

Ornament and body size variation and their measurement in natural populations

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Measurement of intrapopulation variation in secondary sexual traits is a priority in the testing of sexual selection models. However, it is important to take care in the choice of materials and delimitation of populations. The use of museum skins to study variation in male tail ornaments may substantially underrepresent the real degree of intrapopulation variation. Data from live animals in specific areas provide more realistic estimates, and should be used whenever possible. I use as an example field data on male ornament length and body size in *Vidua macroura* (Aves: Ploceidae), a promiscuous, parasitic African finch with elongated tail plumes. Individual males differ in the timing and rate of ornament growth, and females are therefore faced with a large degree of phenotypic variation in male ornament size, even though genetic variation may not be great. By correcting for seasonal variation in the ornament lengths of males caught at different times, I show that mid-season coefficients of variation in ornament length of breeding males in two populations are as high as 18% and 55%. By contrast, tarsus, wing and unornamented tail lengths of the same males vary from 2 to 4%.

KEY WORDS: Ornaments – sexual selection – morphological variation – mate choice – viability indicators – plumage growth – *Vidua macroura*.

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INTRODUCTION

In order for male sexual ornaments to be elaborated through the action of female choice, substantial and discernible variation in the ornament must exist (or have existed) within natural populations. Intersexual selection on ornaments

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may have the effect of reducing genetic variation in a population over many generations (Fisher, 1958; Lande, 1977; Cade, 1984), until variation in the ornament is similar to that in naturally selected morphological traits such as limb measurements (Alatalo, Höglund & Lundberg, 1988a). However, some phenotypic variation in ornament size may be preserved if optimal sizes for individual males depend on their body condition (Andersson, 1982a, 1986), or if ornament size increases with age (Smith, 1965, 1982) or body size (Alatalo *et al.*, 1988a; cf. Møller & Erritzøe, 1988). There may also be variation due to factors such as differential rates of ornament growth and wear.

Alatalo *et al.* (1988a) and Craig (1989) recently examined museum specimens of seven species of long-tailed birds as an important first step towards describing natural variation in ornament size, both between and within populations. Alatalo *et al.*'s primary aim was to establish whether variation *between* populations is sufficient to promote speciation, as predicted by polygenic models of sexual selection (e.g. Lande, 1981). However, it is also important to quantify the degree of *within*-population variation in ornament size, since females must be able to perceive differences between prospective mates in order to use their ornaments as mate choice cues (e.g. Andersson, 1982b; Lambert, Kingett & Slooten, 1982; Møller, 1988).

The contributions of Alatalo *et al.* (1988a) and Craig (1989) to the subject of variation in sexual traits are valuable, and hopefully their examples will promote further empirical work. However, there may be two problems with their approach, which future studies should consider. This short paper addresses these problems: (a) the selection of fresh museum material and (b) the grouping of specimens from broad regions as single populations. I also show that individual males differ in the timing and rate of ornament growth, and that on any given day females are thus exposed to substantial phenotypic variation. While it is unlikely that these factors affect the conclusions of Alatalo *et al.* and Craig, museum surveys can seriously underestimate the degree of within-population variation in sexual characters. As an alternative, field measurements of live animals from specific localities should be used whenever possible. While more labour-intensive and generally yielding smaller samples, field measurement is superior for making biologically meaningful estimates of the variation in ornament size that females actually encounter. The reasons for this are discussed below.

I give an example of field measurements from a preliminary survey of morphological variation in males of a species analysed by Alatalo *et al.* (1988a), the pintailed whydah *Vidua macroura* (Aves: Ploceidae). I then describe variation in the timing and rate of growth of the ornamental plumes in individual males, suggest a corrective method for standardizing the length of ornaments measured at different times in the breeding season (suitable for annually regenerating traits such as breeding plumes in birds), and discuss other potential methodological problems. The pintailed whydah is a promiscuous, brood-parasitic African finch with dispersed, traditional 'call-sites' controlled by breeding males (see Shaw, 1984; Payne, 1985a; Barnard, 1989). These call-sites are visited by females and other males. Payne (1984, 1985a) referred to this mating system as a 'dispersed lek'. This species has four slim, tapered ornamental tail feathers approximately four to five times the unadorned tail length.

RATIONALE AND METHODS

Trapping and measurement methods

Data on body size and ornament length of male pintailed whydahs were collected during capture of adults for colour marking. Data from only 20 colour-ringed males are available, since other analyses (e.g. Barnard, 1989; Barnard & Markus, 1989) required intensive study of a small number of individually known males. Although future field samples should ideally be larger, sample size is limited naturally by intrinsic population size. This should not be seen as a weakness, since individual females in free-living populations have only a limited population of males from which to choose.

