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Relationship of bill morphology to grooming behaviour in birds

DALE H. CLAYTON & PETER COTGREAVE
Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.

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Abstract. Efficient preening by birds is critical for feather care and defence against harmful ectoparasites, yet many species have long, unwieldy bills that are presumably less efficient for preening than short bills. Long-billed taxa such as hummingbirds and toucans could attempt to compensate for inefficient preening by spending relatively more grooming time scratching with their feet than do short-billed taxa. To test this simple hypothesis preliminary data on the grooming behaviour of wild birds in Costa Rica and more extensive data on captive birds in zoos were collected. Comparative analyses of these data support the hypothesis and suggest additional hypotheses for future testing.

Birds' bills are adapted primarily for feeding, as suggested by the congruence of bill morphology and foraging ecology among the members of adaptive radiations, such as the Hawaiian honeycreepers and Darwin's finches (Storer 1971). The functional significance of specialized bills for feeding on particular food items is well documented (Zusi 1987; Benkman & Lindholm 1991) and food availability is known to exert direct selection on bill morphology (Boag & Grant 1981; Grant 1986).

Bills are also important tools for preening. Efficient preening is critical for the straightening and oiling of feathers and removal of dirt and debris from the body surface (Simmons 1985). Preening is also critical for defence against ectoparasites; birds with experimentally impaired preening are subject to rapid increases in ectoparasite load (Brown 1972, 1974; Clayton 1991), leading to reduced survival (Clayton 1989) and mating success (Clayton 1990). Ectoparasites also increase on wild birds that have minor bill deformities which prevent the full occlusion of the mandibles necessary for efficient preening (Clayton 1989). Hence, ectoparasites are another potential source of selection on bill morphology.

Bills that are well designed for feeding are not necessarily well designed for preening. Birds with long, unwieldy bills such as hummingbirds (Trochilidae) and toucans (Ramphastinae) might be less efficient at preening than birds with short or medium length bills. However, comparisons of ectoparasite load indicate that long-billed taxa do not have higher loads than short-billed taxa (D. H. Clayton & R. D. Gregory, unpublished data). This suggests that long-billed taxa may somehow compensate for inefficient preening.

One way long-billed taxa could compensate is to spend relatively more grooming time scratching with their feet than do short-billed taxa. Scratching is important for feather care and ectoparasite control on the head and other regions inaccessible to preening (Simmons 1985). Individuals with a deformed or missing foot often experience an increase in ectoparasite load restricted to the head and upper body (Clayton 1991).

The added importance of scratching to long-billed birds is suggested by Mobbs' (1973) anecdotal account of the swordbilled hummingbird, *Ensifera ensifera*, which has a bill longer than the rest of its body:

> . . . the legs and feet of the Swordbilled have extra manoeuvrability, thus enabling the species to preen [i.e. scratch] areas it could not otherwise reach. . . . As far as I am aware, no other species of hummingbird is able to preen the centre of the back or vent feathers with its claws as the Swordbilled does.

We tested the simple hypothesis that long-billed taxa spend more of their grooming time scratching than do short-billed taxa. Observational data were gathered on the grooming behaviour of a limited number of wild birds in Costa Rica. Analysis of these data suggested that a definitive test of the hypothesis required observations on a more diverse group of taxa. Thus, we collected additional data

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on the grooming behaviour of birds held captive in zoos.

METHODS

Data Collection

Wild birds

We observed the grooming behaviour of 22 species of birds at several sites in Costa Rica during July and August 1984, using binoculars and a 25 × spotting scope. A stopwatch was used to record how long birds spent grooming. Grooming was divided into preening (touching plumage with the bill) and scratching (touching plumage with the foot). A grooming bout was considered terminated if a bird ceased grooming for more than 3 s.

Timed individuals were not chosen at random, but were often chosen because they were grooming when first encountered. This approach maximized the amount of data that could be collected during each field trip, but prohibits use of the data for calculating the proportion of daily time devoted to grooming. Observations continued until the individual flew or ceased grooming for several minutes. Five of the 22 species spent ⩽1 s grooming and were excluded from further consideration, leaving a sample of 17 species for analysis (see below).

Bill length (tip of upper mandible to base of mandible in front of eye) was measured with dial callipers from preserved skins in the Field Museum of Natural History, Chicago. We measured one specimen of each sex and averaged these to estimate mean bill length for each species. Mean body weight was calculated by averaging male and female weights in Stiles & Skutch (1989).

