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## Communication

### Overlap in the wing shape of migratory, nomadic and sedentary grass parrots

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Bird wing shape is highly correlated with mobility, and vagile species have more pointed wing tips than sedentary ones. Most studies of bird wing shape are biased to the Northern Hemisphere, and consider only two migratory syndromes (north–south migrants or sedentary species). There are major gaps in knowledge about the wing shapes of different taxa with other movement strategies (e.g. nomads) in the Southern Hemisphere. Parrots are a prominent Southern Hemisphere bird order with complex movement patterns, but their wing shapes are mostly unstudied. We test whether three metrics of wing shape of grass parrots (*Neophema* and *Neopsephotus* spp.) correspond to their purported migration syndromes (and other factors). We show that two strongly migratory grass parrots and an arid-adapted nomad had pointed wings, with flight feathers longer distally and shorter proximally. However, purportedly sedentary species overlapped extensively with migrants and nomads in all aspects of wing shape. Taxonomic relationships, purported migratory syndromes and ecological barriers did not explain the variation we recorded. The most distantly related species (*Neopsephotus*) had most dissimilar wing shape to the others, but broadly conformed to the expectations of long pointed wings of a nomad. Why purportedly sedentary grass parrots had unexpectedly pointed wings is unclear. We propose the hypothesis that this wing shape may persist in sedentary populations if individuals experience strong but intermittent selection to disperse when environmental conditions are poor. If pointed wings are not costly during good times when individuals are sedentary, this wing shape may persist in populations as a ‘back up’ in bad times. Our study highlights the interesting migration patterns in the Southern Hemisphere that remain largely unstudied. Wing shape offers an interesting way to identify potentially undiscovered capacity for movement in data deficient species, which may also have implications for conservation.

Keywords: austral migration, bird wing, feather, migrant, mobile animals, movement, nomad, resident, sedentary



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## Introduction

Bird wing shape is a trait that is highly correlated with mobility, and vagile species have more pointed wings than sedentary ones (Mönkkönen 1995, Lockwood et al. 1998, Sheard et al. 2020). Pointy wings (i.e. where the longest flight feather is close to the leading edge of the wing) have less drag and allow faster, more aerodynamically efficient flight but less maneuverability than round wings (Lockwood et al. 1998). Vagile species experience intense selection pressure for wing shape, particularly during physically demanding phases of life history like migration or dispersal. Sexual selection (Prum 1998, Carvalho Provinciano et al. 2018) and selection for foraging ability (Gustafsson 1988, Marchetti et al. 1995) or territorial defense (Vanhooydonck et al. 2009) may impose additional, competing pressures on wing shape. The cumulative outcome of these different selection pressures can result in divergent wing shapes between sexes and ages within a species (Fernández and Lank 2007), let alone between related species (Minias et al. 2015). However, the extreme physical demands of migration as a general rule produce more pointed wings in migrants than sedentary conspecifics and congeners (Lockwood et al. 1998) regardless of other selective processes (Sheard et al. 2020).

The majority of studies of bird wing shape are biased to the Northern Hemisphere, and typically consider only two migratory syndromes (north–south migrants or sedentary species). Other migration syndromes, such as nomadism, also occur in the Northern Hemisphere (Newton 2008, 2012), however there has been very little study of wing shape of nomads. This knowledge gap extends to the Southern Hemisphere, where there are few studies of bird wing shape despite evidence of a diverse range of migration syndromes in the region (Dingle 2008a). Furthermore, while passerines and shorebirds are the primary focus of wing shape studies in the literature, a taxonomically diverse array of species exhibit interesting movement patterns in the Southern Hemisphere. For example, parrots are a prominent Southern Hemisphere bird order with complex movement patterns (Webb et al. 2014). However, there has been only limited study of morphological adaptations of parrot wings (Sheard et al. 2020), despite their diverse movement strategies (Dingle 2008b). Given the relationship between wing shape and vagility in the existing literature, this phenotypic trait may be a useful starting point to discover undocumented mobility in data deficient parrots. This may be particularly important for conservation given that mobile animals are disproportionately more threatened than sedentary ones (Runge et al. 2014), and parrots are among the most threatened bird orders (Olah et al. 2016).

