The extraordinaory bill dimorphism of the Huia (*Heteraclocha acutirostris*): sexual selection or intersexual competition?

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ABSTRACT

Morphological comparison of the extinct Huia (*Heteralocha acutirostris*) with its closest known relatives suggests that the pronounced sexual bill dimorphism of the former evolved through selection on female, rather than male bill form. Because sexual selection acts predominantly on males, it cannot readily explain such dimorphism in a non-polyandrous species. Greater female divergence in foraging-related anatomy in a species in which males are the larger (and therefore presumably socially dominant) sex is, however, consistent with the hypothesis that sexual dimorphism can be an adaptation to reduce intersexual competition for food. Determining which sex changed most is a more rigorous means of establishing the evolutionary significance of sexually dimorphic traits than interpretation of current function.

KEYWORDS: Huia, Callaeidae, sexual dimorphism, competition

INTRODUCTION

The extinct Huia (*Heteralocha acutirostris*), a large (450 mm) wood-foraging passerine endemic to New Zealand (Falla *et al.* 1979), displayed the most extreme sexual bill dimorphism known in birds (Rand 1952, Phillipps 1963, Selander 1966, Burton 1974). In contrast to the relatively short, robust bill of the male, that of the female was approximately one third longer, more slender and strongly decurved (Figure 1). With the exception of bill length, the Huia appeared to display the usual avian pattern of sexual size dimorphism, the male being significantly larger than the female in both tarsus and wing length (Selander 1966).

Rand (1952) was the first to suggest that the pronounced bill dimorphism of the Huia was an adaptation to reduce intersexual competition for food, an idea reiterated by Selander (1966, 1972) and Burton (1974). The Huia displayed marked sexual differences in foraging behaviour, consistent with those in bill form (Buller 1888). The most detailed observations were made by Buller who recorded that, "The male always attacked the more decayed parts of the wood, chiselling out his prey after the manner of some woodpeckers, while the female probed with her long pliant bill ... where the hardness of the surrounding parts resisted the chisel of her mate." (Buller 1888, p. 10). While it has been suggested that the sexes foraged cooperatively (Colenso 1887), Buller (1888) noted that the female did not share grubs that were too deep to be reached by the male.

In his "Niche Separation Hypothesis" (NSH) Selander (1966) argued that sexual dimorphism in foraging behaviour and related anatomy had evolved in monogamous, territorial species (or populations), because males and females that diverge in
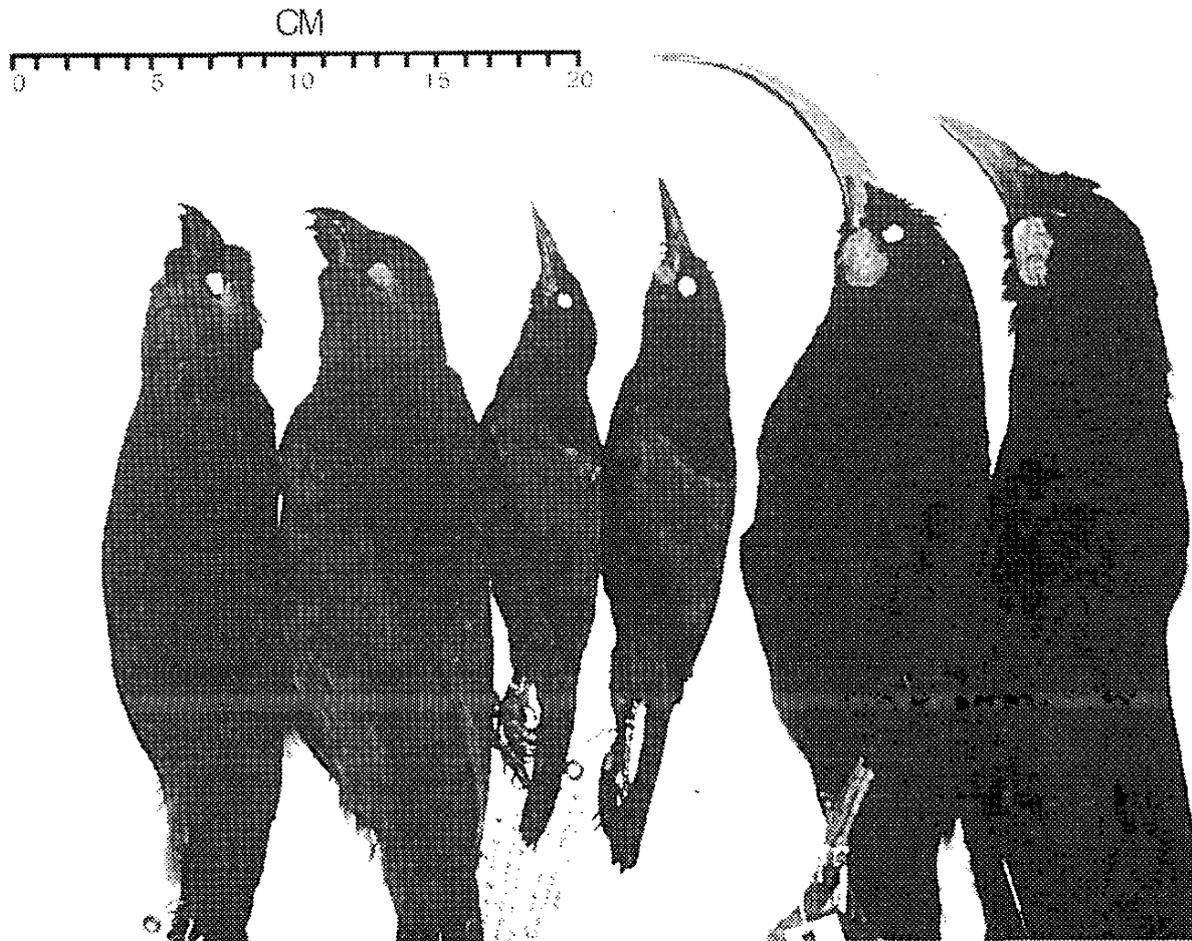

FIGURE 1 - Variation in sexual dimorphsm within the Callaeidae. From left: female and male Kokako, Saddleback and Huia.

foraging ecology would enhance their individual fitness by reducing competition with their mates. Although this mechanism for the evolution of sexual dimorphism has been found to be feasible in population genetic models (Slatkin 1984), a major weakness of the NSH is that it makes few testable predictions, none of which are incompatible with the predominant alternative hypothesis of sexual selection (Shine 1989). Consequently, the bulk of support for the NSH consists of post-hoc arguments linking sexual differences in diet with those in foraging-related anatomy (Shine 1989).

