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How wry is a Wrybill?

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The laterally asymmetrical bill of New Zealand's endemic Wrybill *Anarhynchus frontalis* is unique among birds and has inspired much debate regarding its evolution and functional significance. Despite this, only one previous study has attempted to quantify the range of individual variation in bill shape, but used a single metric of curvature (bill tip angle). Using standardized digital photographs of 40 live Wrybills, we explored a range of metrics of bill length and curvature to describe the variation in bill shape in greater detail. Like the previous study, we found no sexual dimorphism in bill shape, despite males being slightly longer-billed than females, and recorded similar variation in bill tip angle (16–23°). However, we found that this single metric under-represented overall variation in bill shape, due to significant differences in where curvature began and was most pronounced along the length of the bill. Principal component analysis indicated that at least three independent metrics were required to describe the shape variation among individuals. Subtle differences in bill shape could plausibly affect an individual's relative success among the range of Wrybill foraging strategies observed in breeding and non-breeding habitats. Elucidating the potential behavioral and fitness consequences of this variation will require detailed foraging and demographic studies with individuals of known bill morphology.

Keywords

Anarhynchus frontalis
bill morphology
sexual dimorphism
individual variation
morphometrics
curvature
asymmetry

INTRODUCTION

Shorebirds display enormous variation in bill morphology, reflecting specialization to particular diets and partitioning of niches within habitats (Barbosa & Moreno 1999, van de Kam *et al.* 2004). These correlated morphological and behavioral differences are more obvious between species or groups (e.g. curlews vs. plovers), but also occur within species (Durell 2000), according to sex (Puttick 1981, Townshend 1981, Zharikov & Skilleter 2002, Mathot *et al.* 2007, Alves *et al.* 2013, Duijns *et al.* 2014), age (Goss-Custard & Durell 1987, Fasola *et al.* 1996), or even individual specializations, as have been found in curlews (Evans 1988), godwits (Catry *et al.* 2014), phalaropes (Rubega 1996), and oystercatchers (Sutherland *et al.* 1996). Sexual dimorphism in bill size generally follows overall size differences that may result from sex-specific selection unrelated to foraging, such as mating system (Jehl & Murray 1986, Székely *et al.* 2000), but in some dimorphic species, bill differences exceed an isometric scaling with body size (Evans 1988, Mathot *et al.* 2007,

Conklin *et al.* 2011), implying further specialization in foraging behavior by sex. Among shorebirds, the most striking example of sexual dimorphism in bill shape is found in American Avocets *Recurvirostra americana*, in which females have much shorter and more recurved bills than males, despite modest overall size dimorphism (Hamilton 1975). This presumably is associated with sex differences in foraging strategy or efficiency, although this has yet to be clearly demonstrated.

In general, variation in bill size and shape is much less pronounced in Charadriidae than in other shorebird families, particularly Scolopacidae (Durell 2000). Despite the relatively conserved bill structure of plovers, Charadriidae contains one of the most distinctive bills found in all birds: the laterally curved bill of New Zealand's endemic Wrybill *Anarhynchus frontalis* (Fig. 1a). Aside from its unique curvature (always to the right), the bill is unusually long for plovers, lending to the species' historical recognition as a monospecific genus, despite general morphological similarity to *Charadrius* (Piersma & Wiersma 1996).

However, recent phylogenetic analysis has demonstrated the Wrybill's rightful placement in *Charadrius*, as part of a monophyletic sub-group endemic to New Zealand, which includes Banded Dotterel *C. bicinctus* and New Zealand Dotterel *C. obscurus* (dos Remedios et al. 2015). The typical 'plover-type' bills of these closely-related species suggests that Wrybills arose independently from 'normal-billed' ancestors.

The singular bill morphology of Wrybills naturally implies strong selection imposed by foraging ecology. Whether the bill is an adaptation to foraging in the cobble riverbeds where Wrybills breed or on mudflats during the non-breeding season is a matter of centuries-old debate (Potts 1870, Buller 1873, Stead 1932). There is support for both of these non-mutually exclusive propositions (Turbott 1970, Pierce 1979, Hay 1984), as well as a recent suggestion that the unique bill structure is well-suited for biofilm feeding (Withington 2015).

