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COMPARATIVE MATING SYSTEMS AND REPRODUCTIVE ECOLOGY OF THE AFRICAN WHYDAHS (*VIDUA*)

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GENERAL ABSTRACT

This thesis examines territoriality, sexual behaviour, variation in body and ornament size, and the basis of mate choice in two viduine finches (Aves: Viduinae) of southern Africa: the pin-tailed and shaft-tailed whydahs *Vidua macroura* and *V. regia*. Supplementary data are provided where possible for the paradise whydah *V. paradisaea*.

While ecological and behavioural factors are important correlates of male mating success and sexual activity at male-defended call-sites (Chapter 2), male phenotypic characters such as body size and length of breeding plumes are not. Sexually successful males defend centrally located call-sites with permanent water, dense seeding grass and high rates of female visitation. Call-sites attractive to visiting females are sometimes, but not always, the same as those attractive to challenging males. In both field and experimental settings, female sexual responses are also associated with the display vigour of males (Chapters 3 and 5). Male display and defense of desirable resources thus appears important even in these nonparental, promiscuous finches.

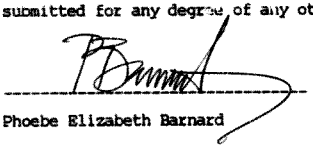
Experimental removals of breeding shaft-tailed whydah males from their call-sites (Chapter 2) confirmed the existence of a floating population of nonterritorial adult and immature males. Such males also occupy places on the periphery of established call-sites as satellites. In addition, males which defend call-sites of low sexual activity constantly seek opportunities to move to more active sites.

Male pin-tailed whydahs copulate infrequently and terminate a high proportion of their courtship displays before copulation, even when females are highly receptive. Receptive females compete aggressively for copulations, disrupting the courtship of other females at a rate (up to 0.6/h) seldom seen even for males in competitive mating systems. In Chapter 3, two alternative explanations, the male choice and sperm depletion hypotheses, are tested using data on colour-ringed individuals. Present evidence favours the possibility that the sperm supply of males in some circumstances is limited.

Male pin-tailed whydahs within two populations show substantial phenotypic variation in ornament length (Chapter 4). With the exception of bill measurements, body size variation is comparatively very small. At the proximate level, ornament variation arises because males differ markedly in the timing and rate of ornament acquisition. Data on tail growth rates of three multiply captured males illustrate the potential for female whydahs to choose as mates those males which grow their tails rapidly and early in the breeding season. In theory, sufficient intrapopulation variation exists for intersexual selection to act on male tail ornaments.

To investigate this possibility, hormone-treated shaft-tailed whydah females were exposed to "choice pairs" of tail-manipulated males in a series of aviary experiments (Chapter 5). Females responded sexually to experimentally tail-lengthened males, in preference to tail-shortened or sham-treated controls. However, males given a tail longer than that of their unseen pairmate became significantly more active in sexual display, aggression, general activity and vocalization, even though their tail treatments changed daily. Secondary sexual responses by females (simple approaches to males, rather than overt solicitation postures) were stronger to active, tail-shortened males than to a tail-lengthened decoy. This fact, together with a strong correlation between male display duration and female sexual response in the field (Chapter 3) and a lack of correlation between male mating success and tail length (Chapter 2), suggests that male display vigour is more important to receptive females than the size of male ornamentation. However, fully developed ornaments should have an additive stimulatory effect on females, since they represent reliable indicators of maturity and fertility.

I declare that this thesis is my own, unaided work, except where explicitly acknowledged in the preface. It has not been previously submitted for any degree of any other university.



Phoebe Elizabeth Barnard

January, 1989



Plate 1. Frontispiece: The pin-tailed (1), paradise (2) and shaft-tailed (3) whydahs, painted by Kenneth Newman

PREFACE

The viduine whydahs are among the most exciting subjects possible for studies of sexual selection, mating behaviour and evolution. They are an extremely sexually dimorphic group (Frontispiece) whose parasitic breeding frees them from many of the assumptions which limit both experimental and observational studies of other birds. Their promiscuity, similarly, frees them from the coevolutionary compromises that characterize pair-bond based mating systems, and renders them an intriguing study in sexual opportunism. They are the sort of group that one could happily study for decades, with each answer spawning half a dozen further questions.

There are, of course, several people whose work or thinking stimulated my own immeasurably. First among these must be Robert Payne of the University of Michigan, whose work on the congeneric widowfinches (or indigobirds) is an impressive example of comprehensive field study imbued with the excitement of evolutionary theory. I have also been influenced by the elegant field and laboratory experiments of Malte Andersson (Goteborg Universitet), William Searcy (University of Pittsburgh), and Sievert Rohwer (University of Washington, Seattle), all of whom have stimulated and clarified research in sexual selection and behavioural dominance.

Admittedly, I did have theoretical biases. Having had a thoroughly adaptationist schooling in animal behaviour at the undergraduate level, where the main textbook used was Alcock (1979), I ran up against a rather anti-adaptationist school of thought at University of the Witwatersrand. While I did not come to embrace many of the views held by my new peers (I would like to mention Mike Allsopp and Martin Villet), exposure to these views created in me an appreciation of the importance of constraints in evolution. To be honest, I did not really believe that Andersson's (1982a) female widowbirds could actually prefer males with supernormal tails, and I resolved to investigate the matter. The fact that in my own aviary work, supernormally-tailed male whydahs did seem to be preferred by females, therefore came as a genuine surprise to me.

There are many more people whose contribution to this thesis is less abstract and more immediate. For critical discussion of chapters, or the papers published from them, I am grateful to Malte Andersson (Goteborg Universitet); Bruce Beehler (Smithsonian Institution); Peter Henzi (University of Natal); Peter Jones (University of Edinburgh), Robert Payne (University of Michigan); Warwick Tarboton (Transvaal Div. Nature Conservation); Mike Anderson, Robin Crewe, Miles Markus and Rob Simmons (all of University of the Witwatersrand); about ten anonymous referees, and of course my thesis examiners.

For advice about study areas I thank Andre Boshoff (Cape Dept. Nature Conservation), Alan Kemp (Transvaal Museum), Carl Vernon (East London Museum), and especially Warwick Tarboton who accurately forecasted that many of my original plans would prove unrealistic. Derek Goodwin (British Museum), David Johnson (Natal Parks Board), Udo Savalli (University of California at Berkeley) and Phil Shaw (then at Aberdeen University) also wrote stimulating letters about various aspects of the study. Enzo Vaccaro smoothed many hurdles in acquiring equipment.

I am particularly grateful to the landowners who graciously allowed access to their properties, often with the privilege of accommodation thereon. These include the Galpin family of Mosdene, whose willingness to let me live and work on their farm means a great deal to me. I also thank Mr. and Mrs K. Hartley of Sedgefield, the Cape Dept. of Nature Conservation, the National Parks Board, and the Transvaal Division of Nature Conservation for assistance and hospitality. For statistical advice and assistance with computers I am very deeply indebted to Neil Caithness, Ignas Heitkonig, Peter Henzi, Denny Meyer, Lucy Randall, Hamish Robertson and Martin Villet. Kenneth Newman of Johannesburg, the only artist who seems to know how it looks and feels to be a whydah, graciously allowed me to use a plate from his book *Newman's birds of southern Africa* for the Frontispiece.

I was funded by the University of the Witwatersrand and the Foundation for Research Development; I thank these bodies for their support. The advisors for this project, Professor Miles Markus and ornithologist

extraordinaire Warwick Tarboton, deserve my greatest thanks. Despite herculean committments elsewhere, Miles was of particular help in processing red tape under unbelievable pressure. I am deeply indebted to both for their complementary and very valuable input.

Finally, my chief critic and editor, sounding board, aviary construction manager, academic stimulus and best friend has been Rob Simmons, my husband. It was he whose irritatingly easy grasp of theoretical issues and encyclopaedic comprehension of the literature brought out the competitive edge in me. If there is any worth in this thesis at all, it is largely due to his example.

Publications arising from the thesis and fieldwork, in chronological order, are:

1. Barnard P. 1988. Ageing and sexing guide: common waxbill *Estrilda astrild*. *Safring News* 17:79-83.

2. Kelsey M.G. & P. Barnard. 1988. Scarlet facial feathering of *Uraeginthus angolensis*: a phenotypic throwback? *Ibis* 130:444 - 445.

3. Barnard P. 1989a. Territoriality and the determinants of male mating success in the southern African whydahs. *Ostrich* 60 (in press).

4. Barnard P. 1989b. Male ornament size, sexual display intensity and female sexual response in a parasitic African finch. *Animal Behaviour* 37 (in press).

5. Barnard P. & M.B. Markus. 1989. Male copulation frequency and female competition for fertilizations in a promiscuous brood parasite, *Vidua macroura*. *Ibis* 131 (in press).

6. Ornament and body size variation and their measurement in natural populations: a cautionary tail. Submitted to *Biological Journal of the Linnean Society*, June 1989.

ABBREVIATIONS USED IN THE TEXT

♂	male
♀	female
cf.	compare
c.v.	coefficient of variation
df	degrees of freedom
E	east
e.g.	for example
et al.	and colleagues
ESMS	Estimated Seasonal Mating Success
Fig.	Figure
g	gram/s
h	hour/s
in litt.	by letter
in prep.	in preparation
km	kilometer/s
lw	length x width
m	meter/s
Max.	maximum
Min.	minimum
min	minute/s
mm	millimeters
N	sample size
n.s.	not significant
P	probability
pers. comm.	personal communication
PW	paradise whydah
PTW	pin-tailed whydah
r	radius
S	south
SD	standard deviation
sec	second/s
STW	shaft-tailed whydah
unpubl.	unpublished
X	magnification
x	mean

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CHAPTER 1. INTRODUCTION

> "I believe...perhaps a dozen distinct laws are all struggling against each other in every variation which ever arises."
>
> -Charles Darwin, 1959, in a letter to Joseph Hooker

RATIONALE

Persistent paradigms and the scientific method

While the scientific method as expounded by Popper (1972) has been widely adopted by the scientific community as a procedural framework, two points of contention about it exist today. Stated simply, these are: (1) the assumption that a phenomenon has a single, universal cause, and (2) the power of theoretical expectations and biases in shaping the outcome of empirical research. In (1), violation of the assumption of universal causation could invalidate Popper's scientific method itself, since the progress of science depends largely on the postulation of universal trends or laws which can be discredited by their falsification in specific circumstances. Clearly, if a phenomenon has multiple rather than universal causation, dependence on Popper's method will delay or mislead us in understanding it. Kuhn (1962, 1977:280-287) has emphasized the importance of this truism for the empirical sciences, and I believe that it is a particular problem for evolutionary biology, which is less subject to rigid "laws" than the physical sciences.

On a different level, (2) the conscious or unconscious theoretical biases of researchers have even greater potential to hamper scientific progress (Kuhn 1977:325-326; Balph & Balph 1983; Gould 1984; Kamil 1988). In ornithology, for example, there exists an uneasy mixture of sometimes mutually disdainful theorists and empiricists, such that some field observers pointedly ignore theoretical developments in order to avoid bias in data collection (e.g. R.J. Dowsett, pers. comm.). Similarly, the tropical ecologist Daniel Janzen (1986) laments

data collection solely for the testing of currently fashionable hypotheses, remarking that theories come and go, but data are "forever." On the other side, some theoreticians blithely write overly simplistic assumptions into their models since the real world is, in effect, too complex for comfort (e.g. Andersson 1986).

I begin with these two points because, as I see it, they pose important problems for many areas of research, and especially evolutionary biology. The phenomenon of theoretical bias, in particular, has received attention from critics such as Gould & Lewontin (1984). However, some areas of research still suffer from paradigm bias. One such area, and the one singled out for criticism by Gould & Lewontin (1984), is behavioural ecology, a vigorous young science which has relied heavily on what Gould (1978) calls "storytelling" for its theoretical advancement.

Behavioural ecology, mating systems and sexual selection

Behavioural ecology originally developed from the empirical studies of ornithologists and the models of evolutionary theorists: John Crook (1964, 1965, 1970), David Lack (1968, 1971), Jerram Brown (1964), Gordon Orians (1961, 1969), W.D. Hamilton (1963, 1964), and John Maynard Smith (1964, 1965, 1974). Their perspectives on the relationships between evolution, ethology and population ecology, initiated by the early work of Charles Darwin (1871) and R. A. Fisher (1930, 1958), were given a framework by E. O. Wilson's (1975) stimulating synthesis of the discipline. As a result, the interface between evolution and behaviour is now the subject of a mushrooming literature, emphasizing the adaptativeness of behavioural phenomena (e.g. Alcock 1979).

With this proliferation of research since the 1960's, there has developed a widening gap between theoretical development and empirical verification. This has made the field vigorous and challenging (Kirkpatrick 1984), but also increasingly subject to intellectual fashions. To some extent, the very nature of behavioural ecology lends itself to trendiness, and has done since its inception. In particular, it has run into trouble by identifying as its primary aim

the discovery of ultimate, as opposed to proximate, explanations of behaviour (see Alcock 1979). The enthusiasm with which researchers have interpreted this dictum, with little regard for the constraints or mechanisms underlying their explanations, has led to Gould and Lewontin's (1984) caricature of the "Panglossian paradigm."

One of the most notably controversial areas stimulated by Wilson's (1975) treatise is the rebirth of mating systems research. While earlier workers (Crook 1964, 1965; Jians 1969) placed the evolution of social and sexual behaviour firmly in the context of ecological resources and constraints, much subsequent work has stressed abstract and non-material benefits to animals through copulatory discretion (e.g. Borgia 1979; Borgia et al. 1985; O'Donald 1980a,b; Partridge 1980; Boake 1985). Beginning with some of Darwin's contemporaries, however, there has been significant skepticism about the validity and evolutionary importance of active intersexual selection or "mate choice" (Wallace 1889; Huxley 1938; Mayr 1942, 1963, 1972; Lambert et al. 1982 and references therein), largely from evolutionary theorists rather than empiricists in the sexual selection field.

Modern criticisms of mate choice theory focus on three aspects:

1. the paucity of genetic variance in fitness-related traits within equilibrium populations, and thus the lack of an adequate selective matrix (Williams 1975; Maynard Smith 1976);
2. the lack of an empirical or theoretical basis for genotype discrimination by the selecting sex (Arak 1983; Kirkpatrick 1982);
3. the difficulty of distinguishing the effects of intrasexual competition and mate choice (Arak 1983; Bell 1983; Payne 1984).

Despite a growing appreciation of these criticisms among influential workers (e.g. Arak 1983; Halliday 1983; Partridge & Harvey 1986), new publications dealing with sexual selection continue to treat its weaknesses and gaps uncritically or perfunctorily (see Wade 1984). As a result, unsubstantiated paradigms of sexual selection are elaborated in the literature. As Wade (1984) remarks in a review of insect mating systems research, the primary weakness of workers in this field is

their "insistently adaptationist interpretation of essentially every aspect of the behavioral phenotype of every individual."

Mating systems research has, nonetheless, begun to move away from its quagmire of hyperadaptationism. Three positive and related developments are (1) an increase in the ratio of empirical tests to theoretical models, (2) a specific move toward manipulative field and laboratory tests, and (3) a renewed appreciation of the importance of immediate resources, rather than abstract evolutionary benefits, to animals searching for mates. These immediate accruals include food and safe breeding sites (e.g. Parker 1971; Searcy 1982; Simmons 1988), quality parental care (Trivers 1972; Halliday 1983; Muldal et al. 1986; Simmons 1988), or simple assurance of fertilization (Dewsbury 1982; Chapter 3). Even in the realm of theory, there is a move toward models based on more realistic assumptions and explicit proximate mechanisms (e.g. Lande 1981; Kirkpatrick 1982; Arnold & Wade 1984a). Ideally, empirical papers on sexual selection will again include sufficient raw data, rather than just summary statistics, to allow reinterpretation of their conclusions by other workers (Janzen 1986).

It was in the context of this theoretical milieu (or perhaps muddle) that I began the work reported in this thesis. Andersson's (1982a) elegant field experiments on female choice and male ornament size had recently been published, apparently showing that supernormal male ornaments were actively preferred by females, in support of Fisher's (1930, 1958) famed "runaway" process of intersexual selection. It seemed to me desirable to carry out similar experiments in controlled conditions, to try to eliminate variables that may have complicated Andersson's conclusions. At the same time, I had been impressed by the manipulative lab techniques of Searcy (1983, 1984), who used hormone-treated birds to analyse the effect of song types on sexual behaviour, and wondered whether these techniques could be combined to investigate visual, rather than vocal, characteristics. While it would be false to claim that I chose my study animals by these lofty theoretical criteria, I did realize that the birds I had already chosen, for largely aesthetic reasons, lent themselves extraordinarily well to such experimentation in both field and laboratory.

The viduine finches

The viduine finches could hardly be better suited to sexual selection research, both from theoretical and logistic angles. They are small (10 - 20 g), brood-parasitic, promiscuous birds of the passerine family Ploceidae (sometimes put in a separate family, Viduidae (Maclean 1985)), inhabiting open savanna/woodland regions of sub-Saharan Africa (Hall & Moreau 1970). As seed eaters, they are easily maintained in captivity, and in the field the availability of their food sources can be experimentally altered without difficulty. Conceptually, they are an exciting group to work with because of their pronounced sexual dichromatism and dimorphism: males of all species have brightly coloured or iridescent plumage, with elaborate tail plumes in many species; the smaller, brown-streaked females are inconspicuous (Frontispiece). Furthermore, their brood parasitism renders them uncomplicated subjects for mate choice study, since neither sex has a substantial investment in offspring. Male resources important to parental females, such as paternal care and control of safe nest sites, are thus irrelevant to female viduines.

