The contour feathers of water birds exhibit adaptations to the impact forces of diving, plunging and alighting

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March 4, 2021

Abstract

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Keywords water birds, contour feathers, water penetration, impact forces, diving, foraging niches.

Introduction

The contour feathers of birds serve a variety of functions that range from intraspecific signaling to such physical qualities as thermal insulation, water repellency, and resistance to impact. It is no surprise, therefore, that they are composed of an array of elements that confer these qualities to the optimal benefit of their avian bearer.

The structural details of contour feathers have been well described in the ornithological literature (Thomson 1964; Stettenheim 1972). The downy (plumulaceous) parts alongside the proximal two-third of the rachis are thought to function as a means to regulate body temperature by entrapping air (King and Farner 1961; Lucas and Stettenheim 1972; Stettenheim 2000; Lei et al. 2002). The distal one-thirds have a patterned, pennaceous structure with barbs extending from the rachis, each sprouting barbules of which the distal ones have hooks that catch upon the curled, proximal barbules of the barb next more distal. They are arranged in an overlapping fashion like shingles on a roof, having their dorsal aspect exposed to air or water. This continuous-looking, hook-and-flange arrangement provides the distal one-third with the rigidity so critical for its mechanical properties. It also confers water repellency and resistance to water penetration to the body plumage.

The water repellency of this part of the contour feather can be rated by the value of the wettability parameter $(r + d)/r$, where $2r$ denotes the diameter of the approximately circular or elliptical cross-section of the barb and $2d$ the separation of the barbs measured in the plane of the long axes of the barbs (Cassie and Baxter 1945; Moilliet 1963; Rijke 1970). Water repellency, expressed in terms of the contact angle with which a drop of water rests on a feather surface, is proportional to $(r + d)/r$, but resistance to water penetration, expressed as the pressure required to force water through the barbs and barbules, is inversely proportional to this parameter as well as to r. Values for the parameter range from about 2.5 for penguins (*Spheniscidae*) to 7 or more for typical land birds, implying that the contour feathers of penguins have poor water repellency, but excellent resistance to water penetration. For the contour feathers of land birds, it is the other way around.

The contribution of barbules to water repellency and resistance to water penetration is not based on the same mechanism as applies to barbs. Instead, barbules provide an interlocking mechanism by preventing the barbs from separating under mechanical forces, for instance, when water penetrates between barbs. They do so by increasing their own separation with their hooks sliding in the flanges of the adjoining barbules. As a result, the pressure required to force water through the feather is determined only by the diameter and spacing of the barbs without recourse to the barbules. Noteworthy is that the wettability parameter for barbules is more or less constant for all bird families at about 4.5 and does not vary with the feeding habits of water bird families as it does for barbs (Rijke et al. 1989).

In this paper, we consider the effects of mechanical forces, specifically the impact of diving, plunging, and alighting, on contour feathers and the structural properties that are identifiable as adaptations to these forces by comparisons of different, ab inito determined, foraging niches. In studies where the trait patterns between biological groups such as foraging niches are compared, it is important to consider the phylogeny of the species in the groups. The standard of establishing evolutionary trends across phylogeny is based on generalized least squares estimation of coefficients for linear models (Blomberg et al. 2003; Adams and Collyer 2018). However, this analysis and its variations are prone to statistical inaccuracy due to high type I errors and use of phylogenetic simulation. Therefore, this simulation infers incorrect parameter estimates if phylogeny is not conditioned in the analysis. Our hypothesis is that the contour feathers of water birds exhibit, in addition to water repellency and resistance to water penetration, morphological and mechanical features that are advantageous for specific aqueous habitats and behavioral patterns.

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Materials and Methods

Feather material

For contour feathers, abdominal feathers were selected as the most likely to interface with water. Our primary source was the same as used in an earlier study of water birds (Rijke 1970). Here, water birds are defined as birds that have habitats with open water and land birds as those that have not. A list of the species in this study is compiled in Table 1, using English names and taxonomic sequence suggested by Handbook of the Birds of the World (HBW) (Del Hoyo et al. 1997 – 2013).

The values for r and d of these feathers, measured at the mid-part of the vane, were collected at the time of the 1970 study using a transmission light microscope equipped with a calibrated scale ocular. The data have been reproduced for convenience in Table 1. We see no reason to suspect the accuracy and precision of these data to be anything less than of those collected with electronic imaging techniques.