Despite much interest in the function of the Wrybill's bill, and its anatomy (Burton 1972), there has been little effort to describe between-individual variation in bill morphology. The only Wrybill study to specifically examine variation in bill curvature (Hay 1984) used a single metric of curvature to show that the bill tip was deflected from straight by 12–26° (mean = 18.3°) among 72 live specimens. Despite slight size dimorphism in most morphological measurements (males > females), that study found a unimodal distribution with no sexual dimorphism in bill curvature.

Measuring bill curvature in the field is far from straightforward, and many metrics have been proposed and explored in a diverse range of avian species, including avocets *Recurvirostra* spp. (Hamilton 1975, Rogers 1990, Ryeland et al. 2017), Eurasian Curlew *Numenius arquata* (Evans 1988), Whimbrel *N. phaeopus* (Mallory 1981), Curlew Sandpiper *Calidris ferruginea* (Ryeland et al. 2017), hummingbirds (Temeles et al. 2009, Berns & Adams 2010), and storks (Ćwiertnia et al. 2006). These various metrics capture different components of bill shape, and each has its own challenges with regard to reproducibility and practicality in the field. Here, we use digital photography of live individuals to quantify bill variation in male and female Wrybills. Specifically, we explore a range of metrics to describe bill shape, determine which metric (or combination of metrics) best captures existing variation, and identify measurable aspects of bill shape for further investigation into the ecological significance of the Wrybill's unique bill morphology.

METHODS

Fieldwork

Wrybills were caught using a cannon-net on 2 March 2014 in the western Firth of Thames, North Island, New Zealand (37°11'S, 175°19'E), as part of a long-term banding and monitoring effort by the New Zealand Wader Study Group. Birds were aged by plumage (Davies 1997). We randomly chose 40 individuals aged second year-of-life

