

Size-dependent beak shape divergence between Parrot and Common Crossbills likely involves major developmental changes

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Abstract

We studied allometry, here defined as shape-size covariation, to explore the unresolved case of divergence between the Parrot and Common Crossbill. Using geometric morphometrics, we compared beak shape and allometry among the Parrot Crossbill, the Common Crossbill and the more distantly related Two-Barred Crossbill. The Parrot Crossbill differed from the two other species in shape changes that cannot be explained by size variations along a common allometric trajectory, and instead shows a deeper and bulkier maxilla than expected by size alone. These results indicate that Parrot Crossbill has likely evolved a distinct beak shape through modulations of developmental processes that are yet to be revealed by genomic investigations.

Introduction

Morphological diversity is very often inherently related to size and growth (Alberch *et al.*, 1979; Klingenberg, 1998), and evolution may be facilitated in directions defined by size-shape relationships, that are, allometric lines of least resistance (Rhoda *et al.*, 2023; Tejero-Cicuéndez *et al.*, 2023). Shifts in allometric trajectories imply developmental repatterning (Alberch *et al.*, 1979), and contrasting allometric slopes have been used to infer processes of divergence when

molecular data are ambiguous or absent (Mitteroecker *et al.*, 2004; Piras *et al.*, 2010; Morris *et al.*, 2019). The bird beak is no exception to allometry (Björklund, 1993; Tokita *et al.*, 2017; Rombaut *et al.*, 2022), and much diversity in beak shape appears to have evolved through size variation along allometric trajectories (Bright *et al.*, 2016). The developmental processes determining beak evolution are highly conserved across extent birds (Fritz *et al.*, 2014), and adaptive divergence in beak morphology can be achieved through perturbations of these processes resulting in changes of allometric trajectories. In Darwin's finches for example, contrasting beak shapes emerge as shifts in beak proportions relative to body size (Grant *et al.*, 2006), most likely through signalling pathways modulating growth parameters of embryonic tissues during craniofacial development (Abzhanov *et al.*, 2004; Campàs *et al.*, 2010).

Here we study beak shape variations in relation to size as a means of exploring the extent of divergence in crossbills (*Loxia spp.*). Crossbills show remarkably specialised beak shapes to feed on conifer cones, and several species have been documented relying mostly on particular conifer species (Lack, 1944; Benkman, 2025). The three species in mainland Europe include the Two-Barred Crossbill (*L. leucoptera*), the Common Crossbill (*L. curvirostra*) and the Parrot Crossbill (*L. pytyopsittacus*). The Two-Barred Crossbill is the smallest of the three species and forages on larch (*Larix spp.*) cones with its slender beak. The Two-Barred Crossbill has diverged from the other two crossbills about 1-3 Mya (Ligon *et al.*, 2016; Kumar *et al.*, 2017; Stiller *et al.*, 2024). The Common Crossbill is generally described as feeding primarily on spruces (*Picea spp.*), at least in northern Europe, but variation in feeding ecology also exists among groups of birds identified as call types. The state of most of these groups remaining contentious with regards to their morphology, ecology and feeding specialism (Robb, 2000; Edelaar *et al.*, 2008; Förschler & Kalko, 2009; Martin *et al.*, 2024). The Parrot Crossbill is sympatric with the Common Crossbill, shows a remarkably larger body size and thicker beak than the latter. The Parrot Crossbill is believed to feed mostly on the tough Scott pine cones,

Pinus sylvestris (Newton, 1967). Because of their morphological distinctiveness, the two species have long been considered separate, although not without discussion (Bonaparte *et al.*, 1850; Gould, 1873). Stunningly, genomic studies have so far been unable to distinguish Common and Parrot Crossbills as separate lineages, even though these same studies succeeded at reporting population structure among several Common Crossbills call types (Björklund *et al.*, 2013; Parchman *et al.*, 2016). Assortative mating between Parrot and Common Crossbills appears to be strong even though interbreeding might occur (Summers *et al.*, 2007), but because of the limited evidence of genomic differentiation, several authors have questioned their status as separate species (Hill & Powers, 2021).

