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Viscous Drag Reduction and Contour Feather Geometry in Water and Land Birds

Roelof D. Coertze and Arie M. Rijke

Abstract

Water birds have contour feathers in contact with water that show in their distal one-third adaptations to water repellency, resistance to water penetration and forceful impact with water. These qualities vary according to their intimacy with open water. In this study, the geometry of this part of the feather was examined to detect additional features that would affect viscous drag in water. The length-to-width ratio was measured and used to calculate the viscous drag coefficients for 48 water birds and, for comparison, 12 land birds. The lowest values for the drag coefficient were observed for birds with foraging niches as diving and swimming, followed by plunging, surface feeding, aerial and ground feeding. Land birds with no open water in their habitat had the highest drag coefficients. Three statistical approaches were used to validate the results. Allowing for the phylogenetic relatedness of the 60 species obscured any significant differences that may exist, but a non-parametric analysis that does not assume the conditions of equal sample size and variance turned out to be the most appropriate method for our data set.

Keywords: viscous drag in water, contour feather geometry, water birds, evolutionary history

1. Introduction

The contour feathers of birds are well-known to serve a variety of functions ranging from intraspecific signaling to such physical qualities as thermal insulation [1], water repellency [2] and resistance to impact [3]. They are arranged on the bird's body in an overlapping fashion like shingles on a roof with the dorsal aspect of their distal one-third exposed to air or water. This outer part of the contour feather has the patterned structure seen in pennaceous feathers 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 [4]. These structural details confer to the plumage the properties of water repellency, resistance to water penetration and resistance to forceful impact. The overall pattern is essentially the same for all regions of the body surface, but differs by location for some species. For instance, a marked difference in barb diameter and spacing was observed for the head, breast and abdominal feathers of Blue Swallows (*Hirundo atrocaerulea*) affecting the water repellency and water resistance of these regions to cope with the swallow's specific habit of foraging along misty mountain slopes [5].

Water birds that swim, dive or plunge can be expected to show adaptations in their contour feathers, compatible with their foraging niches, that are absent in land birds that have no interaction with open water as indeed they do [6]. They show a water repellency and a resistance to water penetration in their contour feathers that vary with the family's specific behavioral patterns. Surface feeders tend to have a predominantly water repellent body plumage whereas those of divers and plungers are more resistant to water penetration and forceful impact.

Birds that swim and dive will also benefit from reduced drag for their locomotion in water, a consideration that applies less to waders and shore birds and not at all to land birds. Viscous drag in water is dependent on the surface microstructure of the distal one-third of the contour feather, but also on the shape of its surface in contact with water, an aspect of feathers that has so far received little or no attention. Drag in air, such as in flight, on the other hand, has been the topic of several studies.

That the shape of the surface area in contact with water varies among bird families has been noticed in the course of previous studies. It was seen to be nearly circular in land birds with a length-to-width ratio (L/W) of approximately 1.0, but oblong with an L/W of about 4 in penguins (*Spheniscidae*), the most aquatic of families. Birds less intimate with open water showed intermediate values for L/W.

In this chapter, we consider the interface between the distal one-third and flowing water to calculate viscous drag for feather shape geometry. Assuming the flow to be parallel to the long axis of the feather, i. e. zero angle of attack, we can derive the total drag coefficient (DC), composed of viscous pressure and frictional drag, from the computational and experimental results of studies on model ship hulls of varying length-to-diameter ratios using solutions to the Reynolds-averaged Navier–Stokes Equations [7]. For the relationship between drag coefficient and L/W, we then find

$$\mathrm{DC}\left(10^{-3}\right) = 4.071\,e^{-0.0595 L/W} \qquad (1)$$

for values of L/W less than 7 which is within the range of feather geometry. The equation predicts that oblong shapes of the tips of contour feathers reduce drag facilitating swimming and diving, whereas a more circular shape would cause an increase in frictional drag. A similar reasoning could be applied to the shape of the area that the body of a swimming bird has in contact with water. If this area is assumed to be elliptical, a drag coefficient for body surface area in contact with water could be determined using the same equation.

