

Huia (*Heteralocha acutirostris*: Callaeidae) - like sexual bill dimorphism in some birds of paradise (Paradisaeidae) and its significance

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ABSTRACT

The rare reversed sexual bill dimorphism of the extinct New Zealand endemic bird species, the Huia (*Heteralocha acutirostris*: Callaeidae) occurs in two Australian riflebird (*Ptiloris*) and three New Guinea sicklebill (*Epimachus [Drepanornis]*) birds of paradise (Paradisaeidae). While less extreme than that of the Huia, the female bill length proportionate to tarsus length is 7-18% longer than in males. In this proportionate bill length, females are longer-billed than males in most typical (polygynous) birds of paradise. More marked examples of reversed sexual bill dimorphism in the Paradisaeidae occur in species with greater proportions of wood-dwelling arthropods in their diets. Ecological studies of these species might provide insights into the way Huia lived and how their bill dimorphism evolved.

KEYWORDS: Birds of paradise, Sexual bill dimorphism, Huia, *Heteralocha acutirostris*

INTRODUCTION

The remarkable sexual dimorphism in bill length and shape of the extinct New Zealand endemic Huia (*Heteralocha acutirostris*: Callaeidae) has long attracted attention (Buller 1871, 1888, Phillipps 1963, Burton 1974 & references therein) and was recently discussed by Jamieson & Spencer (1996) and Moorhouse (1996). The latter two studies present a brief review of wood-probing bird species exhibiting sexual dimorphism in bill structure. The purpose of the present note is to describe and discuss examples of Huia-like sexual bill dimorphism not included in their discussions. These are found in two riflebird (*Ptiloris*) species of Australia and three sicklebill (*Epimachus [Drepanornis]*) birds of paradise (Paradisaeidae) of New Guinea.

The three species of riflebirds are markedly sexually dichromatic. The adult males are jet black, conspicuously decorated with discrete areas of iridescent feathering, with modified outer primaries that produce distinctive sounds in flight and courtship displays (Frith & Cooper 1996). Female riflebirds (and sicklebills) are cryptically coloured (C. Frith & D. Frith 1995). For detailed descriptions of riflebirds and sicklebills see Cooper & Forshaw (1977).

The larger Magnificent Riflebird (*P. magnificus*) occurs throughout much of lowland New Guinea and the extreme north-east tip of Queensland, Australia (D. Frith & C. Frith 1995). Victoria's Riflebird (*P. victoriae*) is restricted to tropical forest between Cooktown and Townsville, north Queensland. The Paradise Riflebird

(*P. paradiseus*) occurs in subtropical forests of the coastal zone of south-eastern Queensland to north-eastern New South Wales (Blakers *et al.* 1984).

Riflebirds exhibit noticeable sexual dimorphism in bill size and shape. In the two endemic Australian species the smaller females have a larger bill than males (Hindwood 1968, Gilliard 1969, Cooper & Forshaw 1977).

MATERIAL AND METHODS

I recently measured *Ptiloris* and *Epimachus* (*Drepanornis*) skin specimens in major world collections (Table 1; see Frith & Frith 1997). Measurements were taken with a stopped steel rule (wing length only) or electronic digital callipers. Wing length was measured by the maximum chord method (Lowe 1989). Bill length was taken from the bill/foreskull union to the tip of the upper mandible.

I note here a point of potential ambiguity with regard to *Huia* bill measurements. Moorhouse (1996) referred to "culmen length: the chord from the tip of the upper mandible to its base" (*Italics mine*). Culmen length is often taken to mean the length of exposed culmen from where forehead feathers no longer cover the culmen to the tip of the bill. Moorhouse's measurement is termed "bill length" in Lowe (1989). While differences between these two measurements could not much, if at all, influence the findings of Moorhouse (1996) on relatively long-billed *Huia*, they can be significant elsewhere. For example, the use of exposed culmen length for the Superb Bird of Paradise (*Lophorina superba*) led Gilliard (1969) and Cooper & Forshaw (1977) to describe bill sexual dimorphism while bill length, when measured to skull, does not differ sexually. This is because the forecrown feathers meet and cover the culmen base differently in the sexes of this species (Frith & Frith, unpubl. data).

Bill length as a percentage of both wing and tarsus length was calculated for each individual specimen. Percentage data were then normalised by applying an arc sin transformation. The resulting mean values for males and for females were then compared using Student's two-tailed *t*-test.