We used allometry to explore the extent of divergence between Parrot and Common Crossbills. The Parrot Crossbill has larger body and beak sizes than the Common Crossbill, and so would be expected to have evolved thicker beak shape by growing larger and reaching higher values along the same allometric trajectory. Alternatively, contrasting beak shapes between Parrot and Common Crossbill independent of size or differing allometric slopes may indicate that the two species possess genomic differences sufficient for divergence through nontrivial developmental processes, even if the majority of the genome shows incomplete lineage sorting.

Methods

Data collection

We conducted landmark-based geometric morphometric analyses from lateral photographs of the head of museum specimens of 70 Common Crossbills, 41 Parrot Crossbills and 19 Two-Barred Crossbills. The specimens belong to the Zoology collection of Lund University, the Natural History Museum in Oslo and the Swedish Museum of Natural History. We only measured specimens of *L. curvirostra* collected in Europe, primarily in Fennoscandia. The camera models were Canon EOS 7D, 100mm focal length; Nikon D3500 focal length 10-20

and Canon EOS 6D Mark II, focal length 50mm. We used StereoMorph 1.6.7 (Olsen & Westneat, 2015) for digitising the landmarks. We digitised three landmarks: at the higher and at the lower posterior extremities of the maxilla, and at the tip of the beak. We also digitised 17 sliding landmarks on each of the dorsal and the ventral (tomium) sides of the maxilla. Because of laterality in the crossing of the beak, we digitised the side of the beak where the maxilla crosses over the mandible. We directly digitised the photograph of specimens with the maxilla crossing on the right side. For specimens with the maxilla crossing over the left side, we mirrored the image before digitising the landmarks.

In addition to landmark data, we extracted maxilla depth as a linear measurement of beak size (Fig S1). Beak depth is a straightforward measure of beak variation in crossbills and is associated with feeding performance and fitness (Benkman, 1993; Summers *et al.*, 2002; Gómez-Blanco *et al.*, 2019). Because of incomplete closure and alignment of the two mandibles in many museum specimens, we only estimated maxilla depth. We used ImageJ 1.54g (Schneider *et al.*, 2012) to extract maxilla depth measurements on 75 Common Crossbills, 44 Parrot Crossbills and 20 Two-Barred Crossbills. This sample size differs for our morphometric analyses because of the state of conservation of some specimens (e.g. broken tip of the beak).

Analyses

The landmark coordinates were processed for scaling, rotation and location with Generalised Procrustes Analyses (GPA) using *geomorph* version 4.0.9 (Adams & Otárola-Castillo, 2013). We studied static allometry (Gould, 1966; Klingenberg, 1998), which in our case corresponds to size-shape covariation within species, including late juveniles (*i.e.* with the beak already crossing) and adults.

We tested for difference in allometry (homogeneity of slope) by performing Procrustes np-MANCOVA and Randomization of Residuals Permutation Procedure (RRPP) with 10,000

permutations, and using the logarithm of centroid size as a measure of beak size (Collyer *et al.*, 2015). We visualised allometric trajectories as (1) predicted values of beak shapes from species-specific regressions over the logarithm of centroid size (PredLine method, Adams & Nistri, 2010), and (2) Common allometric Component of the shape data (CAC) and the first residual shape component (RSC1, Mitteroecker *et al.*, 2004).

Results

While the three species differed in beak size expressed as maxilla depth (Fig 1a), the Parrot Crossbill differed from Common and Two-Barred Crossbills in the shape of the maxilla independently of size (Fig 1b-d). In contrast, the Common and Two-barred crossbills appear not to differ in beak shape and allometry (Fig 1b-d). The results from Procrustes ANOVA revealed strong statistical evidence for the effect of species on beak shape variation (Table 1, results with other Sum of Square Types in Table S1, Table S2). The effect of size on shape was associated with a lower effect size than the effect of species, and received limited statistical support (Table 1, Table S1). Therefore, there was limited statistical evidence for (common) allometry among the three species. We also reported smaller effect size and limited statistical support for an interaction between size and species, meaning that the allometric trajectories were distinct yet likely parallel, differing only in intercept (Table 1). Pairwise comparisons indicated larger phenotypic distances between Parrot and Two-Barred Crossbills, and between the Parrot and Common Crossbills than between Common and Two-Barred Crossbills, with no statistical support for shape difference between the latter pair (Table 2). Note that there was no evidence for an effect of the sex of the specimens on shape (Table S3).

