

The scaling and selection of sexually dimorphic characters: an example using the Marbled Teal

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Current theory and empirical evidence suggests that, if a character is sexually dimorphic as a result of sexual selection, it should be positively allometric (i.e. relatively larger in larger individuals), whereas if the dimorphism is the result of natural selection (e.g. niche divergence), it should be isometric. I show how this can be used to study the selective forces responsible for dimorphic morphological characters, using the monochromatic Marbled Teal *Marmaronetta angustirostris* as an example. In absolute terms, first-year male teals have a higher body mass, wing length, head length and bill length than females. In relative terms (controlling for body size), males still have longer wings, heads and bills. The scaling in Marbled Teal suggests that bill and head dimorphisms are due to sexual selection, whereas wing dimorphism is due to natural selection. Tail length is sexually monomorphic but positively allometric, possibly because of a display function. Such scaling studies are easy to carry out, and provide a useful complement to direct investigation of the influence of variation in the size of dimorphic characters on mating success, foraging efficiency etc.

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Sexual dimorphism in avian morphology can evolve by either sexual or natural selection, and it is generally not self-evident which is responsible (Sigurjónsdóttir 1981, Livezey and Humphrey 1984, Nudds and Kaminski 1984, Price 1984, Shine 1989, Savalli 1995, Craig and Villet 1998). Good morphometric data are available for many species (e.g. for ducks, Cramp and Simmons 1977, Owen and Montgomery 1978, Livezey and Humphrey 1984, Fox et al. 1992, Livezey 1993), yet there are relatively few studies testing the importance of dimorphic characters for e.g. mating success or intersexual niche separation (Nudds and Kaminski 1984, Holmberg et al. 1989, Sorenson and Derrickson 1994). Thus for the great majority of bird species, no direct evidence is available to identify the selective forces responsible for dimorphic characters. However, in this paper I illustrate how morphometric data can be used to study differences in the “scaling” or “allometry” of characters (i.e. the change in their relative size in larger birds) in bird populations, which provides valuable indirect evidence of the selective forces underlying dimorphism.

The scaling of bird morphology has attracted considerable attention at inter- and intra-specific levels (Prange et al. 1979, Peters 1983, Boag 1984, Calder 1984, Schmidt-Nielsen 1984, Livezey and Humphrey 1986, Rayner 1988, Harvey and Krebs 1990, Livezey 1990, Björklund 1994), and mechanical, developmental and other explanations have been sought for the patterns observed. However, little attention has been paid to the use of intraspecific scaling in mature individuals (“static allometry”) in explaining sexual dimorphism in birds. If sexual selection acts to exaggerate a character, current theory and empirical evidence suggests it should be positively allometric (i.e. relatively larger in larger birds). Furthermore, if sexual selection on a character acts more strongly on one sex, leading to dimorphism, the allometry should be more positive in that sex (Emerson and Voris 1992, Petrie 1992, Simmons and Scheepers 1996, Simmons and Tomkins 1996). In contrast, if natural selection (i.e. niche divergence) is responsible for the observed sexual dimorphism, no such positive allometry or sexual difference in scaling is expected.

In this paper I address dimorphism in relative character size, but not dimorphism in body size *per se* (Ranta et al. 1994). With standard morphometric data, the scaling of each character can be compared within and between sexes, and this allows us to identify which characters are likely to be sexually selected, and which are likely to be naturally selected. These hypotheses can then be tested by field or laboratory experiments. For example, the importance of positively allometric characters in mate choice can be tested by manipulative experiments (e.g. Møller 1990, Jones and Hunter 1993).

I illustrate this technique using the Marbled Teal *Marmaronetta angustirostris*, which is highly unusual amongst northern hemisphere members of the subfamily Anatinae (*sensu* Livezey 1986, 1997) in lacking overt sexual differences in plumage (i.e. it is almost monochromatic, Cramp and Simmons 1977, Livezey 1996). This work constitutes the first detailed study of sexual dimorphism in this globally threatened (Collar et al. 1994) species. Firstly, I ask what differences exist between the sexes of Marbled Teal in standard morphometric measures. Secondly, I consider which of these differences persist when taking into account the difference in overall size between sexes (e.g. do males have longer bills simply because males are bigger, or are their bills relatively longer for a given size?). After identifying the scaling of characters in each sex, I then compare the nature of the sexual dimorphism observed for a given character with the sexual difference in its scaling, to determine the likely nature of evolutionary forces leading to the observed sexual dimorphism.

Methods

Marbled Teal become sexually mature in their first year (Cramp and Simmons 1977). The Marbled Teal studied ($N = 56$) were all recently fledged birds measured on 10 September 1996. They were birds rescued in 1996 from a concrete-lined canal in Alicante, Spain within two weeks of hatching (Navarro et al. 1995) then reared in captivity at the Centre for Nature Protection and Study in Valencia. They were released into the wild shortly after measuring.