In this study, we use wing shape to develop new hypotheses about the migratory syndromes of the grass parrots (*Neophema* and *Neopsephotus* spp.) (Joseph et al. 2012). There has been very little direct research on the spatial ecology of most grass parrots, but they are believed to vary from sedentary to nomadic and migratory (Higgins 1999). At least two species undertake annual north–south migrations, but

even sedentary species may occasionally disperse long distances (Higgins 1999). However, evidence for categorization of migration syndromes of the grass parrots is weak except for two species (Dingle 2008b). Given that several grass parrots are of conservation concern (NSW Scientific Committee 2009, Dept of Environment Land Water and Planning 2016) understanding their potential migratory syndromes is important for conservation management of the species, as well as improving knowledge of the diverse movement strategies of animals in an understudied region. To address this knowledge gap we test the hypothesis that purportedly migratory/nomadic grass parrots should have pointier wings than species believed to be more sedentary.

## Methods

### Study species and predictions

Orange-bellied parrots are tentatively considered the sister lineage to a complex comprising rock *N. petrophila*, elegant *N. elegans* and blue-winged parrots *N. chrysostoma* (Provost et al. 2018). Those four species are sister to a clade comprising scarlet-chested *N. splendida* and turquoise parrots *N. pulchella*. Bourke's parrot *Neopsephotus bourkii* is the sister lineage to *Neophema* (Provost et al. 2018). Grass parrots are small (40–50 g) birds endemic to Australia (Higgins 1999). One is a habitat generalist (blue-winged parrots: coastal, woodland and arid habitats), but most are specialists of coastal (orange-bellied and rock parrots), woodland (elegant and turquoise parrots) and arid habitats (scarlet-chested and Bourke's parrots) (Higgins 1999). Movement ecology of grass parrots is mostly unstudied, but we summarize the (largely anecdotal) observations of movements for each species (colated in Higgins 1999). Orange-bellied parrots are obligate migrants. Different subpopulations of blue-winged parrots may be partial/obligate migrants, resident or nomadic. Rock parrots may be sedentary but undertake regular sea crossings between offshore islands and the adjacent mainland, and may disperse when not breeding. Scarlet-chested parrots may be irruptive or nomadic. Bourke's and elegant parrots may be sedentary or nomadic at different locations and times. Turquoise parrots may be sedentary or locally nomadic. Based on this information, we expect that wing shape of orange-bellied, blue-winged, scarlet-chested and Bourke's parrots should reflect their vagile behaviour and be the most pointed. Turquoise and elegant parrots may be the least vagile and should have the roundest wings. Rock parrots may be intermediate due to their flights over the sea, but potentially smaller range than migrants and nomads.

### Quantification of wing shape and comparison among all grass parrot species

We present data from 54 orange-bellied parrots, 46 blue-winged parrots, 30 elegant parrots, 31 rock parrots, 31 scarlet-chested parrots, 34 turquoise parrots and 32 Bourke's parrots.

There was a roughly even split between sexes in data for each species. We measured study skins at the Australian National Wildlife Collection, Australian Museum, American Museum of Natural History, Harvard Natural History Museum, Museum of Victoria, South Australian Museum and the Tasmanian Museum and Art Gallery. The mean collection date was 1946 (range: 1857–2016), and because museum skins stop shrinking after three years (Green 1980, Harris 1980) specimen age was unlikely to influence our study.