Principal Component plots showed that Parrot Crossbills departed from the distribution of Common and Two-Barred Crossbills towards lower values of PC2, which corresponds to a deeper upper maxilla with a more curved upper edge and relatively shorter tomium, giving the

structure a bulkier appearance (Fig 1b, Fig S2). Visualisation of shape allometry suggest that, if influenced by size at all, larger maxilla is shallower and leaner, such that the intercept of the allometric slope of the Parrot Crossbill is shifted towards lower values (Fig 1c). The first residual component of shape regressed out of size (RSC1) clearly separates Parrot Crossbills from Common and Two-Barred Crossbills along the Common Allometric Component (Fig 1d, Fig S3). Overall, these results indicate that the Parrot Crossbill differs from the two other species at least in a size-independent component or in the intercept of the allometric slope of the maxilla.

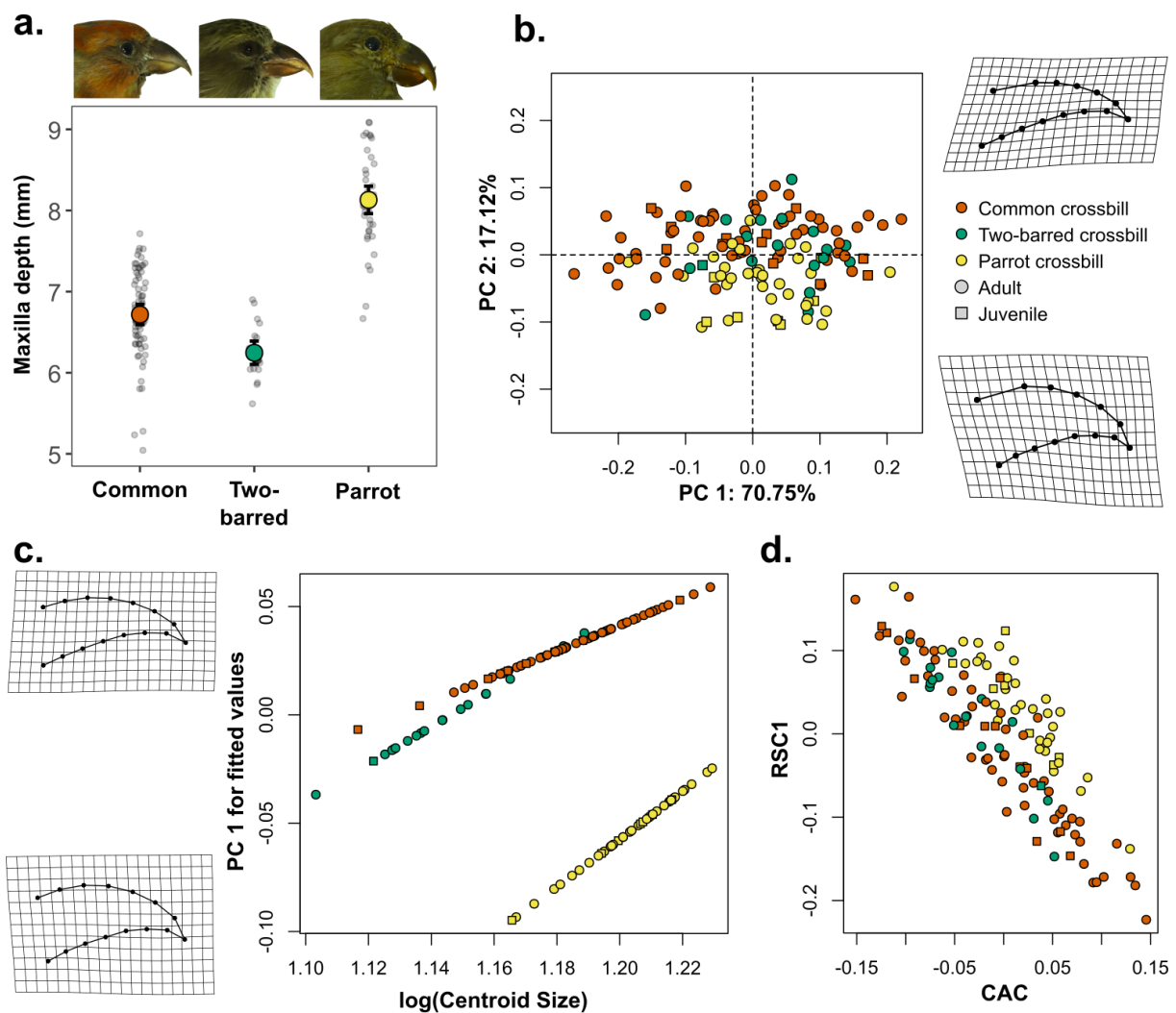


Figure 1. Maxilla size and shape variation among crossbills based on linear measurement (a) and geometric morphometrics (b-d). (a) Linear measurement of the depth of the maxilla.

Coloured dots are species means, error bars are 95% Confidence Intervals and grey dot are individual values. Insets on the top are pictures of representative mounted specimens, not on the same scale. (b) Principal component analysis of landmark coordinates of the maxilla. Right insets are deformation grids depicting shape changes at each extreme of PC2. (c) Allometric trajectories as predicted values over size. (d) Vitalisation of allometry as Residual shape component scores (RSC1) over the Common allometric component scores (CAC).

Table 1. Degrees of freedom, R^2 , effect size (Z) and p-value of Procrustes ANOVA based on randomised residual permutation procedure (RRPP)¹