Birds were sexed by cloacal inspection and weighed to the nearest gram on an electronic balance. Measurements used were folded wing length (distance from carpal joint to the tip of the longest primary), tarsal length (from the middle point of the joint between tibia and tarsometatarsus behind to the middle point of the joint between tarsometatarsus and middle toe), maximum head length, bill length (culmen) and maximum tail length. Folded wing and tail length were measured to the nearest mm with a ruler. Maximum head length, bill and tarsus were measured to the nearest 0.1 mm with digital calipers. Cranium length (excluding bill length)

was also estimated by subtracting bill length from maximum head length.

Statistical analyses

Absolute sexual dimorphism (not accounting for body size) was studied with two sample t-tests using Levene's test to confirm homogeneity of variances.

Sexual dimorphism controlling for size was analysed via generalized linear models using GLIM software (Crawley 1993), including sex (factor) and body mass or wing length (continuous variable as an index of size) as predictor variables and with a morphometric dependent variable. A normal error and identity link functions were used in the GLIM models, and all morphometric variables were \log_e transformed. The significance of the sexual difference in the slope between Y and \log mass or \log wing was tested by adding an interaction term between sex and the linear predictor. Wing length was chosen as a linear measure of size to accompany body mass since wing length is the best linear predictor of avian size, at least in passerines (Gosler et al. 1998). Furthermore, although wing length can be confounded by age or date (Owen and Montgomery 1978, Ormerod and Tyler 1990), this was not the case in this study.

The allometric slopes of each character in relation to body mass were calculated using reduced major axis (RMA) models to place the line of best fit in bivariate plots of \log_e transformed data. The results of ordinary least squares regression (OLS) and RMA regressions are increasingly divergent as r decreases, and slopes become seriously underestimated by OLS methods. RMA is the recommended regression method for scaling studies, particularly where there is no information about error variances, and X and Y variables have different units such as length and mass (Ricker 1984, Rayner 1985, McArdle 1988, Pagel and Harvey 1988, LaBarbera 1989, Sokal and Rohlf 1995, but see Jolicoeur 1990). The RMA slope is equal to the ratio between the standard deviations of Y and X (and also to the OLS slope divided by r). See McArdle (1988) for methods used to calculate the statistical significance of the deviation between observed RMA slopes and those expected under the null hypothesis of isometry (for the purpose of this paper, I consider isometry to be where, in log-log bivariate plots, linear measures scale with a slope of one with each other, and with a slope of one third against body mass).

In studies where it is possible to take morphometric measures of a large number of characters (e.g. in skeletal studies), it can be appropriate to use PC-1 from a principal component analysis of a character set as an indicator of body size, then use RMA to study the scaling of other characters of interest against PC-1 (see e.g. Livezey and Humphrey 1986).

Table 1. Difference in mean measurements in male and female Marbled Teal, tested with two sample t-tests. Mass is in g, other measures are in mm. ** P < 0.01, *** P < 0.001.

Measure	Males (N = 26)		Females (N = 30)		t ₅₄
	Mean	S.D.	Mean	S.D.	
Mass	410.1	28.9	386.4	32.0	2.90**
Wing	202.9	5.2	198.0	4.0	3.99***
Tarsus	38.0	1.3	37.4	1.1	1.96
Tail	61.4 ¹	2.2	62.2	2.5	1.37
Head	96.5	3.5	90.8	2.8	6.75***
Bill	45.4	1.6	43.6	1.3	4.71***
Cranium	51.1	2.9	47.2	2.3	5.66***

¹ N = 24.

Results

Absolute dimorphism

Male Marbled Teal were heavier, and had longer wings, heads, bills and craniums (Table 1) than females. No significant difference was observed between sexes in tarsus or tail length.

Relative dimorphism controlling for size

When controlling for body mass, males had significantly longer wings, heads, bills and craniums than females, whereas there was no significant difference in tail or tarsus length (Table 2). When controlling statistically for wing length as an alternative index of overall size, males still had significantly longer heads, bills and craniums, whereas females had significantly longer tails (Table 2). Partial correlation coefficients (controlling for sex) with body mass were statistically significant for all measures except for tarsus and tail length. Similarly, correlations with wing were significant except for bill length (Table 2).

Table 2. Multiple regression of morphometric measurements in Marbled Teal, using identity link function and normal error distribution in GLIM.

