, suggesting they are more vulnerable to climate change, or demonstrating a greater capacity to undergo adaptive evolution, leading to improved survival prospects. If bill lengthening trends through time are a result of thermal adaptation to climate warming, or adaptation to combat increasing nutritional stress, but long bills become a liability in very hot conditions, longer-billed individuals may be favoured over time but suffer disproportionately during extreme heat events. Unfortunately, climate change continues unabated (Yerlikaya *et al.* 2020; IPCC 2021); with the provision of long-term datasets, there will be ample opportunity to establish whether morphological changes are the result of natural selection (Beausoleil *et al.* 2019; Prokosch *et al.* 2019) and assess the consequences for population survival.

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FIGURES

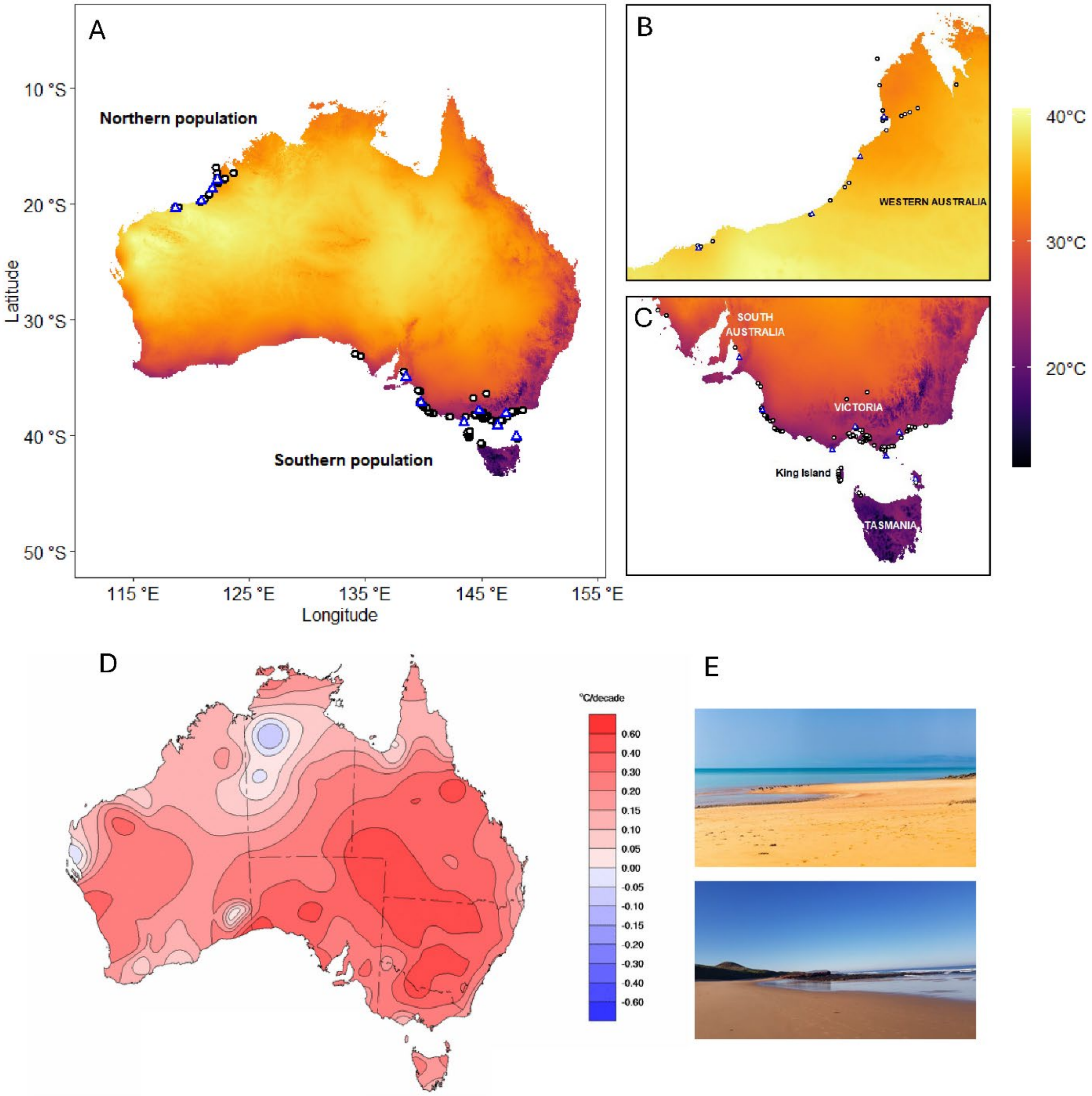

Figure 1.