Two discrete populations were studied. The first inhabited a semi-arid, subtropical region of *Acacia* savanna and open floodplain in the central Transvaal Province, South Africa (24°32'-55'S; 28°40'-58'E), in sympatry with two congeners, *Vidua regia* and *V. paradisaea*. The second, allopatric population inhabited a moist, temperate coastal plain in the southern Cape Province, South Africa (34°00'-01'S; 22°35'-48'E). The study areas and their populations were described in detail by Barnard (1989). Males were trapped at call-sites (in the case of territorial and intruding males) and at water sources (in the case of one male in post-nuptial moult), using mistnets and seed-baited traps. Trapping was undertaken from September to December in the Cape, and December to March in the Transvaal, covering the entire breeding season. The Cape data illustrate the period of ornament acquisition, and the Transvaal data, ornament abrasion. Biometric data for adult females were used for calculation of sexual size dimorphism; only 21 females (sexed by dissection or observed copulatory behaviour) were used. For all birds the following measurement techniques were used: *mass*—with a Pesola spring balance to the nearest 0.1 g; *wing* (flattened chord), *short tail* (excluding ornament), *tail ornament* (see below), *tarsus* and *culmen* measurements—all with ruler, to the nearest 0.5 mm.

Tail length correction methods

While many models of female choice assume that females can perceive (and choose on the basis of) a male's maximum tail length, reflecting his genotype, this hypothetical maximum is rarely if ever expressed phenotypically. Within a population, whydah males differ in the timing and rate of ornament growth, and the maximum length a male achieves in a season may be influenced by factors such as feather abrasion, age (Smith, 1965, 1982), and body condition (Andersson, 1982a). Some males start to grow ornaments much earlier than others (Fig. 1A). On any given day, therefore, a female looking for a mate will actually see a range of ornament lengths, even among territorial males.

To overcome these problems, I corrected my field data on ornament length by standardizing them to a set date, using ornament growth rates of three multiply trapped males (Fig. 2). The standard date chosen (1 November for the temperate area; 1 December for the subtropical area) was an arbitrary, mid-season date designed to represent the time when females are busy mating. For

this reason the corrected ornament lengths for the two areas cannot be directly compared. The ornament lengths of the three retrapped males were corrected using their own growth rates, and those of 16 other males using an average rate.

RESULTS

Timing and rate of ornament growth

Pintailed whydah males differ in the timing and rate of ornament growth, so that at any one time there is a range of tail lengths 'available' to prospective females. There is substantial variation in tail length during both the early-to-middle breeding season (Fig. 1A) and the middle-to-late breeding season (Fig. 1B). In both study areas, males defending call-sites acquire ornaments earlier than non-territorial floaters. However, even among territorial males there is marked variation. This is reduced late in the breeding season, when late-developing males have 'caught up' with early ones and feather abrasion reduces effective ornament length (cf. Fig. 1B, 2C).

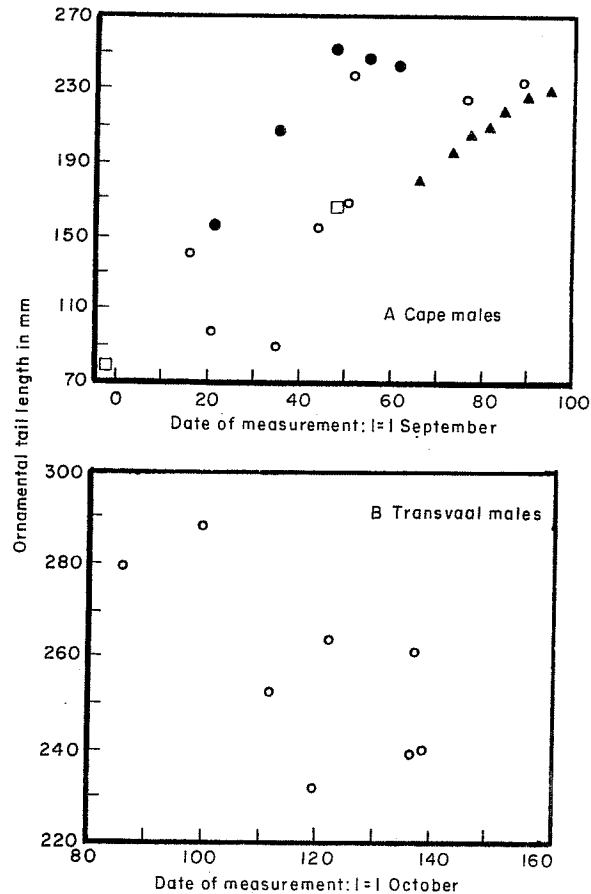


Figure 1. Seasonal distribution of uncorrected ornamental tail lengths of male *Vidua macroura* in A, the Cape and B, Transvaal study areas. ▲, 'Wilderness' male; □, 'Hartley' male; ●, 'uJobela' male; ○, all other (single trapped) males. Units on the x-axis are days.