The Viduinae comprises 10 - 12 species (Payne 1973a; Cooper 1983; cf. Friedmann 1960) of controversial taxonomic affinity and, until recently, uncertain species composition. Payne's extensive work on this family (1970, 1971, 1973a,b, 1977a, 1979a, 1980a,b, 1981, 1982, 1983 1985a,b,c,d, Payne & Payne 1977; Payne & Groschupf 1984) has focused on the taxonomically challenging indigobirds, also called combassous or widowfinches (subgenus *Hypochera*). These are a complex of morphologically similar viduines which differ obviously only in bill and leg colours, and in the host-mimetic male sexual song (Payne 1973a, 1982). The two other recognized subgenera are *Steganura*, the paradise whydahs, and *Vidua*, the slender-tailed whydahs (Traylor 1968), although all viduine finches are now grouped into the single genus *Vidua*. Males in the *Steganura* group have black, russet and cream plumage with long, broad rectrices (Frontispiece: paradise whydah *Vidua paradisaea*), while males of the *Vidua* subgenus are either brightly coloured or pied, with long, slender rectrices (pin-tailed *V. macroura* and shaft-tailed whydahs *V. regia*), often with bright bills.

There are distinct, but more subtle, interspecific plumage differences between females, and these are summarized by Payne (1971,1973a, 1982) and regional avifaunal handbooks (e.g. Maclean 1985).

Objectives

The objectives of this thesis are fourfold, reflecting my diverse but interrelated interests in the behavioural ecology of these birds. My primary, general intention was to analyse, both through quantitative description and judicious experimentation, the basic parameters of whydah behavioural ecology in southern Africa. For this, I planned to study the three whydahs of South Africa: pin-tailed, shaft-tailed, and paradise whydahs. It quickly became apparent that population densities of the two latter species were unpredictable and often very low in response to rainfall. I was able to gather a reasonable amount of data on shaft-tailed whydahs, and used them as subjects in experiments. However, except where noted, I could not study paradise whydahs in any detail, and so this thesis mainly concerns the first two species.

The four specific objectives were:

1. To analyse the spatial dispersion of breeding males, population structure and saturation, and form of territoriality.
2. To investigate visual and vocal modes of intra- and intersexual communication, and if possible interspecific communication. In particular, I wanted to look at phenotypic variation in males in the context of intra- and intersexual selection. Data on vocal communication will be published separately, as they were not sufficiently complete for inclusion in the thesis.
3. To investigate, through observation and experimentation, the basis of call-site visitation and copulation patterns of males and females. This included not only mate choice, but also other aspects of female sexual receptivity and copulation latency.
4. To investigate the relationship between timing of breeding, host breeding, and rainfall in moist-temperate and arid-subtropical areas. This aspect of the study will be published separately, as it fell outside the theme of sexual behaviour and mating systems.

THE STUDY AREAS

Field observations and experiments were based in two widely separated and ecologically distinct regions of South Africa: a temperate coastal plain in the winter-rainfall area of the southern Cape Province, and a subtropical, semiarid savanna in the summer-rainfall Kalahari Sands area of the central Transvaal (Fig. 1.1). The temperate site supports only one whydah, the ubiquitous pin-tailed whydah, while the subtropical area is inhabited by three: pin-tailed, shaft-tailed, and paradise whydahs, with low and unpredictable numbers of two congeneric widowfinches (steel-blue *V. chalybeata* and purple *V. purpurea*) (Tarboton 1971, 1977, 1982). The temperate area was thus treated as a site for supplementary observations only, and the subtropical area as the main study site.

The temperate study area

The Cape study area spanned the southern coastal plain between the towns of Wilderness and Sedgefield (34°00' - 34°01'S; 22°35' - 22°48'E), centered on the Wilderness Lakes (Fig. 1.2). The southern coastal plain is an ancient dune and wetland system along the Indian Ocean, south of the Outeniqua Mountains. Its dunes were formed during fluctuations in sea level since the Pleistocene (Allanson & Whitfield 1983); soils are sandy with overlying alluvium. The Wilderness Lakes, a series of freshwater and brackish coastal wetlands, are interspersed with fynbos- and scrub-covered dunes, indigenous Afromontane forest remnants, pine-eucalypt plantations, scattered human habitation, and small-scale farming. Detailed vegetational accounts of the area are given by Jacot Guillarmod (1982) and Allanson & Whitfield (1983). As is typical of the winter-rainfall Southern Temperate Zone (Weisser & Howard-Williams 1982), annual rainfall at the Wilderness Lakes is moderate (mean total between 1979 - 1986 = 815 mm) and reasonably constant, with small peaks in October and June (Barnard MSb).

The Wilderness study area is of interest for three reasons. First, it lies near the southern limit of the pin-tailed whydah's range in an area of allopatry (Hall & Moreau 1970; Fig. 1.1). Second, it is within

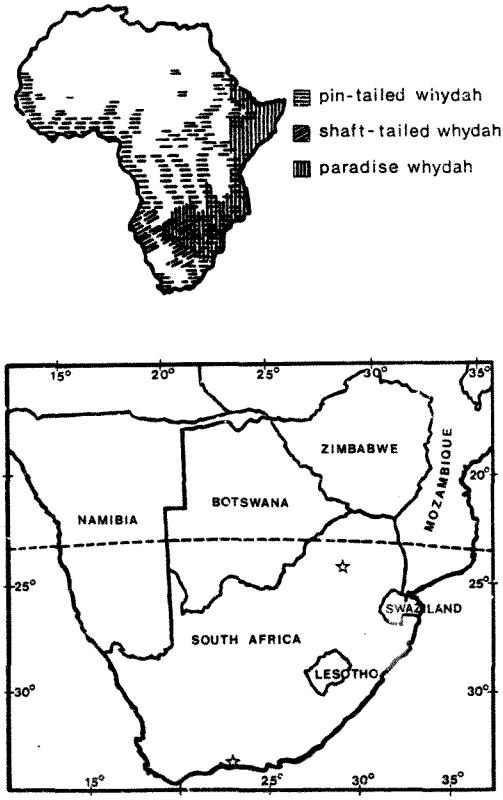


Figure 1.1. Location of the subtropical Transvaal and temperate Cape study areas (stars) within South Africa, showing ranges of the three study species.

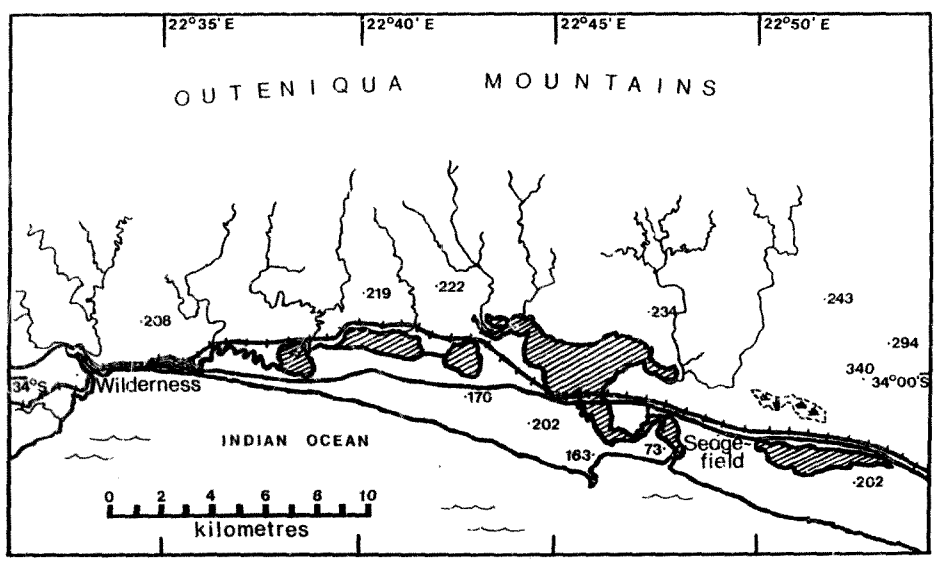


Figure 1.2. The Cape study area, centred on the Wilderness Lakes.

the temperate winter-rainfall area, and may provide substantially different environmental cues and stimuli for reproduction than would the subtropical area (Barnard MSb). Third, it represents a substantially human-fragmented habitat in which whydahs use small homesteads or suburban bird feeders as territorial loci, by contrast to the more natural habitat use of the central Transvaal (Chapter 2).

The subtropical study area

The Transvaal area spanned two adjacent but ecologically distinct sites: the Nyl Floodplain and the extreme northwestern Springbok Flats ($24^{o}32'$ - $24^{o}55'S$; $28^{o}40'$ - $28^{o}58'E$), east of the towns of Naboomspruit and Nylstroom (Fig. 1.3). Work on the Nyl Floodplain was centred on the farm Mosdene (hereafter the Mosdene study site), and that on the Springbok Flats was centred on a road between the grain storage depots of Crecy and Byzonder (hereafter the Crecy study site).

The Nyl Floodplain is a dry grassland during most months, and is seasonally inundated on an irregular basis (Tarboton 1987). Its alluvial and clayey soils are surrounded by comparatively well-drained rocky and sandy soils supporting *Burkea africana* / *Terminalia sericea* and *Acacia* spp. / *Dichrostachys cinerea* open woodlands. The floodplain itself is characterized by the grasses *Panicum schinzii*, *Setaria perennis* and, during floods, *Oryza longistaminata* grasses (Frost 1987). Mosdene Farm is managed as a cattle ranch and nature reserve, with low stocking and high stock rotation rates relative to nearby farms. The adjacent Springbok Flats are underlain by fertile, non-alluvial clayey soils. Primary and secondary savanna remnants persist in uncultivated fields, characterized by *Acacia tortilis*, *A. karroo*, and *A. nilotica*, but most of the area is under intensive agriculture. Chief crops are maize, sunflowers, sorghum, wheat, and cotton (Randall 1989). The entire area is semiarid and has strongly seasonal, but highly variable rainfall. For example, at Nylsvley Nature Reserve, 1.3 km from the southern border of Mosdene, approximately 85% of the mean 620 mm annual precipitation falls between November and April (Frost 1987), but within that period there is substantial variation in the timing and amount of rainfall (Frost 1987; Randall 1989).

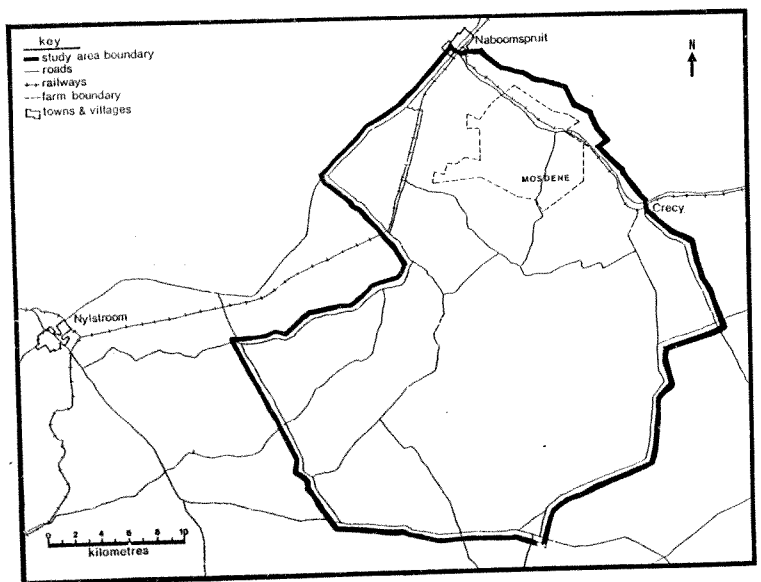


Figure 1.3. The Transvaal study area, showing the positions of the Mosdene and Crecy intensive study sites.

As a semiarid, subtropical area, the Nyl/Springbok Flats study area is of comparative interest for three reasons, related to those cited for Wilderness. First, it is an unusual convergence of the ranges of two arid-country and one mesic-country whydah species. The paradise and shaft-tailed whydahs are common throughout Botswana and Namibia, while the widespread pin-tailed whydah avoids arid regions (Fig. 1.1). Second, the erratic and strongly seasonal rainfall of the area should provide environmental cues for breeding that differ markedly from those of the temperate Wilderness site (Barnard MSa,b). Third, by contrast to the Wilderness site, the area represents a more natural pattern of habitat use, with feeding resources that are potentially more evenly distributed (Chapter 2).

TIMING OF THE STUDY

My research on whydahs began in September 1984 and ended in December 1986. Supplementary observations from outside this period, and from outside the main study areas, have been included where appropriate. Each year, I attempted to spend the entire local breeding season in each of the two study areas. As the late Cape season overlapped to a variable degree with the early Transvaal season, however, this was not strictly possible. In general, I spent the winter and spring months (the nonbreeding period in the Transvaal) at the Cape site, and the summer and autumn months (the late breeding and nonbreeding periods in the Cape) at the Transvaal site. I thus collected data in the Cape between September - December 1984, September 1985 - January 1986, and September - December 1986, and in the Transvaal from December 1984 - May 1985 and January - May 1986. This schedule covered the breeding seasons of both areas as completely as possible; no breeding birds were present at either site between May and September of either year. However, as a result, data are missing for two aspects: the end of the Cape breeding season and the timing of the local postbreeding exodus from that area, and the beginning of the Transvaal breeding season (pin-tailed whydahs only). In lieu of my own observations, I consulted resident ornithologists W.R. Tarboton, A.F. Boshoff and K. Hartley to help fill these two gaps.

STRUCTURE OF THE THESIS

This thesis was written in sections as independent as possible, to facilitate rapid publication. As a result, basic information about the viduine finches is repeated in each chapter. To avoid excessive repetition, however, descriptions of the study areas are confined to Chapter 1 and all references are grouped at the end of the thesis. Each chapter begins with a short linking paragraph, omitted from the published version, for the sake of continuity.

There are four main chapters. Following this introductory chapter, Chapter 2 describes the main ecological attributes of whydah territories, their variation in sexual activity, and some of the correlates of male mating success. It also suggests that the breeding population of males is highly saturated, indicating strong reproductive skewedness and competition (Beehler and Foster 1988). Following from this background, Chapter 3 discusses the mating systems and sexual behaviour of pin-tailed whydahs, in terms of courtship and copulation patterns and female sexual competition.

For the characteristic tail ornaments of the viduine finches to be attributable to sexual selection, there must be variation in the ornaments that is potentially discernible by choosy females or rival males. Chapter 4 presents data on this variation, and points out that while genetic variation (as reflected in a male's maximum ornament size) is difficult to detect or measure in the field, extraordinary phenotypic variation exists within local populations. Such variation is substantially greater than variation in limb, wing and unadorned tail size. Since there is demonstrably large variation in field populations, I undertook a series of aviary experiments to determine whether females could in fact perceive, and act on the basis of, experimentally lengthened and shortened tails (Chapter 5). This chapter presents evidence that ornament size strongly affects the dominance relations of rival males as well as the solicitation patterns of females. In a brief conclusion (Chapter 6), I put the work discussed in the thesis into the context of the broader philosophical problems discussed at the beginning of Chapter 1.

CHAPTER 2. TERRITORIALITY AND THE DETERMINANTS OF MALE MATING SUCCESS

ABSTRACT

Variation in the ecological attributes of traditional mating sites controlled by male pin-tailed (*Vidua macroura*, PTW), shaft-tailed (*V. regia*, STW) and paradise whydahs (*V. paradisaea*, PW) was analysed using data from a three year study in two populations in South Africa. Differences in intersexual and intrasexual behaviour at mating sites (PTW and STW only), and in estimated seasonal mating success (ESMS) of males (PTW only), were related to variation in male-defended resources. In PTWs, ability to control a perennial water source, which ensured a high rate of female visitation, was important to a male's ESMS. Neither body size nor length of breeding rectrices was correlated with ESMS. Female STWs, but not intruding males, were preferentially attracted to mating sites with a high density of seeding grass. Male intrusion pressure in STWs was higher at spatially clumped mating sites than at isolated sites.

Twelve STW males were experimentally removed, or disappeared, from their mating sites. They were replaced by other breeding-plumaged males (75%), a bird belatedly acquiring breeding dress (8.3%), and immature males (16.7%) within as little as 5 5 h. Immatures defended sites successfully only after the consecutive removal of two or more breeding males, suggesting a significant but limited floating population of potential breeders. Territorial males also moved from sites of low to high sexual activity, presumably in an effort to increase their mating success.

INTRODUCTION

In this chapter I describe variation in the habitat characteristics and dispersion of male whydah mating courts or "call-sites," their level of sexual activity, and interactions between the two. Data are most complete for the pin-tailed whydah, but information on the shaft-tailed whydah and paradise whydah is included where appropriate.

As promiscuous, brood-parasitic birds, the whydahs (Viduidae) of southern Africa might be expected to differ in resource use and spatial dispersion from nonparasitic monogamous or polygynous species in the same habitats. For example, while nonparasitic female birds may seek mates controlling resources important for breeding, such as safe nest sites and food for nestlings, female parasites could be more strongly influenced by male behaviour or appearance (Payne & Payne 1977; Chapter 5). The viduine finches, which have been comprehensively studied in many parts of Africa by Payne (e.g. 1973a, 1977a,b, 1979a, 1980a,b, 1981, 1982, 1983, 1985a,b,c, Payne & Payne 1977, Payne & Groschupf 1984) and Nicolai (e.g. 1964, 1969), appear to have a consistent mating system and pattern of spatial dispersion. In the best known species, the steel-blue widowfinch *Vidua chalybeata*, breeding males occupy prominent, traditional "call-sites" (Payne 1973a; Payne & Payne 1977) or "mating courts (*sensu* Beehler 1987) which are visited by females for copulation and/or feeding. Males defend these call-sites against conspecific breeding males, but do not hold a large defended territory. Call-sites may be only a few hundred meters apart (Payne & Payne 1977), often within the hearing range of adjacent males. Female widowfinches visit different call-sites, apparently "sampling" males, and copulate with one or more. Payne & Payne (1977) term this dispersion a "dispersed lek," but it is not certain that extensive sampling is a feature of female choice in other viduines (Chapter 3).