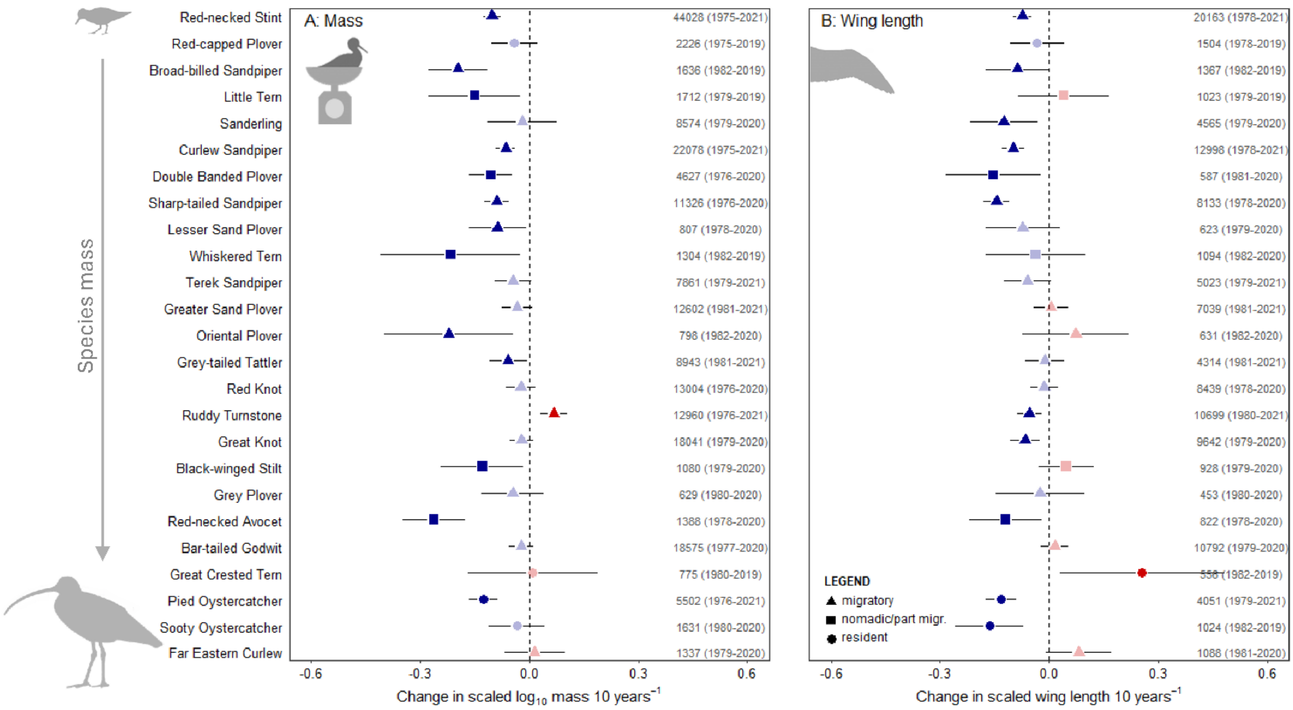

Figure 2.