Specimens were measured using electronic calipers (to the nearest 0.01 mm) and a thin, soft plastic ruler (1 mm). We measured: 1)  $L_w$  – unflattened wing chord, 2) unflattened length of the longest primary flight feather (measured from the point where the calamus inserted into the skin – we followed (Jenni and Winkler 1989) to measure the length of feathers), 3)  $\Delta Q$  values (following the method of Lockwood et al. 1998, including the feather numbering system where p1 forms the leading edge of the wing), i.e. distances between the tip of each primary flight feather from the tip of the longest primary feather and 4)  $S_L$  – the distance between the carpal joint and the tip of the most distal secondary on the folded wing. These measurements are illustrated in Supplementary information. We excluded juveniles (identified from specimen tags and metadata), specimens with broken or worn flight feathers, and specimens where the wings were not in the resting position. Because suitable wild-born specimens of all species (particularly orange-bellied parrots) were scarce in museum collections, we included some birds that had individual missing feathers (p4–p8), and estimated the  $\Delta Q$  value as midway between the two feathers adjacent the gap. We excluded birds missing p1–p3. Either p9 or p10 were missing in 19 skins in our sample, so to minimize impacts on our sample size, we only included  $\Delta Q$ 1–8 values in the analysis and thus included these skins in the study. DS took all the measurements and quantified measurement error using a subset of repeat-measured birds. Measurement repeatability was high, and observer error accounted for mean 12.6% of variance across the traits measured (range: 5–23%).

To quantify variation in wing shapes we undertook our analysis in four steps. We provide code and data in the supplementary materials. We used adjusted  $\Delta Q$  values (length of the longest feather minus  $\Delta Q$ , scaled to account for size differences among species by subtracting the over-all mean length from the length of each individual feather) as the response variable for steps one and two.

First, we used MANOVA to compare adjusted  $\Delta Q$  values of the eight flight feathers between the grass parrots in a multivariate framework. Second, we used a linear mixed model to identify which feathers differed in adjusted  $\Delta Q$  values and to quantify the magnitude of those differences. We fitted an interaction between species and feather number (p1–p8) as the fixed effect and included specimen ID as a random term. Third, we implemented size constrained components analysis (SCCA) using adjusted  $\Delta Q$  values (Lockwood et al. 1998). This produced indices of wing roundness/pointedness (component 2, C2), and concavity/convexity of the trailing edge of the wing (component 3, C3) for all birds in the sample.

C2 and C3 are scaled to remove variation attributable to differences in body size among species, which is critical in interspecific comparisons (Lockwood et al. 1998). Fourth, we calculated hand-wing index (HWI), which is related to dispersal ability of birds (Sheard et al. 2020) because it is a simple index of wing aspect ratio that can easily be measured on skins (Claramunt and Wright 2017). We calculated HWI using the formulation presented by Claramunt et al (2012):

$$HWI = 100 \times \frac{(L_w - S_L)}{L_w}$$

We then used linear models to test for differences in C2, C3 and HWI among the grass parrots and to test whether taxonomic relationships or aspects of species life history explain wing shape. We used the most recent phylogeny for grass parrots (Provost et al. 2018) and assigned the species to the following subgenera: *Neopsephotus* (Bourke’s parrot); *Neophema* (scarlet-chested and turquoise parrots), and; *Neonanodes* (blue-winged, elegant, orange-bellied and rock parrots). We also categorized species migration syndromes based on the available information: migratory (blue-winged and orange-bellied parrots); nomadic (Bourke’s and scarlet-chested parrots); sedentary (elegant, rock and turquoise parrots). Although these categorizations may not account for the true breadth of movement strategies of these animals, they are based on the best (if weak) information about their general migration syndromes (Higgins 1999). Finally, we identified the most resistant ecological barriers faced by each species during potential dispersal: the sea (blue-winged, orange-bellied and rock parrots); arid habitats (Bourke’s and scarlet-chested parrots); woodlands (elegant and turquoise parrots). We also recorded the collection date of specimens, because biometric traits can change over relatively short time frames in birds (Bosse et al. 2017).

For each of our three response variables in turn (C2, C3 and HWI), we fitted linear mixed effects models using the package *lme4* (Bates et al. 2015). Fixed effects included migration syndrome, ecological barriers, collection date, sex and species ID and an interaction between sex  $\times$  species. We limited most models to main effects to avoid overfitting and to simplify interpretation. We included subgenus as a random effect in all models to control for taxonomy. We selected from among competing models based on  $\Delta AIC < 2$  (Burnham and Anderson 2002).