This paper focuses on some determinants of call-site quality and degree of sexual activity in three of the long-tailed whydahs: pin-tailed *V. macroura* (PTW), shaft-tailed *V. regia* (STW), and paradise whydahs *V. paradisaea* (PW). I describe the ecological parameters of male whydah call-sites and their relation to male copulation rate, patterns of female visitation and rival male intrusion, and resource use. The spatial organization and social behaviour of one species, the pin-tailed whydah, have been briefly studied in west Africa by Shaw (1984; see also Payne 1973a), and general behaviour of the Paradise Whydah in east Africa has been discussed by Nicolai (1969).

METHODS

Individual identification

Eighty-four PTWs and 18 STWs were trapped for individual colour-marking using mistnets and four different designs of seed-baited traps. No PWs, which are extremely wary of human attention, could be caught. Males occupying call-sites were caught with mistnets, breeding-plumaged male decoys and playback of male sexual song. In different instances I used painted clay decoys, mounted specimens, and live decoys in increasing order of success. Once the technique was perfected, territorial males could be trapped within 15 min using any decoy type. Females were caught at call-sites using walk-in traps baited with seed. All adults released were given a numbered metal ring and a unique combination of three or four coloured plastic rings. STW males removed from their sites were held in captivity for further experiments on tail length and female choice (Chapter 5). All were released at their sites at the end of the breeding season.

Once colour-ringed, individuals could be identified with the aid of 8X or 10X binoculars. Call-sites were monitored from December or January until May in the Transvaal by checks at weekly (or more frequent) intervals, as committments to other aspects of the study allowed; sites other than at Mosdene and Crecy were checked less regularly. In the Cape, I monitored one or two call-sites intensively over a season; information from other sites was gathered opportunistically.

Ecological parameters

From July 1984 to December 1986, I collected data on 11 habitat and spatial variables from the call-sites of PTWs, STWs and PWs in the Cape and Transvaal study areas. At the end of each variable definition below, I parenthetically mention an equivalent or similar variable used by Payne & Payne (1977:137-142) if one was measured. The 11 variables, and their codenames used in statistical analysis, are:

1. Permanence of nearby accessible water sources (PANPERM): pans,

streams, depressions, birdbaths, and other sources were ranked as 1 (ephemeral: often dry during breeding season), 2 (seasonal: sometimes dry) or 3 (perennial: never dry). Where necessary, field observations on water permanence were supplemented by interviews with landowners. Cattle troughs and other water sources inaccessible to birds were excluded.

2. Surface area and shape of water source (PANSIZE): estimated by measuring the maximum length (l) and width (w) of full, non-flooded pans or other sources in mid-breeding season, and calculating an approximate surface area in m^2 using formulae for rectangles (lw) or circles (πr^2) as appropriate.

3. Call-site type (CSTYPE): species of tree or bush, or type of artificial perch such as telephone wire or fence.

4. Call-site height (CSHEIGHT): height of favoured perch measured to the nearest 0.2 m with a portable ruled 3.0 m stick (equivalent to Payne & Payne's variable PERHT but measured differently).

5. Habitat classification (HABITAT): a qualitative general classification (e.g. "disturbed coastal floodplain," "open Acacia tortilis woodland") determined from habitat photographs centred on the call-site, field notes on vegetative composition, and by examining 1:10 000 orthophotographs and 1:50 000 topographical / land use maps (Government Printer 1981, 1984-86). Classification took into account predominant vegetation, overall habitat structure, and relative vegetation density within a 200 m radius of the call-site. (Similar but not equivalent to Payne & Payne's quantitative variables ANILO, VEGPRO, WOODLAND and OPENLAND).

6. Available food species (GRSTYPES): a list of edible plants known to be eaten by viduines (grasses plus buds of several composite flowers) within 50 m of the call-site.

7. Food availability rank (GRSAVAIL): Quantitative relative grass density indices were calculated according to a modified line-

intercept transect method (Brower & Zar 1977:75-80). Siting of transects was randomized in floodplain habitats, but at call-sites lying linearly along roadsides in otherwise unsuitable habitat (e.g. cultivated fields), spatial constraints imposed a nonrandom, linear transect arrangement. All sampling was done at the height of the local breeding season. I calculated linear density indices for edible seeding grasses in both floodplain and agricultural habitats, and noted the genera present in descending order of stem frequency. These indices were then assigned a relative rank score from 1 (depauperate, $\bar{x}$ = 6 - 10 seeding stems/m) to 5 (super-abundant, $\bar{x}$ = 26+ stems/m). The heterogeneity of seeding grass density in many areas was reflected by large standard deviations of the means in the original transect data. Mean percentage of green stems with milky inflorescences was also noted. Grass genera in the diet of whydahs, as determined from close observation of feeding birds, were Brachiaria, Cynodon (C. dactylon), Eragrostis (E. lehmanniana), Panicum (P. coloratum, P. maximum, P. schinzii) and Urochloa (U. brachyura or panicoides). (Similar but not methodologically equivalent to FECHINO and FSETARIA.)

8. Nearest neighbour distance (NND): the distance (km) of a call-site to the nearest active call-site of a conspecific (equivalent to NEIGHBOR).

9. Conspecific spatial position (CONCLUMP): the sum of distances (km) of a call-site to the two nearest active call-sites of conspecifics. This is an index of microgeographic isolation or centrality relative to other conspecifics (equivalent to CLUMP).

10. Heterospecific spatial position (HETCLUMP): the sum of distances (km) of a call-site to the two nearest active call-sites of other whydah species. This is an index of isolation or centrality relative to other whydahs, and was not calculated for the Cape study area as only PTWs occurred there.

11. Nearest neighbour (NNEIGHB): the name of the nearest active

conspecific call-site.

In addition, two variables represented my observation effort at call-sites:

12. Number of days observation (DAYSOBS)

13. Total observation time (OBSTIME) in h

Behavioural parameters

As an adjunct to the ecological description of call-sites, I collated field data on their "behavioural" attributes: the tenancy periods of individual males, the attendance and intrusion rates of females and other males respectively, the number of observed copulations, and (in the case of PTWs) estimated seasonal mating success or ESMS. These data were compiled following Lyme & Payne (1977) to assess the biological value of each call-site to whydahs themselves, as judged by their behaviour, and to correlate both ecological and behavioural parameters with a male's ESMS. In particular, I surmised that the desirability of defending certain call-sites might be reflected in the intrusion rates of other males, and the desirability of call-sites or their resident males might be reflected in the attendance rates of females. The relative importance of male and call-site quality to breeding females could, in theory, be directly compared by observing changes in male mating success when males change call-sites within a season. Unfortunately, due to very low copulation rates (Chapter 3), the relevant data are too sparse, and confounding variables too difficult to control, to test this.

14. Minimum tenancy period (NDAYS): the minimum period in days during which a known male occupied a call-site (equivalent to NDAY).

15. Mean female attendance rate (FMPH): the mean number of female-minutes per hour during which females were present at a call-site (similar to FPH, which counts only female visits and does not take

into account their duration; cf. Shaw 1984).

16. Mean male intrusion rate (MALEINTRPH): the mean number of intrusions per hour at a call-site by other males (equivalent to MPH).

17. Observed number of matings (OBSMATINGS): the total number of observed copulations by a known call-site owner.

18. Estimated seasonal mating success (ESMS): an estimate of male reproductive success, calculated according to Payne & Payne's (1977:133) equation (for the equivalent index MS):

$$ESMS = \frac{(OBSMATINGS)\ (TENANCY)\ (10\ h/day\ \sigma^{\prime}\ on\ site)}{OBSTIME}$$

Habitat, spatial and behavioural variables were tabulated for each call-site (Appendices 1 - 9) and male (Tables 2.9 and 2.10); those that could be treated numerically (PANPERM, PANSIZE, CSHEIGHT, GRSAVAIL, NND, CONCLUMP, HETCLUMP, FMPH, MALEINTRPH, OBSMATINGS, OBSTIME, ESMS) were entered into STATGRAPHICS © worksheets (Statistical Graphics Corporation 1986) for analysis of the factors influencing male mating success (ESMS), male intrusion and female attendance rates. Analysis of ESMS was possible only for pin-tailed whydahs, as copulations were observed only in this species.

For comparative purposes, I intentionally followed Payne & Payne's (1977) statistical methods as far as possible. Whereas these authors collected data on a larger number of habitat variables, many of which covaried extensively, I restricted my analysis to a smaller number of representative factors. Unfortunately, data on male sexual song were too few to analyse meaningfully here. Like Payne and Payne, I used nonparametric statistics (rank correlation matrices) to identify important covariants of mating success, even though some of the component variables satisfied standard parametric assumptions. Other variables were ranked ordinally (PANPERM, GRSAVAIL), and some (ESMS, FMPH, MALEINTRPH) involved the use of means and ratios. While both Spearman and Kendall rank correlation statistics are given in Tables

2.6 - 2.8, the latter values may be sensitive to small samples (Sokal & Rohlf 1981; but cf. Bradley 1968). Relative to the Spearman test, Kendall's tau tends to generate lower correlation coefficients while inflating their significance. Kendall's tau is thus not necessarily a more conservative test, as Payne & Payne (1977:142) imply.

RESULTS

Ecological variation in call-sites

The call-sites of conspecific whydahs differed appreciably in those habitat and spatial parameters likely to influence their attractiveness to males and females (Tables 2.1 - 2.3), as reflected in large coefficients of variation. These aspects varied to much the same extent as was found in the *V. chalybeata* population studied by Payne & Payne (1977: Tables 7 - 10). Pin-tailed whydah males in the Transvaal occupied call-sites at the edges of seasonal or perennial pans ranging from 0.5 to 1852 m^2 in extent. These water resources clearly increased the attractiveness of call-sites in this semi-arid region. In neither STWs nor PWs were data available on variation in PANSIZE. However, water permanence appeared much more important for all three whydahs than water surface area, and the two variables were only minimally correlated at PTW sites (see Table 2.6).

Most PTW call-sites were spatially clumped, with as little as 200 m between conspecific sites in the Transvaal and 30 m in the Cape, but a few outlying call-sites were over 1 km apart. They tended to be much farther from PW or STW call-sites than the latter two were from each other (cf. Tables 2.1 - 2.3).

At the height of the breeding season in the Transvaal, all whydah call-sites had adequate to excellent food resources (ranked 2 - 5 on a scale of 1 - 5; Tables 2.1 - 2.3), although floodplain sites had a larger expanse of seeding grasses than did roadside, woodland or agricultural sites. The availability of seeding grass and the height of the call-site perch were two potentially important variables that could, in theory, differ widely and influence the attractiveness of

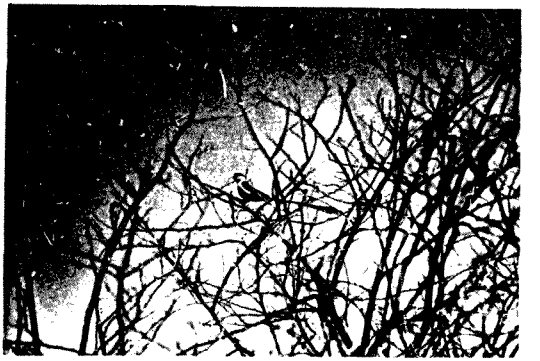


Plate 2. Shaft-tailed whydah ♂ YYY at the Gravel Gate call-site.

call-sites. However, coefficients of variation in GRSAVAIL and CSHEIGHT were among the lowest of all aspects measured. Therefore, it appeared that the permanence of water and proximity of conspecifics were the most variable and potentially most important aspects of call-site quality. The effects of these and other variables are explored statistically below.

Table 2.1. Variation in habitat and spatial parameters of 11 pin-tailed whydah call-sites in the Transvaal study area, 1985-1986.

Variable	Units	Min.	Max.	Mean	SD	c.v.(%)[a]	Skewness	N
PANPERM	rank 1-3	2	3	2.4	0.52	22.14	0.48	10
PANSIZE	m^2	0.5	1852.0	878.8	640.48	75.18	0.20	8
CSHEIGHT	m	2.8	5.0	3.88	0.75	19.74	-0.04	11
GRSAVAIL	rank 1-5	3	5	4.3	0.79	18.92	-0.57	11
NND	km	0.20	1.41	0.54	0.42	79.75	1.27	10
CONCLUMP	km	0.46	4.81	1.71	1.49	89.28	1.52	10
HETCLUMP	km	1.51	11.91	6.65	3.20	49.30	0.01	10

[a]corrected for small samples (Sokal & Rohlf 1981:59)

Table 2.2. Variation in habitat and spatial parame. of ten shaft-tailed whydah call-sites at the Crecy study site, 1985-1986.

Variable	Units	Min.	Max.	Mean	SD	c.v.(%)[a]	Skewness	N
PANPERM	rank 1-3	3	3	3	0	---	0	4
PANSIZE	m^2	---	---	---	---	---	---	---
CSHEIGHT	m	3.8	6.3	4.83	0.99	21.14	0.82	8
GRSAVAIL	rank 1-5	3	4	3.6	0.53	15.23	-0.37	7
NND	km	0.71	1.36	1.12	0.31	28.69	-0.44	7
CONCLUMP	km	2.55	4.46	3.34	0.62	16.68	-1.75	7
HETCLUMP	km	0.29	0.89	0.49	0.26	55.00	0.77	7

[a]corrected for small samples (Sokal & Rohlf 1981:59)

Table 2.3. Variation in habitat and spatial parameters of 30 paradise whydah call-sites in the Transvaal study area, 1985-1986.

Variable	Units	Min.	Max.	Mean	SD	c.v.(%)[a]	Skewness	N
PANPERM	rank 1-3	1	3	2.7	0.70	26.65	-2.12	9
PANSIZE	m^2	---	---	73.5	---	---	---	1
CSHEIGHT	m	4.0	5.0	4.1	0.28	6.90	3.30	25
GRSAVAIL	rank 1-5	2	4	3.2	0.80	24.64	-0.55	15
NND	km	0.58	2.80	1.39	0.87	63.34	0.66	21
CONCLUMP	km	1.54	6.30	4.04	1.40	35.06	0.19	21
HETCLUMP	km	0.30	8.55	2.67	2.30	87.17	1.13	21

[a]corrected for small samples (Sokal & Rohlf 1981:59)

Variation in sexual activity at call-sites

As expected, the "behavioural" attributes of PTW and STW call-sites varied considerably more than simple habitat parameters. Coefficients of variation approached or exceeded 100% in female attendence, male intrusions and, for PTWs, observed copulations and estimated seasonal mating success (Tables 2.4 and 2.5). Males controlling certain sites experienced high rates of both female attendance and male intrusion, while other males were infrequently challenged, seldom if ever visited by receptive females, and were themselves the intruding challengers at more active call-sites (see Tables 2.9 and 2.10 for data on individual sites). PTW and STW populations are thus characterized by a high degree of variation in call-site activity and habitat quality.

Correlates of male mating success, male intrusion and female attendance rates at call-sites

PTW males defending call-sites with a source of permanent water and high rates of female attendance had higher estimated seasonal mating success than those controlling sites with ephemeral water (Table 2.6).

Table 2.4. Variation in behavioural parameters of 11 pin-tailed whydah call-sites occupied by colour-ringed males in the Transvaal study area, 1985-1986.

Variable	Units	Min.	Max.	Mean	SD	c.v.(%)[a]	Skewness	N
FMPH	♀-min/h	0.00	30.84	14.91	10.75	73.74	0.12	11
MALEINTRPH	intrusions/h	0.00	1.09	0.37	0.36	99.51	0.88	11
OBSMATINGS	copulations	0	2	0.45	0.82	186.34	1.50	11
ESMS	copulations/ season	0.00	134.39	26.19	47.41	185.11	1.61	11
OBSTIME	h	4.15	26.47	11.13	6.93	63.71	1.21	11

[a]corrected for small samples (Sokal & Rohlf 1981:59)

Table 2.5. Variation in behavioural parameters of ten shaft-tailed whydah call-sites occupied by colour-ringed males at the Crecy study site, 1985-1986.

Variable	Units	Min.	Max.	Mean	SD	c.v.(%)[a]	Skewness	N
FMPH	♀-mins/h	0.00	24.01	8.14	8.71	109.68	0.78	10
MALEINTRPH	intrusions/h	0.00	0.53	0.16	0.21	134.58	0.88	10
OBSMATINGS	copulations	0	0	0	0	---	0	10
OBSTIME	h	2.08	12.12	5.16	3.20	63.55	1.28	10

[a]corrected for small samples (Sokal & Rohlf 1981:59)

Table 2.6. Rank-order correlations (Spearman r_s and Kendall tau) of estimated seasonal mating success (ESMS) and behavioural, habitat and spatial variables at 14 pin-tailed whydah call-sites. For each variable, Kendall values are given in bold print.