This lack of predictive value has attracted criticism (Power 1980, Payne 1984, Jehl and Murray 1986, Suhonen & Kuitunen 1991). As Jehl & Murray (1986; p. 62) put it, "Our understanding of the influence of ecological factors would be enhanced if the supporters of such hypotheses attempted to cast their views in deductive form. Just what patterns of size dimorphism can be deduced from assumptions about competitive interactions between the sexes?". These authors went so far as to state that, "... sexual size dimorphism is the result of sexual selection and ... ecological factors act only secondarily, if at all, to influence the degree to which the dimorphism is expressed." (op. cit. p. 61).

More rigorous support for the NSH can, however, be provided by demonstrating that sexual dimorphism in foraging-related anatomy was the result of the female, rather than the male, diverging from the ancestral condition. Such evidence has been found in comparative studies at both the species and population level

(Selander 1966, Ebenman 1986, Gosler & Carruthers 1994). Greater female divergence would be predicted by the NSH for species in which males are the larger sex, as, in such species, females are likely to be subordinate in agonistic interactions (Morse 1974, Gaulthreaux 1978, Peters & Grubb 1983) and are therefore more likely to evolve different foraging behaviours and morphology in response to intense intraspecific competition for food or foraging micro-habitat.

Because sexual selection usually affects males more than females (Darwin 1871; Fisher 1930, Huxley 1938, Trivers 1972, Maynard-Smith 1978, Møller 1993) it cannot readily explain sexual dimorphism which is clearly the result of selection on the female rather than the male. While sexual selection can affect females more than males, this is generally the case only in polyandrous species which are the distinct minority in most avian taxa (Jenni 1974, Oring 1982, Murray 1984). It is possible, however, that apparent female divergence in a given trait could be due, at least in part, to sexual selection constraining change in the size of this trait in males. This possibility can only be refuted by a "Rate Test" analysis (Turelli *et al.* 1988, Björklund 1991) which allows the likely influence of stabilising and directional selection on each sex to be evaluated.

As the most extreme avian example of sexual divergence in bill form, the Huia is an important test for the hypotheses that seek to explain the evolution of such dimorphism. Although many aspects of the Huia's ecology, social organisation and mating system are unknown, it is known that it was typically encountered in heterosexual pairs (Colenso 1887, Buller 1888); that the female performed most of incubation (Buller 1892); and that the male assisted the female in feeding the young (Potts 1885, Buller 1892). There is, therefore, no basis to suspect that the Huia was anything other than monogamous (*sensu* Murray 1984). The fact that pairs were strongly attracted to imitations of their call (Buller 1888) suggests that they were highly territorial.

The Huia, together with the extant Kokako (*Callaeas cinerea*) and Saddleback (*Philesturnus carunculatus*), comprises the Callaeidae, a monotypic family of obscure affinities endemic to New Zealand (Williams 1976, Sibley & Ahlquist 1990). The Kokako is similar in size to the Huia (Figure 1) but is predominantly vegetarian, obtaining the relatively small invertebrate component of its diet primarily by gleaning foliage and bark rather than by excavating wood (Powlesland 1987). Like the Huia, males exceed females in tarsus length but the sexes appear monomorphic in bill size (J. Innes unpubl. data). The Saddleback is considerably smaller than the Huia (Figure 1), but, as was the case in the latter, the bulk of its diet is invertebrates extracted from wood or bark (Atkinson & Campbell 1966). The Saddleback displays significant sexual dimorphism in both bill and tarsus length, but unlike the Huia, males exceed females in both variables (Jenkins & Veitch 1991). Both the Saddleback and the Kokako are monogamous and maintain year-round territories (Jenkins 1978, Hay *et al.* 1985).

In this paper I attempt to determine the probable evolutionary significance of the sexual bill difference of the Huia by comparing its bill form to that of the Saddleback and the Kokako.

METHODS

Data collection
Morphometric data on the Huia and Kokako were obtained by measuring study skins and mounts in museum collections. The Kokako measurements were supplemented with those of live birds (J. Innes & I. Flux unpubl. data). The Saddleback data were a randomly selected sub-sample from the measurements used in Jenkins & Veitch (1991) which were taken from live adult birds of known sex. Kokako and Saddleback data were collected from the North Island sub-species (*C. cinerea wilsoni* and *P. carunculatus rufusater*, respectively) only.

The following measurements were analysed for sexual dimorphism:

a) Culmen length; the chord from the tip of the upper mandible to its base (to nearest 0.1 mm).

b) Culmen width; the width of the upper mandible at the widest part of the gape (to nearest 0.1 mm).

c) Culmen-tip width (Huia only); the width of the upper mandible measured as near as possible to its tip. This measurement was taken from Huia as an additional means of corroborating the sexing of museum specimens. The bill of female Huia is more slender than that of the male (Buller 1877, Phillipps 1963) and this difference might be expected to be most pronounced at the bill tip as the bill of the female was primarily used for probing, rather than chiselling or prying as in the male (Buller 1888, Burton 1974).

d) Tarsus length; the oblique distance from the posterior surface of the tibiotarsal joint to the anterior surface of the articulation with the middle toe (to nearest 0.1 mm).

All data were normally distributed and were analysed for sexual differences using a two-tailed Student's *t* - test.

Sexing of specimens
All 30 Huia specimens had been sexed but it was uncertain whether this had been done objectively (i.e. by autopsy). However, given the detail and consistency of the historical literature concerning bill dimorphism in this species (Colenso 1887, Buller 1877, 1888), it seems unlikely that adult specimens were incorrectly sexed. If sex was assigned on the basis of bill length alone, it is possible that juvenile females (in which the bill is of intermediate length; Buller 1877, Phillipps 1963) could have been incorrectly sexed as males. As the bill lengths of such specimens are likely to be closer to the adult male than the adult female mean, their erroneous inclusion in the male sample would increase apparent sexual dimorphism in bill length.