All code and raw data are presented in Supplementary information as markdown script, including additional exploratory analysis.

## Results

### Comparison among grass parrot species

The multivariate test found significant differences in adjusted  $\Delta Q$  values between the grass parrot species (Pillai’s Trace=0.95, F=8.95, df=7,  $p < 0.0001$ ). There were

significant differences in the adjusted  $\Delta Q$  values of each feather among species. Estimated mean lengths of each feather for all species (averaged over the sexes) are in Fig. 1 (standard errors and confidence intervals are given in Supplementary Material, pages 20–22). In Fig. 2 we illustrate the differences in feather lengths between the most extreme examples, i.e. the Bourke’s, orange-bellied and turquoise parrots. Orange-bellied parrots overlapped extensively in wing shape with their closest relatives in the subgenus *Neonanodes*, plus the scarlet-chested parrot, whereas Bourke’s and turquoise parrots had the most divergent wings of the species tested.

The best model of C2 (Table 1) included an interaction between sex and species (raw data, means and standard errors are presented as a beeswarm for each species in Fig. 3). Birds with high values for C2 (wing pointedness) had longer distal feathers but shorter proximal feathers than individuals with low values of C2.

For C3 we found equivalent support for the model that included the effect of species (raw data, means and standard errors are presented as a beeswarm for each species in Fig. 3), and also for the model that contained an effect of ecological barriers (Table 1). Based on the latter model, mean C3  $\pm$  SE was  $1.4 \pm 1.2$  for species in arid environments,  $0.2 \pm 1.3$  for those that fly over the sea and  $-0.01 \pm 1.2$  for woodland species. Pairwise contrasts showed that only arid and woodland species differed significantly to one another in C3 (species that fly over the sea did not differ in C3 to the other two groups – Supplementary information R Markdown script). Based on the raw data and means for each species (Fig. 3),

we preferred the species model rather than the one containing the effects of ecological barriers. This is because the latter model concealed obvious species-level patterns of variation in the data. Specifically, Bourke’s and turquoise parrots were likely responsible for the effects predicted in the ecological barriers model, and Fig. 3 shows they differed in C3 to the other species in their shared ecological barrier category (i.e. respectively, scarlet-chested and elegant parrots). Birds with high values of C3 had shorter distal primaries, but longer proximal primaries than those with low values of C3.

The best model of HWI (Table 1) included only the effect of species (Fig. 3).

Supplementary information (R Markdown script) for all species by sex estimates, standard errors and pairwise comparisons for C2, C3 and HWI plus additional exploratory analysis and visualizations of the raw data.

## Discussion

Support for our hypothesis that the wing shape of grass parrots would correspond to the suspected migration syndrome of species was not clear-cut. This is because in all aspects of wing shape, grass parrots showed extensive overlap among species irrespective of purported migration syndrome. Strongly migratory species (orange-bellied, blue-winged parrots) overlapped in C2, C3 and HWI with one another, but also with related sedentary (elegant parrot) and non-migratory (rock parrot) species in some or all aspects of wing shape. Elegant