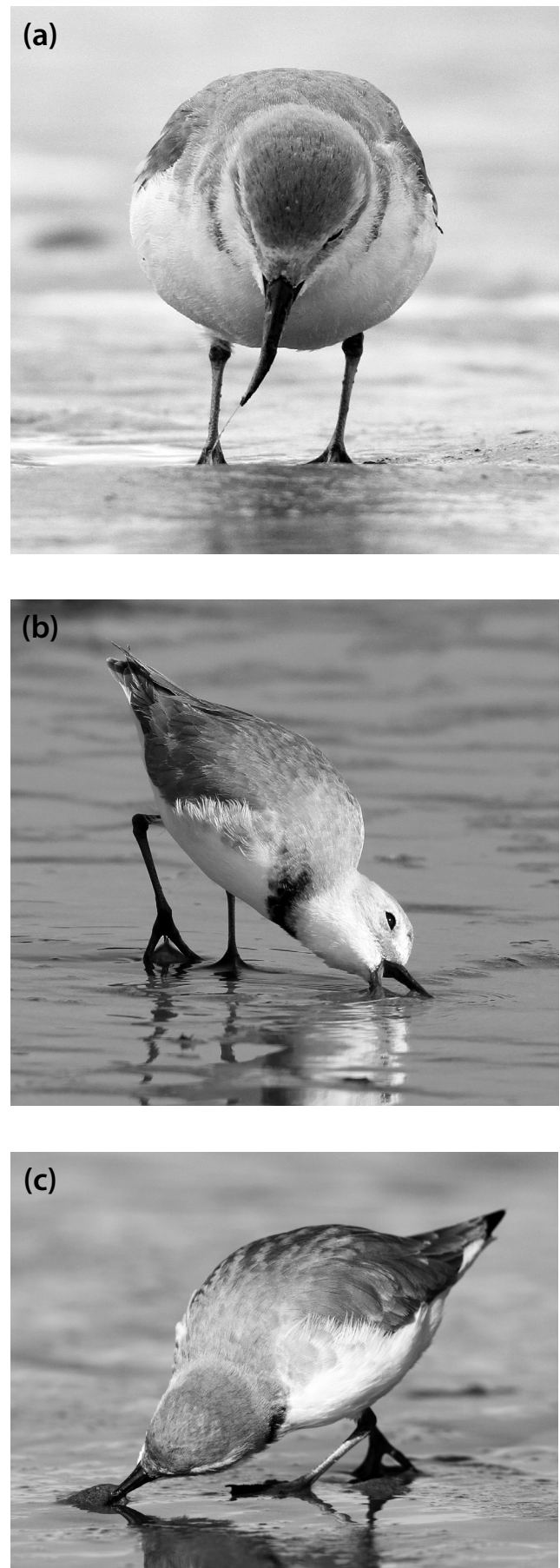


Fig. 1. Wrybills foraging in sandy substrates at the Manawatu River estuary, North Island, New Zealand (photos: Phil Battley).

or older for blood sampling and bill photography. For each individual, we used a 27-gauge needle to extract *ca.* 20 μ l of blood from the brachial vein into a capillary tube, and stored blood samples in Queen's lysis buffer (Seutin *et al.* 1991). We then photographed the head and bill of each bird, positioned over a sheet of paper printed with a standardized grid, from directly above (Fig. 2), using a hand-held digital camera (Canon PowerShot SX270 HS).

Sexing

We extracted DNA from lysed blood samples using the NucleoSpin Blood QuickPure Kit (Macherey-Nagel, Germany). Individuals were molecularly sexed using the wader-specific primers 2602F/2669R, following the method of van der Velde *et al.* (2017).

Bill measurements

Using the *scale*, *rotate*, and *skew* tools in the program Adobe Illustrator (Adobe Inc., USA), we first adjusted photos for slight differences in angle and scale, based on the standardized grid visible in each. Then, using digital measurement and drawing tools in Illustrator, we recorded nine measurements for each bird (see Fig. 3, Table 1).

Three metrics of bill length:

A. Straight length: straight-line length along main axis of the straight portion of the bill from base of bill feathering to the point along this axis parallel to bill tip.

B. Bill chord: straight-line length from base of bill feathering to bill tip.

C. Arc length: curved length following midpoint of bill from base to bill tip.

Four metrics of degree of curvature:

D. Lateral deviation: distance from bill tip to maximum straight-line length (the end point of A).

E. Curve depth: maximum perpendicular distance from bill chord (B) to bill arc (C).

F. Full angle of deviation: angle ($^{\circ}$) between straight (A) and chord (B) axes.

G. Tip angle of deviation: angle ($^{\circ}$) between straight axis (A) and a straight line from bill tip to the point where midline of bill (C) deviates from straight (as in H).

Two metrics of the position of the curvature along the bill length:

H. Distance to curve: distance along bill length from base to the point where midline of bill (C) deviates from straight (A), as in G.

I. Distance to greatest curvature: distance along bill chord (B) from base to the point of greatest distance from bill arc (C), as in E.

From these measurements, we calculated four additional indices of bill shape, which are proportional and thus independent of absolute size (i.e. dimensionless):



Fig. 2. Example of standardized photograph taken in the field.