To create indices of relative bill length, log (bill length) was plotted against log (body weight) across species and residuals from a least squares linear regression were calculated. Residuals were used rather than the ratio of bill length to body weight because the ratio was strongly negatively correlated with body mass ($r_S = -0.88$, $N = 17$, $P = 0.0005$), meaning that any behaviour correlated with relative bill length would automatically be correlated with body size as well. Residuals controlled for this confounding effect of body size by factoring it out.

Captive birds

We collected data on the grooming behaviour of 36 species of captive birds comprising nine pairs of higher taxa (Fig. 1). All species were chosen prior to the collection of data, as follows. We used illustrations in Austin & Singer (1985) to select an array of nine long-billed monophyletic taxa likely to occur in zoos and Sibley & Ahlquist (1990) to select nine short-billed sister groups also likely to occur in zoos. Representatives of each of these taxa were chosen for observation; we tried to locate more than one species per group, though this was not always feasible.

Observations were made with the naked eye for periods of 30 min (1800 s). The data were recorded as described for wild birds beginning with the first individual to start grooming during an observation period. Once a grooming bout was interrupted, additional data were collected from the next bird to start grooming regardless of whether this was the same individual or a new one.

We stopped collecting data for a given species after the observation period in which grooming time, summed across all periods, exceeded 3 min (180 s). The collection of data ended before this criterion was satisfied in the case of two species: *Galbula ruficauda* (58 s), located in a temporary aviary visited only briefly, and *Buceros rhinoceros* (149 s), removed from exhibition following a single period of observation.

Data on body weight and tarsal length were obtained from the literature (British Museum 1874–1895; Moltoni 1939; Sanft 1960; Wetmore 1968; Short 1982; Brough 1983; Stiles & Skutch 1989). Data were unavailable for several species, in which case we used data for similar sized congeners. To create indices of relative leg length, mean log (tarsus length) was regressed on mean log (body weight) across the 18 higher taxa and residuals were calculated.

Data Analysis

Wild birds

The proportion of grooming time spent scratching was calculated by dividing total scratching time (summed across all individuals of a species) by total grooming time. We examined the relationship between relative bill length and scratching across species by calculating a Spearman rank correlation coefficient between residual log (bill length) and the proportion of grooming time spent scratching.