Relatively few Kokako specimens (32/70) had been objectively sexed, either by autopsy (museum specimens) or by observation of nesting behaviour. Because culmen length was rarely measured on live birds (which comprised the bulk of the sexed sample) available culmen length data (from five males and seven females) were insufficient for statistical comparisons. To obtain an adequate sample, museum specimens of unknown sex were sexed on the basis of tarsus length, a technique that is 76% reliable in live birds (J. Innes and I. Flux unpubl. data). Tarsus length data used in statistical tests were from objectively sexed birds only.

Overlap between the tarsus length distributions of objectively sexed Kokako suggested that only the largest 42% of males and the smallest 40% of females could be sexed with greater than 80% reliability. Accordingly, only specimens with tarsi longer than 71 mm were classed as male and those with tarsi shorter than 66 mm were classed as female. As the resultant sample contained a disproportionate number of relatively large males and relatively small females, any apparent sexual dimorphism in bill size could simply be an artifact of this sampling bias. However, an absence of significant sexual size dimorphism in such a size-biased sample would strongly suggest that the Kokako is monomorphic with respect to the variables in question.

All 40 Saddlebacks had been sexed, either by nesting behaviour or song type (Jenkins and Veitch 1991).

Evolutionary analysis

A. Phylogeny

There is no phylogeny currently available for the Callaeidae and consequently the ancestral bill form cannot be deduced with any quantifiable measure of confidence. However, given the rarity of reverse (female larger than male) bill dimorphism in species in which the male is otherwise the larger sex (Rand 1952, Amadon 1959, Selander 1966), and the absence of this trait in both the Saddleback and the Kokako, I consider it reasonable to assume that the bill dimorphism of the Huia is a derived condition.

B. Estimation of the ancestral condition

The obscure affinities of the Callaeidae (reviewed in Sibley & Ahlquist 1990) make it impossible to identify reliable non-callaeitid outgroups and thus objectively estimate the probable ancestral bill form. Therefore, since both the Saddleback and the Kokako are considered to share recent common ancestry with the Huia (Sibley & Ahlquist 1990), but lack the reverse bill dimorphism of the latter, I will use these as approximations of the probable ancestral condition. This is reasonable in this case as the vast majority of bird species with normal (male larger than female) size dimorphism either display slight sexual bill dimorphism in favour of the male, like the Saddleback, or are monomorphic in bill size, like the Kokako (Amadon 1959, Selander 1972). These conditions are thus likely to be ancestral, both in birds generally and in the Callaeidae specifically. Following Björklund (1991), relative change in culmen length in the Huia was estimated by dividing the difference between the species means of the Huia and the other two callaeitids by the standard deviations of the latter.

C. "Rate Test" analysis

The "Rate Test for Neutral Evolution" (Turelli *et al.* 1988, Björklund 1991) provides a means of comparing the degree of variation between sister species in specific variables to that expected through genetic drift. This is useful as even apparently significant differences between related species can be simply due to genetic drift since divergence from the common ancestor (Björklund 1991). Only if between-species differences exceed those expected through genetic drift are they likely to be the

result of directional selection (*op. cit.*). Conversely, a difference between sister species that is less than that expected through genetic drift suggests maintenance of the ancestral condition by stabilising selection (*op. cit.*).

Upper and lower 95% confidence limits for genetic drift are given by

$$V_m \ 2t \ F_{0.025} \ (n\text{-}1, \ \infty) \text{ and } V_m \ 2t \ F_{0.975} \ (n\text{-}1, \ \infty)$$

respectively, where V_m is the neutral mutational input per generation, $F_{0.025}$ and $F_{0.975}$ are values of the F distibution, and t is time (millions of years). As not all mutations are selectively neutral, this equation may overestimate the rate of neutral evolution and the test should therefore be regarded as qualitative (Björklund 1991). As the Callaeidae are thought to be Gondwanic in origin (Stevens 1991) I have estimated genetic drift from 85 million years before present, when all land links between what were to become the principal islands of New Zealand and Gondwanaland were broken (*op. cit.*), to the end of the Pleistocence (10,000 years ago) by which time most modern bird species were in existence (Brodkorb 1971). Following Björklund (1991), I have assumed a neutral mutational input of 10^{-4} per generation.

The between-species variance (S^2) for specific characters was calculated using:

$$S^2 = (MSb - MSw) \ / \ n0$$

where *MSb* and *MSw* are the between and within groups mean squares respectively, taken from a one-way analysis of variance (ANOVA), and *n0* is the average sample size (Björklund 1991).
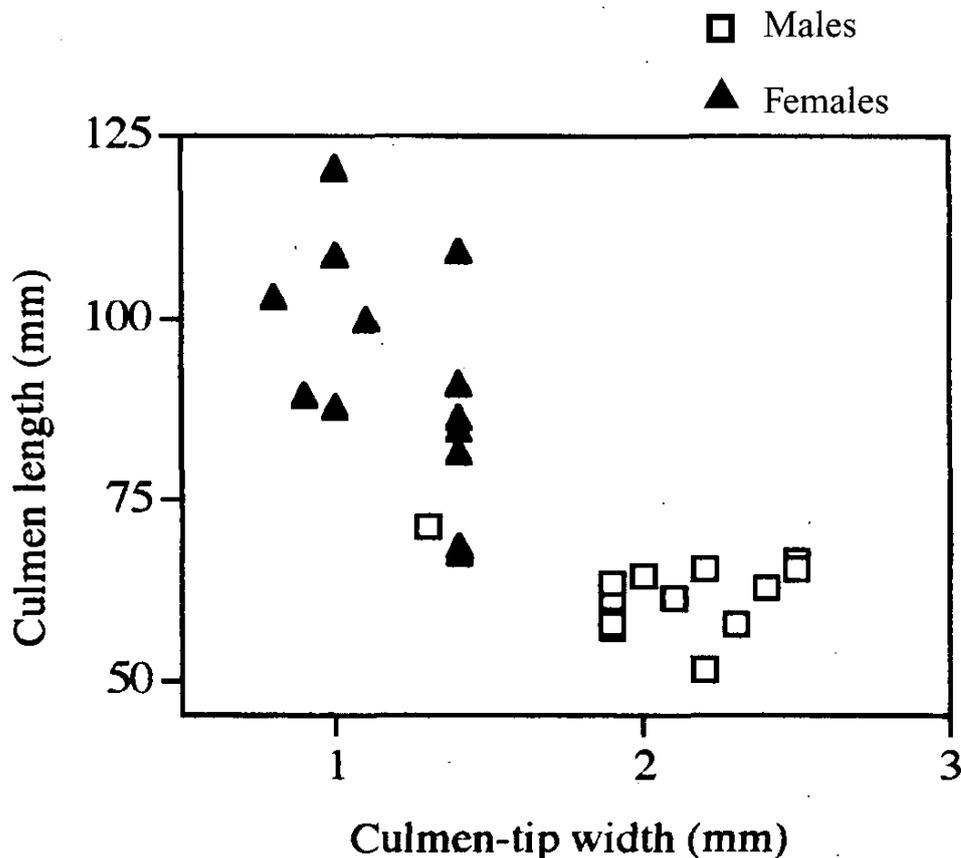