In order to establish if niche-specific adaptations in feather microstructure exist among bird species, various statistical approaches should be considered. Generalized least squares estimation of coefficients for linear models have been commonly used to investigate traits within phylogeny [8, 9]. However, statistical inaccuracies due to high type I errors are widespread without accounting for the evolutionary relationships. A more appropriate approach, described by Adams and Collyer (2018), incorporates phylogeny under a Brownian motion model of evolution while performing ANOVA. This phylogenetic-ANOVA approach offers additional advantages by accounting for group aggregation within phylogeny which could influence results and overall conclusions.

Our hypothesis is that water birds have contour feathers that exhibit in their shapes adaptations to reducing viscous drag according to their interaction with open water.

2. Methods

The measurements on contour feathers were performed on abdominal feathers as these are considered to be most representative of interaction with water. The primary source of feathers was the same as used for earlier studies which included water bird species from 11 orders and, for comparison, land bird species from 9 orders [10]. The species entered in this study are compiled in **Table 1**, using English names and taxonomic sequence suggested by Handbook of the Birds of the World [11].

The length and the width of the closed pennaceous portion of the contour feathers of the 48 water birds and twelve land birds in this study were measured to the nearest millimeter using a traveling microscope with the mid-part of the vane taken for the width. At least three feather specimens of each species were examined. The drag coefficients, listed in **Table 1**, were calculated from L/W values using the above equation.

Grouping the bird species according to their interaction with open water can be achieved by assigning them to foraging niches as proposed by Pigot et al. [12], using a standardized protocol for foraging niche delimitation. Following this procedure, a total of thirty niches has been identified for all of the approximately 10,000 bird species of the world. Of these six major foraging niches were categorized as Aquatic with two more chosen by us to accommodate the 48 water bird species of this study. The twelve land bird species could be grouped into two niches: Ground Feeding and Aerial/Sally.

All statistical analyses were conducted using the R statistical computer software (version 3.6.0). In addition to the foraging niches proposed [12] for aquatic birds (group 1) and land birds (group 2), four more analyses were performed using the values of L/W and DC for both land and aquatic bird species (consisting of the various foraging niches) categorized as the following independent variables: aquatic versus land birds (group 3), swimmers versus land birds (group 4), waders versus land birds (group 5) and swimmers versus waders (group 6). These groupings can be visualized in the context of a phylogeny in **Figure 1** and **Table 4**. Phylogenetic trees comprising of 60 bird species representatives of the independent groups were obtained from www. birdtree.org [13]. A total of 1000 trees were generated and a representative tree was constructed using the *maxCladeCred* function from the *phangorn* package (version 2.5.3).

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. Group aggregation was performed by calculating phylogenetic variance–covariance using the *vcv.phylo* function from the *ape* package (version 5.3), which was followed by performing a two-block partial least squares analysis using the *two.b.pls* function from the *geomorph* package (version 3.2.1). The degree of group aggregation was estimated by the proximity of the R-value to either 1 or 0, where values equal to or larger than 0.6 were considered strong aggregation. Significant group aggregation was considered for p-values <0.05.

In order to determine if the foraging niches for aquatic and land birds as well as the other independent variables, explain feather microstructure while accounting for phylogenetic relationships, a phylogenetic ANOVA (*procD.pgls* function from the *geomorph* package), conventional ANOVA (*aov* function) and non-parametric (*kruskal.test* function) equivalent approaches were followed. Significance among all analyses were accepted for p-values <0.05.