	<i>d.f.</i>	R^2	Z	p
Size	1	0.012	1.039	0.158
Species	2	0.113	3.737	<0.001
Size × Species	2	0.028	1.315	0.096

¹Model : shape coordinates ~ Size + Species + Size × Species, Type I Sum of Squares.

Table 2. Pairwise Procrustes distances (d) and angles of allometric slopes, with respective effect size (Z), and p-value.

		d			Angle	
	d	Z	p	angle (°)	Z	p
Common – Two-barred	0.035	0.126	0.448	6.937	1.541	0.063
Parrot – Common	0.100	3.631	<0.001	6.379	0.446	0.321
Parrot – Two-barred	0.102	2.111	0.014	8.453	1.038	0.142

¹ Full model (*d*): shape coordinates ~ Size + Species. Reduced model (*d*): shape coordinates ~ Size; Full model (angle): shape coordinates ~ Size × Species Reduced model (angle): shape coordinates ~ Size + Species. Type I sum of squares.

Discussion

We showed that the Parrot Crossbill have diverged from the Common Crossbill in their beak shape, and that this differentiation is either independent of size or resulting from allometric shifts. In contrast, the Common and the Two-Barred Crossbills, despite being divergent for more than a million years, show a conserved beak shape, likely varying along a common allometric trajectory. This conservatism in allometry and beak shape between these two distinct species highlight that the uniqueness of the Parrot Crossbill beak. Our results indicate that the Parrot Crossbill beak shape is not explained by extended growth along a common allometric trajectory. Furthermore, the Parrot Crossbill appears to retain the shape expected at smaller beak size, which is tentative evidence of paedomorphosis. Although the ontogenetic processes underlying the pattern of beak divergence in Parrot Crossbill remain to be investigated, our results strongly indicate that the Parrot Crossbill has evolved a divergent morphology through genetic changes modulating craniofacial development.