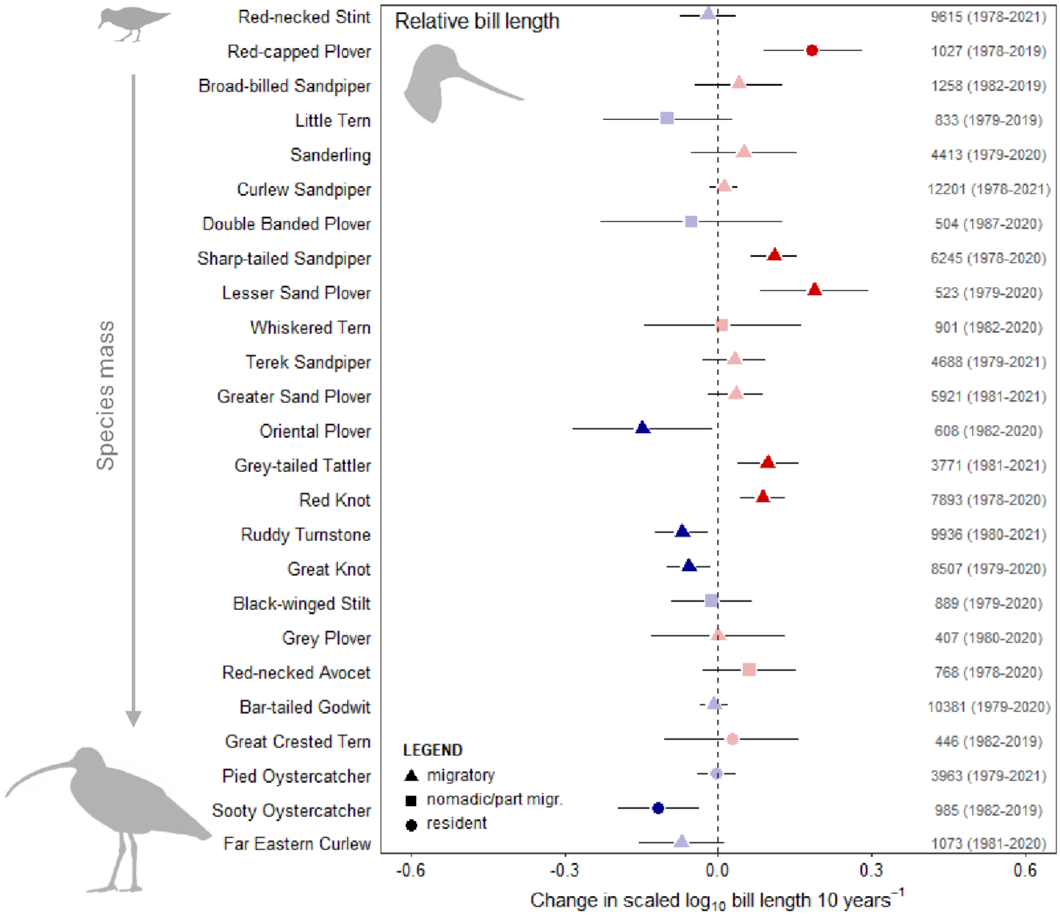

Figure 3.

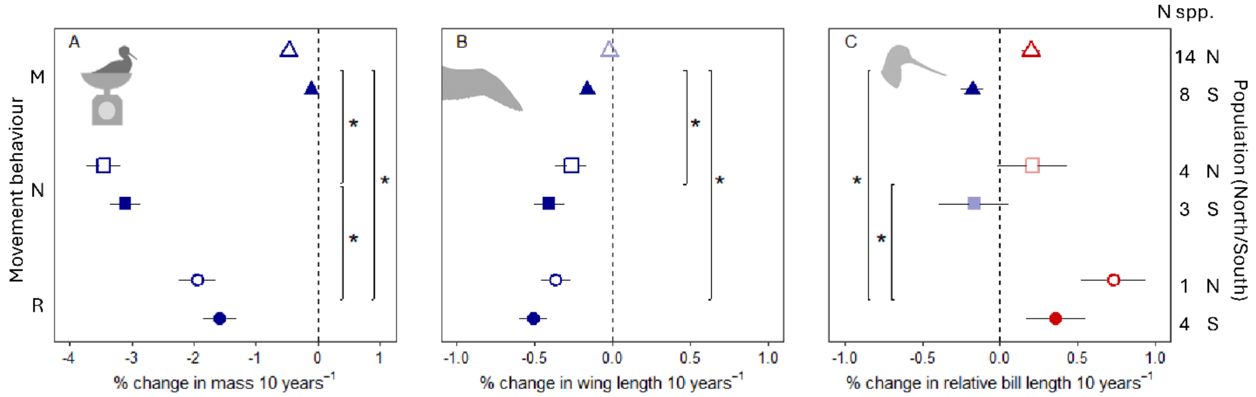

Figure 4.