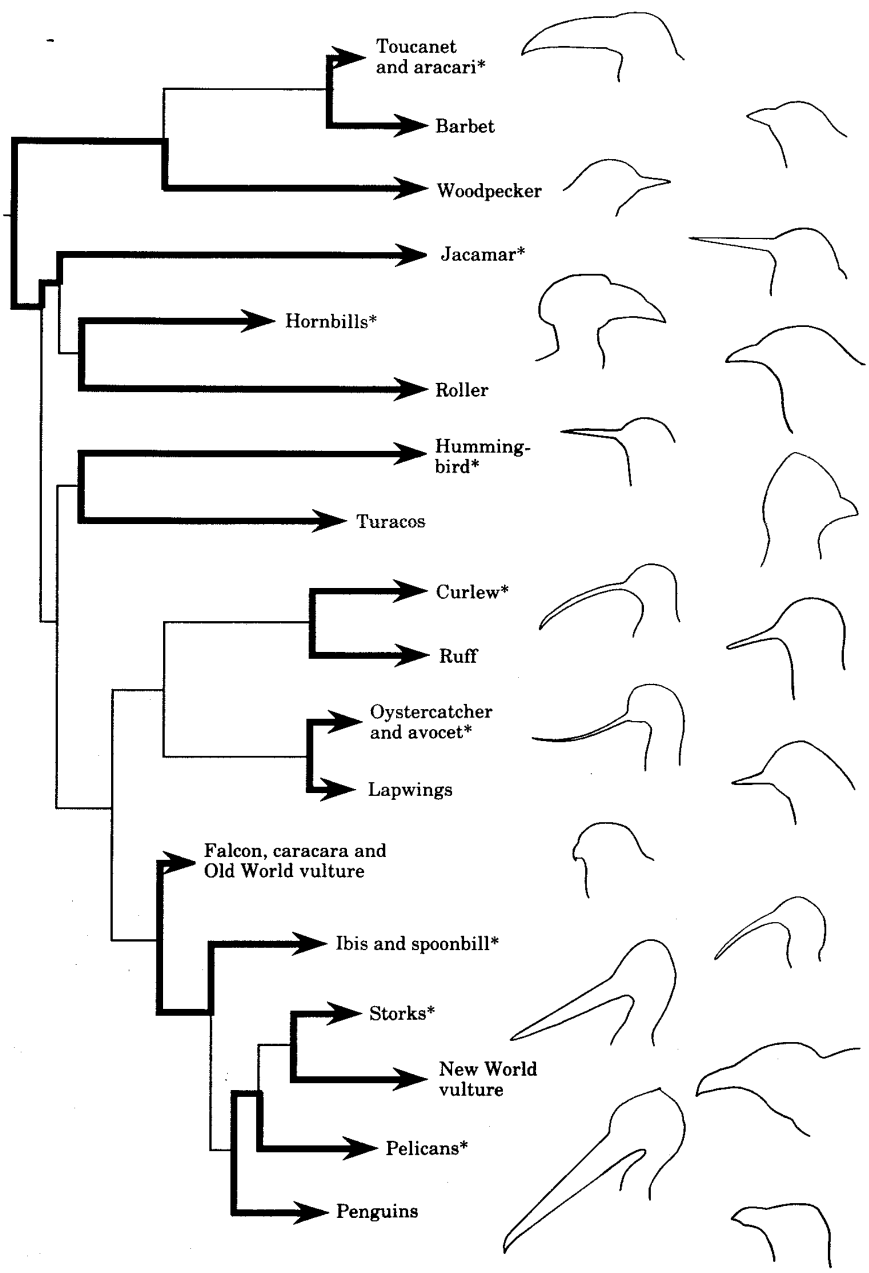

Figure 1. Sister taxa used for matched-pair comparisons of grooming behaviour in captive birds. Long-billed taxa are indicated by asterisks. The phylogeny is from Sibley & Ahlquist (1990).

Captive birds

The proportion of grooming time spent scratching was calculated for each of the 36 species as described for wild birds. Taxonomically weighted averages were then calculated to determine the proportion of grooming time spent scratching by each of the 18 higher taxa: species values were averaged for generic means, generic means were averaged for

Table I. Taxonomically weighted averages for the 18 higher taxa used to perform nine matched-pair comparisons (see text for species names and data for each)

Higher taxon compared	Common names (number) of species observed	Relative bill length	Proportion of grooming time spent scratching
(1) Ramphastinae	Toucanet (1) Aracari (1)	Long	0·32
Capitoninae	Barbet (1)	Short	0·05
(2) Picidae	Woodpecker (1)	Short	0·01
Galbulidae	Jacamar (1)	Long	0·12
(3) Bucerotidae	Hornbills (5)	Long	0·12
Coraciidae	Roller (1)	Short	0·08
(4) Trochilidae	Hummingbird (1)	Long	0·47
Musophagidae	Turacos (3)	Short	0·02
(5) *Numenius*	Curlew (1)	Long	0·03
Philomachus	Ruff (1)	Short	0·01
(6) Recurvirostrinae	Oystercatcher (1) Avocet (1)	Long	0·24
Charadriinae	Lapwings (3)	Short	0·01
(7) Falconides	Falcon (1) Caracara (1) Old World vulture (1)	Short	0·01
Threskiornithidae	Ibis (1) Spoonbill (1)	Long	0·03
(8) Ciconiinae	Storks (2)	Long	0·13
Cathartinae	New World vulture (1)	Short	0·01
(9) Pelecaninae	Pelicans (3)	Long	0·00
Spheniscidae	Penguins (3)	Short	0·01

tribal means, and so on, until an average value was obtained for each higher taxon (Table I).

We tested the relationship between relative bill length and scratching by calculating whether long-billed taxa spent more grooming time scratching than short-billed sister taxa. The nine pairs of taxa were also examined for any association of scratching with two possible confounding factors: body size (weight) and leg length.