Beak morphogenesis is highly constrained across finches by shared developmental processes involving cell proliferation in different growth zones (Fritz *et al.*, 2014; al-Mosleh *et al.*, 2021). Thus, heterochrony (*i.e.* shifts in the timing of development) leading to divergence in beak width and depth are set during embryogenesis by differential expression in key signalling pathways (Mallarino *et al.*, 2012). For example, radiations in Darwin's finches (*Geospiza spp.*) and in Caribbean bullfinches (*Loxigilla spp.*) can each be related to specific scaling of beak dimension (depth and/or length), which likely occurs through differential growth of the prenasal and premaxillary bone cartilages (Mallarino *et al.*, 2012). Beak shape variations in *Geospiza*

can be explained by induced growth in both tissues under the influence of the signalling pathways *Bmp4*, *CaM*, *TGF β II*, *β -catenin* and *Dkk3*, while divergence among *Loxigilla* species involves premaxillary bone growth through *Bmp4* and *Indian Hedgehog* (Mallarino *et al.*, 2012). The Parrot Crossbill shows either size-independent changes or shift in the intercept of allometric trajectory, indicating that its unique beak shape might have evolved through variations in a growth parameter within a developmental programme shared among crossbills. In contrast, a profound reshaping of developmental processes would likely have implied a differentiation in the slopes of the trajectories. The deeper and bulkier beak relative to size of the Parrot Crossbill might be patterned by modulating and timing the relative growth rate of cell proliferation in the beak primordia through the same signalling as in large-beaked species of *Loxigilla* or *Geospiza*.

Our results based on static allometry identify exciting directions to further investigate ontogeny and developmental dynamics in crossbills. Coupled with more thorough genomic studies, such work could decipher the evolutionary-developmental processes of divergence in crossbills and shed light on the taxonomic status of the Parrot Crossbill. The most up-to-date genomic investigations on Parrot and Common Crossbills, using over 18 000 SNPs from Genotyping-by-Sequencing, only reported low levels of differentiation and a lack of population structure (Parchman *et al.*, 2018). Further analyses based on whole-genome sequencing will provide a higher resolution investigation of genomic regions associated with the signalling pathways underlying beak scaling. These processes would warrant particular attention according to the patterns of beak shape variation we have described here for the Parrot Crossbill. Many additional cases of divergence are still unresolved and poorly understood among the crossbills species complex, the emblematic Scottish crossbill being worthy of note in this regard (Marquiss & Rae, 2002; Summers *et al.*, 2002). Here we showed that developmental considerations using the concept of allometry can shed light on the remarkable patterns of

morphological differentiation in the many populations and call types of crossbills amid their unsettled phylogeny. Our results showcase the importance of studying allometry in the genomic era, emphasising that size-shape covariation provides powerful means to characterise morphological divergence and to infer candidate developmental processes that otherwise might be unnoticed when using only a molecular approach. **Authors contributions**

Quentin Horta-Lacueva: Conceptualization, Methodology, Software, Data curation, Formal analysis, Investigation, Resources (equal), Validation, Visualization, Writing – Original draft, Writing – Review & editing (lead), Funding acquisition (lead)

Mark Ravinet: [add more or upgrade to lead/equal if you judge it to be fair] Resources (equal), Writing – Review & editing (support), Funding acquisition (support)

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Data availability

The datasets and code will be available after publication on Zenodo, doi:10.5281/zenodo.23503185

Conflict of interest

The authors declare no conflict of interest.

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Supplementary Material

Table S1. Degrees of freedom, effect size (Z) and p-value of Procrustes ANOVA based on randomised residual permutation procedure (RRPP)¹, Type II Sum of Squares.

	<i>d.f.</i>	<i>R</i> ²	<i>Z</i>	<i>p</i>
Size	1	0.017	1.418	0.079
Species	2	0.113	3.737	<0.001
Size × Species	2	0.028	1.315	0.096

¹Model : shape coordinates ~ Size × Species

Table S2. Degrees of freedom, effect size (Z) and p-value of Procrustes ANOVA based on randomised residual permutation procedure (RRPP)¹, Type III Sum of Squares.

