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Relationship of bill morphology to grooming behaviour in birds

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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load indicate that long-billed taxa do not have higher loads than short-billed taxa (D. H. Clayton & R. D. Gregory, unpublished data).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 $\leqslant 1$ 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 ($r_S = -0{\cdot}88$, $N = 17$, $P = 0{\cdot}0005$), 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.

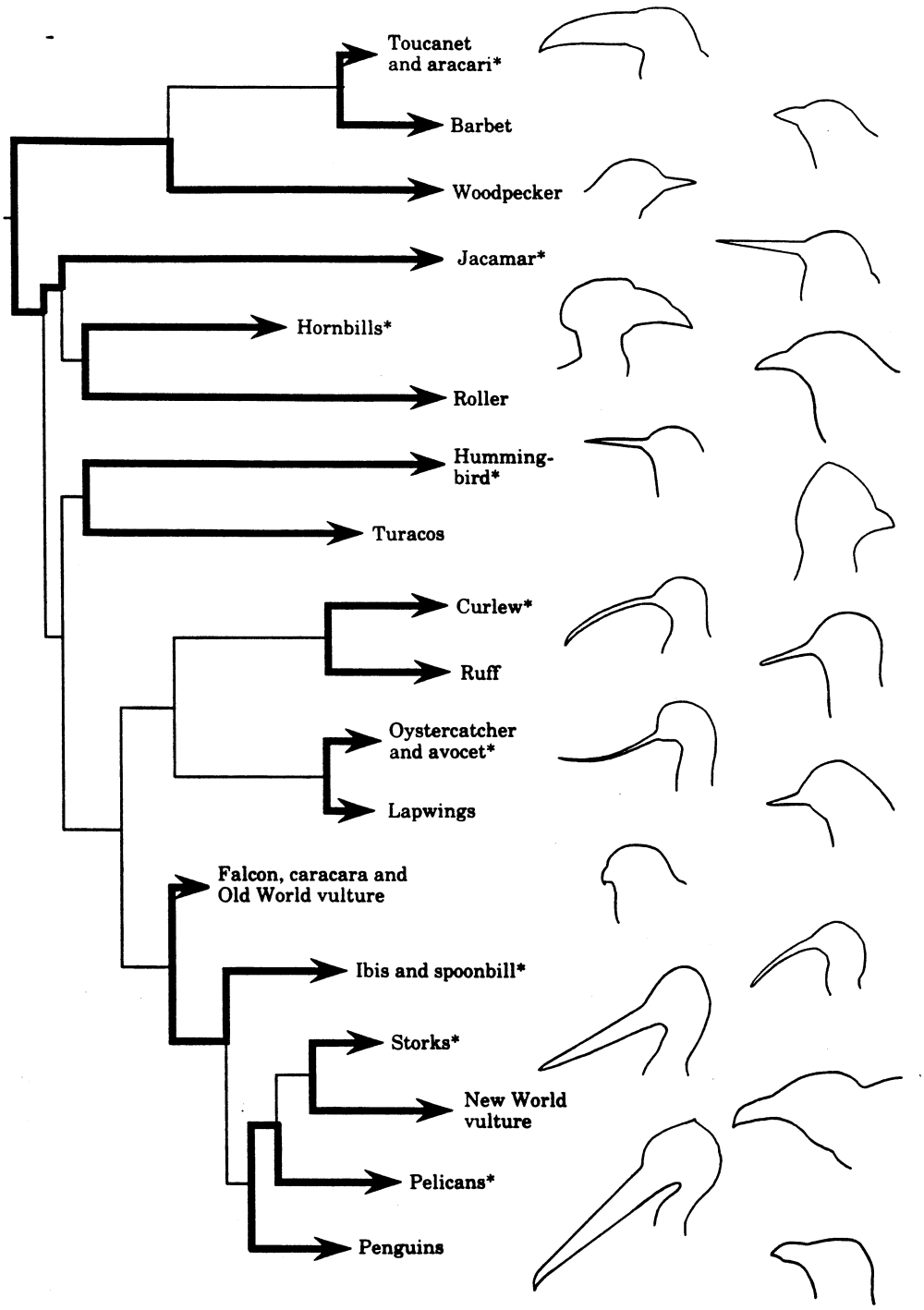

Figure 1. Sister taxa used for matched-pair comparisons of grooming behaviour in captive birds. Long-billed taxa are indicated by asterisks. The phylogeny is from Sibley & Ahlquist (1990).

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),