The values for barb length l of the closed pennaceous portion of the contour feathers were measured at the mid-part of the vane to the nearest half millimeter using a traveling microscope. At least three feather specimens of each species were examined. For the calculation of body feather density and the extent of contour feather overlap, we measured the length of the rachis L_f to the nearest millimeter. The extent of overlapping can be approximated by the product of L_f and the square root of the number of feathers per surface area.

To estimate the latter, we made use of the data on number of feathers and body weights as reported by several authors (Wetmore 1936; Hutt and Ball 1933; Dwight 1900; McGregor 1903; Knappen 1932; Lowe 1933; Kuhn and Hesse 1957). For the weights of the birds we used as our source HBW (Del Hoyo et al. 1997 – 2013), the weight ranges for both male and female birds being averaged for our purpose. By fitting a second-order polynomial to these data (ignoring those on very small birds and penguins), an estimate of the number of contour feathers as a function of the mass of the bird was obtained. For the relationship between body surface area and body mass, expressions proposed by Perez, Moye and Pritsos (2014) and Mitchell (1936) were used to estimate surface area as a function of body weight. Combining the results of these two sets of calculations, contour feather densities expressed in number of feathers per surface area were found to be approximately 100,000 to 150,000 per m^2 for water birds weighing less than 1.2 kg for all species studied. This number increases with body weight to $200,000/m^2$ at about 7 kg. The extent of feather overlap, according to these calculations, yields about 10 to 15 feathers in a stack for families in the lower weight range with twice that number for heavier birds. Land birds show an average of nine feathers in a stack.

Feather measurements

The mechanical forces involved in diving, plunging, and alighting are not accessible to direct measurement by current technologies in any reliable or representative way. Any such data would not be meaningfully correlated to the resulting yield or flexure of barbs and vanes during forceful interaction with water. However, the bending and flexing of materials of different shapes and sizes have been well described in engineering physics and it is from these considerations that a number of conclusions in relation to our hypothesis can be drawn.

When a force F is applied over the length of a single barb, the barb will bend in the direction of the applied force with its tip flexing over a distance S. This relates to the barb length l and barb radius r as

$S = F \cdot l^3 / 2\pi \cdot r^4 \cdot E$ (1)

where E stands for the Young's elastic modulus of the feather keratin (Bonser and Purslow 1995, Greenwold et al. 2014). For the purpose of modeling, barbs are here assumed to be cylindrically shaped. When the force is applied to the vane, the flexural displacement of the tips of the vane per repeating unit $2(r + d)$ can be written as

$S_v = F_v \cdot l^3 \cdot 2(r + d)/2\pi \cdot r^4 \cdot E$ (2)

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where the subscript v refers to the repeating unit of the vane. Rearrangement of Eqn 2 then yields

$\pi.E.S_v/F_v = (l/r)^3 \cdot (r + d)/r$ (2a)

Apart from π and the elastic modulus E , the left-hand side of Eqn 2a represents the extent of flexing of the tips of barbs per unit of force applied over the lengths of the barbs and measured over a distance $2(r + d$). For the bending of the entire vane,F_v needs to be considered for the number of repeating units per vane. Note that the right-hand side of the equation is made up of the feather variables l , r and d , which, unlike S_v and F_v , are easily and directly accessible to measurement. These considerations allow us to predict semi-quantitatively the bending of the vane under an applied force from the dimensions and spacing of the barbs alone.

The role of the barbules in resisting bending of the vane is to be considered in the light of their primary function, i.e., keeping the barbs from separating under an applied force and doing so by their hooks sliding in the flanges of the barbule next more distal. For this reason, but mostly for their small size, barbules are assumed to make only a minimal, if any, contribution to the over-all resistance to bending.

According to Eqn 2a, the bending of the vane of the contour feather under the impact of forces associated with diving or alighting - here referred to as the deflection parameter - consists of two factors: (1) the ratio of the length to the thickness of the barbs expressed asl/r and (2) the wettability parameter $(r + d)/r$. The first factor indicates that short and thick barbs make the vane stiff resisting bending, whereas long and thin barbs favor flexibility that promotes bending. The appearance of the wettability parameter in the deflection parameter shows that feathers resistant to water penetration also help prevent their bending, whereas highly water repellent feathers do not. Note that l/r enters the equation in the form of a third power which markedly enhances its contribution to the deflection parameter and dwarfs that of the other factor: over its range of 2.5 to 7 or higher, $(r + d)/r$ increases by only a factor of 3 or 4, whereas $(l/r)^3$ does so by about three orders of magnitude.