RESULTS

Mean adult male bill length of the majority of the 42 bird of paradise species is slightly longer than or the same as respective females except in the following species: Yellow-breasted Bird of Paradise (*Loboparadisea sericea*), Carola's Parotia (*Parotia carolae*), Buff-tailed Sicklebill (*Epimachus albertisi*), Paradise Riflebird, and Victoria's Riflebird. In these species, females have slightly longer bills than males do (Frith & Frith 1997; Table 1).

Measurements of the three riflebird and four closely related sicklebill species (Table 1) show that in *P. paradiseus* and *P. victoriae*, in which adult females are smaller overall than adult males, the female bill was by 8% and 4% longer than male bill, respectively. In the larger, more widespread and polytypic *P. magnificus* adult female bill length on average was 11% shorter than adult male. Sexual bill

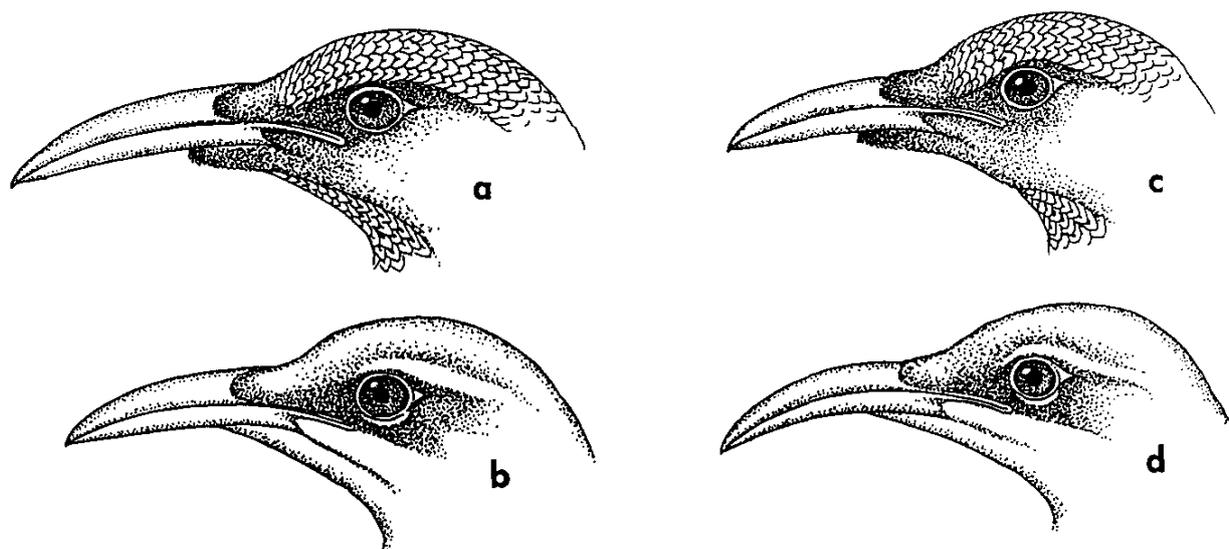


FIGURE 1 – Head of adult male (a) and adult female (b) Magnificent Riflebird *Ptiloris magnificentus* and adult male (c) and female (d) Paradise Riflebird *P. paradiseus* to show sexual dimorphism in bill length and shape. Drawing by William T. Cooper.

dimorphism in *P. magnificentus* and *P. paradiseus* is shown in Figure 1; the female *P. paradiseus* bill is clearly longer and more decurved than the male. Bill length in adult female Buff-tailed Sicklebills was also longer (4%) than that of adult males, but in the other three sicklebills the female bill was shorter (Table 1).

Bill length proportionate to wing length are presented in Table 1 as the latter is widely used as indicative of body size in birds. This may not be the best indicator of body size, however, because males with elaborate nuptial plumage (specifically elongated tail feathers) that presumably reduces flight performance have longer wings as a compensatory adaptation (Andersson & Andersson 1994). Tarsus length is therefore a better indicator of overall body size than wing length (Andersson & Andersson 1994) particularly as the wing is also subject to variation due to moult and feather wear.

As a proportion of both wing and tarsus length, female bird of paradise bill length was typically longer than (in 31 and 29 species respectively) or the same size as (in 6 and 2 species respectively) male bill length.

In bill length proportionate to wing length, females have a 3-7% longer bill than adult males in all riflebirds and sicklebills except the Pale-billed Sicklebill (*E. bruijnii*). The difference in means between the sexes is significant in the three riflebirds: *P. paradiseus* ($t_{57} = 11.04$, $P < 0.001$); *P. victoriae* ($t_{81} = 10.56$, $P < 0.001$); *P. magnificentus* ($t_{157} = 11.74$, $P < 0.001$). It is also significant in the sicklebills: *E. fastuosus* ($t_{110} = 16.14$, $P < 0.001$), *E. meyeri* ($t_{100} = 10.28$, $P < 0.001$) and *E. albertisi* ($t_{72} = 4.53$, $P < 0.001$) but not in *E. bruijnii* ($t_{34} = 1.64$, $P > 0.1$).