Y	Mass	Wing	Sex	F _{2,53}	r ²
Wing	4.87*	–	(–)8.87**	10.7***	0.288
Tarsus	2.16	–	(–)1.69	3.03	0.164
	–	16.7***	0.00	10.8***	0.290
Tail	1.37	–	(+)1.69	1.59	0.059
	–	11.7**	(+)10.2**	6.92**	0.214
Head	15.6***	–	(–)32.3***	37.2***	0.584
	–	6.22*	(–)26.0***	28.5***	0.518
Bill	10.0**	–	(–)12.5***	17.8***	0.402
	–	1.83	(–)12.4***	12.0***	0.312
Cranium	8.14**	–	(–)21.1***	22.4***	0.459
	–	4.90*	(–)17.3***	19.9***	0.428

The Y variable and the predictors Mass and Wing are log_e transformed. F-values are presented for the partial effects of sex (factor of two levels) and body mass or wing. F_{2,53} and r² refer to the whole regression. (+) represents cases where the fitted value of the dependent variable was higher for females whilst controlling for Mass or Wing, and vice versa. ** P < 0.01, *** P < 0.001. N = 56 except for log Tail (N = 54). The effect of an added interaction term (Sex × Mass or Sex × Wing) was not significant with the exception of Y = Bill, for which Sex × Mass had a significant effect (F_{1,52} = 4.74, P < 0.05).

Table 3. Scaling of Marbled Teal linear morphometric measures against body mass, by sex.

Measure	Males (N = 26)		Females (N = 30)	
	RMA slope	r	RMA slope	r
Wing	0.371	0.337	0.242	0.260
Tarsus	0.483	0.365	0.361	0.066
Tail ¹	0.580*	0.376	0.482	0.047
Head	0.507*	0.434	0.368	0.522
Bill	0.489*	0.619	0.352	0.225

¹ for males, N = 24. Both body mass and the linear measure were log_e transformed. The deviation of the RMA slope from that expected under isometry (1/3) was tested for statistical significance. * P < 0.05.

Scaling

When related to body mass, wing and tarsus length did not deviate significantly from isometry for either sex (Table 3). For males, tail length, head length and bill length were all positively allometric (Table 3). For females, no character deviated significantly from isometry (Table 3). For all characters, the allometric slope was more positive for males than for females (Table 3, Fig. 1). However, differences in slopes between sexes were only significant in the case of bill length (Table 2, Fig. 1).

Discussion

Empirical evidence in integrated studies of insects, amphibians and mammals so far supports the hypothesis that sexually selected characters are positively allometric whereas naturally selected characters tend to be isometric (Emerson and Voris 1992, Green 1992, Petrie 1992, Simmons and Scheepers 1996, Simmons and Tomkins 1996). However, there have been almost no tests of this hypothesis in birds. The frontal shield of

the Moorhen *Gallinula chloropus* is positively allometric, apparently because of its importance in defence of breeding territories (Petrie 1988). In steamer-ducks (*Tachyeres*), wings are used in male-male combat and, compared with other skeletal characters, wing bones are positively allometric in males but not in females (Livezey and Humphrey 1984, 1986). There is evidence that extreme sexual tail dimorphism in some species of widows and bishops *Euplectes* is a result of sexual selection, and positive allometry of male tails has been shown at the interspecific level (Savalli 1995, but see Craig and Villet 1998).

If the increased expression of a character is sexually selected, the character is predicted to be positively allometric, essentially owing to the relatively greater benefits obtainable for a larger individual from making a given investment in a character (Green 1992, Petrie 1992). There are several reasons why these benefits may increase in larger individuals, although no empirical studies have so far distinguished between them. One possible explanation on the basis of age (that larger animals are older and therefore invest relatively more in reproduction since their life expectancy is lower) is excluded from the current study because there was no age variation in the sample of Marbled Teal. If sexual selection acts more strongly in one sex than the other, as is usually the case, the character should be both relatively larger and more positively allometric in that sex. In theory, mate choice could alternatively select for reduced character size, although no such cases have been documented (see Andersson 1994 for review). In the sex in which smaller characters were sexually selected, the character would be expected to be both relatively smaller and negatively allometric in that sex.

On the other hand, where natural selection leads to dimorphism in a character, there is much less reason to

expect positive allometry and a sexual difference in allometric slopes (although these are possible under some theoretical conditions: see Green 1992). Thus, the scaling relationships of the characters concerned provide a potential means to distinguish between sexual and natural selection as causes of dimorphism.

This is the first avian study to explicitly compare the sexual dimorphism in a set of morphometric characters with the scaling of those same characters at an intraspecific level, in order to investigate the likely causes of dimorphism. First year male Marbled Teal are significantly larger than females in most absolute morphometric measurements, with the exception of tarsus and tail length. Similar results have been obtained for sexual dimorphism in both first year and older Marbled Teal at Slimbridge, UK (A. Chisholm unpubl. data), with the additional finding that males have a greater absolute bill height (at the front edge of the nostrils). This apparent sexual dimorphism is not merely a consequence of differences in overall size between the sexes: for a given size, males have longer wings, heads and bills. It is not just the culmen which is relatively longer in males, but the cranium itself. For a given wing length, females have relatively longer tails, although this appears to reflect their shorter wings.