Phylogenetic ANOVA

As seen in Table 2, the 49 species of aquatic birds in this study, excluding the darter and dippers, were assigned to nine foraging niches (independent groups) in accordance to Pigot et al. (2020). Twelve land bird species were included for the purpose of similarity comparisons. These twelve species were divided into two foraging niches (ground feeders and aerial/sally). Darters were excluded on account of their exceptional feather microstructure (see Discussion). The datasets of the two dippers were incomplete and have not been included in the calculations (reported here for archival purpose).

All statistical analyses were conducted using the R statistical analysis software (version 3.6.0). Significance for all analyses was recognized for values of $p < 0.05$. Normality of datasets was calculated using the Shapiro-Wilk test of normality with the *shapiro.test*function from the R base functions. It was shown that the deflection parameter dataset was not normally distributed (W = 0.824, $p < 0.001$). Significance of differences of deflection parameters between groups were calculated to determine which foraging niche represented higher/lower deflection parameter values. These results were used in comparison with the phylogenetic ANOVA results to substantiate the influence of phylogeny. Significance of the differences of deflection parameter values between aquatic and land bird species was calculated using the Mann-Whitey U Test with the *wilcox.test*function. Significance of differences between foraging niches of aquatic birds was calculated using the Kruskal-Wallis H Test with the*kruskal.test* function.

For both aquatic birds and land birds, phylogenetic ANOVA was used to determine whether feeding niches explain differences in feather microstructure while accounting for phylogenetic relationships. Two independent phylogenetic trees, consisting of 49 aquatic and 12 land bird species, were obtained from www.birdtree.org (Jetz and Thomas 2014). A 1000 trees were generated for both land and aquatic birds and representative trees were constructed using the *maxCladeCred*function from the *phangorn* package (version 2.5.3). Phylogenetic trees depicting the phylogenetic relationships between bird species as well as placement of groupings in the different feeding niches are illustrated in Fig. 1 and Fig. 2.

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Group aggregation of the bird groups on the phylogenetic trees was calculated using the *two.b.pls* function from the *geomorph* package (version 3.1.2). An R-value of 1 was indicative of total group aggregation and a value of 0 indicated no group aggregation. The foraging niches listed in Table 2 were regarded as the independent variable. Data on feather microstructure with regard to deflection parameter were considered as dependent variables.

In this study, a randomizing residuals in a permutation procedure (RRPP) phylogenetic ANOVA approach was used as described by Adams and Collyer (2018). This analysis was performed in 1000 iterations using the *procD.pgls* function from the *geomorph* package (version 3.1.2). This method is beneficial since it has demonstrated the importance of accounting for group aggregation in phylogenetic ANOVA. Moreover, it has shown that group differences can be detected, if they exist, in a phylogenetic context more accurately than in phylogenetic simulation models. RRPP is also more appropriate for highly multivariate datasets.

Results

In assigning the bird species to foraging niches, we have followed procedures proposed by Pigot et al. (2020) based on a standardized protocol for foraging niche delimitation. Thirty niches were identified for all of the approximately 10,000 bird species of the world. Of these six major foraging niches were categorized as Aquatic with three more chosen by us to accommodate the 49 water bird species of this study, darters and dippers excluded. The 12 land bird species could be grouped into two niches: Ground Feeding and Aerial/Sally (Table 2).

We found a significant difference between the deflection parameter medians of aquatic (260.10^6) and land (1595.10^6) bird foraging niches ($p < 0.001$), thereby demonstrating an evolutionary distinction between these groups. There was no significant difference between the deflection parameters of the two land bird foraging niches ($p = 0.600$), Ground Feeding (1228.10^6) and Aerial/Sally (2864.10^6), which indicates similarity among land birds. The aquatic bird species however, expressed significant differences between Aquatic Dive (328.10^6) and Aquatic Surface (37.10^6) ($p = 0.012$), Aquatic Surface and Aquatic Plunge (935.10^6) ($p < 0.001$), and Aquatic Surface and Aquatic Perch (276.10^6) ($p = 0.001$). These results show that differences in feather microstructure are identifiable with respect to differences in aquatic niches.