Variable	ESMS	OBSTIME	FMPH	MALEINTRPH	PANPERM	PANSIZE	CSHEIGHT	GRSAVAIL	NND	CONCLUMP	HETCLUMP
ESMS											
OBSTIME	0.57*										
	0.44*										
FMPH	0.48	0.25									
	0.38*	**0.19**									
MALEINTRPH	0.18	-0.11	0.11								
	0.15	**-0.08**	**0.08**								
PANPERM	0.45	0.45	0.62*	-0.37							
	0.41**	**0.38***	**0.52***	**-0.32**							
PANSIZE	-0.47	-0.13	-0.62	0.42	-0.17						
	-0.40	**0.00**	**-0.44**	**0.28**	**-0.15**						
CSHEIGHT	-0.72*	-0.20	-0.82*	-0.08	-0.73*	0.51					
	-0.63**	**-0.22**	**-0.46***	**-0.05**	**-0.64****	**0.38**					
GRSAVAIL	0.09	0.28	0.10	-0.24	0.32	-0.30	-0.09				
	0.09	**0.20**	**0.07**	**-0.27**	**0.31**	**-0.24**	**-0.05**				
NND	0.38	-0.04	-0.24	-0.15	-0.14	-0.51	-0.26	-0.20			
	0.32	**-0.02**	**-0.21**	**-0.15**	**-0.13**	**-0.42**	**-0.20**	**-0.16**			
CONCLUMP	0.24	0.11	-0.41	-0.16	-0.21	0.02	-0.18	-0.21	0.90**		
	0.21	**0.11**	**-0.33**	**-0.13**	**-0.18**	**0.07**	**-0.13**	**-0.15**	**0.78****		
HETCLUMP	-0.15	-0.53	0.38	0.13	0.03	-0.32*	-0.42	0.05	-0.13	-0.42	
	-0.11	**-0.56***	**0.38**	**0.04**	**0.08**	**-0.62**	**-0.35**	**0.05**	**-0.16**	**-0.[illegible]**	
N =	14	14	14	14	13	[illegible]	13	14	11	11	10

*P < 0.05; **P < 0.01

The association of PANPERM and FMPH as two major correlates of ESMS is expected, since females visited water daily to drink and, if receptive, copulated with the resident male. FMPH is itself significantly correlated with PANPERM. Surprisingly, however, call-sites with permanent water were not under significantly more pressure from challenging males, although intruder pressure was very high at certain of these sites (see **Sexual activity** of individual males).

Male PTWs controlling sites with low favoured perches had significantly higher ESMS than those with higher perches (Table 2.6). This apparently arbitrary relationship is a function of habitat type, which could not be expressed on a linear scale for statistical purposes. Floodplain dwelling males, with low bushes, tended to have higher mating success than those in agricultural or roadside habitats, with tall call-site trees. The limited sample also exaggerates data from males at the extreme of any range, such as ♂ BWR at the uJobela 86 site, which had an extremely high ESMS (Table 2.9) and a low favoured call-site perch (Appendix 3). ESMS was also correlated with observation time (Table 2.6), owing to very low copulation rates and a low probability of detecting copulations in any one observation period.

Although ESMS was not calculable for STWs and PWs, limited data are available on behavioural and/or ecological aspects in the correlation matrices of Tables 2.7 and 2.8. Female STWs spent significantly more time at call-sites with abundant grass seed than at more depauperate sites (Table 2.7), although inter-site variation in grass density was low (Table 2.2). Intruding STW males, by contrast, did not appear preferentially attracted to sites with abundant food. However, the intrusion rates of males were significantly higher at sites with a close conspecific neighbour, implying that the pressure from challenging males was substantially greater at clumped than isolated sites (see **Population saturation: male removal** experiments). Unfortunately, due to time and cost constraints I spent more time at clumped, active sites (see also Payne & Payne 1977:115), so that data from isolated sites may be less accurate: observed female attendance rates were significantly related to observation time in STWs.

Table 2.7. Rank-order correlations (Spearman r_s and Kendall tau) of behavioural, habitat and spatial variables at ten shaft-tailed whydah call-sites. For each variable, Kendall values are given in bold print.

Variable	OBSTIME	FMPH	MALEINTRPH	CSHEIGHT	GRSAVAIL	NND	CONCLUMP	HETCLUMP
OBSTIME								
FMPH	0.67*							
	0.49*							
MALEINTRPH	0.30	0.09						
	0.27	**0.08**						
CSHEIGHT	0.33	-0.02	0.00					
	0.34	**0.10**	**-0.14**					
GRSAVAIL	0.14	0.73	0.00	-0.86				
	0.24	**0.65***	**0.00**	**-0.60***				
NND	0.06	0.24	-0.82*	0.52	-0.24			
	0.00	**0.18**	**-0.81***	**0.43**	**-0.23**			
CONCLUMP	0.14	-0.18	-0.40	-0.07	-0.29	0.18		
	0.10	**-0.05**	**-0.34**	**-0.10**	**-0.26**	**0.12**		
HETCLUMP	-0.35	-0.67	0.45	-0.39	-0.15	-0.79	0.20	
	-0.35	**-0.51**	**0.35**	**-0.32**	**-0.13**	**-0.61**	**0.15**	
N =	10	10	10	8	7	7	7	7

*P < 0.05

Table 2.8. Rank-order correlations (Spearman r_s and Kendall tau) of habitat and spatial variables at 30 paradise whydah call-sites.

Variable	PANPERM	CSHEIGHT	GRSAVAIL	NND	CONCLUMP	HETCLUMP
PANPERM						
CSHEIGHT	0.00[a]					
	0.00					
GRSAVAIL	0.66	-0.44				
	0.63	**-0.43***				
NND	-0.58	0.09	0.05			
	-0.52	**0.08**	**0.06**			
CONCLUMP	-0.58	-0.03	0.10	0.84**		
	-0.51	**-0.03**	**0.10**	**0.69****		
HETCLUMP	-0.08	-0.42	-0.09	0.13	0.30	
	-0.07	-0.34	-0.07	0.08	0.20	
N =	9	25	15	21	21	21

[a]constant association of values
*P < 0.05; **P < 0.01

Only habitat and spatial data were collected at PW sites. There were no persistent associations between variables, other than the predicted one between NND and CONCLUMP (as the latter was based partly on the former), although low call-site perches characterized sites with high grass availability. Although I would expect PWs to show the same broad relationships between habitat, spatial and behavioural variables as PTWs and STWs, an intensive behavioural and ecological study is needed before generalizations can be extended to this species with confidence.

Sexual activity of individual males

As reflected in Table 2.4, the sexual behaviour of individual PTW males and their male and female visitors was extremely variable (Table 2.9). Many males, possibly a majority, do not appear to mate during the breeding season even if they defend a call-site. There was extreme variation in sexual activity among even the three intensively studied males in the Cape study area, where observations were undeniably sufficient to detect copulations. For example, ♂ XYY at the Wilderness 84 call-site never copulated in 115 h observation, while ♂ XXR at the Tandy 84 site copulated twice in 95 h, and ♂ BWR at uJobela 86 copulated at least 50 times in less than 280 h (Table 2.9). The corresponding data for the less intensively studied Transvaal males, therefore, are probably a true reflection of intermale variation despite my much briefer observations there (see also comparable data of Payne & Payne 1977: Tables 5 and 6).

In the Transvaal population, only two of four colour-ringed call-site owners (♂ XPu and ♂ XXB) were seen to copulate in 1985, and only one of seven such males (♂ RRR) in 1986. The latter male defended the Central Pan floodplain call-site, which was the only permanent water within a radius of several kilometers, and also included abundant seeding grass in both years (Appendices 4 and 5). Furthermore, large flocks of the host *Estrilda astrild* visited Central Pan to drink (unpubl. data). As a result, ♂ RRR had unusually high rates of both female attendance and male intrusion (Table 2.9), both during the main breeding season and in the late-season transitional period between breeding and flock formation, when dozens of breeding and immature PTWs congregated and attempted to court females. Other call-sites at permanent or seasonally reliable water, such as Nyl Pan 1 (N1) in 1986 and Nyl Pan 2 (N2) in both years, were similarly characterized by high female and male visitation rates (Table 2.9).

Unexpectedly, there was no statistical association between female visitation and male intrusion rates at PTW (Table 2.9) or STW call-sites (Table 2.10). On average, sites popular among females tended to have low rates of male intrusion. While in STWs this may have been a

Table 2.9. Pin-tailed whydah estimated seasonal mating success (ESMS), female attendance and male intrusion rates, and observed copulations at the call-sites of eleven colour-ringed males.

♂	Call-site[a]	OBSTIME[b]	NDAYS	DAYSOBS	FMPH	MALE-INTRPH	OBS-MATINGS	ESMS[c]
XXR	T 84	95.28	14	12	13.40	0.00	2	2.94
XYY	W 84	115.17	32	22	9.12	0.00	0	0
BWR	U 86	278.77	91	65	58.22	0.04	50	163.22
XPu	H 85	15.80	108	37	6.65	0.51	1	68.35
	H 86[d]	8.15	32	13	20.49	0.86	0	0
RRR	CP 86	10.12	68	11	23.52	1.09	2	134.39
XWW	N1-EP 85	18.78	91	20	8.36	0.05	0	0
	EP 86	7.45	57	10	3.49	0.13	0	0
DGYY	N1 86	6.38	54	10	23.04	0.47	0	0
OOO	N2-BP 85	13.88	75	14	13.90	0.50	0	0
	N2 86	4.15	34	8	30.84	0.00	0	0
BWRR	GD 86	6.37	53	7	5.49	0.31	0	0
OBO	N 86	4.85	20	8	0.00	0.00	0	0
XXB	SC 85	26.47	113	7	28.18	0.19	2	85.38

[a]Listed with year: T = Tandy; W = Wilderness; U = uJobela; H = Highway; CP = Central Pan; N1 = Nyl Pan 1; EP = East Pan; N2 = Nyl Pan 2; BP = Big Pan; GD = Graham Dam; N = Nilotica; SC = Sericea

[b]Includes time budgets and site-occupancy checks; excludes ringing-oriented time

[c]Estimated Seasonal Mating Success (no. copulations) calculated using Payne & Payne's (1977:133) equation:

$$ESMS = \frac{(OBSMATINGS)\ (NDAYS)\ (10\ h/day\ \delta\ on\ site)}{(OBSTIME)}$$

[d]♂ removed on 12-2-86 for amputation of a ring-induced gangrenous tarsus. Released after a 2-day recuperative period, he regained and defended his site successfully for at least 7 days before disappearing from the area

Table 2.10. Shaft-tailed whydah female attendance and male intrusion rates at the call-sites of ten colour-ringed males[a].

♂	Call-site[b]	OBSTIME[c]	FMPH	MALEINTRPH	OBSMATINGS	Trapping dates[d]
BBB	F 85a	2.08	0.00	0.00	0	t 24-2-85
						r 5-5-85
OOO	GG 85a	12.12	24.01	0.00	0	t 6-4-85
						d 7-4-85
GGG	AP 85a	5.68	13.56	0.53	0	t 9-4-85
						r 6-5-85
YGYG	AP 85b	4.32	3.01	0.46	0	c 12-5-85
GGW	GG 86a	3.33	19.22	0.00	0	t 26-2-86
						r 24-4-86
YRR	F 86a	8.50	6.35	0.00	0	c 8-2-86
YYY[e]	F-N/GG 86b	6.82	12.76	0.29	0	c 16-2-86
BRRR	SF 86a	3.10	0.65	0.00	0	t 27- -86
						r 24-4-86
YBY	CD 86a	2.13	1.88	0.00	0	t 1-3-86
						r 24-4-86
WRW	AP 86a	3.52	0.00	0.28	0	t 2-3-86
						r 24-4-86

[a]Observation effort for individual ♂♂ was severely curtailed because most were removed from their call-sites in mid-season for aviary experiments (Table 2.12; Chapter 5). NDAYS and DAYSOBS could thus not be meaningfully compared for PTWs and STWs. This, along with the lack of observed copulations, prevented calculation of ESMS

[b]Listed with year: F = Fork; GG = Gravel Gate; AP = Abandoned Pasture; N = Nilotica; SF = Small Farm; CD = Cornfield (all Transvaal sites)

[c]Inclusion criteria as in Table 2.9

[d]t = trapped and brought into captivity; r = released from captivity; d = died in captivity; c = colour-ringed and released immediately

[e]♂ was resident at both the adjacent Fork and Nilotica sites until at least 18-2-86; from 26-2-86 he controlled the nearby Gravel Gate site (Table 2.12). Data are from the residency period at Gravel Gate

Table 2.10. Shaft-tailed whydah female attendance and male intrusion rates at the call-sites of ten colour-ringed males[a].

♂	Call-site[b]	OBSTIME[c]	FMPH	MALEINTRPH	OBSMATINGS	Trapping dates[d]
BBB	F 85a	2.08	0.00	0.00	0	t 24-2-85
						r 5-5-85
CCO	GG 85a	12.12	24.01	0.00	0	t 6-4-85
						d 7-4-85
GGG	AP 85a	5.68	13.56	0.53	0	t 9-4-85
						r 6-5-85
YGYG	AP 85b	4.32	3.01	0.46	0	c 12-5-85
GGW	GG 86a	3.33	19.22	0.00	0	t 26-2-86
						r 24-4-86
YRR	F 86a	8.50	6.35	0.00	0	c 8-2-86
YYY[e]	F-N/GG 86b	6.82	12.76	0.29	0	c 16-2-86
BRRR	SF 86a	3.10	0.65	0.00	0	t 27-2-86
						r 24-4-86
YBY	CD 86a	2.13	1.88	0.00	0	t 1-3-86
						r 24-4-86
WRW	AP 86a	3.52	0.00	0.28	0	t 2-3-86
						r 24-4-86

[a]Observation effort for individual ♂♂ was severely curtailed because most were removed from their call-sites in mid-season for aviary experiments (Table 2.12; Chapter 5). NDAYS and DAYSOBS could thus not be meaningfully compared for PTWs and STWs. This, along with the lack of observed copulations, prevented calculation of ESMS

[b]Listed with year: F = Fork; GG = Gravel Gate; AP = Abandoned Pasture; N = Nilotica; SF = Small Farm; CD = Cornfield (all Transvaal sites)

[c]Inclusion criteria as in Table 2.9

[d]t = trapped and brought into captivity; r = released from captivity; d = died in captivity; c = colour-ringed and released immediately

[e]♂ was resident at both the adjacent Fork and Nilotica sites until at least 18-2-86; from 26-2-86 he controlled the nearby Gravel Gate site (Table 2.12). Data are from the residency period at Gravel Gate

simple function of brief observation times, FMPH and MALEINTRPH were negligibly correlated in both PTWs (Table 2.6) and STWs (Table 2.7). However, the STW sites Gravel Gate (1985 and 1986) and Abandoned Pasture (1985) were visited most frequently by females, and were also the sites of all male challenges observed in both years.

Body size, tail length and mating success

The relationships between ESMS, body size, and length of breeding rectrices of ten PTW males are analysed in Table 2.11. (Summary statistics and intrapopulation variation in those traits are described later, in Tables 4.1 and 4.2.) Because breeding males differ in the timing of ornamental plumage growth (Chapter 4), and because trapping difficulties and feather abrasion make it impossible to record each male's maximum tail length, I corrected field measurements by using tail growth rates of three known males to standardize all males' tail ornaments to an arbitrary mid-season date (see Chapter 4). There was no significant association between ESMS, body size, or corrected ornamental tail length. In fact, contrary to current theory, the smallest-bodied males tended to have slightly higher mating success. In a related experimental study, however (Chapter 5), the manipulation of tail length strongly influenced both the activity levels of test males, and the sexual responses of females to them.

Population saturation: male removal experiments

Twelve STW males were removed, or disappeared, from their call-sites in 1985 and 1986 (Table 2.12). Their replacements were other fully plumaged breeding males in nine cases (75%), a late-developing breeding male with newly emergent rectrices in one case (8.3%), and immature males in two cases (16.7%). Other immature males were seen contending for two sites after the removal of breeding males, but were successfully displaced by adults before they could establish themselves. It is important to note that the two immatures successfully replacing males at the Fork and Gravel Gate sites did so only after the second removal or disappearance of a male from those sites in quick succession. There thus appeared to be at least as many

adults in the floating population as there were call-sites, but once these replacements were themselves removed, immature males gained occupation of some vacated sites.

Not all of the males assuming control of vacated sites were floaters. At least three replacements were territorial males moving from other sites. One male, ♂ PuPuPu, first appeared in the study area in 1985 as an unringed, adult replacement after the removal of a male from the Fork site (Table 2.12). He was resident at Fork for a month before transferring to the neighbouring Gravel Gate site, which had an extremely high female visitation rate (Table 2.10), when it became vacant at the removal of ♂ OOO. Fork was then inhabited by an unringed immature, as was Gravel Gate shortly afterwards when ♂ PuPuPu was removed from that site.

In 1986, males again increased their potential mating success by transferring from Fork to the more active Gravel Gate site (cf. FMPH values, Table 2.10). When ♂ YRR temporarily deserted Fork after colour ringing, he was replaced by a new and unringed adult, ♂ YYY. The latter male transferred to Gravel Gate upon the removal of its resident ♂ GGW, at which point ♂ YRR reappeared and regained control of Fork. Male YRR was subsequently seen twice challenging ♂ YYY for control of Gravel Gate, both times unsuccessfully.

Tradition and species overlap in call-site use

Tradition plays an important part in the placement of whydah call-sites from year to year (Table 2.13). Although my three-year study can only estimate the degree of temporal stability in call-site occupancy, it is clear that many sites are occupied from one year to the next.

In the Cape study area, two of the three PTW sites studied in 1984 were active in 1986; one of these, Tandy, had been inactive in 1985 (Fig. 2.1). PTWs in the Transvaal were even more traditional in their use of sites (Table 2.13); twelve of fourteen sites studied in 1985 and 1986 were active in both years (Fig. 2.2 for the Hosdene study

Table 2.11. Rank-order correlations (Spearman r_s and Kendall tau) of estimated seasonal mating success (ESMS) and body size of ten colour-ringed pin-tailed whydah males. For each variable, Kendall values are given in bold print. Pearson r coefficients only are reported for body measurement correlations, since these can be treated parametrically.