FIGURE 2 - Culmen length vs culmen-tip width in the Huia (n=26).

RESULTS

Description of sexual dimorphism

A. Huia

Males were significantly larger than females in all variables except culmen length (Table 1). Plotting culmen length against culmen-tip width resulted in clear separation of the sexes with the exception of one putative male specimen (Figure 2). This suggests that the majority of specimens had been correctly sexed. Plotting culmen length against tarsus length (an index of overall body size) indicated nearly complete separation of the sexes in the former but considerable overlap in the latter variable (Figure 3A). The greater variation in female culmen length (Figure 2) is expected as the culmen lengths of juvenile females are intermediate between those of adult females and males (Buller 1877, Phillipps 1963).

B. Saddleback

Males were significantly larger than females only in culmen and tarsus length (Table 1). The "t" statistic for tarsus length in the Saddleback was the highest for all three species (Table 1) and, unlike the Huia (Figure 2), there was no overlap between the sexes in this variable (Figure 3B). This could, however, reflect the absence of juveniles in the Saddleback sample. Despite this absence, there was much greater overlap between male and female Saddleback in culmen length (Figure 3B) compared to male and female Huia (Figure 3A).

C. Kokako

The only significant sexual size difference was in tarsus length in which males were the larger sex (Table 1). There was no obvious potential sexual segregation in the culmen and tarsus length data (Figure 3C) comparable to that in the Huia (Figure 3A) and Saddleback (Figure 3B). As the Kokako sample was comprised of a disproportionate number of relatively large males and relatively small females, the absence of significant dimorphism in culmen length and width (Table 1) strongly suggests that this species is monomorphic with respect to these variables.

TABLE 1. Sexual differences in the Callaeidae. All Measurements are in mm. Values are means, compared by Student's *t*-test.

| Species & variable	Male	Female	t	d.f.	Significance
Huia					
Culmen length	62.3	91.6	7.83	26	0.001
Culmen width	12.4	11.0	3.15	26	0.005
Culmen-tip width	2.1	1.1	6.83	24	0.001
Tarsus length	83.8	78.7	2.40	26	0.05
Saddleback					
Culmen length	34.8	33.3	3.97	38	0.001
Culmen width	8.7	8.6	0.50	38	0.7
Tarsus length	41.7	39.0	12.51	38	0.001
Kokako					
Culmen length	30.9	30.4	0.69	30	0.5
Culmen width	15.8	15.4	0.84	22	0.5
Tarsus length	69.6	66.5	2.40	22	0.025
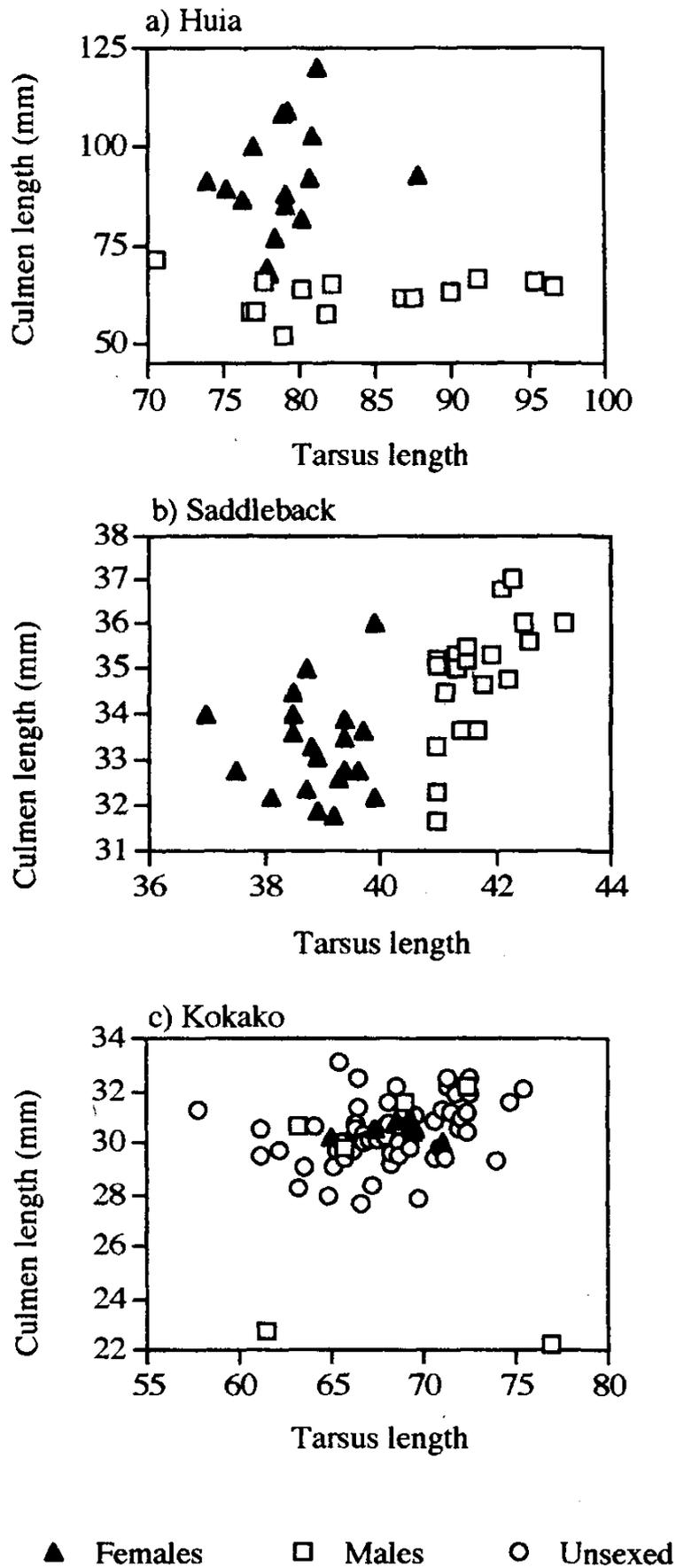
FIGURE 3 - Culmen length vs tarsus length in (a) the Huia, (b) the Saddleback,and (c) the Kokako. Note difference in scale.