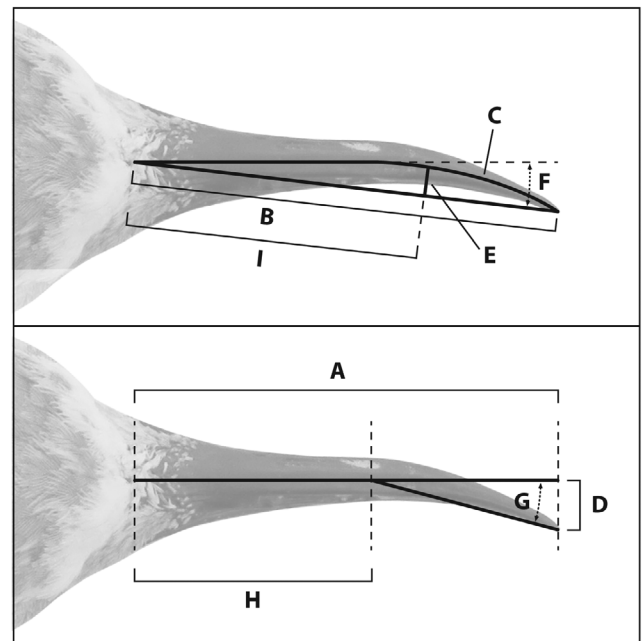


Fig. 3. Metrics of bill length and shape: A. straight length; B. bill chord; C. arc length; D. lateral deviation; E. curve depth; F. full angle of deviation; G. tip angle of deviation; H. distance to curve; I. distance to greatest curvature. See text for details.

J. Arc:chord ratio: ratio of curved length to bill chord (C/B).

K. Proportion straight: proportion of arc length from base to start of curvature (H/C).

L. Proportion to greatest curvature: proportion of bill chord from base to point of greatest curvature (I/B).

M. Depth ratio: ratio of curve depth to bill chord (E/B).

Statistical analysis

Linear measurements were unitless when recorded, then converted to mm using the known size of the standardized grid. We do not have caliper-measured bill chords for these 40 individuals. However, our values for bill chord (not shown) were systematically 2–3 mm smaller than

those reported in previous studies (Hay 1984, Davies 1997); this is likely an artefact of our method of converting digital photographic measurements to ‘real’ lengths. This discrepancy does not affect our analysis of bill shape, which is intentionally based on scale-independent metrics. However, to present the range of variation while avoiding the presentation of potentially confusing raw data, we transformed all linear measurements (A–C) by $\times 1.104$ to conform to the mean bill chord found by Hay (1984); these transformed values are presented in Table 2.

In Wrybills, males are slightly larger than females in most linear measurements, including bill length (Hay 1984); therefore, we tested for sex differences in metrics of bill length (A–C) using one-tailed *t*-tests. We tested for sex differences in angular and proportional metrics of bill shape (F, G, J–M) using non-parametric, two-tailed Wilcoxon rank-sum tests.

We explored the contribution of different metrics of bill shape using principal components analysis (PCA) in R

(built-in function *prcomp*), and visualized results using the *ggbiplot* function in the R package *ggplot2* (Wickham 2016). For this analysis, we removed the effect of absolute size by excluding length measurements (A–C) and including only six scale-independent metrics (F, G, J–M); thus, metrics D, E, H, and I were not tested, as these were used only to derive scale-independent metrics.

RESULTS

Among 40 Wrybills measured, the range of variation was *ca.* 6 mm in all three length measurements (A–C; Table 2). Although capturing potentially different variation, these three metrics were essentially redundant: straight length (A) and arc length (C) were almost perfectly correlated ($r^2 = 0.99$, $P < 0.0001$). Despite the pronounced visible curvature of the bill, an individual’s arc length (C; mean = 29.8 mm) exceeded its bill chord by only 1–2% (J; mean 1.3%). Overall, the curvature of the Wrybills measured resulted in a bill tip that deviated 5.9–9.3°

Table 1. Metrics of bill length and shape used in this study (see *Methods* and Fig. 3 for details). The terminology used for equivalent metrics in previous studies of decurved or recurved bills is provided for reference.