Data on the rate of ornament growth are available from three territorial males trapped two or more times. The 'Wilderness' male's tail plumes grew at the rate of 1.81 mm day^{-1} (Fig. 2A); the 'Hartley' male, caught only twice, averaged 1.74 mm day^{-1} (Fig. 2B), and the intensively studied 'uJobela' male averaged 3.77 mm day^{-1} during the growth period, with a subsequent phase of feather abrasion (Fig. 2C). All males held call-sites in rural gardens supplied *ad libitum*

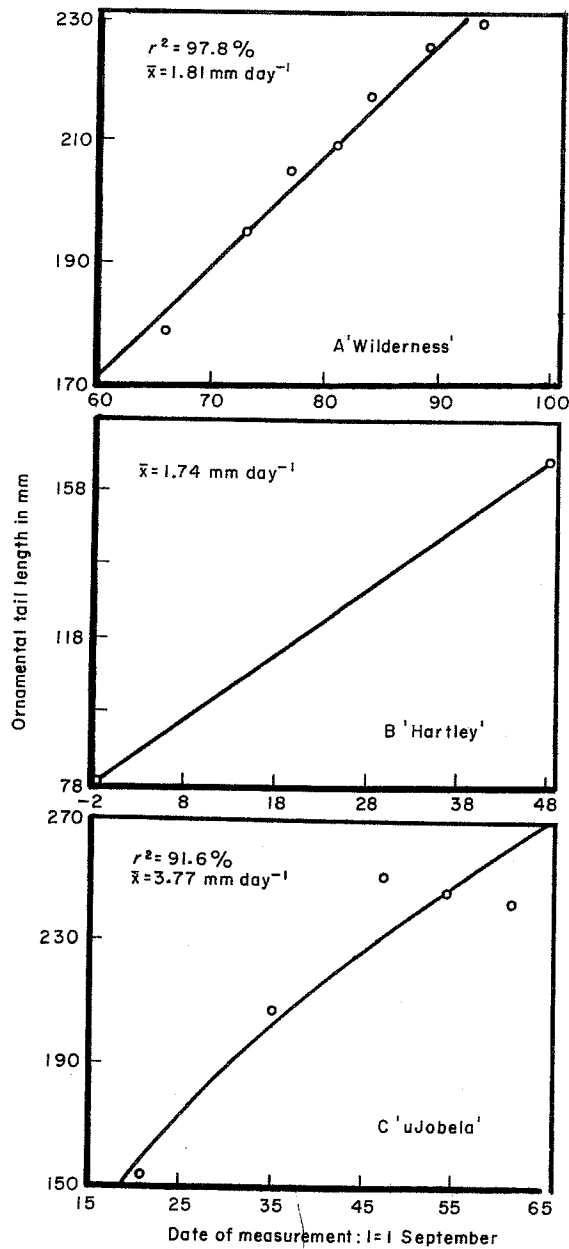


Figure 2. Rates of ornamental tail growth of three male *Vidua macroura* in the Cape Province with *ad libitum* food supplies: A, 'Wilderness', B, 'Hartley', C, 'uJobela'. Units on the x-axis are days.

TABLE 1. Summary statistics of male body size, corrected ornamental tail length, and sexual dimorphism of live *Vidua macroura* in two populations in South Africa, 1984–1986. *P*-values refer to two-sample *t*-tests