In order to determine if the foraging niches for aquatic and land birds explain feather microstructure while accounting for phylogenetic relationships, a phylogenetic ANOVA approach was followed. The degree of group aggregation was determined in order to establish if the ANOVA methodology would be affected by the association between the independent variable, i. e. foraging niche, and the phylogeny. The results indicated no significant group aggregation for either aquatic birds ($r = 0.468$ and $p = 0.122$) or land birds ($r = 0.650$ and $p = 0.120$) which confirmed the statistical reliability of the ANOVA approach. The phylogenetic ANOVA results demonstrated that there is a significant difference in feather microstructure between aquatic bird groups ($p = 0.001$), regardless of phylogenetic relatedness. In contrast, no significant difference in feather microstructure for the two land bird feeding niches was observed ($p = 0.971$).

Discussion

Birds, in particular water birds, are protected from water penetrating to the skin by the diameter and spacing of the barbs as determined by the parameter $(r + d)/r$ and the absolute value of r (Baxter and Cassie 1945; Rijke and Jesser 2011). The smaller these values are, the greater the resistance to water penetration. Only darters are known to benefit from water reaching the skin in order to reduce buoyancy while stalking prey on the bottoms of shallow lakes and streams. Their contour feathers show unusually large values for the parameter and lack barbules all together. However, all other species, with the possible exception of the Flightless Cormorant (*P. harrisi*), have a contour feather structure that optimizes water repellency and resistance to suit the specific requirements of their habitat and behavior.

Swimming birds, by their weights, exert a pressure on their surface area in contact with water that remains well below that required to force water through the barbs. This is particularly true for the most aquatic of families, but, as shown in Table 3, decreasingly so for the families less intimate with open water. Swimmers

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are subject to a more or less static equilibrium between the pressure exerted by the weight of the bird and the capability of the outer contour feathers to resist penetration. Once the pressure exceeds this resistance, the underlying layers of feathers will eventually be penetrated as well and will provide no further protection against wetting (Rijke, Jesser and Mahoney 1989).

Diving birds, on the other hand, are subject to much greater, albeit temporary, pressures. On immersion, their bodies will be quickly surrounded by water. Initially, some air will be expelled, but the remaining air within the plumage as well as in air sacs and airways, will be trapped and compressed by hydrostatic forces. As they dive deeper, the pressure difference across the water-feather interface will no longer increase, but balance out as the compliant feather coat further compresses the trapped air at greater depths, thereby decreasing the volume and the buoyancy of the bird.

For birds alighting on water, the pressure on impact will not be balanced by compressed trapped air, but will instead produce a pressure gradient with the atmospheric air in the plumage. It is not known if this gradient is large enough to force water through the barbs of a single contour feather or a stack of multiple feathers. The available experimental data, few as they are, seem to suggest that each additional feather layer adds another 50 percent increase to water resistance (Rijke, Jesser and Mahoney 1989). Experiments of this kind, in which water is forced through feathers, may well closely resemble the conditions of birds landing on water. However, water on impact could also reach the skin by the flexing and bending of stacked feathers. How much each of these two dynamic mechanisms contributes to water penetration, if at all, is unknown. It is likely, however, that stacked layers mostly serve to reduce the bending and flexing of vanes in diving and alighting birds - and thus aid in preventing water from reaching the skin - but not in swimming birds.

As the data in Table 1 show, the contour feathers of penguins have barbs that are much shorter and thicker, and therefore more resistant to bending than those of less aquatic species: thirty times more so than those of divers, grebes and cormorants, fifty times more so than those of finfoots, jacanas and storm petrels, and six hundred times more so than those of waders. Compared with those of land birds, these contour feathers are more resistant to bending by as much as three orders of magnitude. We posit that these differences in magnitude as well as the wide range of resistance to bending represent evolutionary adaptations to the forces of impact associated with specific feeding habits and habitats.

The families in each foraging niche share a similar behavior with respect to their feeding habits and interaction with water. This is evident for families in the Aquatic Dive foraging niche, but less so for the taxonomically more distant families in other niches. Penguins, divers, grebes and cormorants all pursue their prey in much the same way, but this holds less true for families in the other foraging niches. In parallel with this observation, we find that the values for l/r are small for species in the Aquatic Dive niche, but larger in the others. In other words, the most aquatic species have stiff and very similar vanes in their contour feathers that resist bending, providing increased protection against water reaching the skin, whereas species with less interaction with open water have, apart from more diverse feeding habits, more flexible and dissimilar vanes with no such protection.