Metric	Name	Equivalent to	Reference
A	Straight length	Culmen length Tangent to straight base Lower straight line (recurved)	Hamilton 1975 Evans 1988 Ryeland <i>et al.</i> 2017
B	Bill chord	Bill chord Culmen length Upper straight line (recurved)	Hamilton 1975, Berns & Adams 2010 Temeles <i>et al.</i> 2009 Ryeland <i>et al.</i> 2017
C	Arc length	Arc Arc length Middle curved profile	Berns & Adams 2010 Temeles <i>et al.</i> 2009 Ryeland <i>et al.</i> 2017
D	Lateral deviation	Height Bill depression	Hamilton 1975, Ryeland <i>et al.</i> 2017 Evans 1988
E	Curve depth	Mandibular curvature index	Berns & Adams 2010
F	Full angle of deviation	Alpha angle	Evans 1988
G	Tip angle of deviation	Beta angle Angle of curvature	Evans 1988 Hay 1984
H	Distance to curve	Length of straight bill	Evans 1988
I	Distance to greatest curvature	Length to perpendicular	Hamilton 1975
J	Arc:chord ratio (C/B)	Arc:chord ratio	Berns & Adams 2010
K	Proportion straight (H/C)	Inverse of % decurved	Evans 1988
L	Proportion to greatest curvature (I/B)	–	This study
M	Depth ratio (E/B)	–	This study

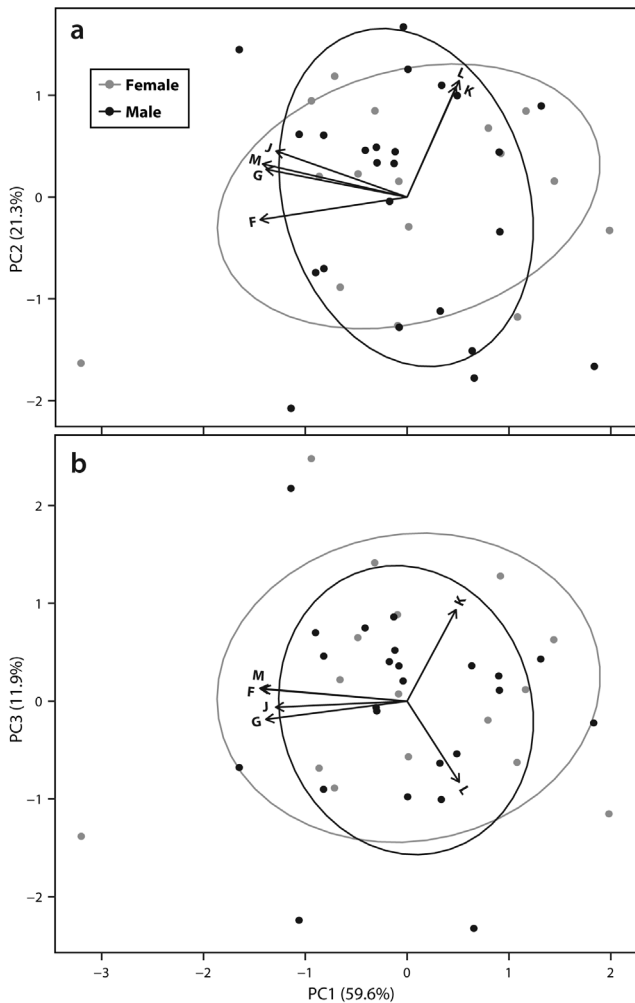


Fig. 4. Principal component analysis of six metrics of bill shape (letters indicate different metrics; see *Methods*) grouped by sex (gray = females, $n = 16$; black = males, $n = 24$). **(a)** Two major axes (% = amount of total variation explained) explaining 81% of total variation are described by two groups of highly correlated metrics: degree of curvature (F, G, J, M) and position of curvature along length of bill (K, L). **(b)** An additional 12% of variation is largely explained by differences in two metrics of position of curvature (K, L). In both **(a)** and **(b)**, overlap of ellipses (68% probability) indicates a lack of sexual dimorphism in curvature.

from a perpendicular axis when measured from the base of the bill (F), or 15.9–23.0° when measured from the point of first visible curvature (G).

According to molecular sexing, our sample included 16 females and 24 males. On average, male bills were slightly longer than female bills, in all three metrics of bill length (A–C; Table 2). However, variation in bill length was slightly higher in females (e.g. in A: range = 25.6–30.6 mm, SD = 1.41) than in males (range = 27.5–31.5 mm, SD = 0.94). We found no sex differences among six size-independent metrics of bill curvature (F, G, J–M), despite considerable overall variation in all aspects of bill shape.