	Body size characters (mm)						Tail ornament length (mm) ^a	Maximum mass (g)
	Culmen length	Culmen width	Culmen depth	Tarsus length	Wing length	Short tail		
<i>Southern Cape Province</i>								
Mean	9.14	4.94	7.17	16.59	72.91	52.41	202.09	15.89
1 s.d.	0.45	0.30	0.66	0.49	1.51	1.64	34.79	0.76
Minimum	8.5	4.5	6.5	16.0	71.0	50.0	155.0	14.8
Maximum	10.0	5.5	8.5	17.5	76.0	55.0	263.0	16.7
<i>N</i>	11	9	9	11	11	11	11	9
Dimorphism ^b	1.02	1.08	1.04	1.04	1.06	1.07	4.13	1.07
<i>Central Transvaal Province</i>								
Mean	10.06	6.00	8.06	16.94	75.25	52.88	117.13	15.07
1 s.d.	0.58	0.87	0.50	0.63	2.38	1.93	62.81	1.27
Minimum	9.5	5.0	7.5	15.5	72.0	51.0	52.0	13.8
Maximum	11.0	7.5	9.0	17.5	79.0	55.5	221.0	17.8
<i>N</i>	9	7	8	9	8	4	8	9
<i>P</i> <	0.001	0.005	0.01	N.S.	0.02	N.S.	— ^c	N.S.

^aCorrected for date of measurement (see Methods); ^bratio of mean male : mean female measurement (*N* = 21 females); no data available for Transvaal; ^cnot calculable since tail length is standardized to different arbitrary dates in the two areas.

with commercial seed in the Cape study area, so differential food availability is an unlikely source of variation in growth rates. The uJobela male, with the fastest growth, also had the highest mating success of 11 males studied (Barnard, 1989).

Within-population variation

Male pintailed whydahs in the semi-arid Transvaal population were significantly larger than their counterparts in the moist Cape in terms of culmen (bill) measurements and wing length (Table 1). For this reason, morphological variation within the two populations was analysed separately. In both areas, corrected ornament length was many times more variable than any body size character (*F*-tests, *P* < 0.001; see also Alatalo *et al.*, 1988: 368). Tarsus, wing and short tail lengths showed the least intrapopulation variation (coefficients of variation, CVs, ranging from 2 to 4%), while CVs for body mass and bill

TABLE 2. Coefficients of variation^a for body size characters and tail ornaments of live male *Vidua macroura*

Study area	Body size characters						Tail ornament length	Maximum mass
	Culmen length	Culmen width	Culmen depth	Tarsus length	Wing length	Short tail		
Cape	5.04	6.24	9.46	3.02	2.12	3.20	17.61	4.92
Transvaal	5.93	15.02	6.40	3.82	3.26	3.88	55.30	8.66

^aCorrected for small samples (Sokal & Rohlf, 1981: 59).

measurements were intermediate (Table 2). Corrected ornament length, however, was extraordinarily variable in both populations.

DISCUSSION

Timing and rate of ornament growth

For sexual selection theory to make a real contribution to our understanding of animal behaviour in the wild, it must take more account of the constraints of real-life situations. Particular problems are the perceptual and temporal constraints faced by females in choosing mates (e.g. Alatalo, Carlson & Lundberg, 1988b; Barnard & Markus, 1989), and the intimidating effect of male ornaments or body size on competing males (e.g. Peek, 1972; Smith, 1972; Siegfried, 1985; Enquist, Ljungberg & Zandor, 1987; Barnard, 1990). We often assume that phenotypic variation between males reflects genetic variation, but the real situation is not that simple. In the case of sexual ornaments, environmental sources of variation include abrasion, the timing and rate of ornament growth, and the overall nutritional condition of males, although these may have an underlying genetic component. There are unfortunately no data on heritability of ornament size in whydahs, due in part to the daunting nature of such a study with a parasitic bird. However, heritability is likely to be low (R. V. Alatalo, *in litt.*), especially if ornaments form a major component of fitness (Gustafsson, 1986).

Rather than maximum ornament size, which is an intractable measurement for population comparisons, we might use the timing of ornament acquisition or rate of growth as an index of male 'quality'. Both of the latter measurements are obtainable in field studies of individually known animals, particularly where repeated capture is possible. While these values are more difficult to obtain than museum measurements, they are undoubtedly more accurate and biologically meaningful.

In this study, males which grew their long tails early in the breeding season were the first to acquire call-sites, and drove off later-developing males with which they had previously flocked. Particularly during the period of call-site acquisition, early-developing males were behaviourally dominant to later ones, and their call-sites were the focus of greater sexual activity (see also Barnard, 1989). The early sexual readiness of these males could simply reflect superior nutritional condition, although three wild males with *ad libitum* food grew their tails at very different rates (Fig. 2). It seems likely that stimulation from competing subordinate males influences the rate of ornament growth, via increased plasma concentrations of androgens (e.g. Ralph, Grinwich & Hall, 1967; Wingfield, 1985), but this needs experimental study.