For swimming birds, we have seen that water may ultimately reach the skin if the weight of the bird exceeds the pressure required to force water through the barbs of the outer contour feathers, but in plunging and diving birds or birds landing on water surfaces, water penetration may also be caused by bending of the vanes. Closely stacked contour feathers should impede bending, but to which extent is difficult to measure experimentally. One would expect the denser the feather coat and the more the feathers overlap the more restriction to bending is attained. However, our calculations have shown there are approximately 100,000 to 150,000 feathers per m^2 for water birds weighing less than 1.2 kg regardless of group. Furthermore, the extent of overlapping amounts to about 10 to 15 feathers in a stack for birds in all groups with approximately double that number for heavy birds. Apparently, feather overlapping is the same for all water birds and, as a result, the restriction stacking provides to bending is also the same. Only for birds weighing more than 1.2 kg do we find an increase in feather density and overlap with weight: up to 250,000 per m^2 and stacks of 18 for the pink-backed pelican (*P. rufescens*). This observation is in line with expectation as impact forces are directly proportional to mass.

The above findings may be explained by any of two or both possibilities: 1) the feather density and number of feathers in a stack are sufficiently large to prevent feather bending regardless of behavioral pattern and 2) the barb stiffness and resistance to water penetration of the contour feathers of each species are large enough to prevent water reaching the skin on their own account and do not benefit from a further increase in feather density or stacking.

The results of phylogenetic ANOVA have demonstrated that regardless of the phylogenetic relationships between bird species in this study, there is a significant difference in feather microstructure between the water bird groups. That no such significant difference was found for the land bird feeding niches supports the hypothesis of this study that the contour feathers of water birds exhibit features that are advantageous for specific aqueous habitats and behavioral patterns such as diving, plunging and alighting.

In summary, we have observed that the length and diameter of the barbs of contour feathers vary considerably among water birds with their stiffness parameters covering an eight-fold range however evolutionarily adapted to a specific niche. By referring to the mechanical properties of materials in general, we were able to show that short and thick barbs are stiff and resist bending, whereas long and thin barbs are flexible which facilitates bending. The value for l/r and, in particular the deflection parameter $(l/r)^3 \cdot (r+d)/r$, is small for penguins, the most aquatic of bird families, but increases by orders of magnitude for birds with less interaction with open water. The families in each of these groups are taxonomically different, but have in common their method of feeding. This is particularly true for the species in the Aquatic Dive niche, but less so for other niche representatives, which populate a wider range of habitats and have more diverse feeding habits. This effect was not observed among terrestrial birds, although other terrestrial traits may remain conserved due to the birds' respective niches.

Acknowledgements:

Data Accessibility Statement

All data used in this study have been reported in the text, Tables and Figures and have not been separately archived in a repository.

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Table 1 List of the 64 bird species of this study along with their corresponding feather microstructure measurements. N/A stands for number of feathers per unit of surface area.

ID	English Name	Genus species	r (μμ)	d (μμ)	$(r+d)/r$	l (mm)	l/r	l
1	Jackass Penquin	*Spheniscus demersus*	34	51.3	2.51	2	58.8	2
2	Magellanic Penquin	*Spheniscus magellanicus*	32	47.9	2.50	2.5	78.1	2
3	Gentoo Penquin	*Pygoscelis papua*	27.8	38.9	2.40	3	107.9	2
4	Rockhopper Penguin	*Eudyptes chrysocome*	30	49.4	2.65	2.5	83.3	2