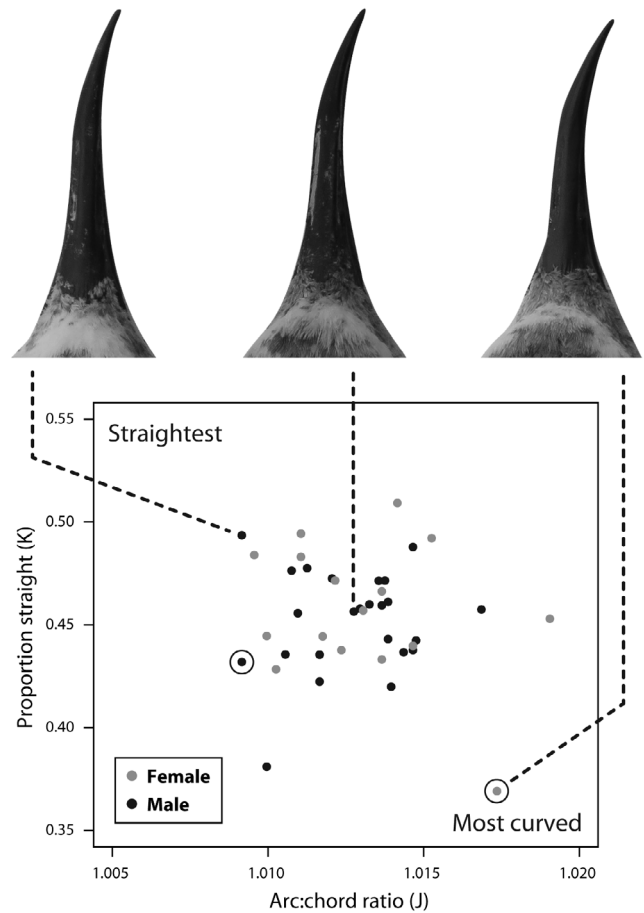


Fig. 5. Variation in bill shape among 40 individual Wrybills (gray = females, $n = 16$; black = males, $n = 24$) along two main axes identified in PCA (see Fig. 4a): degree of curvature (arc:chord ratio; J) and position of curvature along length of bill (proportion straight; K). Three individuals representing the continuum from straightest to most curved are highlighted. Circles indicate the individuals with lowest (left) and greatest (right) values of the single metric (bill tip angle; G) used by Hay (1984).

PCA analysis confirmed a lack of differences in bill shape by sex (Fig. 4).

After excluding differences in relative size among individuals, PCA analysis indicated two major axes that together explain 81% of the total variation in bill shape (Fig. 4a): degree of curvature (represented by metrics F, G, J, M) and position of the curvature along the length of bill (K, L). These two groups of variables lie approximately perpendicular to each other (i.e., orthogonal) with little variation within each group, suggesting that two metrics (one from each group) are sufficient to characterize most variation in bill shape in Wrybills. To illustrate this, we plotted arc:chord ratio (J) against proportional distance from base of the bill to the point of first curvature (K; Fig. 5); these metrics are not correlated ($r^2 = 0.01$, $P = 0.55$). Here, it is possible to identify the range from straightest to most curved bills in our sample.

The third axis (PC3) explained an additional 12% of

variation and confirmed that the two metrics of position of curvature (K, L) describe somewhat different aspects of bill shape. However, proportion of the bill that is straight (K) is to some extent correlated with the position of the greatest curvature (L; $r^2 = 0.10$, $P = 0.049$).