Variable[a]	ESMS	MASS	WING	TAIL	TARS	CULML	CULMW	CULMD
ESMS								
MASS	-0.06							
	-0.11							
WING	-0.14	-0.07						
	-0.10							
TAIL	0.23	0.25	0.11					
	0.19							
TARS	-0.09	0.12	-0.41	-0.35				
	-0.09							
CULML	-0.20	0.16	0.57*	0.13	0.17			
	-0.14							
CULMW	-0.43	0.42	-0.13	-0.09	0.19	0.77**		
	-0.39							
CULMD	-0.46	-0.44	0.24	0.11	0.01	0.67**	0.51	
	-0.40							
N =	10	10	9	10	10	10	6	7

[a]ESMS calculated as in Table 2.9 and Methods. Mass to nearest 0.1 g; tail (longest rectrix, corrected to a standard date of measurement) to nearest mm; wing (flattened chord), tarsus length, culmen length, culmen width and culmen depth all to nearest 0.5 mm

*$P < 0.05$; **$P < 0.01$

Table 2.12. Call-site takeovers after the removal or disappearance of twelve shaft-tailed whydah males from their sites in 1985 and 1986. All sites were checked 21-26 h after removal unless otherwise noted. A male was considered a replacement if he sang at the vacated call-site during observations.

Date	Call-site[a]	Removed ♂	Replacement ♂	Status of new ♂	Replacement time (h)[b]
24-2-85	P	BBB	PuPuPu[c]	br	263.0[d]
6-4-85	GG	OOO	PuPuPu[c]	br	21.5
7-4-85	P[e]	PuPuPu[c]	unringed	imm	72.0[f]
9-4-85	GG	PuPuPu[c]	unringed	imm	23.5
9-4-85	AP	GGG	YLGYLG	br	24.0
24-4-85	L	WWW	unringed	br	269.0[g]
8-2-86	P[e]	YRR	YYY	br	188.5[h]
26-2-86	P[e]	YYY	YRR	br	22.0[f]
26-2-86	GG	GGW	YYY	br	5.5
27-2-86	SI	BRRR	unringed	br	26.0
1-3-86	CC	YBY	unringed	br[i]	45.5[j]
2-3-86	AP	WRW	unringed	br	573.0[k]

[a]Abbreviations as in Table 2.10; L = Locatie

[b]To nearest 0.5 h

[c]This ♂ unringed until 9-4-85 but easily recognizable by pattern of rectrix abrasion

[d]Checked only at 261 h, and apparently vacant then

[e]"Natural" experiments due to the transfer of a ♂ to another site

[f]Estimated by assuming that ♂ 's first observed appearance at Gravel Gate immediately followed his desertion of the adjacent Pork site

[g]Checked only at 24 h and 269 h; immature ♂ visited call-site at 24 h check but did not sing

[h]Checked only at 1 h and 188.5 h

[i]Replacement breeding ♂ with long rectrices only just emerging

[j]Checked only at 45.5 h

[k]Checked at 20.5, 24.0, 44.0, 76.0, 221.0, and 573.0 h

Table 2.13. The year-to-year stability of whydah call-sites.

Species	Study area	Period	Sites still active	Sites known inactive	Unknown sites	% stability
PTW	Cape	1984-1985	1	2	---	33.33
		1985-1986	5	2	1	71.43
		1984-1986	2	1	---	66.67
	Transvaal	1985-1986	12	2	11	85.71
STW	Transvaal	1985-1986	5	4	6	55.56
PW	Transvaal	1985-1986	7	8	2	46.67

Table 2.14. Persistence of individual male pin-tailed whydahs at call-sites in consecutive years.

Cape		Transvaal	
Male	Call-site & year	Male	Call-site & year
OYY	Graveyard 85	XPu	Highway 85
	Graveyard 86		Highway 86
WWX	Hartley 85	OOO	Nyl Pan 2/Big Pan 85
	Hartley 86		Nyl Pan 2 86
		WXWX	Nyl Pan 1/East Pan 85
			East Pan 86

site, and Fig. 2.3 for the Crecy study site). In the Cape and Transvaal, five individual males controlled the same sites in consecutive years (Table 2.14); these data may underrepresent the real degree of male persistence, since not all call-site holders could be colour-ringed in the first year of study.

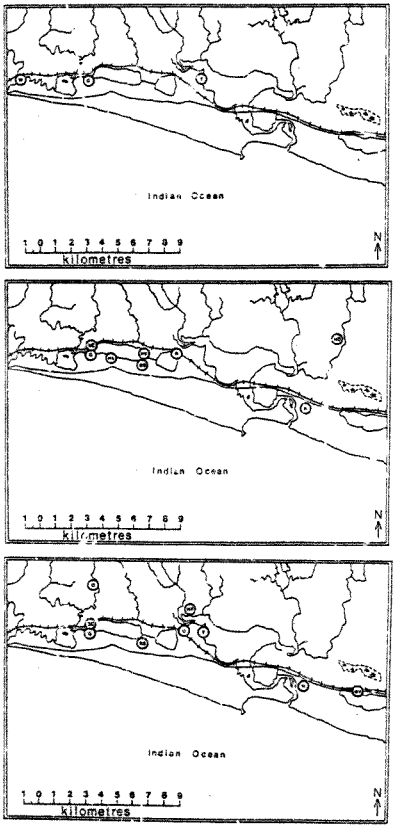


Figure 2.1. Position of pin-tailed whydah call-sites studied in the Cape study area in (a) 1984; (b) 1985; (c) 1986. BC = Bolang Channel; BS = Bolang Southeast; G = Graveyard; GV = Groenvlei; H = Hartley; HD = Herd; HF = Hopfields; HX = Hexagons; O = Oakhurst; R = Rondevlei; RV = Rondevlei Village; T = Tandy; U = uJobela; W = Wilderness.

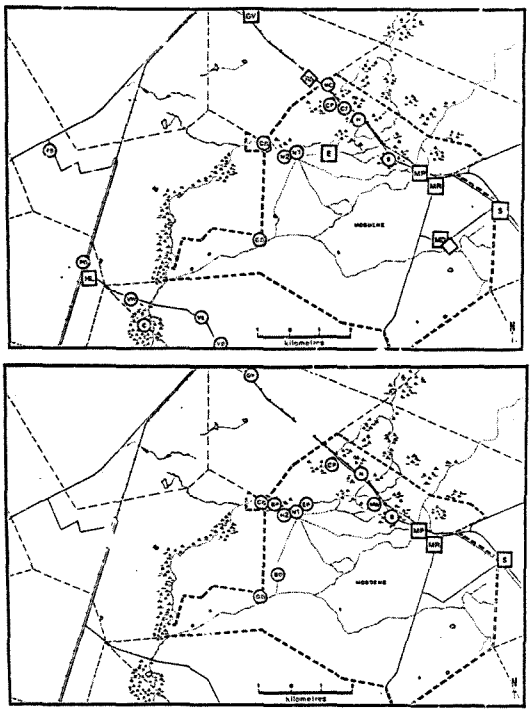


Figure 2.2. Position of pin-tailed (circles), shaft-tailed (diamonds) and paradise (squares) whydah call-sites studied on Mosdene and surrounding areas in (a) 1985; (b) 1986. B = Borrow Pits; BD = Bypass Dam; BP = Big Pan; C = Cobra; CG = Cargnellutti; CF = Central Fence; CP = Central Pan; E = Everglades; EP = East Pan; FS = Farm Stall; GD = Graham Dam; GV = Great Valley; H = Highway; HL = Hamlet; MD = Mosdene Drive; MP = Mud Pools; MR = Mosdene Road; MW = Midway; N1 = Nyl Pan 1; N2 = Nyl Pan 2; NC = Northwest Corner; PG = Power Grid; R5 = R519 Road; S = Sunflowers; VB = Vogel Bush; VE = Vogel East; VW = Vogel West.

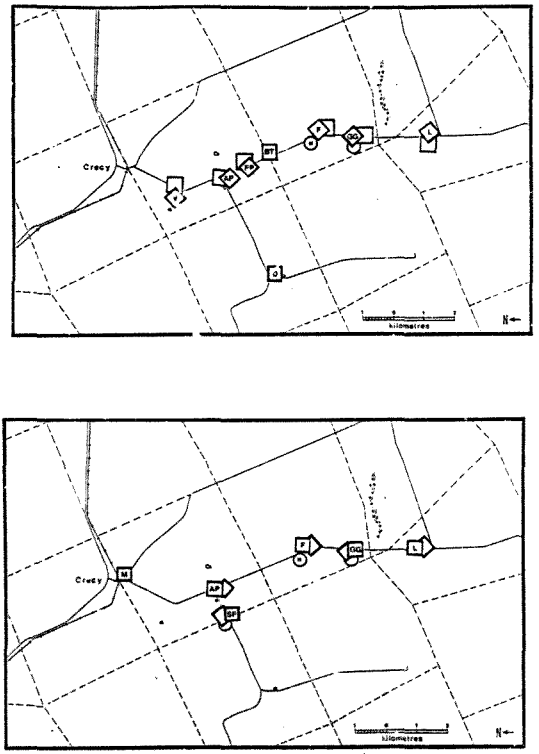


Figure 2.3. Position of pin-tailed (circles), shaft-tailed (diamonds) and paradise (squares) whydah call-sites studied at Crecy in (a) 1985; (b) 1986. AP = Abandoned Pasture; BT = Black Turf; D = Depot; F = Fork; FP = Fallow Pasture; GG = Gravel Gate; L = Locatie; M= Marolong; N = Nilotica; V = Village.

Most of the STW and PW sites observed in 1985 and 1986 were active in both years (Table 2.13, Figs. 2.2 - 2.3). Because STW males were removed from their sites in both years and released late in the season, and because no PW males were colour-ringed, no data are available for these species on the persistence of individual males at call-sites.

In the Transvaal, STW and PW males commonly shared call-sites (Figs. 2.2 and 2.3), whereas PTW males in this area seldom shared a site with either congener. Of 17 STW call-sites, 47.1% were shared with a male PW (and five of six well-established sites). Similarly, 34.8% of 23 PW call-sites were shared with a STW male (as were all three well-established sites). By contrast, only 10.3% of 29 Transvaal PTW sites were shared with any congener (9.1% of 11 well-established sites). Although interspecific aggression was a feature of all shared sites, it was normally subtle, manifested chiefly by displacement and singing (see also Payne & Groschupf 1984). The larger PWs nearly always dominated PTWs and STWs at mutual call-sites.

DISCUSSION

Variation in ecological parameters and sexual activity at call-sites

There was considerable intraspecific variation in the habitat and spatial parameters of pin-tailed, shaft-tailed and paradise whydahs, yet only a few key factors seemed to influence the degree of sexual activity at sites. The permanence of available water appeared to affect the rate of female visitation at PTW call-sites, and consequently the mating success of their resident males. Call-site perch height was inversely correlated with ESMS simply because highly successful males controlled floodplain or garden sites, which tended to have low bushes (Appendices 1 - 5) rather than tall trees.

STW females were preferentially attracted to call-sites with high grass density; water permanence and other habitat variables were uncorrelated with female attendance. STW males, by contrast, intruded

frequently at the call-sites of close neighbours, apparently checking their continued occupancy. Isolated sites were seldom visited by challenging males, and their isolation may have made them intrinsically poor spots for encountering females (see also Bradbury et al. 1986).

Variation in the degree of sexual activity at PTW and STW call-sites was even greater than ecological variation, with strongly skewed distributions. Statistically, female visitation rates at call-sites were unassociated with male intrusion rates, although individual sites with a high intruder pressure were also very attractive to females. Male body size and ornamental tail length (corrected for date of measurement) were uncorrelated with male mating success, although there appears to be more than enough intrapopulation variation in ornament length in the viduines (Alatalo et al. 1988a; Chapter 4) for sexual selection to occur.

There are probably quite a few factors which influence the attractiveness of call-sites to males and females, both measured and unmeasured by my study. However, only a few are likely to be critical.

Ecological resources important to both sexes on a daily basis, such as water, appear critical. While some male PTWs and STWs did not defend a water source and travelled up to 500 m to drink, those with a water source had the highest rates of female visitation. On the other hand, defense of a water source carried with it a greater burden of intermale competition. The Central Pan PTW male, for example, aggressively drove out all intruding males which attempted to drink at the pan. While his energy expenditure on resource defense was probably much higher than that of his waterless neighbours, he did not run the same risk of losing copulation opportunities to intruding males while away at a distant water source. Intruding males appear, sing, and court females at call-sites within minutes of the owner's departure. Also, it appears that females stop visiting call-sites where the male is too often absent (see also Payne 1973a:16). Since whydahs must drink several times daily, an on-site water supply allows greater monopolization of sexual opportunities there.

Although food resources at call-sites were thought to be relatively unimportant to female *V. chalybeata*, so that on-site feeding by females serves only a "ritual" function to help reduce aggression after copulation (Payne 1973a:32-34,38), female *V. macroura*, *V. regia* and *V. paradisaea* do feed extensively at call-sites. This occurs whether or not females copulate during their visit (although there is some evidence that males are less tolerant of unreceptive feeding females: Chapter 3; Barnard unpubl. data). Without continuous observations of individual birds, it is difficult to say whether a female's food intake at a call-site forms a significant portion of her daily total. Yet female PTWs do feed at call-sites for up to 1 h at a time, particularly before sunrise when they feed continuously and rarely solicit the resident male (Barnard unpubl. data). These observations suggest that food resources at call-sites are of considerably more than ritual importance to females, as recognized by Payne & Payne (1977:136, 158-159) for *V. chalybeata*. Food is probably not a critical determinant of call-site quality for females, simply because grass seed is widespread and not monopolizable by individual males. However, it probably is of importance to males, for much the same reasons as those cited above for water. A male which has little grass seed at his call-site must leave the area to feed, with the concomitant risks of leaving the site unattended (see also Payne & Payne 1977:124). It may be partly for this reason that floodplain sites are highly sought-after by PTW males.

Finally, it appears that spatial position relative to conspecific sites is a critical determinant of call-site attractiveness, for both males and females. Females probably range over an area encompassing a number of male call-sites (Payne 1983, 1985a,b) and concentrate their attentions on spatially clumped sites. They may do so because clumped sites reflect patches of prime habitat with abundant resources (including breeding hosts), or because they can visit clumped sites most economically, or both. Spatially isolated sites generally have low rates of male intrusion and female attendance, as indicated by negative correlations between CONCLUMP and MALEINTRPH or FMPH. Similarly, this may be either because isolated sites are in marginal habitat, or are uneconomical for females to visit, or both.

In Payne & Payne's (1977) parallel and more thorough study of mating success in the steel-blue widowfinch *V. chalybeata*, the proximity of a water hole to a call-site perch (as opposed to its permanence, which was not analysed) was significantly associated with mating success of the resident male. Other habitat variables correlated with ESMS in that study were the distance of the call-site to dense mature woodland, the openness of the call-site tree (an index of male conspicuousness), and its "twigginess." I observed that males often sang from partly dead or particularly twiggy trees, but did not collect data on call-site parameters other than height and type. Unlike Payne & Payne's (1977) study area in a national park in Zambia, most of my study sites were crossed by roads with telephone lines, and these lines were adopted by whydahs of all species as conspicuous call-site perches. Although tradition plays an important role in the siting of call-sites from year to year, it is undoubtedly advantageous for a male to further advertise his presence by perching as prominently as possible on the site as he sings. In the Zambian study, a male's tenancy period on a call-site (a component variable of ESMS) and the attendance rate of females were also significantly associated with male ESMS. In particular, the mating success of male *V. chalybeata* was closely linked to their song behaviour, an aspect that was unfortunately inadequately studied in my work. Payne considered male mating success to arise from both male competition for favoured call-sites, and from female choice based primarily on male song (see also Payne 1973a, 1977b).

Habitat use by whydahs

Floodplains and gardens near wetlands (Appendices 1 - 5) are especially suitable habitat for breeding PTWs, due to the abundance of available grass seed (and, in the case of many gardens, provided commercial seed), the existence of seasonally reliable or perennial water, and the proximity of breeding hosts. In the Cape study area, the Wilderness Lakes and associated marshes and rank grass edge habitats provide abundant nesting habitat for the PTW's host, the common waxbill *Estrilda astrild*. The Tandy, Wilderness and Hartley call-sites in the Cape, and the Sericea site in the Transvaal, are

examples of garden-based sites with an abundant artificial food source (commercial millet or mealies). The importance of reliable food is exemplified by the extremely active Hartley site, with up to three resident breeding males spaced at the far corners of a small suburban garden, an aviary filled with breeding estrildid finches including *E. astrild*, and an artificial food supply of 500 g millet/day provided by the landowner. The garden also abuts a large expanse of rank grass, mixed coastal scrub and estuarine floodplain suitable for host nesting, and was used as a major ringing site (Barnard 1988) with up to 300 common waxbills and 16 female PTWs visiting daily to feed, drink and bathe.

Although it is difficult to generalize about two such ecologically different areas, PTW sites in the Transvaal study area may be spatially more homogeneous than those in the Cape in terms of food availability, and temporally less homogeneous in terms of rainfall. The coastal scrub vegetation and sandy soils of the southern Cape are not very suitable for PTWs, except where grazing or human habitation have created patches of palatable grass. The Transvaal study area's *Acacia* savanna and floodplain habitats, by contrast, support a vast expanse of seeding grass in the rainy season. Similarly, rainfall is an important stimulus for host and parasite breeding in both the semiarid Transvaal and mesic Cape (Chapter 3; Barnard unpubl. data). While PTW breeding seasons are highly predictable in the winter-rainfall area of the Cape, the summer rains of the Transvaal are extremely unreliable and variable in amount (Frost 1987). This unreliability may be a more important determinant of male lifetime reproductive success than variation in food availability. Also, since the Cape area has a higher human density where PTWs occupy gardens with bird feeders, which are not always supplied each year, I would expect the degree of long-term stability in call-site use to be less than that in the more "natural" setting of the Transvaal area. As much as the data from a short study can be relied upon, this was in fact the case (Table 2.13).