TABLE 2 - Average sexual dimorphism calculated as the difference between male and female means, expressed as percentage of the male mean. Negative values indicate variables in which the female was the larger sex.

Variable	% Sexual dimorphism		
	Huia	Saddleback	Kokako
Culmen length	-47.2	4.4	1.4
Culmen width	11.4	0.9	3.0
Tarsus length	6.0 ·	6.6	4.5

Interspecies comparison

Culmen length dimorphism in the Huia was seven times that of the most sexually dimorphic variable in the Saddleback and Kokako, and was the only variable in which females exceeded males in size (Table 2). The Huia also displayed over twelve and three times as much sexual dimorphism in culmen width as the Saddleback and Kokako respectively (Table 2). However, in contrast to the marked variation in the degree of dimorphism in culmen length and width, that in tarsus length was similar in all three species (Table 2).

Evolutionary analysis

Direction of change

The ancestor of the Huia presumably resembled either the Saddleback, and displayed slight allometric dimorphism in culmen length as a consequence of overall dimorphism in body size, or the Kokako, and was monomorphic in culmen length (Table 2). Burton's (1974) comparison of skull structure and associated musculature suggests that the former scenario is the most probable, however, in the absence of a rigorously constructed phylogeny it is prudent to consider both possibilities. The Huia has become considerably more dimorphic than either the Saddleback or the Kokako in culmen length, but is only slightly more dimorphic than the Saddleback, and no more dimorphic than the Kokako, with respect to tarsus length (Figure 4).

Rate Test analysis

Without a "molecular clock" for evolution within the Callaeidae it is impossible to obtain an objective estimate of when the modern species diverged. The fossil record suggests that most modern bird species evolved within the Pleistocene (ten thousand to one million years ago) and that most modern genera diverged within the last ten million years (Brodkob 1971). In the absence of other information I can only assume that the modern callaeitids also evolved within this general time-frame. If this was so, then the observed variation between species in male and female culmen and tarsus length is consistent with directional selection (Figure 5).

Female culmen length displayed the highest between-species variance, sufficient to exceed the upper limit of genetic drift if divergence occurred within the last 3.75 million years (Figure 5), and is therefore the variable most likely to have been influenced by directional selection. The between-species variances of male culmen length and male and female tarsus length are sufficient to suggest directional selection only if divergence occurred relatively recently, within the last 430,000 or 750,000 years respectively (Figure 5). Excluding the female Huia decreased the between-
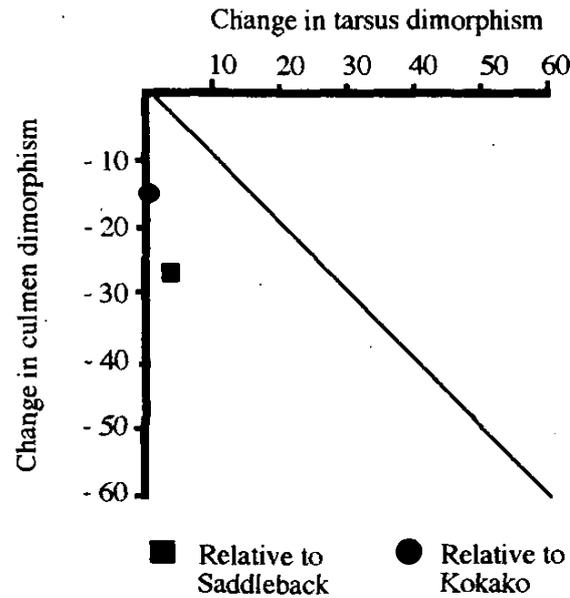
FIGURE 4 - Comparison of sexual dimorphism in Huia culmen and tarsus length relative to the Saddleback and the Kokako. Units are standard deviations of the Saddleback and Kokako. Units are standard deviations of the Saddleback and Kokako. Diagonal line represents slope of equal dimorphism in both variables, diameter of symbols indicates 90% confidence limits.

species variance in female culmen length by three orders of magnitude, sufficient to suggest either stabilising selection or genetic drift (Figure 5). The between-species variance in male culmen length is likely to have been constrained by stabilising selection only if divergence occurred earlier than 70 million years ago (Figure 5).

DISCUSSION

The Huia is clearly unique with respect to the magnitude of its sexual dimorphism in culmen length and width, and the fact that the direction of dimorphism in culmen length is reversed with respect to that in body size. This indicates that the culmen length dimorphism of the Huia is evolutionarily independent of that in body size and may be the result of directional selection. As the culmen length dimorphism of the Saddleback is both of similar magnitude and direction to that in tarsus length, it is probably an allometric consequence of dimorphism in body size and therefore has no adaptive significance.

The Kokako data suggest another explanation; because dimorphism in culmen length and width are significantly less than that in body size (as indicated by tarsus length), culmen size is likely to have been constrained by stabilising selection. The similar tarsus dimorphism of all three species suggests there has been little evolutionary divergence in body size dimorphism within the Callaeidae. As sexual size dimorphism in many avian taxa is positively correlated with the intensity of male competition for females or breeding territories (Murray 1984, Oakes 1992, but see also Höglund & Sillén-Tullberg 1994), the apparent uniformity of sexual size dimorphism within the Callaeidae is consistent with the monogamous habit of the group.