The evidence from scaling suggests that sexual selection is the main cause of sexual dimorphism in bill and head morphometry in the Marbled Teal. Heads and bills are positively allometric in males but isometric in females, the sexual difference in allometric slope being statistically significant for bill length. Wings are dimorphic, but are isometric in both sexes, suggesting that natural selection is responsible for the sexual difference in wing morphology. Tarsus length is sexually monomorphic and isometric. Tail length is sexually monomorphic, but tails are positively allometric in both sexes (although significantly so only in males). It is possible that tail length is sexually selected in both sexes (see Jones and Hunter 1993).

Sexual dimorphism in mass, wing length and bill and head length such as that observed in Marbled Teal is typical of that observed in other Anatinae species (Cramp and Simmons 1977, Livezey 1990, 1993, Fox et al. 1992) and suggests that, whereas the Marbled Teal is unusual amongst northern hemisphere Anatinae in its monochromatism, there is nothing particularly unique about the dimorphism in its morphometrics. Although males may make a limited contribution to brood rearing (Green 1997), Marbled Teal show the serial monogamy and much greater reproductive investment of females that is common to the Anatinae (Batt et al. 1992, Green 1998). Little previous attempt has been made to investigate the causes of sexual dimorphism in Anatinae. Nudds and Kaminski (1984) suggested that bill dimorphism is selected by natural selection (reduced intersexual competition for food) based on divergent distributions of bill length in each sex. Sorenson and

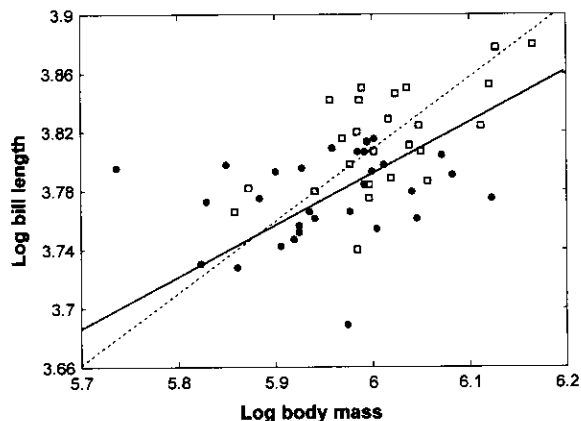


Fig. 1. Scaling of bill length against body mass in Marbled Teal. Lines are plotted by reduced major axis (males: $y = 0.873 + 0.489x$; females: $y = 1.682 + 0.352x$). ---□---, males; —●—, females.

Derrickson (1994) found no evidence that the larger tails of male Northern Pintail *Anas acuta* confer a mating advantage.

So far there is little evidence available from field studies to assess the contribution of sexual or natural selection to the sexual dimorphism observed in Marbled Teal. Males display their heads repeatedly to females during group courtship (Cramp and Simmons 1977, Green in press), and larger heads and bills may confer an advantage through female choice or male-male competition. This is supported by the sexual differences in plumage, which are most pronounced in the greater development of a crest on the nape and forehead of the male, whilst bill coloration differs between sexes (Navarro and Robledano 1995, Green in press). Wings are not displayed overtly when Marbled Teal court on the water, and it seems less likely that they are sexually selected, although some courtship occasionally appears to occur on the wing (Navarro and Robledano 1995). Wing size can also be dimorphic to provide aerodynamic compensation for exaggerated, sexually selected characters such as tails (Andersson and Andersson 1994), but tail length is not exaggerated in Marbled Teal compared with other Anatinae (Cramp and Simmons 1977). Tails are always visible during Marbled Teal courtship (Johnsgard 1965) and, on the water, Marbled Teal always hold their tails well above the horizontal in full view to conspecifics (pers. obs.).

Sexual selection thus offers the most likely explanation for the bill and head dimorphism observed in Marbled Teal, and alternatives based on natural selection are not supported by scaling. Scaling suggests that natural selection is more likely to explain the observed wing dimorphism (e.g. via sexual differences in migration strategies, Carbone and Owen 1995). However, further research is required to confirm the hypotheses made on the basis of such scaling studies.

Scaling studies such as the one conducted here are easy to carry out, often with pre-existing data, and provide a useful complement to direct investigation of the influence of variation in the size of dimorphic characters on mating success, foraging efficiency etc. For example, they could be used *a priori* to identify characters most worthy of manipulation in mate choice experiments. In order to clarify the relationships between scaling and sexual selection in birds, it would be enlightening to carry out studies similar to this one of sexual differences in scaling in bird species in which the significance of dimorphic characters for mating success has been studied in more detail (e.g. Møller 1990, Jones and Hunter 1993).

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