By contrast to the floodplain- and garden-dwelling PTWs, STW and PW call-sites are found in semiarid, secondary *Acacia* savanna and on

edges of agricultural lands. Roadsides with telephone wires and tall Acacia nilotica or A. tortilis trees are especially suitable. Roadsides also offer easily locatable grass seed resources (Payne & Payne 1977) and are used heavily by both PWs and STWs. Nearly all well-established call-sites of these two species were shared with each other in my study, whereas only one in ten PTWs in the Transvaal shared a site with either congener. It is apparent, then, that STWs and PWs overlap extensively in semi-arid thorn savanna, while PTWs occupy more mesic, open terrain.

Population saturation

The experimental removal (or disappearance) of twelve STW males from their call-sites provoked a reshuffling of territorial affinities, as well as an influx of previously nonterritorial males. Males moving from one call-site to another substantially improved their rates of encountering females, and presumably also their potential mating success. Similar removals of male V. chalybeata (Payne 1973a:15-16,27; Payne & Payne 1977), and V. macroura (Shaw 1984) also showed large numbers of "surplus males" in their populations. As pointed out by W. R. Tarboton (in litt.), a male strategy of floating may be "a form of prospecting for better sites (which) is practiced by all males to a greater or lesser extent." This view places males along a continuum of nomadism, ranging from continuous floaters to established residents which shift to better quality sites when they can. It is probably the most meaningful way to view territoriality in the viduine finches.

To summarize, there is greater intraspecific variation in sexual activity than ecological variation at whydah call-sites. Basic habitat characteristics such as water permanence and food availability influence the mating success of resident male PTWs and the female visitation rate of male STWs, respectively; body size and length of the ornamental tail plumes are uncorrelated with male PTW mating success. Females appear to visit call-sites primarily because of their ecological resources, and less for any intrinsic qualities of their resident male. More detailed analyses of differential female responses to the sexual behaviour of males are found in Chapters 3 and 5.

CHAPTER 3. SEXUAL DISPLAY AND COPULATION PATTERNS: FIELD STUDIES

> "(Promiscuity) represents an exceptional mating system found in a few aberrant groups...feeding habits (of both sexes) may make a degree of independence necessary, so facilitating this odd mating behaviour."
>
> -- R.K. Murton & N.J. Westwood (1977:444-445)

> "A male..., who can produce millions of sperms every day, has everything to gain from as many promiscuous matings as he can snatch... (he) can never get enough copulations with as many females as possible: the word excess has no meaning for a male."
>
> -- R. Dawkins (1976:176)

ABSTRACT

Precopulatory displays, the degree of promiscuity, male copulation latencies, and female sexual interference were analysed in an African parasitic finch, the pin-tailed whydah Vidua macroura (PTW). Limited supplementary data are compared for the shaft-tailed whydah V. regia (STW). Males copulated infrequently and terminated most courtship displays, even when females were highly receptive; 43% of 128 displays to fully-soliciting females were terminated by an intensively studied PTW male. Although 36% of male-terminated displays were < 2 h after a copulation, the mechanism of this apparent reduced sexual capacity was unclear. Present evidence favours the possibility that some males may be sperm-limited at times.

Female sexual interference in PTWs occurred at a rate (up to 0.6 disruptions/h) seldom seen even for males in competitive mating systems, and was aimed at preventing other females from copulating. Disruptions nearly always ended the courtship of another female. Females showed periods of receptivity, apparently when they were ovulating. However, male display intensity was important in stimulating female solicitation both within and outside of receptivity peaks.

INTRODUCTION

In many animals which form mating aggregations such as leks, sexual interference by intruding males is a common phenomenon. In recent years, such interference has gained theoretical prominence as an alternative reproductive "strategy" (e.g. Rubenstein 1980; Gross 1982; Trail 1985). However, not only males may disrupt copulation. In cases where female reproduction is highly synchronized and a premium is placed on successful and rapid fertilization, there is every reason to expect females to compete for access to mates. In an astute review of lekking in birds, Avery (1984) predicted that sperm depletion and female competition may develop if females are "kept waiting" for access to dominant males at a lek. We might also expect female competition where males are not clumped, as on a lek, but rather hold isolated call-sites and are visited in rapid succession by many receptive females. In particular, females may disrupt courtship where the breeding season is restricted or tightly synchronized to extrinsic events, and where the operational sex ratio is highly female-biased.

On a local scale, the viduine finches (Viduidae) fit these criteria. They are sexually dichromatic, promiscuous brood parasites of open and wooded African savannas. Males occupy spatially separated call-sites (Payne 1973a; Payne & Payne 1977; Shaw 1984; Chapter 2) which are visited by many different females for copulation and/or feeding. Ovulation is closely synchronized with nest-building and egg-laying by the host species (Payne 1973a), so appropriate laying opportunities may be very restricted (Payne 1977a), and the number of fertilizations may be limited at times of peak sperm demand. In this chapter I test this idea informally, using activity data.

Issues of male fertility, timing of breeding, and reproductive competition are central to our theories of sexual selection and the evolution of mating systems. Unfortunately, measuring the sexual behaviour of known individuals is difficult, especially with free-living vertebrates (but see Clutton-Brock et al. 1982 and references therein). Consequently, much of what we know about the selective forces and constraints shaping mating systems derives from

invertebrates or laboratory-housed vertebrates. We cannot be certain that experimental conditions are artifact-free, or that the models applicable to other taxa are appropriate to vertebrates. The factors which shape sexual behaviour in intelligent mammals may differ fundamentally from those acting on instinct-driven invertebrates; similarly, the determinants of sexual behaviour in social primates may have little in common with those shaping the mating patterns of asocial fish. Only long-term field studies of individually-known vertebrates can generate the data needed for such comparisons and contrasts to be made (see Bateson 1983; Clutton-Brock 1988).

It is a truism of field biology that the depth with which one knows one's subjects is inversely proportional to their number, and insights from intensive studies of small populations are often marred by the difficulty of couching them in persuasive statistical terms. In this study, I monitored the sexual behaviour of a large sample, but focused on a small subsample of marked individuals. This strategy proved more insightful than diluting my efforts to study individuals more equally. However, it may limit the extent to which I can generalize individual behaviour to species-characteristic behaviour.

METHODS

In the field from 1984 through 1986, I monitored sexual activity at traditional, dispersed "call-sites" (Payne 1973a) or "courts" (Beehler 1987) of male pin-tailed (PTW) and shaft-tailed whydahs (STW). Although male paradise whydahs *V. paradisaea* often shared call-sites with one or both congeners at the subtropical study site (Chapter 2), their extreme wariness prevented me from colour-marking them or collecting any substantial comparative data. Therefore, this chapter concerns the first two species only, primarily the PTW.

Individual identification

Mist-netting and colour-ringing of whydahs and their hosts formed a large part of early-season field time. Unlike Shaw (1984), I was unable to mark birds at roosts, as these were scarce and inaccessible

(one Cape roost was atop a 25 m eucalypt tree). Breeding males were trapped at call-sites using a combination of small nets, song playbacks, and live or stuffed male decoys; females were caught in walk-in traps baited with seed at call-sites, and post-breeding males and juveniles were trapped at drinking sites late in the season. Breeding birds were ringed with 2 - 3 plastic rings on the left tarsus, and 1 - 2 plastic rings and a numbered aluminium or steel ring on the right. Juveniles were given only a numbered metal ring. I refer to call-sites by name, and to birds by colour ring combination (following Payne & Payne 1977). Call-site owners were additionally known by their territorial affiliation at any particular time. For example, the male STW wearing metal ring AA88897 was known both as ♂ YLG-YLG and as ♂ Abandoned Pasture 1985b (the second male resident at the Abandoned Pasture site in 1985).

Behavioural observations

Field observations totalled 706.6 h in the temperate study area and 902.3 h in the subtropical area, or 1608.9 h in sum. Approximately half of this was spent in regular road and foot surveys of call-site activity. Another third was spent sampling activity of individual males during 0.5 - 6.0 h periods, using instantaneous and scan-sampling methods (Altmann 1974). The remaining time was spent mist-netting, recording songs, or censusing host nests. In the temperate area these proportions varied,as I emphasized activity sampling at focal sites and mist-netting, and did not census host nests.

I collected data at 23 PTW and seven STW call-sites on three main activities: female and male visits to call-sites, sexual display and copulation rates, and courtship disruption. I studied some PTW sites intensively, particularly "uJobela" and secondarily "Tandy," "Wilderness," and "Sericea." Most sampling (316 h) was done at the uJobela call-site, where I sampled the activity of a male and 16 females (all colour-ringed) daily between 25 October and 19 December 1986, systematically covering all daylight hours. This site was unusual in being 1.3 km from the nearest call-site; elsewhere adjacent sites may be as close as 30 m (Chapter 2).

Sexual and aggressive behaviours

During activity sampling, I recognized the following seven sexual/aggressive behaviours in addition to activities such as feeding, perching, preening and roosting. Payne (1973a:29-32) describes some of these behaviours for the steel-blue widowfinch V. chalybeata:

1. Hover Displays are female-directed sexual displays, illustrated by Shaw (1984:Fig. 3b). A male performs a bouncing, hovering flight above and in front of a perched female, without significant horizontal movement. I excluded all displays of < 3 sec in which males supplanted nonsoliciting females, as these were associated with attempts to drive females from the call-site. Males also approach females in a directional hovering flight; for distinction I termed this Hover Display Flight.

2. Solicitation: If receptive to male Hover Display, a female droops and flutters her wings, crouches, raises her head, and raises and fans her tail (Nicolai 1964:179; Shaw 1984:Fig. 3a). I have adopted Shaw's three levels of solicitation to quantify female receptivity: 1/3 (mild), 2/3 (moderate), and 3/3 (strong or "full" solicitation).

3. Copulation: Viduine matings are typical of other passerines. They appear to be wholly controlled by the female, since they occurred only during full solicitation (ranked 3/3) and forced copulations were never seen.

4. Wing-Shake: a female-directed pre- or postcopulatory display (Shaw 1984:Fig. 3c) in which the male drops to a feeding site, crouches and fluffs his plumage, and rapidly shakes his wings. It appears to encourage the female to join the male and/or feed.

5. Supplant: Males and occasionally females aggressively displace other birds, especially at feeding sites. Males often displace unreceptive females or other granivores; a flying Supplant was termed a Dive-Bomb. Females displace other brown-plumaged

conspecifics, but rarely breeding males or other granivores.

6. Whistle: a multi-contextual whistling call given by males in response to the presence of a predator, human, or whydah decoy, or in apparent warning to females that they will shortly be supplanted (heard only with PTWs).

7. Bill-Point: Shaw (1984:Fig. 3d) has illustrated this aggressive, intrasexual display for PTW males a the "Upright" posture; I also saw it used in female-female conflicts, particularly during sexual disruption.

RESULTS

Appropriate and misdirected male sexual displays

Of 887 Hover Displays by 32 male PTWs, 99.32% were directed at conspecifics in adult female-type plumage, and only 0.68% at other brown-plumaged passerines. These six inappropriate displays were all performed by three unsuccessful or immature males. A territorial adult male which was never seen to copulate ("Borrow Pits" 1985 ♂) displayed four times to black-throated canaries *Serinus atrogularis* and an unidentified brown passerine; a "satellite" adult ("Northwest Corner" 1985 ♂) displayed jointly to two fan-tailed cisticolas *Cisticola juncidis*, and an immature male in female-type plumage even displayed to a juvenile conspecific ensnared in a mist-net. However, these sexual displays were very short and mainly terminated by the male; most adult males never displayed to heterospecifics, and abandoned any approaches begun. Furthermore, in an unusual incident, a territorial adult male repeatedly rebuffed a (probably adult) *Anthus* pipit which approached it in a sexual solicitation posture.

Of a small sample of 22 STW Hover Displays by four males, two (9.09%) were inappropriately directed at a female cut-throat finch *Amadina fasciata* and a southern grey-headed sparrow *Passer griseus*. Both were by territorial adults which abandoned the display in < 2 sec. It thus seems as though male whydahs, although they may be initially attracted



Plate 3. The uJobela male pin-tailed whydah (♂ BWR).

to birds resembling conspecific females, quickly realize their error and do not approach closely. Those that do persist appear to be inexperienced and with an imperfect sexual repertoire.

Mating systems

PTWs were highly promiscuous in this study, with no pair bonding between copulation partners. At the intensively studied uJobela call-site, the resident ♂ BWR copulated with at least 12 of the 16 females ringed at the site in 1986. Females appeared less extensively promiscuous; they formed no pair bonds but seemed to have fewer partners than males (see also Payne 1973a:28). Some females associated with only one or two call-sites and males in a season, as indicated by regular attendance at one site; this more likely reflects a lack of reason to seek other partners than any sexual "loyalty." I saw only one PTW female actually copulate with more than one male; a female at the "Hartley" call-site copulated with both resident males within a 3-min period in mid-breeding season. However, other PTW and STW females (PTW ♀ YBX; STW ♀ LGLGLG) actively solicited two males each, although I did not see other multiple copulations. To establish the extent of female promiscuity with accuracy, a team of field observers would have to simultaneously watch neighbouring call-sites for lengthy periods.

Male display and copulation frequency

There is much individual variation in the courtship and copulation frequency (Table 3.1) of nine PTW males whose mid-season activity was quantified for 2 - 13 h. Although the chance of detecting copulations increases with observation time, data from six males with activity samples of 2 - 3 h are included to indicate variation in Hover Display intensity, which was unrelated to observation time (r^2 = 0.002, n.s.).

PTW copulations are most common in the morning, and their frequency decreases sharply thereafter with a small late-afternoon peak (Fig. 3.1). Courtship and copulation rates may also vary seasonally. The Hover Display rate of the uJobela male varied between 0.25 - 7.00 displays/h ($\bar{x} \pm 1$ SD = 2.44 ± 1.41, N = 316 h), and copulation

frequency from 0.00 - 2.00 copulations/h (0.22 ± 0.35). While courtship rates by this male declined gradually over the season, copulation rates were more variable (Fig. 3.2c,d). Both rates showed a late-season peak during a week with high rainfall (Fig. 3.2a; see also **Female receptivity**). I have no comparable data for STWs.

Outcomes of sexual displays

Of the 887 PTW Hover Displays noted, males in breeding plumage accounted for 874 (98.53%) and nonbreeding/immature males for the other 1.47%. Despite the effort breeding males devoted to these displays, only 7.87% were followed by mating. Copulations lasted, on average, 4 sec (SD = 1.03 sec, range = 1.5 - 6.0 sec, N = 68). In at least five of 68 cases sperm transfer probably did not occur.

Table 3.1. Variation in observed courtship and copulation frequency of nine adult pin-tailed whydah males, arranged in descending order of courtship frequency. Data from mid-season activity budgets only.

Male	Courtship rate (Hover Displays/h)	Copulation rate (matings/h)	Time sampled (min)
Nyl Pan 1[86]	3.03	----[a]	178
Borrow Pits[85]	2.73	----	132
Highway[85]	2.44	0.49[b]	123
uJobela[86]	2.01	0.18	18970
Tandy[84]	1.97	----	122
Central Fence[85]	1.80	----	133
East Pan[85/86]	1.16	----	464
Sericea[85]	0.82	0.09	1303
Northwest Corner[85]	0.48	----[c]	126

[a] --- = no copulations seen

[b] value probably inflated artificially by short observation time

[c] "satellite" male of Central Pan call-site

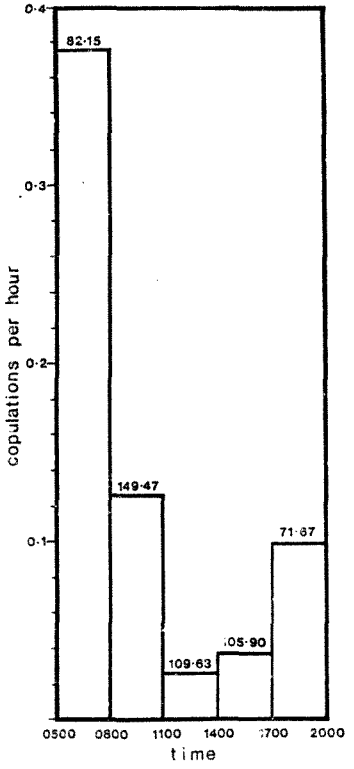


Figure 3.1. Diurnal variation in copulation frequency of pin-tailed whydah males at 23 call-sites (N = 64 copulations), excluding copulations noted outside of formal observation periods. Numbers atop bars indicate observation effort (h) during each time period.

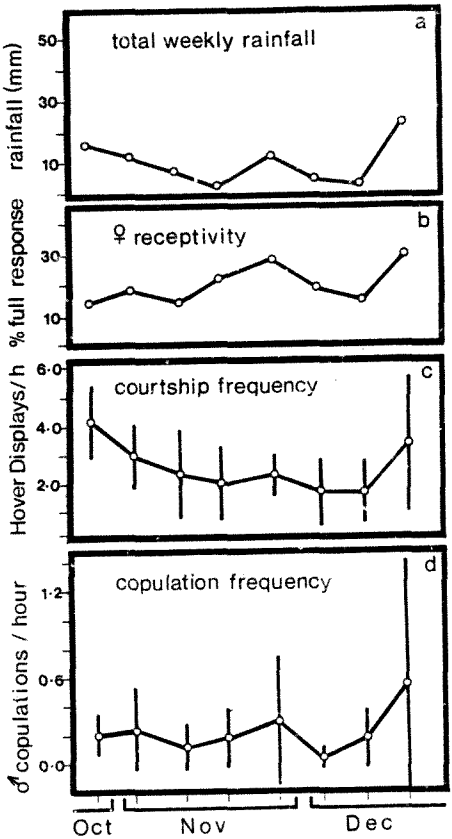


Figure 3.2. Seasonal variation in copulation opportunities in relation to rainfall at the uJobela pin-tailed whydah call-site: (a) total weekly rainfall; (b) female receptivity (% of Hover Displays eliciting full solicitation); (c) courtship frequency; (d) male copulation frequency. Vertical lines indicate ± 1 SD.