TABLE 1 – Bill, tarsus and wing measurements and bill/wing and bill/tarsus proportions of adult riflebird *Ptiloris* spp. and sicklebill *Epimachus* spp. bird of paradise (Paradisaeidae) specimens from various world collections.

Species/sex	Bill length			Wing length			Tarsus length			Bill length relative to	
	Mean±s.d.	Range	n	Mean±s.d.	Range	n	Mean±s.d.	Range	n	wing (%)	tarsus (%)
<i>Ptiloris paradiseus</i>											
Male	54.1±2.48	49.3-61.6	34	160±2.75	153-165	37	33.3±1.34	30.1-36.2	35	34	163
Female	58.5±2.97	51.1-65.8	25	144±5.07	137-156	26	32.3±1.41	29.5-35.6	24	41	181
<i>P. victoriae</i>											
Male	43.2±1.24	40.1-46.7	51	139±3.06	133-148	51	32.1±1.00	29.8-34.6	51	31	135
Female	44.7±2.22	40.1-49.0	33	125±5.00	116-136	34	30.3±1.55	28.0-33.1	31	36	148
<i>P. magnificus</i>											
Male	56.8±2.89	50.9-63.5	89	188±7.13	174-200	96	39.1±1.57	35.6-42.7	91	30	145
Female	50.4±3.10	44.6-56.9	70	153±6.89	139-165	71	35.3±1.95	31.1-44.2	71	33	143
<i>Epimachus alberti</i>											
Male	76.1±2.62	69.2-82.6	43	153±3.45	145-161	51	34.4±0.89	32.2-35.8	49	50	221
Female	79.0±5.16	68.1-91.0	31	148±2.99	143-156	34	34.0±0.87	32.3-36.5	34	53	232
<i>E. s. bruijni</i>											
Male	79.0±2.21	73.5-82.6	26	160±3.07	153-165	28	33.0±0.93	30.8-34.8	26	49	239
Female	75.1±3.16	68.3-79.1	12	155±4.78	148-162	14	32.1±1.21	30.2-33.9	14	48	234
<i>E. fastuosus</i>											
Male	77.9±3.96	69.9-85.8	57	201±9.70	188-232	63	50.9±2.14	46.5-55.4	62	39	153
Female	75.3±4.28	66.4-88.5	55	171±9.52	152-193	58	47.2±2.68	42.7-55.0	58	44	160
<i>E. meyeri</i>											
Male	84.4±2.72	78.4-90.4	42	182±6.69	171-206	51	50.2±1.78	46.3-54.0	50	46	168
Female	82.1±4.19	69.1-90.5	60	157±9.59	142-185	63	45.6±2.81	39.0-53.2	63	52	180

Considering the more significant (see above) bill length proportionate to tarsus length: it is 13-18% larger in females than in males in the two reverse dimorphic riflebird species but 2% smaller in the Magnificent Riflebird. The difference in means between the sexes is significant in *P. paradiseus* ($t_{53} = 5.56$, $P < 0.001$) and *P. victoriae* ($t_{78} = 5.32$, $P < 0.001$) but is not significant in *P. magnificus* ($t_{152} = 2.09$, $P > 0.02$). In three sicklebills bill length proportionate to tarsus length is 7-12% larger in females than in males, but 5% larger in male Pale-billed Sicklebills than in females (Table 1). These sexual differences in sicklebills are significant in *E. fastuosus* ($t_{109} = 4.60$, $P < 0.001$), *E. meyeri* ($t_{99} = 6.37$, $P < 0.001$) and *E. albertisi* ($t_{70} = 2.93$, $P < 0.01$) but not significant in *E. bruijnii* ($t_{34} = 2.35$, $P > 0.02$).

DISCUSSION

Riflebirds are highly 'insectivorous' and commonly excavate insects and their larvae from accumulated detritus and wood (D. Frith 1984, Frith & Beehler unpubl. data). Ecological data are inadequate to determine the cause of the reversed sexual dimorphism in bill size in the two smaller endemic Australian species (Table 1; Fig. 1). A review of bird of paradise diets suggested riflebirds might eat approximately equal amounts of fruit and animal food (Beehler & Pruett-Jones 1983). Victoria's, and possibly also Paradise, Riflebirds take a higher proportion of animal than fruit food (D. Frith 1984, C. Frith & D. Frith 1995). This is consistent with the apparent relationship between wood-foraging and the marked sexual bill dimorphism in several unrelated avian taxa (Jamieson & Spencer 1996, Moorhouse 1996 and references therein). Of the four scimitar-billed sicklebills that all regularly extract arthropods from sites such as pandanus (*Pandanus* spp.) frond bases and tree crevices, *E. albertisi* is considered the most insectivorous (Schodde 1976, Beehler & Pruett-Jones 1983, Beehler 1987, Frith & Beehler unpubl. data).