ID#	Bird Name	FN Group	L/W	DC (10⁻³)
1	Jackass Penguin, *S. demersus*	Aquatic Dive	3.4	3.326
2	Magellanic Penguin, *S. magellanicus*	Aquatic Dive	4	3.209
3	Gentoo Penguin, *P. papua*	Aquatic Dive	3.33	3.339
4	Rockhopper Penguin, *E. chrysocome*	Aquatic Dive	3.4	3.326
5	Great Northern Diver, *G. immer*	Aquatic Dive	2.85	3.437
6	Little Grebe, *T. ruficollis*	Aquatic Dive	2	3.615
7	Black-necked Grebe, *P. nigricollis*	Aquatic Dive	1.73	3.673
8	Yellow-nosed Albatross, *T. chlororhynchos*	Aquatic Surface	1.87	3.643
9	Great-winged Petrel, *P. macroptera*	Aquatic Aerial	2.37	3.536
10	Blue Petrel, *H. caerulea*	Aquatic Surface	2.75	3.457
11	Gray Petrel, *P. cinerea*	Aquatic Surface	3.13	3.38
12	European Storm-Petrel, *H. pelagicus*	Aquatic Aerial	2	3.615
13	Common Diving-Petrel, *P. urinatrix*	Aquatic Dive	1.63	3.695
14	Great White Pelican, *P. onocrotalus*	Aquatic Surface	2.68	3.472
15	Pink-backed Pelican, *P. rufescens*	Aquatic Surface	2.17	3.579
17	Northern Gannet, *M. bassanus*	Aquatic Plunge	2.5	3.509
18	Cape Gannet, *M. capensis*	Aquatic Plunge	2.4	3.53
19	Cape Cormorant, *P. capensis*	Aquatic Dive	2.6	3.488
20	Darter, *A. melanogaster*	Aquatic Dive	3.14	3.377
21	Great Frigatebird, *F. minor*	Aquatic Aerial	2.28	3.555
22	Gray Heron, *A. cinerea*	Aquatic Ground	1.46	3.733
23	Black-headed Heron, *A. melanocephala*	Aquatic Ground	1.45	3.734
24	Little Egret, *E. garzetta*	Aquatic Ground	2	3.61
25	Hamerkop, *S. umbretta*	Aquatic Ground	2.33	3.544
26	Yellow-billed Stork, *M. ibis*	Aquatic Ground	2.22	3.568
27	Saddlebill, *E. senegalensis*	Aquatic Ground	1.82	3.654
28	Sacred Ibis, *T. aethiopicus*	Aquatic Ground	2.12	3.589
29	Greater Flamingo, *P. ruber*	Aquatic Ground	2	3.615
30	Horned Screamer, *A. cornuta*	H.A. Ground	1.19	3.794
31	Egyptian Goose, *A. aegyptiaca*	Aquatic Surface	1.55	3.713
32	Yellow-billed Duck, *A. undulata*	H.A. Surface	2.08	3.597
34	Coqui Francolin, *F. coqui*	Ground Feeding	1.57	3.708
35	Blue Crane, *G. paradisea*	Ground Feeding	2.69	3.469
36	Limpkin, *A. guarauna*	Aquatic Ground	2.58	3.491
37	Red-knobbed Coot, *F. cristata*	Aquatic Surface	1.5	3.724
38	African Finfoot, *P. senegalensis*	Aquatic Surface	2.89	3.428
39	African Jacana, *A. africanus*	Aquatic Ground	1.73	3.673
40	Greater Painted-snipe, *R. benghalensis*	Aquatic Ground	2	3.615
41	Crab Plover, *D. ardeola*	Aquatic Ground	2	3.615
42	African Black Oystercatcher, *H. moquini*	Aquatic Ground	2.23	3.566
43	Pied Avocet, *R. avosetta*	Aquatic Ground	2.36	3.538

ID#	Bird Name	FN Group	L/W	DC (10^{-3})
44	Spotted Dikkop, *B. capensis*	Ground Feeding	2.43	3.523
45	White-fronted Plover, *C. marginatus*	Aquatic Ground	1.78	3.662
46	Eurasian Curlew, *N. arquata*	Aquatic Ground	1.94	3.628
47	Red Phalarope, *P. fulicarius*	Aquatic Ground	2	3.615
48	Pale-faced Sheathbill, *C. albus*	Ground Feeding	2.25	3.561
49	Pomarine Skua, *S. pomarinus*	Aquatic Aerial	2.57	3.494
50	Lesser Black-backed Gull, *L. fuscus*	Aquatic Surface	2.36	3.538
51	Sooty Tern, *S. fuscata*	Aquatic Plunge	2.13	3.586
52	African Skimmer, *R. flavirostris*	Aquatic Aerial	2.01	3.613
53	Common Murre, *U. aalge*	Aquatic Dive	3.33	3.339
54	Namaqua Sandgrouse, *P. namaqua*	Ground Feeding	1.2	3.799
55	Dusky Turtle-dove, *S. lugens*	Ground Feeding	1.27	3.775
56	Brown-necked Parrot, *P. robustus*	Ground Feeding	1	3.836
57	White-browed Coucal, *C. senegalensis*	Ground Feeding	1.13	3.807
58	Rufous-cheeked Nightjar, *C. rufigena*	Aerial/Sally	1.22	3.786
59	White-rumped Swift, *A. caffer*	Aerial/Sally	1.18	3.795
60	Narina Trogon, *A. narina*	Aerial/Sally	2.2	3.572
61	Half-collared Kingfisher, *A. semitorquata*	Aquatic Perch	1.87	3.643
64	European Starling, *S. vulgaris*	Ground Feeding	1.33	3.762