Between 55% - 74% of all Hover Displays were terminated prematurely by the displaying male (Table 3.2). There appears to be poor behavioural synchrony between males and females during courtship displays, and PTW males often Supplant females aggressively. In many cases males Supplant unreceptive females, but in a surprising number of cases fully-soliciting, responsive females were also aggressively chased. Since males can only copulate when a female solicits fully, displays eliciting a full response constitute obvious copulation opportunities. To investigate why PTW males passed up such opportunities to fertilize receptive, presumably ovulating females, I first analysed patterns of female receptivity, and then looked at the relationship between receptivity and display outcome.

Table 3.2. Outcomes of sexual displays by male pin-tailed and shaft-tailed whydahs.

Outcome	pin-tailed whydah	shaft-tailed whydah
Male supplants female	382 (43.07%)	---
Male flies off or drops to feeding site in Wing-Shake display	278 (31.34%)	12 (54.55%)
Female flies off or drops to feed	139 (15.67%)	10 (45.45%)
Sexual interference	17 (1.92%)	---
Predator alarm	3 (0.34%)	---
Copulation	68 (7.67%)	---
N =	887	22

Female receptivity

Female solicitation intensity (an index of sexual receptivity) was a strong function of male sexual display duration in PTWs. Hover Display duration and solicitation score were highly significantly linked in 837 displays for which both aspects were known (Spearman rank correlation coefficient $r_s = 0.49$; $P < 0.0001$). However, females also varied seasonally in their receptivity (Figs. 3.2b, 3.3a), and Hover Displays were not always necessary to enhance female responsiveness. At times, females solicited spontaneously on arrival at an occupied call-site, before the male's approach, and did not feed or leave the territory until they had copulated. Payne (1977a) has argued that female steel-blue widowfinches solicit only when they are ovulating, and this may also be true of the other viduines.

At the uJobela site, where data are most complete, seasonal variation in female receptivity showed a mild three week cycle synchronizing with periods of higher rainfall (Fig. 3.2a,b). Rainfall thus appeared to have a mild stimulatory effect on sexual behaviour even in this temperate area. Total weekly rainfall was linked to mean weekly male copulation rate (Fig. 3.2d; $r^2 = 0.67$, $t_6 = 3.47$, $P < 0.02$) and the frequency of competitive female sexual disruptions (Fig. 3.3c; $r^2 = 0.51$, $t_6 = 2.50$, $P < 0.05$; see **Female sexual interference**), although not to the frequency of full female receptivity (Fig. 3.2b; $r^2 = 0.24$, n.s.). Although female receptivity is predictably linked to male copulation frequency ($r^2 = 0.54$, $t_6 = 2.67$, $P < 0.05$), the correlation would have been much stronger had females been able to copulate whenever they solicited fully. However, they were not always able to mate, due to premature termination of display by the male.

Missed mating opportunities and postcopulatory intervals

Failure of males to mate after Hover Displays eliciting a full female response (ranked 3/3) was noted at four PTW call-sites. At the uJobela site (Fig. 3.3b), the male copulated at only 44.5% of 128 such opportunities. Of the other 71 3/3 displays, the male ended the display

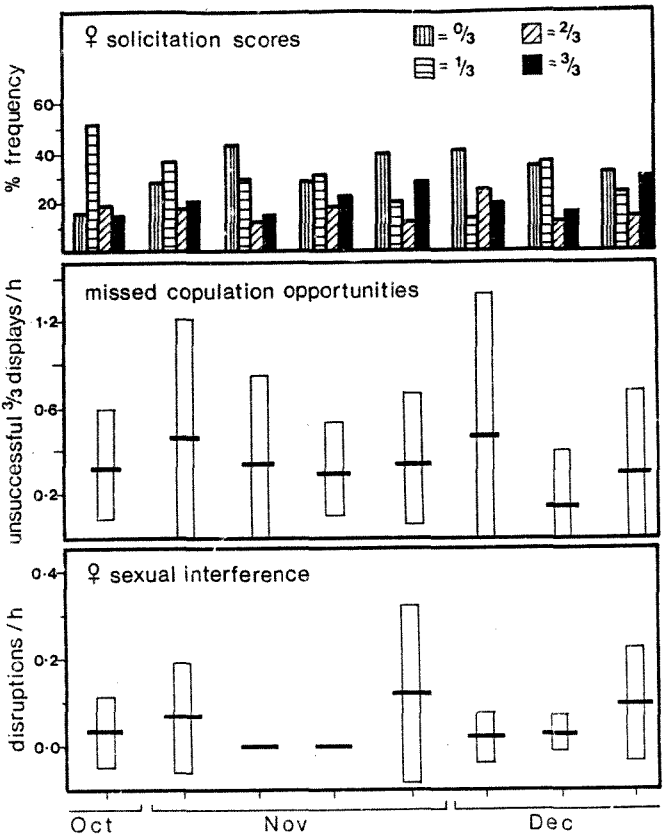


Figure 3.3. Seasonal variation in other sexual behaviour at the uJobela pin-tailed whydah call-site: (a) overall female sexual response; (b) missed copulation opportunities; (c) female sexual interference. In (b) and (c) the horizontal bar indicates the mean, and the vertical bar 1 SD.

in 55 (77.5%). Why should a male pass up 43% (55/128) of his chances to fertilize a receptive, probably ovulating female?

The uJobela male missed at least 13 opportunities to mate in the hour following a copulation, based on activity data. It is difficult to analyse the effect of copulations on subsequent sexual behaviour, partly because mating opportunities are spaced unevenly throughout the day (Fig. 3.1), and partly because sperm transfer cannot be reliably determined in the field. However, even though highly receptive females were often unsuccessful in mating with the uJobela male, their chances of mating were three times better on days with high male copulation rates (Table 3.3; n.s.), not worse as would be predicted if sperm depletion was a factor. If a male's short-term capacity to copulate is adversely affected by high mating frequency, it is not reflected in the ratios of successful to unsuccessful 3/3 displays on days with high and low male copulation rates.

Table 3.3. The probability of a female achieving copulation on days with above and below average male copulation rates at the uJobela pin-tailed whydah call-site.

	Above average		Below average	
Mean ratio of successful: unsuccessful 3/3 displays	2.3 : 1.9		0.6 : 1.6	
SD	1.3	2.1	0.5	1.4
N days	20		22	

$X^2 = 2.12$, df = 1, n.s.

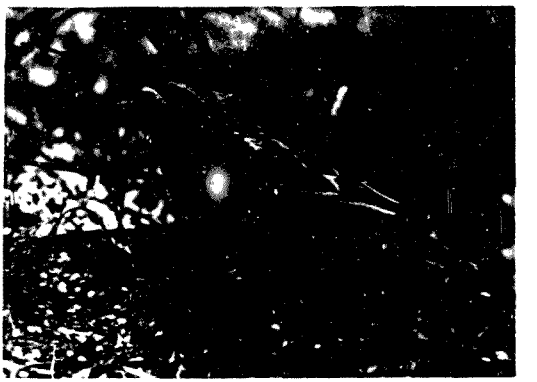


Plate 4. Pin-tailed whydah ♀ DGBDG at the uJobela call-site.

Data on the latency period between copulations by the uJobela male bear out this point. If sperm depletion, or other form of diminished copulation ability was at work, copulation latency should increase after the second and subsequent copulations in an hour. However copulation latency in fact decreased slightly (although nonsignificantly) after the second copulation (Table 3.4), possibly because of the increased stimulation feedback between the male and receptive females.

Table 3.4. Mean copulation latency periods during activity samples with two or more copulations per hour at the uJobela pin-tailed whydah call-site.

	Latency period (min)[1]
After first copulation	
$\bar{x} \pm 1$ SD	35.0 ± 33.4
range	2 - 102
N periods	10
After second and subsequent[2] copulations	
$\bar{x} \pm 1$ SD	28.2 ± 30.0
range	6 - 85
N periods	9

[1] $t_{17} = 0.46$, n.s.

[2] Three latency periods after third copulations, and one after a fourth, were included in this category

Female sexual interference

Attempted disruption of courtship or copulation by intruding birds was noted on 18 occasions at five PTW call-sites. Three disruptions involved intruding males; 15 involved females. Sexual interference by females took four forms, all aimed at the soliciting female rather

than the display. male, and listed here by increasing aggression.

(a) Flying to perch next to the female (N = 7)
(b) Bill-Pointing (N = 4)
(c) Supplanting one or more times (N = 3)
(d) Chasing and pecking (N = 1)

Some disruptions combined two or more elements, and once four females jointly disrupted courtship by simultaneously flying to the soliciting female.

Disruptions appeared to be aimed at preventing other females from copulating with the resident male. Female solicitations ranked 3/3 at the uJobela site were disrupted over four times as often as partial solicitations (5.47% of 128 full solicitations, vs. 1.36% of 513 partial ones; $P < 0.025$). Most disruptions succeeded in ending a Hover Display to another female. At the uJobela site, 13 of 14 attempts were successful; only one display proceeded to copulation despite the intruder's efforts. However, only 31% of the 13 single intruders then solicited after displacing the previous female, and of these, only one female was seen to copulate later that day.

DISCUSSION

Viduine mating systems

Because pin-tailed whydahs and other viduines were conspicuous to early ornithologists, yet led apparently novel sex lives, a number of myths grew up about their mating and breeding habits. It was not until 1907 that Austin Roberts first established that pin-tailed whydahs were parasitic on estrildid finches (Friedmann 1960; Jensen 1971); previous observers had searched in vain for their nests. As common garden birds, PTWs were thought to be harem-polygynous (Jensen 1971:188-189) or even monogamous (Friedmann 1960:99-100; Wing 1956:236), and males were thought to show host nests to females (Jensen 1971:189; but see van Someren in Friedmann 1960:100). Similarly, a misleadingly captioned photograph of paradise whydahs at

a feeding site (Jensen 1971:190) erroneously suggests classical lek behaviour. However, there is no evidence for female-directed group display by any viduine finch, and this study has established a system of call-site based promiscuity for PTWs (quantitatively) and STWs (qualitatively). My data on mating systems accord with both Shaw's (1984) one-season PTW study in Ghana (Shaw observed too few copulations to classify the mating system), and Payne's extensive studies on *V. chalybeata* (Payne & Payne 1977). In terms of the general patterns of male dispersion, site-based sexual display, and promiscuity, there do not appear to be substantive differences between PTWs, STWs, and the widowfinches studied by Payne (see Payne 1973a).

Male mate recognition and sexual competence

It is widely believed that male viduine finches copulate indiscriminately (e.g. Nicolai 1959; Jensen 1971; Payne 1973a:175,182; 1980a), and that the role of selecting a conspecific partner lies with the female. Indeed, interspecific mating attempts and congeneric hybridizations do occur intermittently both in captivity (Nicolai 1959) and in the wild (Payne 1973a:185; 1980a; Hockey & Brooke 1987 and references therein).

However, I saw inappropriate sexual approaches by only three individual immature or unsuccessful adult male whydahs. The large majority of call-site owners, including all males seen to copulate, never misdirected their sexual displays; if they began to approach another passerine, they abandoned the approach rapidly. Adult PTW and STW males therefore do discriminate between conspecific females and other similarly-plumaged species, even in areas where the two whydahs are sympatric. This discrimination appears to be a learned part of the sexual repertoire which may be inexpertly manifested in young males. Nonetheless, where several very similar viduines occur sympatrically, such as widowfinches in parts of southern and western Africa (Payne 1973a, 1980a, 1982, 1985b; Payne & Groschupf 1984), the correct species identification of females may be more problematic for males, as well as human observers (Payne 1973a).

It is a commonly believed corollary of parental investment theory (Parker et al 1972; Trivers 1972) that males, especially in species with *no* paternal care, should copulate with whomever possible since sperm are cheaply produced (for a typically extreme view, see the quote by Dawkins which prefaces this chapter). However, Trivers' (1972) insightful discussion of the consequences of male and fema gamete size has been perversely oversimplified, to the point that spermatozoa are now implicitly regarded as an unlimited resource freely dispensed by indiscriminate males (see attitudes quoted by Dewsbury 1982).

The truth lies somewhat short of this scenario, as recognized by Dewsbury (1982), Avery (1984), Svärd & Wiklund (1986), Rutowski et al. (1987) and workers cited therein. While it is well established both theoretically and empirically that females are generally more discriminating than males, it does not follow that males incur no costs through sexual profligacy. In PTWs, at least, spatial and temporal constraints acting on laying females may contribute to a short-term, temporary inability by males to fertilize them.

The sexual behaviour of PTW males in this study was characterized by low copulation rates and, at least for the intensively studied uJobela male, a high number of missed copulation opportunities. Payne (1973a:24-27; 1977a) has argued that female *V. chalybeata* solicit only when they are ovulating, and this seems to be true of PTWs. If so, males miss a large proportion of their chances to fertilize females. At least four males in my study passed up copulations, and the uJobela male failed to respond to nearly half of the full solicitations by receptive females.

However, this apparently reduced sexual competence (*sensu* Trivers 1972:167-168) was not immediately attributable to sperm depletion. Although the uJobela male often passed up mating opportunities within 2 h of an earlier copulation, missed chances were not clearly associated with rapid serial copulations. Also, copulation latency decreased after a second or subsequent copulation in an hour, rather than increasing as predicted by a sperm depletion hypothesis.

While other explanations for missed fertilization opportunities are possible, such as male choice and rejection of copulation partners, at least 11 of 13 females soliciting unsuccessfully at the uJobela site copulated with this male at other times. Similarly, although a male might avoid multiple matings with the same female in a short period (thereby fertilizing females "thriftily"), this was not the case with the uJobela male. Only one female soliciting unsuccessfully had already copulated with this male in the previous 48 h, and at least five females copulated successfully twice or more in 48 h.

In summary, three lines of evidence suggest reduced male sexual capacity:

(a) missed mating opportunities in over 12% of displays eliciting full female solicitations;

(b) missed opportunities in over 34% (20/58) of such displays occurring < 2 h after a previous copulation;

(c) apparent female competition for fertilization opportunities.

Two weak lines of evidence are inconsistent with sexual incompetence:

(d) a (nonsignificant) decrease in male copulation latencies after a second or subsequent copulation in an hour;

(e) a (nonsignificant) improvement in a female's chances of mating on days with high male copulation rates.

Additionally, two points are incompatible with the hypothesis that males rejected individual females as partners:

(f) at least 11 of 13 fully receptive females ignored by one male copulated with him at some other time;

(g) there was no trend for a male to avoid multiple copulations with the same female within a two day period.

I conclude that the the available evidence favours the possibility of reduced male sexual capacity, or "male sexual incompetence."

These analyses constitute only informal, *a posteriori* tests of the sperm depletion and male choice hypotheses, but I include contrary evidence to illustrate the maxim that things (such as sexual behaviour) are rarely as simple as they seem. In this case, although

my data were gained through intensive study of marked individuals, they are probably either inadequately detailed, or inappropriately structured, to answer questions about the fine-scale patterning of copulatory behaviour. Obviously, definitive tests of the sperm depletion hypothesis must include sperm counts and other physiological tests with captive males.

Although sperm depletion is only inferred here, and not proven, it remains a distinct possibility. As Dewsbury (1982) pointed out, although individual spermatozoa are cheap to produce, the functional unit in the evolution of copulatory behaviour is the ejaculate, which is millions of times more costly. Males simply cannot produce ejaculates continuously, and sperm depletion is possible when demand by females is unusually high. Sperm depletion has been documented in invertebrates, mammals, amphibians, and fish (Dewsbury 1982; Svard & Wiklund 1986; Rutowski et al. 1987) and domesticated birds (summarized by Avery 1984). There are as yet no comparable data for wild birds; the study of sperm limitation in wild populations must normally rely on circumstantial evidence (R. Simmons, D. MacWhirter & G. Hansen unpubl. data). However, there are abundant data on sperm depletion with frequent ejaculation in poultry, as well as correlations of sperm count and fertility (Avery 1984). Therefore, ornithologists' dismissal of the phenomenon in wild birds (e.g. W.D. Koenig *in litt.* to R. Simmons) must result either from simplistic interpretation of the paradigm of differential gamete cost (Parker et al. 1972, Trivers 1972), and/or an unfamiliarity with the relevant literature.

Promiscuity and female competition for fertilizations

The term "promiscuity" has been used to mean many different things, as discussed in several reviews (e.g. Selander 1972; Wittenberger 1979; Oring 1982; Wickler & Seibt 1983). There are two historical problems with its use. First, some authors have objected to its connotations of indiscriminate mating (Oring 1982). Second, most authors have classified mating systems simply by the number of partners of each sex and not by the timing of pairing and duration of association between partners (but see Selander 1972; Wittenberger 1979). In my view, this

has led to a misleading "lumping" of certain mating systems (such as polygyny and promiscuity) which may arise from different ecological circumstances and which should, therefore, be distinguished.

Promiscuity is best regarded as a system of one or more ephemeral, unbonded associations between copulation partners, in the sense of Selander's (1972) terms "mono-" or "polybrachygamy" (one or many brief matings). This obviates the tendency to view promiscuity as a subset of polygamy, which it is not. Promiscuity implies a lack of adaptive "compromises" made by both males and (in nonparental species) females in the pair bonding process; both sexes pursue a simple strategy of looking after their own reproductive interests without postcopulatory ties to each other. This may or may not involve multiple partners. For example, most breeding male whydahs are polybrachygamous while some individual females may only be monobrachygamous. Yet both are promiscuous by the nature of their brief, unbonded association(s). This view contrasts with one in which males of a promiscuous species are "polygynous" while their female partners are "monogamous" or "polyandrous" (e.g. Payne 1973a:28); such an awkward combination is impossible under a temporal classification of mating systems.