Far better data on foraging sites, methods and diet of riflebirds and sicklebills are required to adequately interpret bill morphology. Notwithstanding this, the available evidence does suggest that sexual dimorphism in bill length in *P. paradiseus*, *P. victoriae* and *E. albertisi* correlates with a relatively greater proportion of arthropods in the diet. In their close relatives, difference in bill size is proportionate to overall size (Frith & Frith unpubl. data).

Moorhouse (1996) pointed out that the sexual dimorphism in bill length of the Huia is consistent with Selander's (1966) hypothesis that sexual difference in foraging-related morphology should be larger in populations lacking competitors. Two birds of paradise also conform with this hypothesis. The Australian *Ptiloris* spp. lack specialist wood probing/excavating competitors whereas New Guinea-dwelling *P. magnificus* has some potentially sympatric relatives (*Epimachus* spp., Twelve-wired Bird of Paradise (*Seleucidis melanoleuca*)) that may feed similarly. There is larger sexual dimorphism in bill length in the Australian-endemic *Ptiloris* spp..

While reversed sexual bill length dimorphism in Huia, the smaller two riflebirds and three sicklebills could be linked to wood foraging and perhaps reduction of

intersexual competition for food, much remains to be learnt about possible underlying selective pressures and physical mechanisms involved. Given that a species has the potential for marked bill size sexual dimorphism, it is possible that in some species sexual or social visual signal functions of the bill and head shape dictate which sex develops the larger and/or more decurved/slender bill. Thus when the bill in males is shorter and less decurved than in females it may reflect stabilising sexual selection on males (D. Goodwin *in litt.*).

Sexual dimorphism in bill length of wood foraging birds enable the species to utilise an expanded range of foods (Lack 1971). The interesting question is why is this achieved in the Huia, two riflebirds and three sicklebills by reversed sexual bill dimorphism and not by normal (male bill larger) dimorphism? The birds of paradise involved are all polygynous species in which only the female feeds offspring predominantly animal foods (C. Frith & D. Frith 1995 and unpubl. data, Frith & Beehler unpubl. data). Is it in highly 'insectivorous' wood-probing/tearing species the female that has the longer and more decurved bill because this was advantageous in providing young with a high-protein diet? This raises an unanswerable but intriguing question. Did female Huia collect most food for offspring?

Since sexual bill dimorphism presumably reflects ecologically significant differences in bill/body proportions, examination of sexual differences in foraging behaviour in each species (foraging sites, techniques and diet) and a phylogenetic analysis of the dimorphism in question is required (Moorhouse 1996). Mechanically important body proportions including bill length and its degree of downward curvature, bill width, skull and neck length and (particularly pertinent to scansorial foragers) tarsus and/or foot length/thickness/strength are doubtless of much significance to the foraging efficiency of the bill. Such data are not yet available for birds of paradise.

The unusual and 'reversed' sexual dimorphism in bill length and shape in the above birds of paradise is probably a further example of convergent evolution of this character as documented in Huia and wood-foraging members of several other bird groups. However, many authors suggested a close relationship between the Callaeidae and the Paradisaeidae (Gadow 1888, Beecher 1953, Mathews 1930, Mayr & Greenway 1962, Fleming 1964, 1985, Borecky 1977). Currently they are considered adjacent families within the superfamily Corvoidea but separated by three subfamilies and seven tribes (Sibley *et al.* 1988, Sibley & Ahlquist 1990). New Zealand wattlebirds possess some typical birds of paradise characters such as: coloured wattles at the gape, pale bill colour, small central shaft points to rectrices and use of the feet to hold food (Frith & Beehler unpubl. data).

It is demonstrated above that the typical (polygynous) bird of paradise has females with a longer bill than males; most exceptions to this being the monogamous species. This is contrary to the held-to-date impression, gained by simply comparing bill lengths between the sexes, and suggests fertile ground for further comparative morphological and ecological studies. Field studies of the feeding ecology of and foraging mechanics employed by both sexes of the bird of paradise species *P.*

paradiseus, *P. victoriae* and *Epimachus (Drepanornis)* spp. could possibly provide insights into the way in which the extinct Huia lived and why and how its bill dimorphism evolved.

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