5	Great Northern Diver	*Gavia immer*	31.6	92	3.91	7	221.5	2
6	Little Grebe	*Tachybaptus ruficollis*	26.1	137	6.25	6	229.9	2
7	Black-necked Grebe	*Podiceps nigricollis*	31.1	122	4.92	7	225.1	2
8	Yellow-nosed Albatross	*Diomedea chlororhynchos*	30.5	100.8	4.30	21	688.5	8
9	Great-winged Petrel	*Pterodroma macroptera*	33.8	121	4.58	13	384.6	4
10	Blue Petrel	*Halobaena caerulea*	23.9	83.2	4.48	9	376.6	2
11	Grey Petrel	*Procellaria cinerea*	36.1	93.8	3.60	12	332.4	5
12	European Storm-Petrel	*Hydrobates pelagicus*	16.6	93.8	6.65	4	241.0	1
13	Common Diving-Petrel	*Pelecanoides urinatrix exsul*	21.1	83.8	4.97	5	237.0	2
14	Great White Pelican	*Pelecanus onocrotalus*	23.3	103.3	5.43	9	386.3	4
15	Pink-backed Pelican	*Pelecanus rufescens*	26.6	114.3	5.30	8	300.8	3
16	Brown Pelican	*Pelecanus occidentalis*	18.9	73.8	4.90	4	211.6	4
17	Northern Gannet	*Sula bassana*	28.9	65.5	3.27	9	311.4	3
18	Cape Gannet	*Sula capensis*	21.1	57.2	3.71	8	379.1	3
19	Cape Cormorant	*Phalacrocorax capensis*	26.6	99.9	4.76	5	188.0	3
20	Darter	*Anhinga melanogaster*	25.9	239.6	10.25	10	386.1	
21	Great Frigatebird	*Fregata minor*	26.8	125.1	5.67	11	410.4	4
22	Grey Heron	*Ardea cinerea*	25	132	6.28	14	560.0	8
23	Black-headed Heron	*Ardea melanocephala*	24	155.5	7.48	12	500.0	7
24	Little Egret	*Egretta garzetta*	20.3	157	8.73	8	394.1	3
25	Hamerkop	*Scopus umbretta*	23.3	115.5	5.96	9	386.3	5
26	Yellow-billed Stork	*Mycteria ibis*	28.9	125	5.33	18	622.8	6
27	Saddlebill	*Ephippiorhynchus senegalensis*	36.1	213.7	6.92	23	637.1	6
28	Sacred Ibis	*Threskiornis aethiopicus*	29.6	139	5.70	21	709.5	4
29	Greater Flamingo	*Phoenicopterus ruber*	26.6	99	4.72	16	601.5	5
30	Horned Screamer	*Anhima cornuta*	29.4	101	4.44	9	306.1	2
31	Egyptian Goose	*Alopochen aegyptiacus*	30	103.2	4.44	22	733.3	5
32	Yellow-billed Duck	*Anas undulata*	30.5	95	4.11	10	327.9	4
33	Wild Turkey	*Meleagris gallopavo*	27	124.5	5.53	36	1333.3	
34	Coqui Francolin	*Francolinus coqui*	23.3	92.1	4.95	10	429.2	4
35	Blue Crane	*Anthropoides paradisea*	26.8	186	7.94	18	671.6	8
36	Limpkin	*Aramus guarauna*	33.3	174	6.23	14	420.4	4
37	Red-knobbed Coot	*Fulica cristata*	26.6	120.5	5.53	15	563.9	4
38	African Finfoot	*Podica senegalensis*	33.2	110	4.31	8	241.0	4
39	African Jacana	*Actophilornis africanus*	23.3	150	7.44	6	257.5	3
40	Greater Painted-snipe	*Rostratula benghalensis*	19.4	107	6.52	9	463.9	4
41	Crab Plover	*Dromas ardeola*	20	126	7.30	11	550.0	6
42	African Black Oystercatcher	*Haematopus moquini*	28.9	126.5	5.38	9	311.4	3
43	Pied Avocet	*Recurvirostra avocetta*	21.6	103.3	5.78	12	555.6	4
44	Spotted Dikkop	*Burhinus capensis*	25	173.9	7.96	8	320.0	4
45	White-fronted Plover	*Charadrius marginatus*	15.7	125	8.96	5	318.5	4
46	Eurasian Curlew	*Numenius arquata*	25	129.8	6.19	16	640.0	4
47	Red Phalarope	*Phalaropus fulicaria*	17.2	70.4	5.09	4	232.6	2
48	Pale-faced Sheathbill	*Chionis alba*	16.6	93.3	6.62	15	903.6	5
49	Pomarine Skua	*Stercorarius pomarinus*	25.5	123.8	5.85	14	549.0	5
50	Lesser Black-backed Gull	*Larus fuscus*	25.5	131.6	6.16	14	549.0	5
51	Sooty Tern	*Sterna fuscata*	17.8	88.3	5.96	8	449.4	3
52	African Skimmer	*Rynchops flavirostris*	21.1	106	6.02	8	379.1	4
53	Common Murre	*Uria aalge*	26.6	97.2	4.65	8	300.8	2
54	Namaqua Sandgrouse (M)	*Pterocles namaqua*	16.65	77.7	5.67	10	600.6	2
54	Namaqua Sandgrouse (F)	*Pterocles namaqua*	16.65	84.92	6.10	10	600.6	2