The Rate Test indicates that the between-species variation in female culmen length is likely to have been the result of directional selection. As exclusion of the
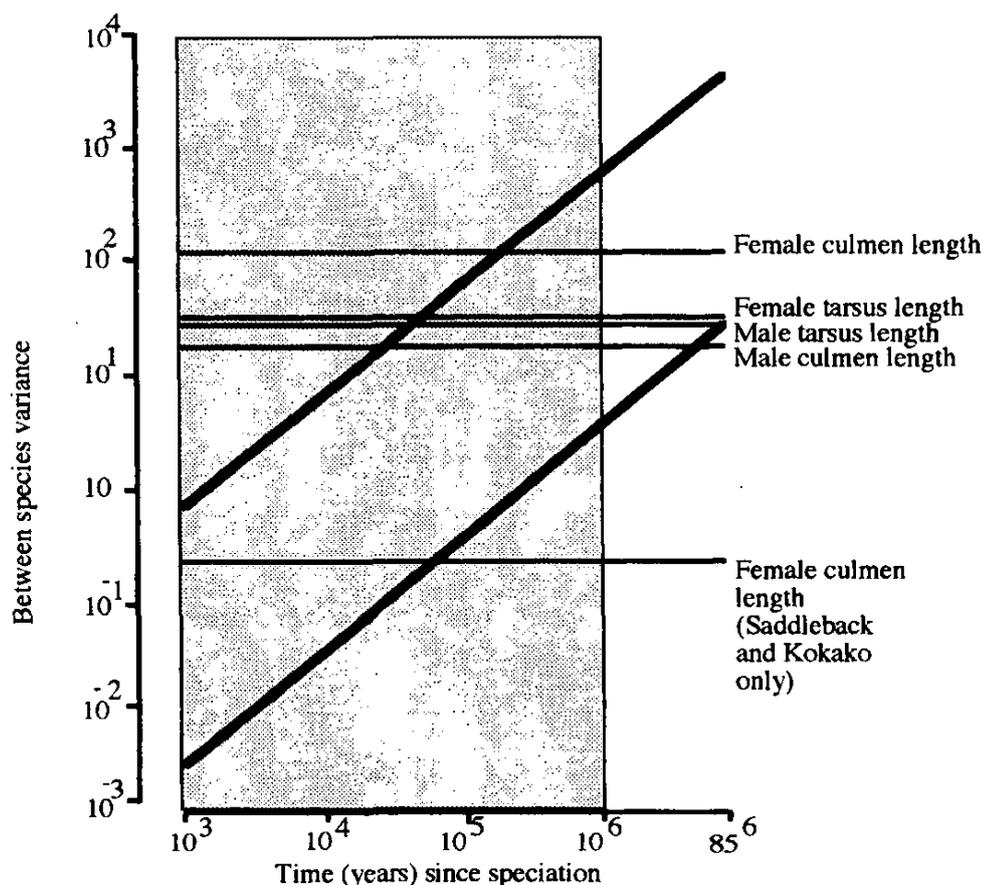
FIGURE 5 - Between-species variance in culmen and tarsus length in the Callaeidae in relation to estimated genetic drift over the time-scale within which speciation has occurred. Diagonal lines demarcate the 95% confidence interval for genetic drift, stippled area indicates the time-frame for divergence suggested by the avian fossil record. Between-species variance that exceeds the confidence limits for drift suggests directional selection over the corresponding time interval. Between-species variance less than the lower limit of drift suggests stabilising selection over the corresponding time interval.

female Huia reduced the between-species variance in this variable to a level consistent with either genetic drift or stabilising selection, it seems likely that directional selection has influenced culmen length in the female Huia alone. Male culmen length is unlikely to have been constrained by stabilising selection as the corresponding divergence date of 70 million years is much earlier than the time-frame for the evolution of modern genera suggested by the fossil record (Brodkorb 1971).

Although in the absence of a chronology for evolution within the Callaeidae these results are not conclusive, they are consistent with the available information on systematic relationships with the group. As most of the between-species variance in female culmen length was contributed by the Huia, if this were due to genetic drift the Huia should have diverged from the ancestral stock earlier than the Saddleback and the Kokako. The available information on systematic relationships within the Callaeidae (Burton 1974), however, suggests that the Huia and Saddleback are more closely related to each other than to the Kokako. In view of this, directional selection is the most probable explanation for the increased culmen length of the female Huia. As there is no evidence that the Huia was polyandrous, sexual selection cannot

readily explain the evolution of longer female culmen length in this species. There-fore, the most parsimonious evolutionary explanation for the divergent bill of the female Huia is the NSH -   i.e. that this was an adaptation to reduce intersexual competition.

An alternative hypothesis consistent with greater female divergence in bill form is the Sexual Division of Labour Hypothesis (Ralls 1976, Power 1980); that sexual dimorphism has evolved as an adaptation for sex-specific functions such as parental care or nest-building. Since both sexes of the Huia fed the young (Potts 1885, Buller 1892), nest-building would seem the only sex-specific activity involving the bill that could have been performed exclusively by the female Huia. It is unlikely that the bill of the female Huia was primarily an adaptation for nest-building as female Saddleback and Kokako construct very similar nests to that of the Huia (Oliver 1974).

The hypothesis that the bill of the female Huia was primarily an adaptation for foraging is supported by the fact that several unrelated wood-probing species have similar long decurved bill forms. These include a Hawaiian honeycreeper (Drepaniidae) *Hemignathus procerus* (Amadon 1950), some Woodhoopoes (Phoeniculidae) *Rhinopomastus* spp. (Burton 1974), some Woodcreepers (Dendrocolaptidae) *Campyloramphus* spp. (Storer 1971), and a Babbler (Timaliidae) *Xiphirhychus superciliaris* (op. cit.). Species with similar bill forms to the male Huia also occur in many wood-foraging species, such as *Phoeniculus* spp. in the Woodhoopoes (Burton 1974) and *Pomatorhinus* spp. in the Babblers (Storer 1971). The African Green Woodhoopoe (*Phoeniculus purpureus*) displays less extreme but otherwise remarkably similar bill dimorphism to the Huia but in this species it is the male which has the longer, more decurved bill (Ligon & Ligon 1979, Jamieson & Spencer 1996).