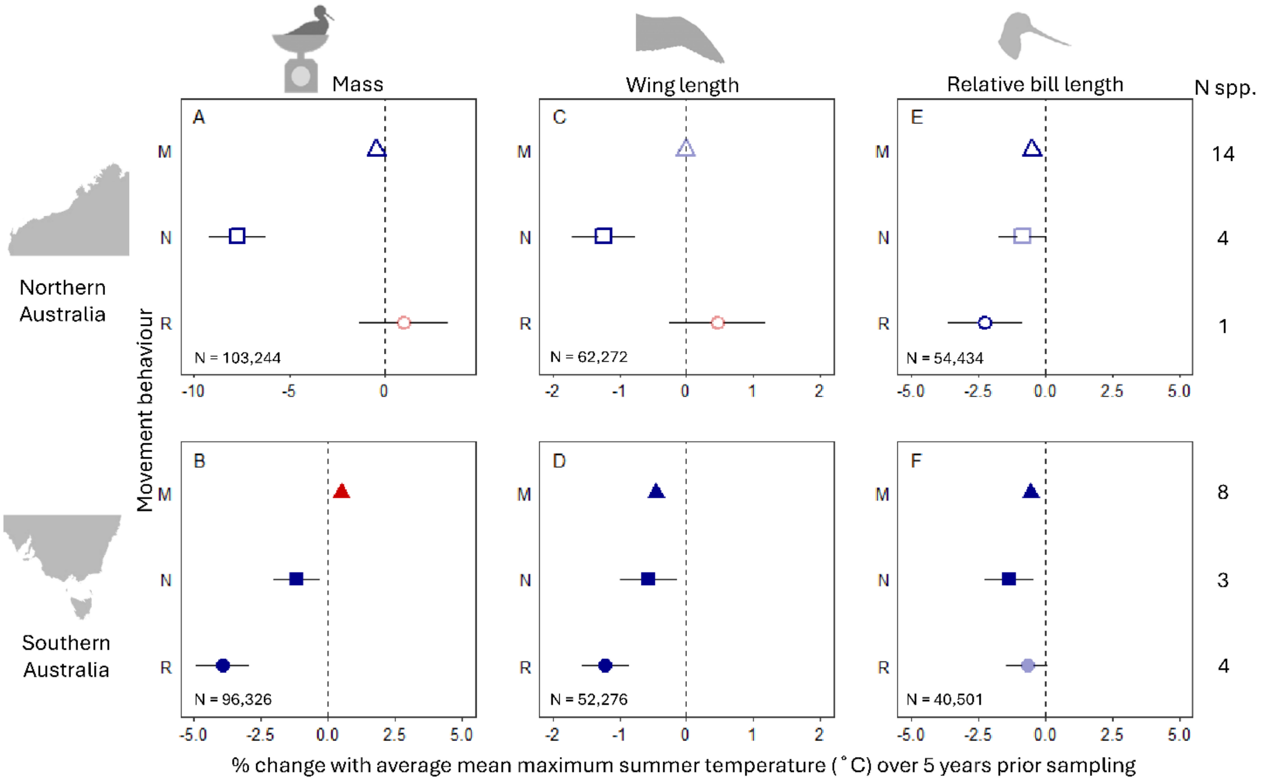

Figure 5.

FIGURE CAPTIONS

Figure 1: Field sites and climate information for northern and southern Australian shorebird populations. Panels A-C show locations where shorebirds have been sampled by members of the VWSG and AWSG (black circles) and nearby Australian Bureau of Meteorology weather stations with summer temperature data from 1970-2021 (blue triangles); colour scale shows average summer daily maximum temperatures (December-February). Northern Australian field sites are regularly subject to hot conditions; southern Australian field sites are generally cooler but subject to transient hot weather and heat wave events (average of 5 days ≥ 35˚C per year across south-eastern Australian coastal weather stations over the past decade). Panel D shows the estimated change in mean maximum summer temperature (December-February) from the summer of 1970/71 to 2021/2022, obtained from the Australian Bureau of Meteorology, based on the ACORN-SAT v2.3 data. Panel E shows example of shorebird habitat in northern Australia (top) and southern Australia (bottom). Shorebirds forage by wading in shallow water, flying, and running along sand, mudflats, and rocky outcrops; shorebird habitats are harsh in hot conditions, with limited access to shade and freshwater.

Figure 2. Estimated change in (A) mass and (B) wing length per decade for 25 shorebird species. Log-transformed mass and wing length data were centred and scaled to make effect sizes comparable across species. Species are sorted from smallest to largest on the y axis. Estimates are from linear mixed models run separately for each species; error bars show 95% confidence intervals; negative effects are shown in blue, positive effects are red; darker points show effects with 95% confidence intervals that do not overlap zero. Sample sizes and year ranges are listed on the right side of each panel.

Figure 3. Estimated change in relative bill length (i.e., bill length controlling for body size) per decade for 25 shorebird species. Log-10 transformed bill length was centred and scaled to make effect sizes comparable across species. Species are sorted from smallest to largest on the y axis. Estimates are from linear mixed models run separately for each species; error bars show 95% confidence intervals; negative effects are shown in blue, positive effects are red; darker points show effects with 95% confidence intervals that do not overlap zero. Sample sizes and year ranges are listed on the right side of the panel.

Figure 4. Estimated percentage change in shorebird mass (A), wing length (B) and relative bill length (C) per decade. Estimates are from Bayesian phylogenetic linear mixed models that include the interactions year*movement behaviour and year*population location. Error bars show 95% confidence intervals. Percentage changes are shown according to movement behaviour (M = migratory, N = nomadic or partly-migratory and R = resident species) and region sampled (N = northern Australia, S = southern Australia). Sample sizes (number of observations) are (A) mass = 203,444, (B) wing length = 117,570 and (C) bill length = 97,756 from 25 species. The number of species per population location and movement behaviour are shown to the right of panel C. See Tables S8-10 for full statistics.

Figure 5. Estimated percentage change in shorebird mass (A, B), wing length (C, D) and relative bill length (E, F) according to mean maximum summer temperatures over the five years prior to measurements being taken in the field. Estimates are from Bayesian phylogenetic linear mixed models and error bars show 95% confidence intervals. Estimates were made separately for shorebirds sampled in northern (A, C, E) and southern Australia (B, D, F), and percentage changes are shown for shorebirds with different movement behaviours (M = migratory, N = nomadic or partly-migratory and R = resident species). Sample sizes for each analysis are shown on the bottom left of each panel; the number of species per sample location and movement behaviour category are shown to the right of panels E and F. See Tables S12-17 for full statistics.