Table 1.
*Bird species, foraging niches (FN) and drag coefficients (DC) of the 60 species in this study. Their full scientific names are provided in **Figure 1**.*

3. Results

The results of the various forms of analyses are collected in the **Tables 2–4**. In **Table 2**, the 60 species of our study are presented as four categories. The 48 aquatic birds are subdivided into swimmers and waders. Their values for DC show a viscous drag coefficient for swimmers significantly lower ($p < 0.05$) than that of waders and, predictably, land birds. In **Table 3**, these categories are further subdivided into eight aquatic foraging niches and two terrestrial ones according to Pigot et al. [12]. It is seen that divers have the lowest recorded drag coefficient increasing in order for plungers, surface feeders, aerials, herbivore surface feeders, ground feeders, perchers to herbivore ground feeders. Land birds experience an even higher drag with no significant difference between ground feeders and those that catch their prey by aerial or sally sorties.

In **Table 4**, the 60 species are divided among six groups to show the outcomes of the various statistical analyses used in this study. In the phy-ANOVA analysis, the closeness of the phylogenetic relatedness of the groups is accounted for whereas in conventional ANOVA it is not. However, the value of the latter suffers of shortcomings due to lack of equal sample size and equal variance among the populations in groups one to six. The non-parametric variant does not assume the conditions of equal sample size and variance and, for this reason, is a more appropriate method of analysis for our data set.

Group aggregations were performed to determine if phylogenetic relatedness and independent groupings could influence the reliability of the phylogenetic
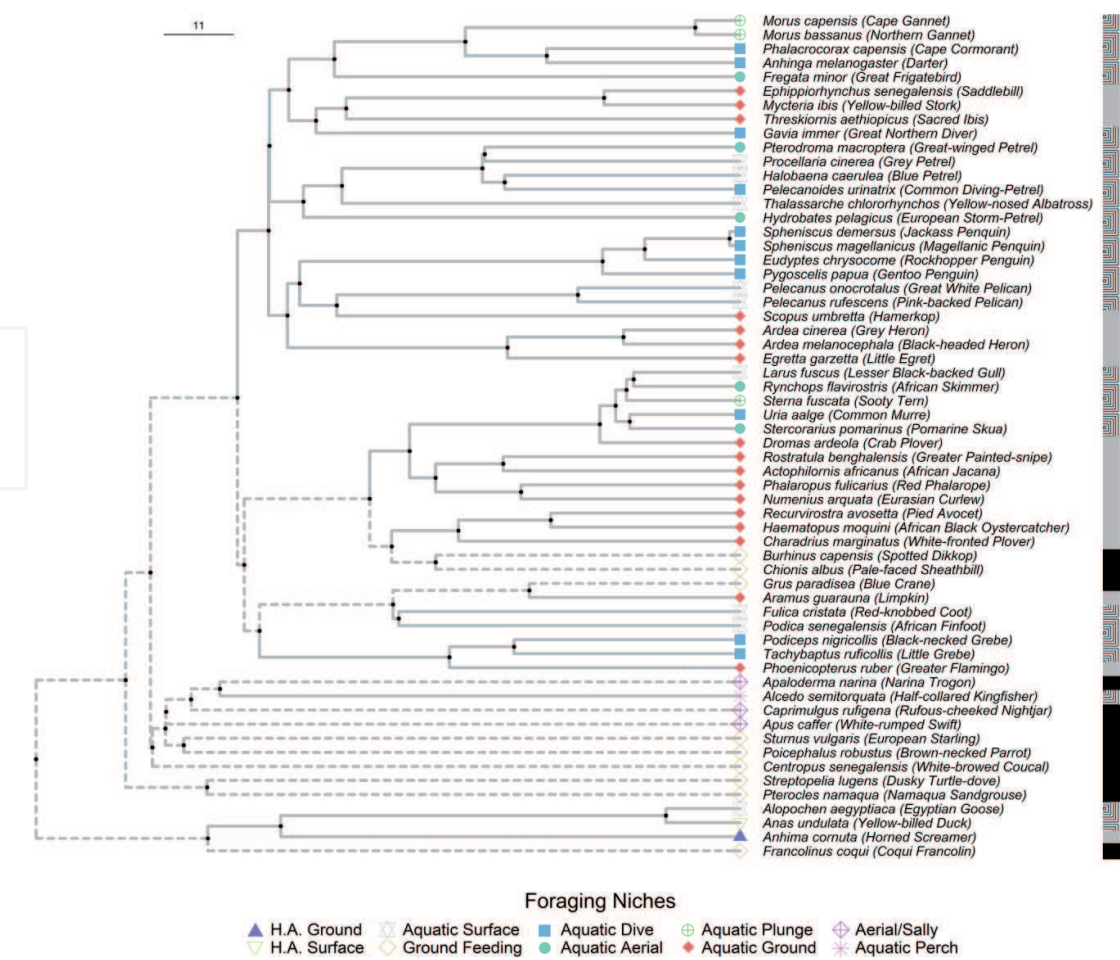
Figure 1.
Phylogenetic tree depicting the phylogenetic relationships between the 60 bird species. The various foraging niches are displayed at the tree tips. Land bird species are illustrated on the tree edges as dashed lines and aquatic birds as solid lines. Swimming characteristics are illustrated by the right-hand bar between land birds (black), waders (gray) and swimmers (dark gray).