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| 55 | Dusky Turtle-dove | *Streptopelia lugens* | 15 | 109.3 | 8.29 | 7 | 466.7 | 2 |
56	Brown-necked Parrot	*Poicephalus robustus*	20.1	103.7	6.16	9	447.8	2
57	White-browed Coucal	*Centropus senegalensis*	20.5	137.7	7.72	14	682.9	3
58	Rufous-cheeked Nightjar	*Caprimulgus rufigena*	16.7	100.5	7.02	12	718.6	2
59	White-rumped Swift	*Apus caffer*	13.3	89.4	7.72	6	451.1	1
60	Narina Trogon	*Apaloderma narina*	14.8	126.9	9.57	11	743.2	3
61	Half-collared Kingfisher	*Alcedo semitorquata*	18.3	79.9	5.37	7	382.5	2
62	White-capped Dipper	*Cinclus leucocephalus*	13.5	93.15	7.90			
63	Rufous-throated Dipper	*Cinclus schulzi*	12	81.6	7.80			
64	European Starling	*Sturnus vulgaris*	17	103.7	7.10	6	352.9	2

Table 2 Foraging niches in accordance with Pigot et al. (2020) for the 49 water bird species and 12 land bird species in this study with ranges for stiffness and deflection parameters (DP).

| Grp	Foraging Niches	Stiffness parameter range l/r	Deflection Parameter range $(l/r)^8\,(r+d)/r$ (10^6)	Median DP (10^6)
1	**Aquatic Dive** Penguins, Divers, Grebes, Diving Petrels, Cormorants and Murres	59 - 301	0.5 – 126.5	37
2	**Aquatic Plunge** Gannets and Terns	311 - 449	99 – 541	202
3	**Aquatic Surface** Albatrosses, Blue Petrel, Grey Petrel, Pelicans, Geese, Coots, Finfoot, Gulls	241 - 733	46 - 1751	276
4	**Aquatic Aerial** Great-winged Petrel, Storm Petrels, Frigate Birds, Skuas and Skimmers	241 - 549	93 - 968	328
5	**Aquatic Ground** Herons, Egrets, Hamerkop, Storks, Saddlebill, Ibises, Flamingos, Limpkin, Jacanas, Greater Painted-snipe, Crab Plover, Oystercatchers, Avocets, Plovers, Curlews and Phalaropes	233 - 710	64 - 2036	935

Grp	Foraging Niches	Stiffness parameter range l/r	Deflection Parameter range $(l/r)^8$ $(r+d)/r$ (10^6)	Median DP (10^6)
6	**Aquatic Perch** Kingfishers	383	301	301
7	**Herbivore Aquatic Surface** Ducks	328	145	145
8	**Herbivore Aquatic Ground** Horned Screamer	306	127	127
9	**Invertivore Ground** Dikkops	320	261	261
10	**Land birds Ground Feeding** Wild Turkey, Francolins, Blue Crane, Sheathbill, Namaqua Sandgrouse, Turtle-dove, Parrots, Cougals and Starlings	353 – 1333	312 – 13107	1228
11	**Aerial/Sally** Nightjars, Swifts and Narina Trogon	451 - 743	709 - 3929	2605

Table 3 Maximum weights for no water penetration through abdominal feathers compared with weights per body surface area in contact with water. (Rijke, 1970)