	<i>d.f.</i>	<i>R</i> ²	<i>Z</i>	<i>p</i>
Size	1	0.007	0.392	0.357
Species	2	0.028	1.306	0.099
Size × Species	2	0.028	1.315	0.096

¹Model : shape coordinates ~ Size × Species

Table S3. Degrees of freedom, effect size (Z) and p-value (P) of Procrustes ANOVA based on randomised residual permutation procedure (RRPP)¹

	<i>Df</i>	<i>SS</i>	<i>MS</i>	<i>Rsq</i>	F	Z	Pr(>F)
sex	1	0.013	0.013	0.007	0.948	0.363	0.364
size	1	0.028	0.028	0.015	2.057	1.186	0.123
pop	2	0.223	0.112	0.119	8.166	3.658	0
size:pop	2	0.056	0.028	0.03	2.033	1.325	0.095

¹Model : shape coordinates ~ Sex + Size + Species + Size × Species, Type I Sum of Squares.

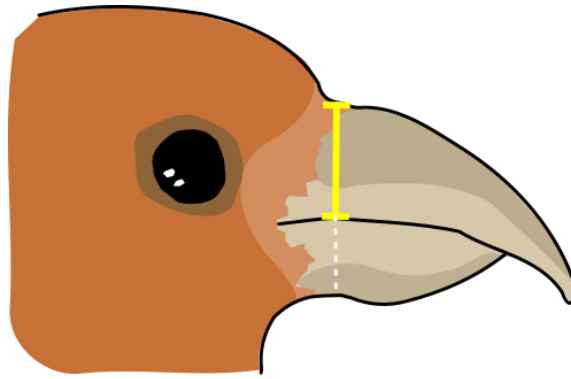
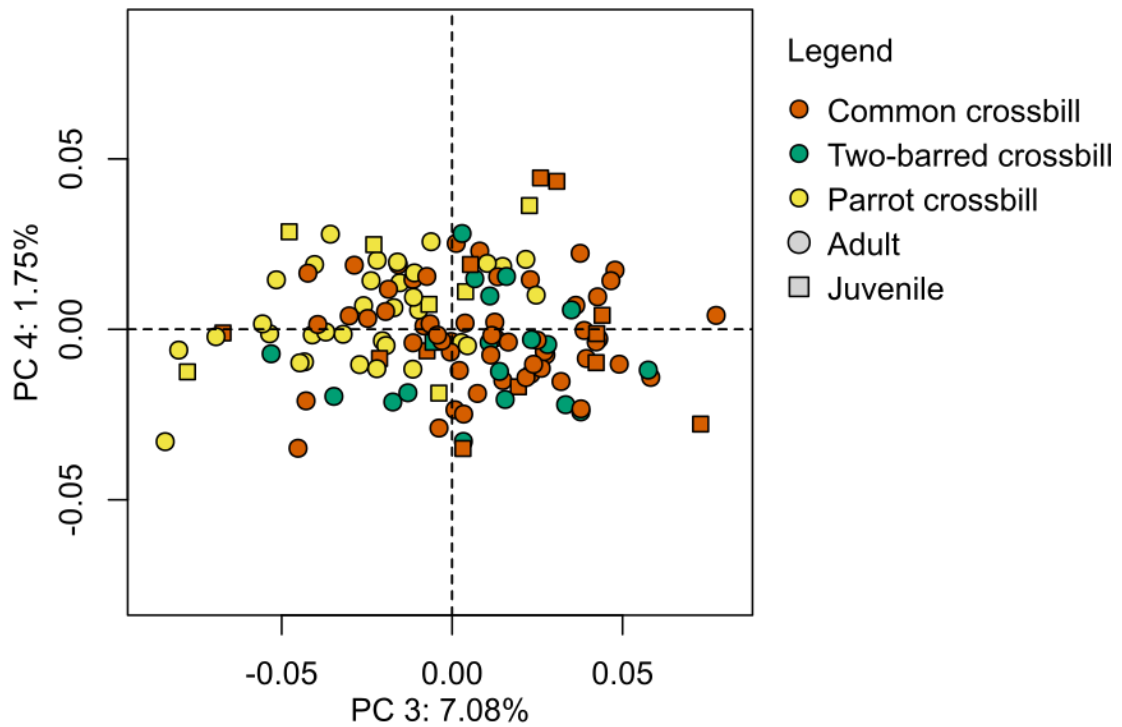