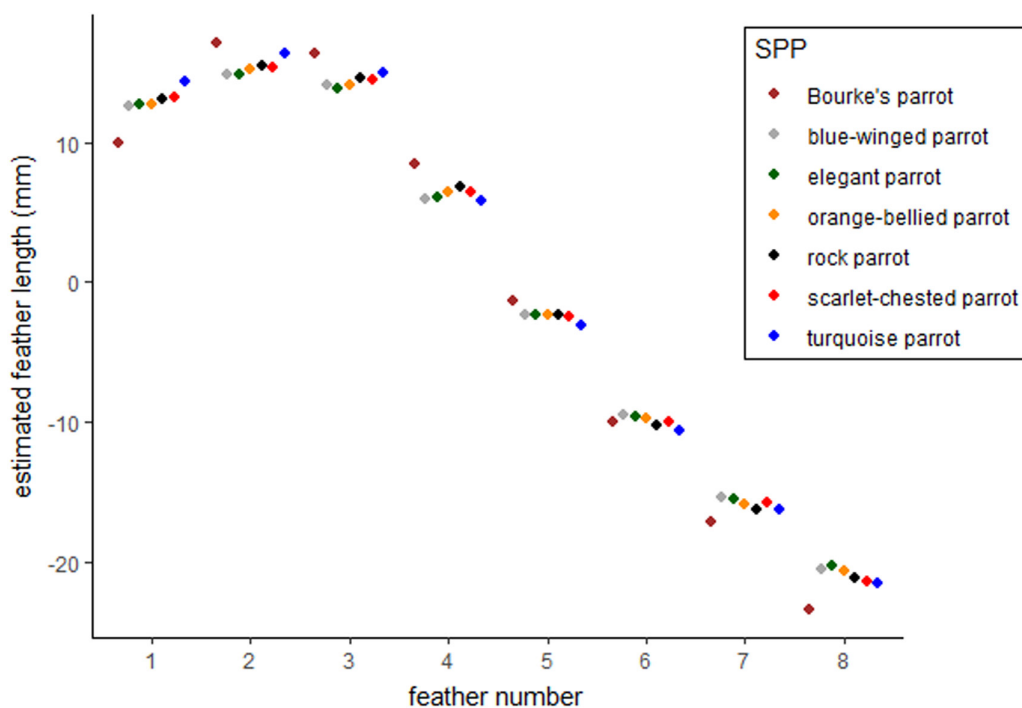
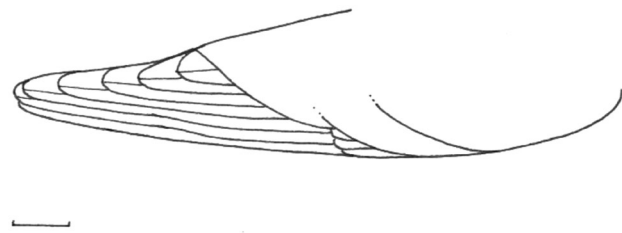


Figure 1. Modeled estimates of the mean length of each primary flight feather of the grass parrots. The feather that forms the leading edge of the wing is numbered one, and numbers increase proximally. Feather lengths are adjusted to account for differences in size among species (mean feather lengths for each species were subtracted from the overall length of each feather to maintain the mm scale).

Orange-bellied parrot



Turquoise parrot



Bourke's parrot



Figure 2. Illustrated examples of wing shape among three grass parrot species with 1 cm scale bars. The Bourke's parrot lives in arid areas and may be nomadic; orange-bellied parrots live in coastal areas and migrate over the sea; turquoise parrots live in woodlands and are sedentary. These images are based on real feather lengths of each species. When size is accounted for the relative lengths of the individual feathers among species are independent of taxonomy, purported migratory syndrome or the most resistant ecological barriers faced by each species. The best model of feather length in the grass parrots included effects of species ID and sex. The wing shape of orange-bellied parrots overlapped with that of most other grass parrots, whereas Bourke's and turquoise parrots are most different to the other species.

parrots, believed to be mostly sedentary, had the lowest HWI of any species in its clade. This is in line with expectations under our hypothesis, but HWI, C2 and C3 of elegant parrots substantially overlapped with migrants. This suggests they are to some extent capable of dispersal and that HWI is too coarse to differentiate among closely related species. Turquoise parrots, also believed to be sedentary, overlapped with migrants in HWI. However, C2 and C3 of turquoise parrots were higher and lower (respectively) than most other species. This is at least partly attributable to the lengths of

Table 1. List of models fitted to each response variable ranked by AIC. \* indicates the preferred model.