RESULTS

Wild Birds

The 17 species of wild birds (names as in Sibley & Monroe 1990) and data for each are as follows (number of individuals observed, number of seconds grooming, proportion of grooming time spent scratching): *Campephilus guatemalensis* (1, 237, 0·00), *Ramphastos sulfuratus* (1, 6, 0·50), *Ramphastos swainsonii* (2, 434, 0·01), *Crotophaga sulcirostris* (5, 805, 0·01), *Amazona farinosa* (3, 1629, 0·01), *Panterpe insignis* (2, 7, 1·00), *Amazilia rutila* (1, 38, 0·03), *Elvira cupreiceps* (1, 35, 0·20), *Eugenes fulgens* (1, 8, 0·62), *Columbina inca* (2, 390, 0·00), *Harpagus bidentatus* (1, 500, 0·00), *Pitangus sulphuratus* (1, 214, 0·02), *Notiochelidon cyanoleuca* (2, 598, 0·02), *Zonotrichia capensis* (2, 45, 0·00), *Myioborus miniatus* (1, 28, 0·00), *Gymnostinops montezuma* (4, 2180, 0·01), *Agelaius phoeniceus* (1, 22, 0·09).

Across these species the proportion of grooming time spent scratching was positively correlated with relative bill length (Fig. 2). However, this comparison is not controlled for phylogenetic effects (see Discussion).

Captive Birds

The 36 species of captive birds and data for each are as follows (conventions as for wild birds): Ramphastinae: *Baillonius bailloni* (2, 282, 0·23), *Pteroglossus castanotis* (1, 1379, 0·41), Capitoninae: *Capito niger* (3, 198, 0·05); Picidae: *Melanerpes candidus* (1, 188, 0·10); Galbulidae: *Galbula ruficauda* (1, 58, 0·12); Bucerotidae: *Buceros bicornis* (1, 279, 0·09), *B. rhinoceros* (2, 149, 0·16), *Anthracoceros albirostris* (2, 210, 0·18),

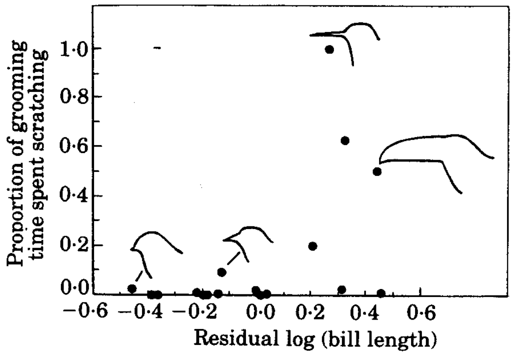

Figure 2. Scratching versus relative bill length for 17 species of wild birds in Costa Rica (see text for species names and data); $r_S = 0{\cdot}61$, $N = 17$, $P = 0{\cdot}01$). Outlines are the heads of (clockwise from top) fiery-throated hummingbird, *P. insignis*, keel-billed toucan, *R. sulfuratus*, red-winged blackbird, *A. phoeniceus*, and blue-and-white swallow, *N. cyanoleuca*.

Ceratogymna subcylindricus (2, 182, 0·16), *Tockus flavirostris* (2, 689, 0·03); Coraciidae: *Coracias caudata* (1, 546, 0·08); Trochilidae: *Amazilia* sp. (3, 216, 0·47); Musophagidae: *Tauraco leucotis* (2, 318, 0·03), *T. erythrolopus* (2, 215, 0·02), *T. hartlaubi* (2, 252, 0·00); *Numenius*: *N. arquata* (1, 334, 0·03); *Philomachus*: *P. pugnax* (1, 339, 0·01); Recurvirostrinae: *Haematopus ostralegus* (2, 323, 0·13), *Recurvirostra avosetta* (2, 220, 0·34); Charadriinae: *Vanellus coronatus* (5, 388, 0·03), *V. spinosus* (1, 418, 0·00), *V. armatus* (1, 241, 0·00); Falconides: *Polihierax semitorquatus* (2, 342, 0·02), *Phalcoboenus australis* (3, 334, 0·02), *Torgos tracheliotus* (2, 294, 0·00); Threskiornithidae: *Eudocnemus ruber* (5, 557, 0·05), *Platalea alba* (4, 416, 0·00); Ciconiinae: *Ciconia ciconia* (3, 515, 0·13), *C. abdimii* (7, 546, 0·12); Cathartinae: *Cathartes aura* (1, 231, 0·01); Pelecanidae: *Pelacanus oncrotalus* (4, 451, 0·00), *P. rufescens* (1, 550, 0·00), *P. occidentalis* (1, 1190, 0·00); Spheniscidae: *Eudyptes chrysocome* (4, 642, 0·02), *Spheniscus demersus* (4, 1121, 0·00), *S. humboldti* (12, 301, 0·00).