A review of the literature suggests that sexual dimorphism in foraging related anatomy is relatively common among wood-foraging birds (Amadon 1950, 1959, Selander 1966, Storer 1971, Noske 1986, Gosler & Carruthers 1994). This may, at least in part, reflect the fact that this polyphyletic group, and particularly the Woodpeckers (Piciformes), have become the focus for research on sexual foraging differences since the publication of Selander's (1966) seminal work. Nonetheless, the fact that species as unrelated as the Huia, and the Giant Sunbird (*Cyanomitra thomensis*) both display unusual sexual dimorphism in bill size, and are the most specialised wood-foragers in their respective families (Selander 1966, Burton 1974), suggests a link between this foraging mode and the evolution of such dimorphism.

Hogstad (1976) suggested that the wide range of textural variation of bark and wood may favour the evolution of sexual bill dimorphism in wood-foraging birds. While the evidence for a link between wood-foraging and sexual bill dimor-phism is, at present, merely suggestive, the independent evolution of pronounced sexual bill dimorphism in unrelated wood-foraging species suggests that this dimor-phism has an ecological basis. Although sexual selection predicts that sexual dimor-phism should be most pronounced in polygynous species (Oring 1982, Payne 1984, Oakes 1992), many wood-foraging species with marked sexual bill dimorphism are

highly monogamous (e.g. the Huia, Buller 1888; the Hispaniolan woodpecker [*Centurus striatus*], Wallace 1974; the Three-toed Woodpecker [*Picoides tridactylus*], Hogstad 1991).

The question remains as to why only the Huia, but not the Saddleback, evolved such pronounced sexual dimorphism in bill form. Burton (1974) suggested that this was because the Huia appears to have been primarily a specialist predator of the large (c. 50 mm long) wood-boring larvae of the Huhu Beetle (*Prionoplus reticularis*) (Buller 1888), while the Saddleback, consistent with its smaller size, takes a greater diversity of smaller, more abundant prey (Atkinson & Campbell 1966). As the Saddleback is able to exploit a greater diversity and abundance of invertebrate prey than the Huia, it would be expected to experience less intersexual competition for food. Indirect support for this hypothesis is provided by Schoener (1964) who found that variation in bill form among sympatric avian congeners tended to be greater in larger-bodied genera, presumably because these tend to feed on larger, less abundant food particles.

The bill dimorphism of the Huia is consistent with a further prediction derived from the NSH. Selander (1966) argued that sexual differences in foraging-related morphology should be more pronounced in species (or populations) that are isolated from competitors as these should have a greater range of alternative foraging modes potentially available to each sex. The Woodpeckers (Piciformes) are absent from New Zealand, the wood-probing/excavating guild having been comprised of only three-species, the Huia, the considerably smaller Saddleback, and the Kaka (*Nestor meridionalis*), an endemic parrot (it is notable that the latter also displays an unusual degree of sexual dimorphism in bill size [Moorhouse *et al.* unpubl.). The Saddleback and Kaka forage for invertebrates primarily by chiselling and prying, as did the male Huia (Buller 1888, Burton 1974, Beggs and Wilson 1987). The female Huia was, therefore, the only specialist wood-prober in the New Zealand avifauna.

CONCLUSIONS

Although in the absence of rigorous phylogeny and evolutionary chronology the results are not conclusive, they indicate that the most parsimonious explanation for the remarkable sexual bill dimorphism of the Huia, and more specifically the divergent bill of the female, is that this was an adaptation to reduce intersexual competition. In contrast to sexual selection, the Niche Separation Hypothesis is consistent with the Huia's pronounced sexual differences in foraging behaviour, its monogamous mating system, and the absence of other specialist wood-probers in New Zealand's avifauna. In view of the greater explanatory power of the NSH in this case, and evidence of greater female divergence in foraging-related anatomy in other species, dismissal of intersexual competition as a causal factor in the evolution of sexual dimorphism is clearly unjustified.

ACKNOWLEDGEMENTS

LITERATURE CITED

AMADON, D. 1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Am. Mus. Nat. Hist. 95: 151-262.

AMADON, D. 1953. Avian systematics and evolution in the Gulf of Guinea: the J. G. Correia collection. Bull. Am. Mus. Nat. Hist. 100: 393-452.

AMADON, D. 1959. The significance of sexual differences in size among birds. Proc. Am. Phil. Soc. 103: 531-536.

ATKINSON, I. A. E.; CAMPBELL, D. J. 1966. Habitat factors affecting Saddlebacks on Hen Island. Proc. N. Z. Ecol. Soc. 13: 35-40.

BEGGS, J. R., WILSON, P. R. 1987. Energetics of South Island Kaka (*Nestor meridionalis meridionalis*) feeding on the larvae of Kanuka Longhorn Beetles (*Ochrocydus huttoni*). N. Z. J. Ecol. 10: 143-147.

BJÖRKLUND, M. 1991. Evolution, phylogeny, sexual dimorphism and mating system in the grackles (*Quiscalus* spp: Icterinae). Evolution 45: 608-621.

BRODKOB, P. 1971. Origin and evolution of birds. Pp. 20-55 *in* Farner D.S.; King J. R. (eds) Avian Biology. Vol. I. Academic Press, New York.

BULLER, W. L. 1877. Further descriptive notes of the Huia (*Heteralocha acutirostris*). Trans. Proc. N. Z. Inst. 10: 211.

BULLER, W. L. 1888. A history of the birds of New Zealand. The author, London.

BULLER, W. L. 1892. Further notes on the birds of New Zealand. Trans. Proc. N. Z. Inst. 25: 63-68.

BURTON, P. J. K. 1974. Anatomy of the head and neck in the Huia (*Heteralocha acutirostris*) with comparative notes on other Callaeidae. Bull. Brit. Mus. Nat. Hist. 27: 148.

COLENSO, W. 1887. A description of the curiouslydeformed bill of a Huia (*Heteralocha acutirostris*, Gould) an endemic New Zealand bird. Trans. Proc. N.Z. Inst. 19: 140-145.

DARWIN, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

EBENMAN, B. 1986. Sexual size dimorphism in the Great Tit *Parus major* in relation to the number of coexisting congeners. Oikos 47: 355-359.

FALLA, R. A.; SIBSON, R. B.; TURBOTT, E. G. 1979. The new guide to the birds of New Zealand. Collins, Auckland.

FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon Press, Oxford.

GAUTHREAUX, S. A. Jr. 1978. The ecological significance of behavioural dominance. Pp. 17-54 *in* Bateson, P. P. G.; Klopfer, P. H. (eds) Perspectives in ethology. Vol. 3. Plenum Press, New York.