Response variable	Fixed effect	df	AIC	$\Delta$ AIC
C2	Sex $\times$ species*	16	937.74	0.00
	Species	9	940.59	2.85
	Migration syndrome	5	955.96	18.22
	Sex	4	956.08	18.34
	Null	3	956.43	18.69
	Ecological barriers	5	957.88	20.14
	Collection date	4	966.46	28.72
C3	Species*	9	839.86	0.00
	Ecological barriers	5	841.68	1.82
	Migration syndrome	5	841.98	2.13
	Sex $\times$ species	16	843.93	4.07
	Null	3	847.09	7.23
	Sex	4	850.10	10.25
	Collection date	4	858.62	18.77
HWI	Sex $\times$ species	16	913.29	0.00
	Species*	9	913.59	0.30
	Migration syndrome	5	917.50	4.21
	Ecological barriers	5	920.13	6.84
	Null	3	926.62	13.34
	Sex	4	929.23	15.94
	Collection date	4	936.46	23.17

the most distal three primary feathers, which were longer in turquoise parrots than most other grass parrots, and likewise, their proximal primaries were shorter than most other species (except for Bourke's parrots). The two purportedly nomadic, arid adapted species had some overlap with one another in C2 and C3, but little overlap in HWI. Taxonomic relationships may explain these differences. Scarlet-chested parrots had similar wing shapes to more closely related migratory *Neophema* spp., but Bourke's parrots differed in all aspects of wing shape to the other grass parrots. Bourke's parrots are the sister lineage to *Neophema*, and had shorter first flight feathers, longer second and third feathers, and shorter proximal flight feathers than any grass parrot.

Our results highlight major gaps in knowledge about the grass parrots. The (mostly) speculative categorization of grass parrots as migratory, sedentary or nomadic did not correspond to obvious differentiation in the wing shape of different species. Our results suggest that 'sedentary' grass parrots have wings suited to long distance dispersal, which may explain anecdotal evidence of occasional irruptive movements of these species reported in the literature (Higgins 1999). Given that wing shapes are subject to multiple discrete selective pressures, our results raise new questions about the ecology of grass parrots in the wild. Intense selection on wing shape during migration over the sea or nomadism in arid environments intuitively would produce the pointed wings of migratory or nomadic grass parrots. However, the similar wing shapes of non-migratory species suggests that there may be strong selection on ordinarily sedentary grass parrots to undertake long movements, even if these dispersal events are irregular. For example, droughts may exert strong but temporary selection for individuals capable of moving over inhospitable habitats