While ornament size in some animals may be a simple allometric function of body size, the longest-tailed male whydahs were not the biggest (Barnard, 1989; cf. Alatalo *et al.*, 1988a; Craig, 1989). Nor were they the most successful at obtaining copulations (Barnard, 1989). However, male shaft-tailed whydahs *V. regia* with experimentally lengthened tails were preferred by females to control and short-tailed males in aviary trials (Barnard, 1990), suggesting that females are attracted to supernormal ornaments. If the development of breeding plumage correlates closely with testicular development (e.g. Ralph *et al.*, 1967),

females may benefit from mating with the longest-tailed males available simply because they are most likely to be fully fertile.

Natural populations and museum surveys

This field study generated coefficients of variation substantially greater than the museum values reported for *Euplectes progne* by Craig (1989), and similar to, but usually somewhat greater than, those reported for *V. macroura* by Alatalo *et al.* (1988a: Table 3). There are four possible reasons for this. First, my ornament length data were corrected for date of capture, whereas Alatalo *et al.* and Craig used raw data. I also applied Sokal & Rohlf's (1981: 59) correction for small-sample coefficients of variation, which increases CVs incrementally. Second, my sample was smaller than those of Craig and two of the three analysed by Alatalo *et al.*, and was subdivided further than theirs. Third, my tarsus and bill measurements were made with a millimetre rule, whereas Alatalo *et al.* used calipers (Craig did not specify his methods). My method is less accurate and would normally yield higher estimates of variation. However, the most obvious difference between the three studies is that I used live birds and not museum skins. This affects the selection of data at two levels: the choice of appropriate males, and the delimitation of populations. These are discussed below.

As the tail ornaments of birds such as the pintailed whydah reach their full length, sheaths of the emergent feathers turn from bluish to grey, and then dry and flake from the base of the rectrix. In both live birds and prepared specimens, the disintegrating sheaths of nearly-grown feathers may be rapidly lost, making it difficult to evaluate the state of feather growth in study skins more than a few years old. Alatalo *et al.* (1988a) measured "only males with intact and fully grown ornaments with no blood quills at the base of rectrices". However, the study skins they examined were collected between 1843 and 1967. Craig (1989), who measured only skins showing no wing or tail moult, did not give the collection dates of his material. No matter how meticulous the examination (or preparation) of skins, it may be risky to classify old study skins with no visible blood quills as having fully grown ornaments. If some incompletely developed males are included, estimates of variation may be overinflated (but see below). This need not adversely affect the conclusions of a study, provided that the date of collection is reasonably standardized within regions.

Although the decay of feather sheaths may be a problem for museum studies, incompletely plumaged males are likely to be underrepresented in museum series anyway. Museum collections sometimes overrepresent 'perfect' specimens, in this case males with immaculate, fully developed ornaments. Males with incomplete or heavily abraded tails are likely to be collected less often than their relative frequency in a population warrants. This bias would underestimate the variation in natural populations, since incompletely ornamented males do court females, compete with other males, and sometimes gain territories. Furthermore, most museum collections span many years, with specimens taken in different months and from widely different localities.

Of course, females (and rival males) are exposed only to phenotypic variation within their home range, and not within huge regions (e.g. West Africa; southern South America) of the magnitude grouped by Alatalo *et al.* (1988a). Similarly,

Craig (1989) grouped his material broadly, according to subspecies. Natural (intrinsically defined) populations are the preferable unit for consideration here, and the concept of 'song populations' may be useful for songbirds, insofar as these represent naturally defined breeding populations (cf. Payne & Payne, 1977; Payne, 1981, 1985b; Hafner & Petersen, 1985; Baker *et al.*, 1985). To my knowledge, there are only three other publications reporting coefficients of variation in tail ornament length from local field studies. These are Andersson (1982b) on the polygynous widow *Euplectes progne* (CV = 9.4%, $N = 7$ males); Møller (1988) on the monogamous swallow *Hirundo rustica* (CV = 9.6%, $N = 74$), and Barnard (1990) on the promiscuous whydah *Vidua regia* (CV = 5.7%, $N = 12$). These figures are probably not comparable, since they were uncorrected for seasonal variation and, with the notable exception of Møller (1988), were calculated using small samples. I urge future workers to calculate standard, mid-season coefficients of variation in order to allow biologically meaningful comparisons.

The museum-based approach of Alatalo *et al.* (1988a) and Craig (1989) is a valuable first step in quantifying variation. Yet there is a need for more field studies comparing males within populations delimited by traits of the animals themselves (see especially Payne & Payne, 1977), rather than by external criteria imposed by taxonomists. Since females seeking mates have only a limited number from which to choose, highly localized samples from field studies provide the most realistic estimates of male variation in phenotypic traits.

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