Figure S1. Schematic depiction of the linear measurement for maxilla depth. Maxilla depth was measured as the distance from the upper edge of the maxilla to the lower edge (tomium) as depicted by the yellow segment. The longitudinal location of the measurement was defined at the edge of the feathered crown and the nostril (top) and the convex point of curvature of the mandibula (bottom) as indicated by the white dashed line.

a.



b.

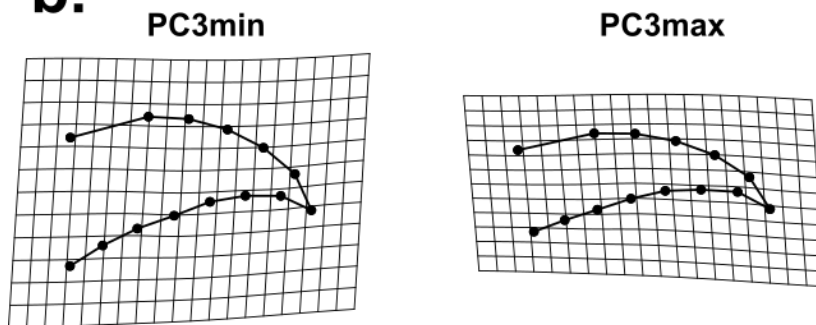


Figure S2. Principal component analysis of landmark coordinates of the maxilla. (a) Projection along Principal Components 3 and 4. (b) Deformation grids depicting shape changes at each extreme of PC3.

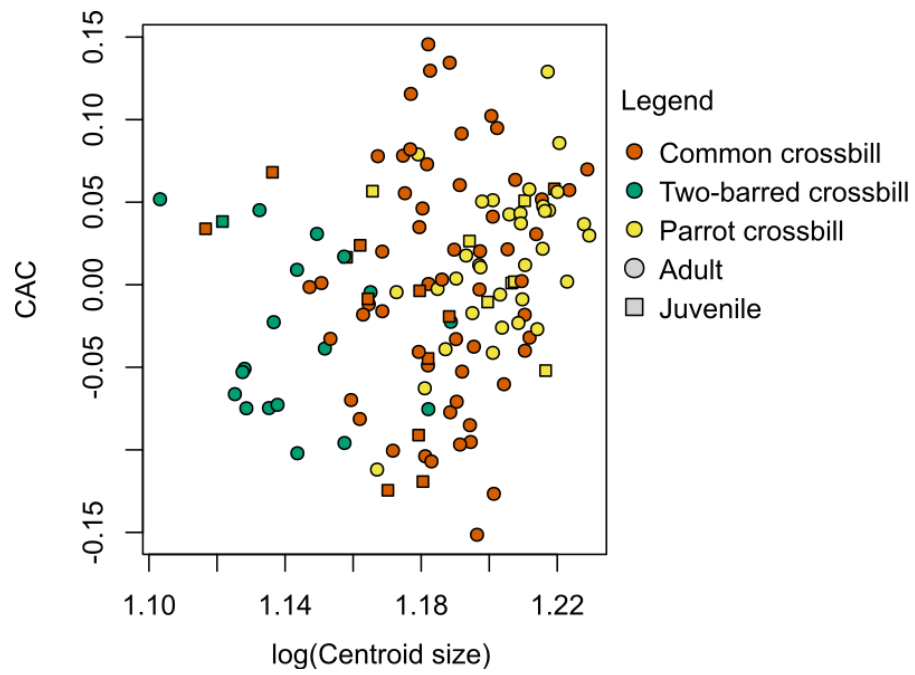


Figure S3. Visualisation of allometry as Common allometry component scores (CAC) over the logarithm of centroid size.