Category	Sample Size	LW	DCf
Aquatic Birds	48	2.304 +/− 0.587	3.56 +/− 0.124
Swimmers	30	2.484 +/− 0.625	3.515 +/− 0.130
Waders	18	1.986 +/− 0.325	3.625 +/− 0.074
Land Birds	12	1.623 +/− 0.570	3.699 +/− 0.125

Table 2.
Sample size with L/W and DC values (including means (+/− standard deviation) of the various independent categories used in this study.

ANOVA analysis. The results revealed the presence of a relatively strong ($r > = 0.6$) and significant ($p < 0.05$) group aggregation for groups 2, 4 and 6, thus showing its limiting effect on the reliability on the outcome of the ANOVA analysis. Groups 1, 3 and 5 reveal weaker group aggregation ($r < 0.6$) but significance ($p < 0.05$) only for group 3.

The results of statistical significance for LW and DC values are comparable for all groups and analyses and therefore significance among groups will be discussed as a single result. Results among the various independent groupings yielded inconsistent results between the three statistical approaches. Results of the phylogenetic ANOVA approach indicated that no significance was observed for all groups

Foraging Niche	Sample Size	LW	DCf
Aquatic Dive[1]	11	2.855 +/− 0.739	3.439 +/− 0.156
Aquatic Plunge[1]	3	2.343 +/− 0.156	3.542 +/− 0.032
Aquatic Surface[1]	9	2.322 +/− 0.557	3.548 +/− 0.118
Aquatic Aerial[1]	5	2.246 +/− 0.218	3.562 +/− 0.046
H.A. Surface[1]	1	2.080 +/− NA	3.597 +/− NA
Aquatic Ground[1]	17	2.036 +/− 0.264	3.615 +/− 0.063
Aquatic Perch[1]	1	1.87 +/− NA	3.643 +/− NA
H.A. Ground[1]	1	1.19 +/− NA	3.794 +/− NA
Ground Feeding[2]	9	1.652 +/− 0.596	3.693 +/− 0.130
Aerial/Sally[2]	3	1.533 +/− 0.472	3.718 +/− 0.103

[1]*Aquatic Niches.*
[2]*Terrestrial Niches.*

Table 3.
Sample size with L/W and DC values (including means (+/− standard deviation) of the eight aquatic and two terrestrial foraging niches according to Pigot et al. [12]. **Figure 1** *Lists the birds that belong to each foraging niche.*

Group		Phy-ANOVA	Parametric	Non-Parametric
1	Aquatic Birds	NS	S	NS
2*	Land Birds	NS	NS	NS
3	Aquatic vs. Land	NS	S	S
4*	Swimmers vs. Land	NS	S	S
5	Waders vs. Land	NS	S	NS
6*	Swimmers vs. Waders	NS	S	S

S: Significant ($p < 0.05$). NS: Non-significant ($p > 0.05$). *: Significant ($p < 0.05$) and strong ($r > = 0.6$) group aggregation.