DISCUSSION

Despite the obvious potential ecological and evolutionary significance of the Wrybill's singular bill, our study is the first to explore how best to describe its unique shape. The only previous attempt to quantify individual variation in the bill shape (Hay 1984) used a single metric to describe curvature: the angle at which the bill tip deviated from straight. Using the same metric (G), we found a similar range of variation among our sample of 40 individuals: 16–23° (mean 18.9°) compared to 12–26° (mean 18.3°) from 72 live specimens in that study. These results are remarkably similar, given the potentially subjective nature of identifying the point along the bill where curvature begins (see Fig. 3), particularly in the field. Hay (1984) did so by tracing bills on paper and marking reference points for later calculations; presumably greater precision and repeatability is possible with digital photos. We used a hand-held camera and later digitally corrected for slight scale and angle variation. A rigid camera set-up could easily be devised to ensure greater standardization of photos, to minimize potential measurement error.

Despite the slightly longer bills of male Wrybills, we found no sexual dimorphism in any metric of bill shape. Using a sample of birds sexed by a combination of plumage and breeding behavior, Hay (1984) similarly found a uni-

modal distribution and no sex difference in bill tip angle, despite males having greater average mass and length of bill, tarsus, and tail. Due to overlap in all characters, these small differences were insufficient to devise a discriminant function for reliable sexing based on morphometrics (Hay 1984), consistent with generally low sexual dimorphism found in the subfamily Charadriinae (Piersma & Wiersma 1996). The lack of dimorphism in bill shape suggests that its unique curvature plays little role in sexual selection or in niche partitioning between sexes.

We found that a single metric of degree of curvature was insufficient to describe the variation in overall bill shape. According to PCA, bill tip angle (G) was a good proxy for two other metrics of degree of curvature (J, M), but all of these failed to capture additional variation related to where the curvature is situated along the length of the bill (L, K; Fig. 4a). By simple geometry, these two primary attributes should be summarized, or at least partly captured, by the angle of deviation of the full bill length (F). In fact, the main axis of variation in F lies intermediate between the two orthogonal groups (Fig. 4a), suggesting this is true to some degree. Although the two main PCA axes explained 81% of variation in bill shape, PC3 (Fig. 4b) indicates that including a third metric (i.e., combining J, K & L) can increase the total variation explained to *ca.* 93%. It should be noted that the individual identified in Fig. 5 as 'most curved' based on two metrics (J, K) also had the extreme value (23.0°) of the single metric (bill tip angle; G) used by Hay (1984), and here the studies would agree. However, the lowest value of bill tip angle (G) corresponded to an intermediate value of proportion of straight bill (K; Fig. 5), illustrating how much overall

Table 2. Wrybill males had slightly longer bills than females in all three metrics of bill length (A–C, in mm), but there was no sexual dimorphism in any size-independent metric of bill curvature (F & G, in degrees; J–M, proportional). Linear metrics (A–C) are transformed values from digital measurements (see *Methods* for description of metrics). COV = Coefficient of variation.

Metric	Sexes combined ($n = 40$)				Female ($n = 16$)		Male ($n = 24$)		One-tailed <i>t</i> -test		
	Mean	Min	Max	COV	Mean	SD	Mean	SD	<i>t</i>	df	<i>P</i>
A	29.19	25.56	31.46	4.05	28.78	1.41	29.47	0.94	-1.71	23.8	0.051
B	29.42	25.84	31.67	3.97	29.00	1.38	29.70	0.93	-1.77	24.1	0.045
C	29.80	26.15	32.09	3.98	29.38	1.41	30.08	0.94	-1.72	23.9	0.049
									Two-tailed Wilcoxon test		
									<i>W</i>	<i>P</i>	
F	7.18	5.92	9.31	8.63	7.20	0.79	7.16	0.50	187.0	0.901	
G	18.92	15.87	22.98	7.45	18.84	1.58	18.98	1.32	171.5	0.581	
J	1.013	1.009	1.019	0.22	1.013	0.003	1.013	0.002	194.5	0.955	
K	0.454	0.369	0.509	6.28	0.457	0.034	0.452	0.025	216.0	0.516	
L	0.622	0.561	0.647	2.77	0.620	0.014	0.622	0.019	169.0	0.534	
M	0.068	0.056	0.082	7.85	0.068	0.006	0.069	0.005	155.5	0.318	

variation in shape is missed with a single metric. Furthermore, our 'straightest' individual (Fig. 5) had a bill tip angle (18.0°) near the mean value in our study (18.9°); here, the overall straightness of the bill would be missed by focusing only on bill tip angle.