GOSLER, A. G.; CARRUTHERS, T. D. 1994. Bill size and niche breadth in the Irish Coal Tit *Parus ater hibernicus*. J. Avian Biol. 25: 171-177.

HAY, J. R.; BEST, H. A.; POWLESLAND, R. G. 1985. Kokako. John McIndoe and the New Zealand Wildlife Service, Dunedin, New Zealand.

HÖGLUND, J.; SILLÉN-TULLBERG, B. 1994. Does lekking promote the evolution of male biased size dimorphism in birds? On the use of comparative approaches. Am. Nat. 144: 881-889.

HOGSTAD, O. 1976. Sexual dimorphism and divergence in winter foraging of Three- toed Woodpeckers *Picoides tridactylus*. Ibis 118: 41-50.

HOGSTAD, O. 1991. The effect of social dominance on foraging by the Three-toed Woodpecker *Picoides tridactylus*. Ibis 133: 271-276.

HUXLEY, J. 1938. The present standing of the theory of sexual selection. Pp. 11-42 in de Beer, G. R., (ed.) Evolution. Clarendon Press, Oxford.

JAMIESON, I. G.; SPENCER, H. G. 1996. The Huia's bill and foraging behaviour: were they unique? Notornis 42: 14-18.

JEHL, J. R. Jr; MURRAY, B. G. Jr. 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. Current Ornithol. 3: 1-76.

JENKINS, P. F. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. Anim. Behav. 26: 50-78.

JENKINS, P. F.; VEITCH, C. R. 1991. Sexual dimorphism and age determination in the North Island Saddleback (Philesturnus carunculatus rufusater). N. Z. J. Zool. 18: 445-450.

JENNI, D. A. 1974. The evolution of polyandry in birds. Am. Zool. 14: 129-144.

LIGON, J. D.; LIGON, S. H. 1979. The communal social system of the Green Woodhoopoe in Kenya. Living Bird 17: 159-197.

MAYNARD-SMITH, J. 1978. The evolution of sex. Cambridge University Press, Cambridge, U.K.

MØLLER, A. P. 1993. Sexual selection in the barn swallow Hirundo rustica. III. Female tail-ornaments. Evolution 47: 417-431.

MORSE, D. H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108: 818-830.

MURRAY, B. G. Jr. 1984. A demographic theory on the evolution of mating systems as exemplified by birds. Pp 71-140 in Hecht, M.; Wallace, B. and Prance, G. (eds) Evolutionary Biology. Vol. 18. Plenum Press, New York.

NOSKE, R. A. 1986. Intersexual niche segregation among three bark-foraging birds of eucalypt forests. Aust. J. Ecol. 11: 255-267.

OAKES, E. J. 1992. Lekking and the evolution of sexual dimorphism in birds:comparative approaches. Am. Nat. 140: 665-684.

OLIVER, W. R. B. 1974. New Zealand Birds. A. H. and A. W. Reed. Wellington.

ORING, L. W. 1982. Avian mating systems. Pp. 1-92 in Farner, D. S.; King, J. R.; Parkes, K. C. (eds) Avian Biology. Vol. VI. Academic Press, New York.

PAYNE, R. B. 1984. Sexual selection, lek and arena behaviour, and sexual size dimorphism in birds. Am. Ornithol. Union, Ornithol. Monogr. No. 33.

PETERS, W. D.; GRUBB, T. C. Jr. 1983. An experimental analysis of sex specific foraging in the Downy Woodpecker, Picoides pubescens. Ecology 64: 1437- 1443.

PHILLIPPS, W. J. 1963. The book of the Huia. Whitcombe and Tombs Ltd, Auckland.

POTTS, T. H. 1885. Oology of New Zealand. N. Z. J. Sci. 2: 373-484.

POWER, H.W. 1980. The foraging behaviour of Mountain Bluebirds, with emphasis on sexual foraging differences. Am. Ornithol. Union, Ornithol. Monogr. No. 28.

POWLESLAND, R. G. 1987. The foods, foraging behaviour and habitat use of the North Island Kokako in Puketi State Forest, Northland. N. Z. J. Ecol. 10: 117- 128.

RALLS, K. 1976. Mammals in which females are larger than males. Quart. Rev. Biol. 51: 245-276.

RAND, A. L. 1952. Secondary sexual characteristics and ecological competition. Fieldiana-Zoology 34: 65-70.

SCHOENER, T. W. 1964. The evolution of bill size differences among sympatriccongeneric species of birds. Evolution 19: 189-213.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilisation in birds. Condor 68: 113-151.

SELANDER, R. K. 1972. Sexual selection and dimorphism in birds. Pp. 180-230 in Campbell, B. (ed.) Sexual selection and the descent of man 1871-1971. Aldine, Chicago.

SHINE, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64: 419-461.

SIBLEY, C. G.; AHLQUIST, J. E. 1990. Phylogeny and classification of birds: a study in molecular evolution. Yale University Press, New Haven, Conn.

SLATKIN, M. 1984. Ecological causes of sexual dimorphism. Evolution 38: 622-630.

STEVENS, G. R. 1991. Geological evolution and biotic links in the Mesozoic and cenozoic of the Southwest Pacific. Acta XX Cong. Int. Ornithol. 1: 361-382.

STORER, R. 1971. Adaptive radiation in birds. Pp. 149-188 in Farner, D. S.; King, J. R. (eds) Avian Biology. Vol. I. Academic Press, New York.

SUHONEN, J.; KUITUNEN, M. 1991. Intersexual foraging niche differentiation within the breeding pair in the Common Treecreeper Certhia familiaris. Ornis Scand. 22: 313-318.

TRIVERS, 1972. Parental investment and sexual selection. Pp. 136-179 in Campbell, B. (ed.) Sexual selection and the descent of man 1871-1971. Aldine, Chicago.

TURELLI, M.; GILLESPIE, J. H.; LANDE, R. 1988. Rate tests for selection on quantitative characters during macroevolution and microevolution. Evolution 42: 1085-1089.

WALLACE, R. A. 1974. Ecological and social implications of sexual dimorphism in five melanerpine
      Woodpeckers. Condor 76: 238-248.
WILLIAMS, G. R. 1976. The New Zealand Wattlebirds (Callaeatidae). Proc. 16th Int. Ornithol. Cong.: 161-179.