The long-billed taxa averaged 16·2% of their grooming time scratching (range = 0·0–47·0), whereas short-billed taxa averaged only 2·3% scratching (range = 1·0–8·0; Table I). In eight of the nine paired comparisons the long-billed taxon scratched more than its short-billed sister group (one-tailed binomial $P = 0{\cdot}02$), thus supporting the hypothesis that long-billed taxa devote more of their grooming time to scratching than short-billed taxa.

There was no association between body size (weight) and scratching ($P = 0{\cdot}25$) or between relative leg length and scratching ($P = 0{\cdot}50$).

DISCUSSION

The results for wild birds show that scratching covaries significantly with bill length across species, but this comparison is not controlled for phylogenetic effects. Because similar adaptations of related taxa may be due to shared ancestry rather than parallel or convergent evolution, related taxa do not constitute statistically independent points for comparative analysis (Felsenstein 1985; Harvey & Pagel 1991). The six long-billed, wild species (Fig. 2) represent only two unrelated groups: toucans (*Ramphastos* spp.) and hummingbirds (*Panterpe, Amazilia, Elvira, Eugenes*). The data set therefore does not contain enough independent taxa for a more rigorous comparative analysis.

To control for the problem of 'phylogenetic inertia', it is necessary to compare the immediate descendants of a common ancestor, viz. sister taxa. The sister taxa compared must also vary in the independent variable of interest. We performed a phylogenetically controlled test of the scratching hypothesis using data on the grooming behaviour of sister taxa with obviously long or short bills (Fig. 1). The taxa were chosen expressly to maximize the variation in bill length because the wild bird data suggested that unwieldiness may be a threshold trait; species with a residual log (bill length) <0·1 hardly ever scratched (Fig. 2). We wanted to ensure that our comparisons were of sister taxa falling on either side of the presumed threshold.

The results for captive birds support the hypothesis that long-billed taxa spend more of their grooming time scratching than short-billed taxa. The sole exception involved pelicans, which averaged no time scratching (Table I). Pelicans were the only long-billed taxa with webbed feet. The only other web-footed taxa in the study were penguins, which averaged a mere 1·0% of their grooming time scratching. It is worth noting that penguins are the only birds known to control ectoparasites by allopreening. Unmated individuals with no opportunity to allopreen have significantly more parasites on the head and neck than mated individuals, despite scratching significantly more often than mated individuals (Brooke 1985). These results suggest that foot morphology may limit scratching efficiency just as bill morphology appears to limit preening efficiency.

Inefficient groomers may attempt to compensate with other anti-parasite behaviour. During this study, for example, a wild chestnut-mandibled toucan was observed rubbing its face (not the bill) vigorously on a tree trunk for several seconds. This behaviour could dislodge louse eggs, which are unusually abundant on the facial feathers of toucans (D. H. Clayton, personal observation). Other suggested anti-parasite behaviour includes anting, dust-bathing and sunning (Brooke 1985; Simmons 1985). Unfortunately, rigorous experiments testing the role of such behaviour in parasite control have not been published (Murray 1990), but see Clayton & Wolfe (1993).

Our results indicate that scratching does not covary significantly with body size or leg length, both potentially confounding variables. However, we have not performed a general test of whether these traits influence grooming behaviour. Such a test would require the collection of data from taxa showing greater variation in body size and leg length than did the taxa chosen for this study. A comparison of long-legged to short-legged birds would be of particular interest.

Proximal data on the mechanics and efficiency of grooming are needed to test more precise questions about the relationship of morphology to grooming. Are long bills really less efficient preening instruments than short bills? If so, is this because they cannot be used to reach upper regions of the body, because they lack dexterity, or both? What other bill characteristics, for example, width, depth and curvature, govern preening efficiency?

Data are available on the mechanics of grooming for rock doves, *Columba livia*, which spend about 20% of their grooming time preening the breast and neck (Clayton 1991). Similar data are not available for long-billed species. However, we predict that such species would devote less time than rock doves to preening of the breast and neck. Additional simple observations would shed further light on the relationship of morphology to grooming behaviour.

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