The use of standardized digital photos minimizes handling time of birds in the field, and also creates a permanent record that is available for multiple, or even unforeseen, analyses of bill shape. However, it may be desirable to develop simple metrics that can be measured in the field. We have shown that metrics G, J, and M provide roughly equivalent information and capture the bulk of variation in curvature (PC1). We expect arc-chord ratio (J) is the most repeatable of these in a field situation, as it relies on the ratio of two length metrics, bill chord (B) and arc length (C), which are straightforward measurements requiring no potentially subjective decisions, such as the precise point where curvature begins or is greatest. For more subtle description of curvature (PC2 & 3), such decisions appear unavoidable and may be difficult in the field. However, further exploration of the best way to characterize variation in bill shape, for example with geometric morphometric analysis (GMA; Adams & Otárola-Castillo 2013), may reveal simpler but useful metrics.

Ultimately, the research question should dictate whether a coarse single metric or detailed combination of metrics is sufficient to characterize variation in bill shape. Currently, there is little empirical evidence for which aspects of bill shape, if any, are functional and adaptive in Wrybills, and what range of variation is ecologically relevant. The morphological variation is considerable (COV of 6–9 in the most variable traits; Table 2), similar to variation found in the bill curvature of Whimbrel (COV 8–10; Mallory 1981), but less than that of Eurasian Curlew (COV 10–20; Evans 1988). Despite this, we found no bimodality in size or shape that would imply diversifying selection based on ecological differences, such as specialization on a certain foraging strategy. Such variation could be maintained by a range of foraging strategies in the population or fluctuating selective conditions across time. Alternatively, it could be non-adaptive variation that has simply not been removed through selection. This small, island population (*ca.* 4,000–5,000 individuals; Riegen & Dowding 2003) provides a good opportunity for rare but non-detrimental traits to proliferate and persist, even with only marginal adaptive advantage.

Following decades of dispute about whether the Wrybill's asymmetrical bill was an adaptation to the breeding or non-breeding season, behavioral research suggested different adaptive function in each season. During breeding seasons spent on braided rivers, the bill seems to allow better chasing and extraction of mayfly and caddisfly larvae as they hide under rocks to escape detection and capture (Pierce 1979). On mudflats in the non-breeding season, the bill is used for a different type of motion, a 'swishing' through wet muddy substrate (Turbott 1970). However, other foraging modes on mudflats, such as stalking and probing (Hay 1984), and biting the sediment

with the head tilted nearly 90° to the left (Fig. 1b), make no obvious use of the curved bill. American Avocets similarly use their recurved bill for both probing and scything motions (Boettcher *et al.* 1994). Interestingly, riverine probing by Wrybills involves a largely left-to-right motion (Pierce 1979), whereas mudflat 'swishing' (Fig. 1c) is largely done with a right-to-left motion (Turbott 1970, Withington 2015); this involves scything with the convex left side as the leading edge, rather than the more intuitive 'scooping' motion with the concave edge. Such a combination of foraging strategies may explain why the Wrybill has skeletal and muscular symmetry of the head and neck, contrary to expectations (Burton 1972).

It is easy to conceive how bill shape could influence effectiveness at various foraging modes, and thus influence an individual's true or perceived tradeoffs between prey types, local habitats, or even site choice. For example, Eurasian Curlews appear to specialize to some extent based on their bill curvature, with shorter, straighter bills (in both sexes) found more often in fields than on mudflats (Evans 1988). For Wrybills, what part of the bill shape is important for each foraging method? Is simple bill tip angle important for particular angles of approach, or does the precise location and length of the curvature offer certain advantages for leverage or prey detection? Answering these questions, and determining the potential demographic consequences of bill shape, requires cross-seasonal observational or experimental foraging studies involving individuals with known variation in bill morphology, which has yet to be attempted.

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