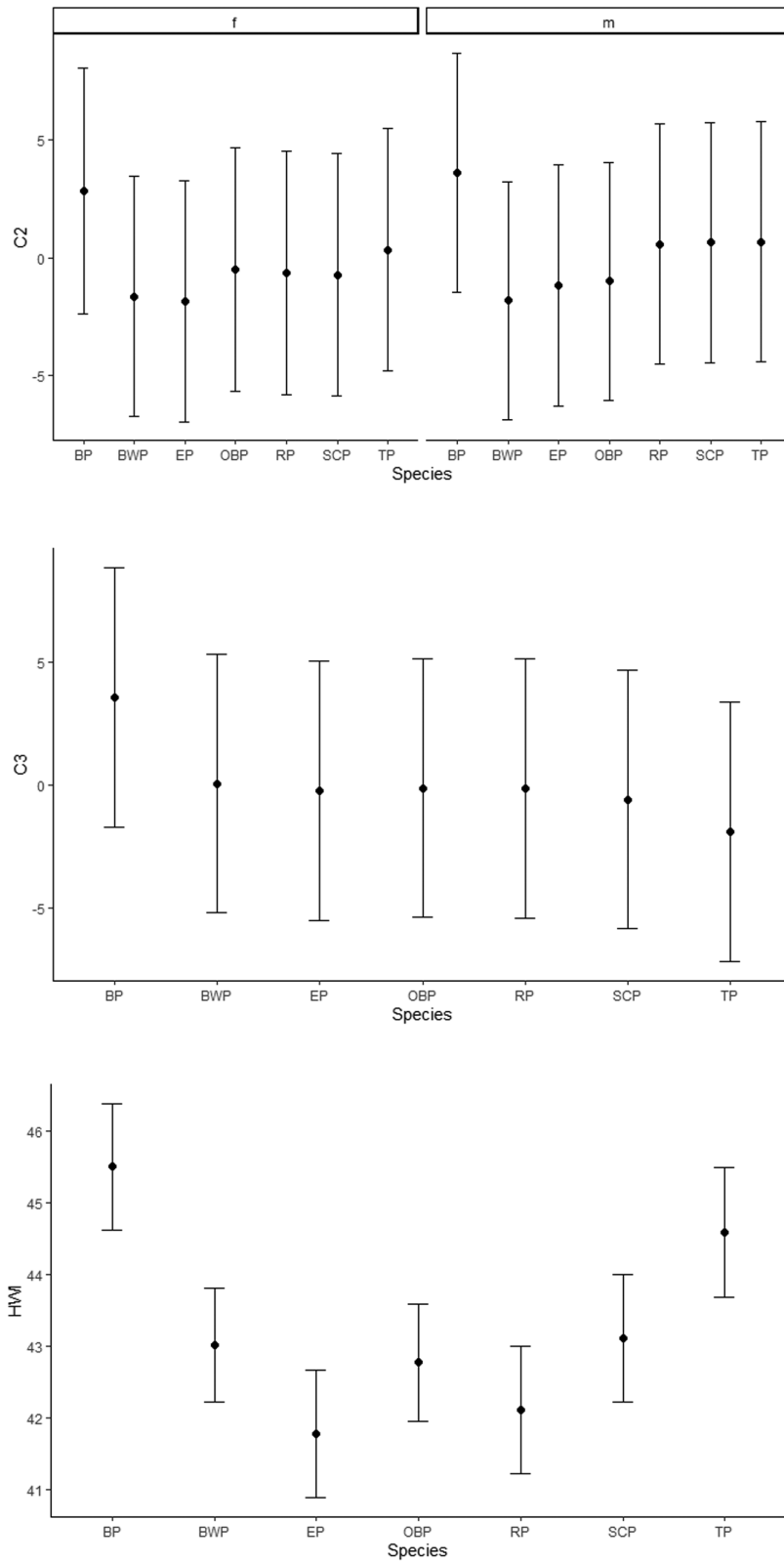


Figure 3. Estimates of means and confidence intervals from the preferred models for C2 (wing pointedness), C3 (wing convexity) and HWI (hand-wing index) for each grass parrot species. For C2 the species are broken into sexes (f= female, m= male). Species are: BP= Bourke's parrot, BWP= blue-winged parrot, EP= elegant parrot, OBP= orange-bellied parrot, RP= rock parrot, SCP= scarlet-chested parrot, TP= turquoise parrot.

efficiently while searching for refugia. This pattern of movement falls within the continuum between sedentary, nomadic and regular migratory behavior (Dingle 2008b). If infrequent but long-distance dispersal events are an important selective process, pointed wings should persist in sedentary populations provided they do not incur fitness costs during ordinary life. Further research could test this hypothesis, which may provide important new information about the ecology of grass parrots and an important nuance to the study of migratory syndromes and wing shapes. In environments that experience extreme fluctuation between good and bad times, the need for a 'back up' ability to disperse in bad times may be an important but overlooked selective pressure.

Our study provides a taxonomically controlled example of the complex interplay of environment, life history and taxonomy on wing shape. Mobile animals are disproportionately vulnerable to threats encountered at different locations and life stages, so understanding how and why species move is fundamental to conservation. Our study leads to a new hypothesis that intermittent, temporary dispersal phases of life history experienced in variable environments may be crucial to understanding population dynamics and evolution in otherwise sedentary species. As global heating increases the variability of habitat suitability of the world's habitats, our results provide an interesting new direction for research on how less vagile species may cope during bad times.

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*Conflicts of interest* – None.

*Permits* – Permission was received from all museums to handle study skins.

## Author contributions

**Dejan Stojanovic:** Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (lead); Writing – review and editing (lead). **Teresa Neeman:** Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization (lead); Writing – review and editing (supporting). **Robert Heinsohn:** Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

## Transparent Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/jav.02612>

## Data and code

Data and code will be archived at Dryad on acceptance. Data will be available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.5qfttdz3q>>.

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