Family/species	Avg. r	Avg Wt	Wt per surface area	Max. wt for no penetration
	(μm)	(kg)	(kg/m^2)	(kg/m^2)
Penguins	32	2.84	63.6 – 78.8	95.3 – 98.4
Ducks/geese	30	1.40	32.5 – 43.3	45.0 – 58.3
Black-backed Gull	25	0.66	27.0	39.0 – 47.5
Herons	25	1.48	38.3 – 48.0	35.2 – 48.0
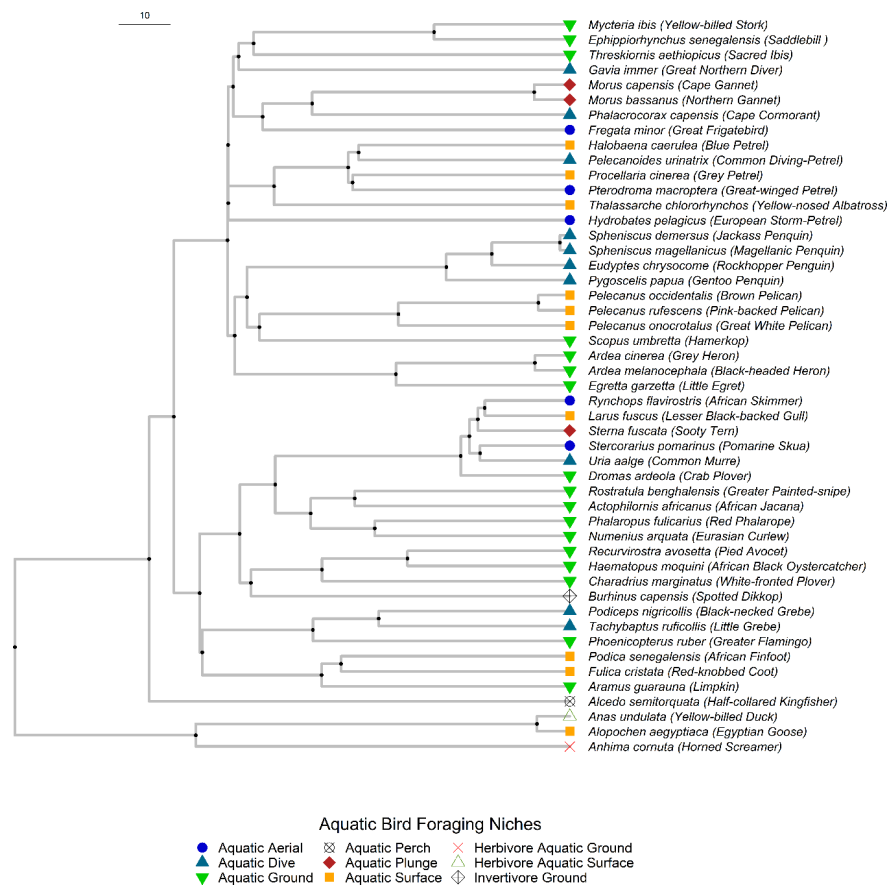
Fig. 1 Phylogenetic tree depicting the phylogenetic relationships of 49 aquatic bird species represented in this study. Each node tip illustrates the feeding niche/independent group into which the associated bird species is assigned.
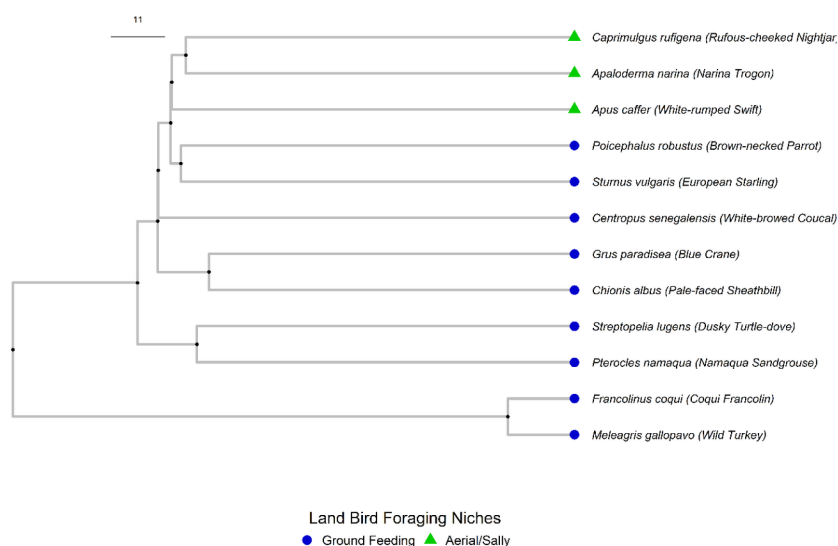
Fig. 2 Phylogenetic tree depicting the phylogenetic relationships of 12 land bird species represented in this study. Each node tip illustrates the feeding niche/independent group into which the associated bird species is assigned.