Table 4.
Summary of the outcome of the statistical analyses used in this study.

($p < 0.05$). Parametric results were highly contrasted against this result in that all groups with the exception of land birds indicated significant differences in feather microstructures. The non-parametric equivalent results in significance for groups 3, 4 and 6 and therefore corresponds with the results of phylogenetic ANOVA for groups 1, 2 and 5. The only consistent result across all analyses was group 2, the foraging niches of land birds, which indicated non-significance ($p < 0.05$).

4. Discussion

The present study has shown that adaptations in feather microstructure and body surface area in contact with water that bring about a reduction in viscous and frictional drag while swimming increase according to the bird's intimacy with open water. Swimming and diving birds, such as penguins and grebes, benefit the most from reduced viscous drag, more so than plungers such as gannets. Aerials such as terns even less so, but much more than herbivore surface feeders such as ducks.

The body feathers of ducks, in turn, appear to be better adapted to their watery habitat than those of aquatic ground feeders such as herons or kingfishers. The single herbivore aquatic ground feeder in this study, the Spotted Dikkop, is a bird of open scrubby habitat with comparatively little interaction with open water. Its drag coefficient is more in line with those of land birds in which adaptations to locomotion in water are not expected to have evolved.

Land birds do not only show drag coefficients higher than those of water birds, they also show no significant difference among the two foraging niches examined in this study. This is in line with expectation as their lack of interaction with open water and their locomotion in air only suggest that forces that foster reduced drag in water have been absent in their evolutionary history.

Of the three methods of statistical analyses, the phy-ANOVA test shows us that allowing for phylogenetic relatedness negates any differences among feather microstructure that may exist. Only for land birds would non-significance be expected. There is no doubt that group aggregation among the 48 water bird species is quite strong which detracts from the reliability of our positive and negative findings. Adding more species to the study or identifying more foraging niches could, statistically speaking, affect the results either way depending on numbers of species and their phylogenetic relatedness. Alternatively, it could be argued that relatedness is not necessarily a force that would make the evolution of an isolated trait impossible. Several examples support this notion. For instance, the Flightless cormorant (*Phalacrocorax harrisi*) is undoubtedly closely related to all other cormorants, yet a small change in the diameter and spacing of its barbs has rendered the bird better adapted to its bottom feeding habits than other cormorants are. The contour feathers of Brown pelicans (*Pelecanus occidentalis)* that, unlike their congeners, dive from the air to procure their prey, are more water repellent than those of other pelicans that catch their fish while swimming. Similar considerations apply to the differences in the contour feathers of dippers (*Cinclidae*) [6].

As argued above, a conventional statistical test while avoiding the condition of equal sample size and variance among populations, may the more suitable. Following this line of thought, the non-parametric variety of analysis would show that among group 1 consisting of all 48 aquatic birds, no significance is apparent, but when compared to land birds, it is. Subdividing into swimmers and waders shows comparison of the first group with land birds to be significant whereas that of waders with land birds is not. However, comparison between swimmers and waders is significant again indicating that, in terms of feather microstructure, waders stand between swimmers and land birds, but closer to land birds. This interpretation is entirely plausible, particularly if we assume that water birds have evolved from land birds.

In summary, the length-to-width ratio of the dorsal aspect of the distal one-third of abdominal feathers, the part that is in contact with water in aquatic birds, varies with the extent of interaction with open water as formulated by our hypothesis. This ratio and the total drag coefficient, composed of viscous pressure and frictional drag and calculated from Reynolds-averaged Navier–Stokes equations, are lowest for swimming and diving birds and increase for birds with less intimacy with open water. The highest values were found for land birds that have no open water in their habitat.

Due to the limited number of foraging niches and close phylogenetic relatedness among water bird families, statistically significant differences among water birds was not observed if allowance for phylogeny was made. However, using conventional statistical tests, in particular the non-parametric variety that does not assume conditions of equal sample size and variance, did show significant results when comparing water birds with land birds, swimming birds with land birds and

swimming birds with waders, but not waders with land birds. This finding suggests, in terms of feather microstructure, a closer evolutionary relationship between waders and land birds than between waders and swimmers. In line with expectation, land birds showed no significant differences in their contour feather geometry that could be related to interaction with open water.

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