It may not be clear why this apparently trivial semantic argument is of interest. Promiscuity, as opposed to various forms of prolonged association, implies a primitive strategy uncomplicated by adaptations for behavioural coordination and cooperation between the sexes (except, of course, for the basic sexual synchrony needed to breed). By contrast, promiscuity as a subset of polygamy seems to imply a derived condition, an "emancipation" of both sexes from a supposed tendency towards cooperative sexual bonding (see, for example, Shaw 1984 and the quote by Murton & Westwood 1977 which prefaces this chapter). I believe that this latter approach is anthropomorphic and misleading, for the following reasons.

Most authors since Lack (1968) have implicitly regarded monogamy as the ancestral avian condition (e.g. Shaw 1984; Beehler 1987). Shaw's (1984) implicit assumption of a derived evolutionary state for promiscuous, nonparental birds such as pin-tailed whydahs (involving a

"dissolution of the monogamous pair-bond") contrasts strongly with the view that mate fidelity and biparental care are instead complex adaptive derivations. Why should brood parasites ever have a pair bond to dissolve (see also Selander 1972:195; Payne 1977b; Yokel 1986)? They also have no parental duties from which to be emancipated. While it is natural and logical to assume, at first glance, that the most widespread trait is the most primitive, this is not necessarily so (see also Selander 1972:194). If pair bond-based mating systems evolved in one or two key groups during the early evolutionary history of birds, and these later branched extensively, other mating systems could be key evolutionary lines without being the sole one. I see promiscuity as resulting from an absence of selective pressures toward cooperation, rather than from elaborate presures toward the "dissolution" of prior adaptations; it is thus a default condition.

Female promiscuity has been explained in a number of adaptive terms, which have recently been reviewed by Halliday & Arnold (1987). These include increased genetic diversity of offspring fathered by different males, and uncertainty of paternity arising from female promiscuity, which ostensibly fosters an increase in paternal care by mating partners. In brood parasites, however, there seems no need to invoke more elaborate explanations than the assurance of egg fertility (see Birkhead et al. 1987). If a single male is unable to copulate with receptive, probably ovulating females, they may seek fertilizations elsewhere. In the case of the uJobela call-site, its isolation made travel to other sites costly and created an unfavourable ratio of females to males, so females competed aggressively for copulations at peak mating times. Females at less isolated sites behaved promiscuously in soliciting from, and copulating with, neighbouring males (see also Shaw 1984). The difficulty of finding suitable host nests at the right stage in a limited area probably puts significant pressure on females to be fertilized rapidly and efficiently (Payne 1977a). However, female parasites may be better able to cope with temporal constraints on nest-finding and egg-laying if they have sperm storage glands, as Birkhead (1987) has shown for the zebra finch, Poephila guttata. The possibility of such an adaptation in the related viduine finches is strong, and merits investigation.

CHAPTER 4. ORNAMENT AND BODY SIZE VARIATION AND THEIR MEASUREMENT IN NATURAL POPULATIONS

> "Females will be selected to respond to a character only if it varies among potential mates."
>
> -- M. Andersson (1982a)

> "The extraordinary variation in tail ornament size, as opposed to naturally selected morphological traits, (needs) to be explained by (more) realistic sexual selection models."
>
> -- R.V. Alatalo et al. (1988a)

ABSTRACT

Measurement of intra-population 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 material and delimitation of populations. The use of museum skins to study variation in male tail ornaments (Alatalo et al. 1988a; Craig in press) may substantially underrepresent the 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 thus 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 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 - 4%.

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 may have the effect of reducing genetic variation in a population over many generations (Fisher 1930, 1958; Lande 1977; Cade 1984), until variation in the ornament is similar to that in naturally selected traits such as limb measurements (Alatalo et al. 1988a). However, some phenotypic variation in ornament size may be preserved if optimal sizes for individual males depend on their body condition (Andersson 1982b, 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 (in press) recently examined museum specimens of seven species of long-tailed birds as a first step towards describing variation in ornament size 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 1982a,b; Lambert et al. 1982; Møller 1988).

Alatalo et al.'s (1988a) and Craig's (in press) contributions to the subject of variation in sexual traits are extremely 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. 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 severely affect the conclusions of these authors, museum surveys can seriously underestimate the degree of within-population variation in sexual characters. As an alternative, field measurements of live animals from specific locales 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 pin-tailed 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 pin-tailed whydah is a promiscuous, brood-parasitic African finch with dispersed, traditional "call-sites" controlled by breeding males (see Shaw 1984; Payne 1985d; Chapter 2). These call-sites are visited by females and other males. Payne (1984, 1985d and references therein) refers to this mating system as a "dispersed lek." This species has four slim, tapered elongated rectrices approximately 4 - 5 times the unadorned tail length (Table 4.1).

RATIONALE AND METHODS

Trapping and measurement methods

Data on body size and ornament length of male pin-tailed whydahs were collected during capture of adults for colour marking. Data from only 20 colour-ringed males are available, since other analyses (Chapters 2 and 3) required intensive study of a small number of individually known males. Although future samples will ideally be more complete, sample size will be limited naturally by intrinsic population size. This should not be seen as a weakness, since females in free-living populations have only a limited number of males from which to choose.

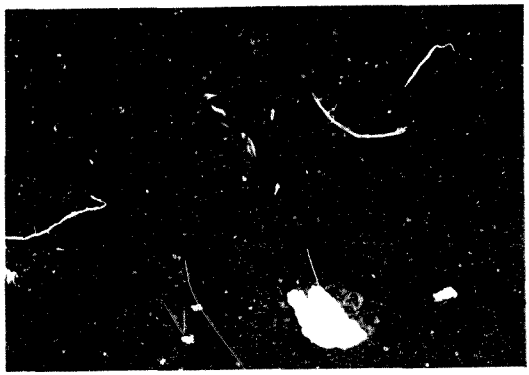


Plate 5. The uJobela male (♂ BWR) with fully grown tail ornament.

Two discrete populations were studied; these are described in Chapter 2. 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 (Table 4.1); only 21 confirmed females (by dissection or observed copulatory behaviour) were used. The following measurements were taken: *mass* - with Pesola spring balance to nearest 0.1 g; *wing* (flattened chord), *short tail* (excluding ornament), *tail ornament* (see below), *tarsus* and *culmen* measurements - all with ruler, to 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, which reflects his genotype, this hypothetical maximum is probably rarely 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 feather abrasion, age (Smith 1965, 1982), and body condition (Andersson 1982b). Some males also grow ornaments much earlier than others (see Fig. 4.1). 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 this factor, I corrected field data on ornament length by standardizing them to a set date, using ornament growth rates of three multiply trapped males (see Fig. 4.2). The standard date chosen (1 November for the temperate area; 1 December for the subtropical area) was an arbitrary, mid-season date representing the time when females are busy mating. Because of this arbitrariness, 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

Pin-tailed 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. 4.1a) and in the middle-to-late breeding season (Fig. 4.1b). In both study areas, males defending call-sites acquire ornaments earlier than nonterritorial 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. Figs. 4.1b and 4.2c).

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 (Fig. 4.2a); the "Hartley" male, caught only twice, averaged 1.74 mm/day (Fig. 4.2b), and the intensively studied "uJobela" male averaged 3.77 mm/day during the growth period, with a subsequent phase of feather abrasion (Figure 4.2c). All males were in rural gardens supplied with ad libitum 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 (Chapter 2).

Within-population variation

Male pin-tailed whydahs in the semi-arid Transvaal population had significantly stouter bills and longer wings than their counterparts in the moist Cape (Table 4.1). 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, $P << 0.01$). Tarsus, wing and short tail lengths showed the least intrapopulation variation (coefficients of variation, c.v.s, ranging from 2 - 4%), while c.v.s for body mass

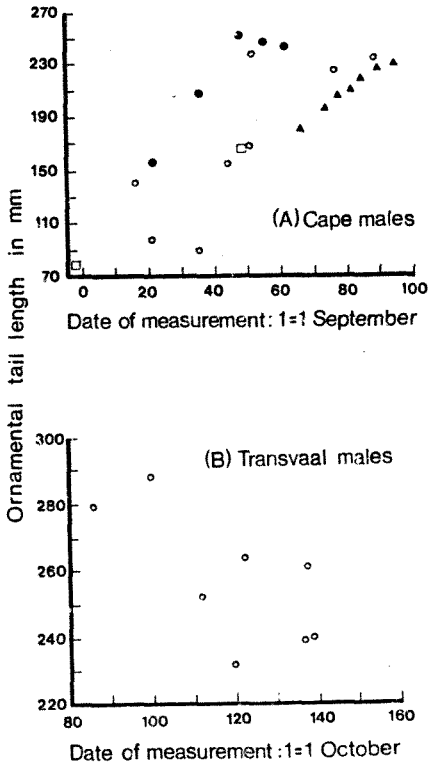


Figure 4.1. Seasonal distribution of uncorrected ornamental tail lengths of male pin-tailed whydahs in the Cape (a) and Transvaal (b) study areas. Triangles: Wilderness male; squares: Hartley male; closed circles: uJobela male; open circles: all other (singly trapped) males.

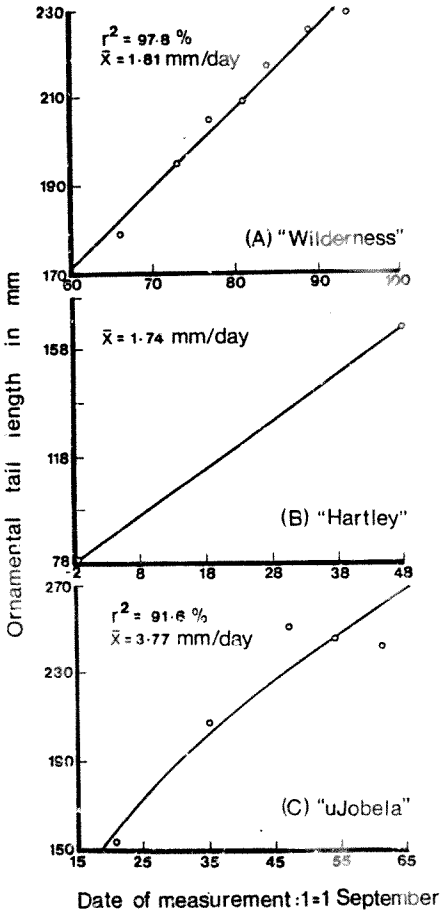


Figure 4.2. Rates of ornamental tail growth of three male pin-tailed whydahs with *ad libitum* food in the Cape study area: (a) Wilderness; (b) Hartley; (c) uJobela.

Table 4.1. Summary statistics of male body size, corrected ornamental tail length, and sexual dimorphism of live pin-tailed whydahs in two populations, 1984-1986.

	Body size characters (mm)						Tail ornament length (mm)[a]	Maximum mass (g)
	Culmen			Tarsus	Wing	Short tail		
	length	width	depth					
Southern Cape Province								
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
N	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
Central Transvaal Province								
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
N	9	7	8	9	8	4	8	9
P <	0.001	0.005	0.01	n.s.	0.02	n.s.	---[c]	n.s.

[a] corrected for date of measurement (see Rationale and methods)

[b] ratio of mean male : mean female measurement (N = 21 females); no data available for Transvaal

[c] not calculable since tail length is standardized to different arbitrary dates in the two areas

and bill measurements were intermediate (Table 4.2). Corrected ornament length was extraordinarily variable in both populations. There were no allometric correlations between ornament length and any body size measure (Chapter 2; cf. Alatalo et al., 1988a; Craig in press), nor between ornament length and male mating success (Chapter 2). By contrast, male shaft-tailed whydahs *V. regia* with experimentally lengthened ornaments were preferred by oestradiol-treated females in a series of choice-pair aviary trials (Chapter 5).

Table 4.2. Coefficients of variation[a] for body size characters and tail ornaments of live male pin-tailed whydahs.

	Body size characters							
Study area	Culmen length	Culmen width	Culmen depth	Tarsus	Wing	Tail	Tail ornament length	Max. mass
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

[a]corrected for small samples (Sokal & Rohlf 1981:59)

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 et al. 1988b; Chapter 3), and the intimidating effect of male plumage, ornaments or body size on competing males (e.g. Peek 1972; Smith 1972; Siegfried 1985; Enquist et al. 1987; Chapter 5). We often assume that phenotypic variation

between males accurately reflects genetic variation, but the real situation is probably not that simple. In the case of sexual ornaments, environmentally induced variation (such as feather wear) adds to the apparent variation due to differences in timing of ornament growth, although the latter may have a genetic component.

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 energy-intensive to obtain than museum measurements of ornament size, they are undoubtedly more accurate and biologically meaningful.

In this study, males which began growing tail ornaments 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 this 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 Chapters 2 and 3). The early sexual readiness of these males may reflect superior nutritional condition, although the ornament growth rates of three wild males with *ad libitum* food varied substantially (Fig. 4.2). It seems likely that stimulation from competing subordinate males mediates the rate of ornament acquisition, via increased plasma concentrations of androgens (e.g. Ralph et al. 1967; Wingfield 1985), but this needs experimental study.

Natural populations and museum surveys

This field study generated coefficients of variation substantially greater than the museum values reported for Euplectes progne by Craig (in press), and similar to, but usually somewhat greater than, those reported for V. Lacroura 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 c.v.s 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). The former 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 pin-tailed whydah reach their full length, sheaths of the emergent feathers turn from bluish to grey, and quickly dry and flake from the base of the rectrix. In both live birds and prepared specimens, the disintegrating sheaths are rapidly lost and it is problematic to evaluate the state of feather growth in study skins more than a few years old. While Alatalo et al. (1988a) were careful to point out that they attempted to measure "only males with intact and fully grown ornaments with no blood quills at the base of rectrices", the study skins they examined were collected between 1843 and 1967. Craig, 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 is risky to classify old study skins with no apparent blood quills as having fully grown ornaments. If some incompletely developed males are included, estimates of within- and between-population 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.

Although the decay of feather sheaths may be a problem for museum studies such as Alatalo et al.'s (1988a), incompletely plumaged males are likely to be underrepresented in museum series anyway. Museum collections often 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 frequency in a population warrants. (Possibly reflecting a similar bias of museum collectors, the series Craig analysed were substantially larger for breeding males than for non-breeding or immature males or females.) 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 locales.

Of course, females (and rival males) are exposed only to phenotypic variation within their home range, and not within huge regions (e.g. W Africa; S South America) of the magnitude grouped by Alatalo et al. (1988a). Similarly, Craig (in press) 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 they represent naturally defined gene pools (cf. Baker 1974, 1975; Payne & Payne 1977; Payne 1981, 1985b; Hafner & Petersen 1985; Baker et al. 1985).

While Alatalo et al.'s (1988a) and Craig's (in press) approach is an important first step in quantifying variation, there is a need for more field studies which explicitly compare males within populations delimited by traits of the animals themselves, rather than by external criteria imposed by taxonomists (see especially Payne & Payne 1977). 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.

CHAPTER 5. SEXUAL DISPLAY AND COPULATION PATTERNS: AVIARY STUDIES

> "With notable exceptions, the study of female choice has limited itself to showing that females are selected to decide whether a potential partner is of the right species, the right sex and sexually mature. While the adaptive value of such choices is obvious, the adaptive value of subtler discriminations among broadly appropriate males is much more difficult to visualize..."
>
> -- R.L. Trivers (1972:165)

ABSTRACT

Controlled aviary experiments on male ornamentation and female sexual response were carried out with a promiscuous, nonparental finch, the shaft-tailed whydah (Vidua regia), in its natural breeding habitat. Oestradiol-treated females, presented with choice pairs of males with widely differing tail lengths, performed copulation-solicitation displays to tail-lengthened males in preference to normal-tailed controls, and to controls in preference to tail-shortened males. However, even though choice pair males were continuously visually isolated, individual males vocalized and displayed more when their tails were lengthened, and less when their tails were shortened. In a short test to distinguish between male activity and tail length, females presented with a long-tailed decoy and a short-tailed live male did not solicit, but spent much more time with live males. I suggest that sexual display activity, as a stimulant to female courtship, is a simpler and more logical explanation for female mating patterns than is phenotypic discrimination of ornament variability or presumed genetic quality.

INTRODUCTION

Darwin's (1871) distinction between the roles of "rival males" and "choosy females" in producing and perpetuating male ornaments has

stimulated intense disagreement, as well as semantic confusion (e.g. Blum & Blum 1979), since its publication. While the importance of competition between males for breeding opportunities is widely acknowledged (e.g. Baker & Parker 1979; Searcy 1982; Avery 1984; Beehler & Foster 1988), the theoretical basis of mate choice has historically been tenuous, and supportive evidence has been lacking (see Huxley 1938; Searcy 1982). Most of Darwin's contemporaries, with the exception of E.B. Poulton (1890), dismissed the concept. Did females of other species really have an "aesthetic sense"? Why distinguish sexual from natural selection? Why attribute some sexual traits (such as genitalia and mammae) to natural selection, and not others (such as weapons)? In many cases, the controversies of Darwin's day have continued, in somewhat modified and more sophisticated form, to the present day.

Despite the landmark work of Fisher (1930, 1958), who postulated a mechanism whereby mate choice could select for phenotypic traits, the other leading evolutionary biologists of this century, Dobzhansky (1937), Huxley (1938), Mayr (1942, 1963) and Lack (1968), all regarded intersexual selection as of little evolutionary significance. Even the coauthor of natural selection theory, Wallace (1889), roundly denounced Darwin's belief in mate choice, and viewed sexual differences in conspicuousness as products of both intrasexual competition and differential selection for predator-avoidance during the breeding season (see also Baker & Parker 1979; Baker & Hounsome 1983; Baker 1985). Athough Wallace invoked erroneous mechanisms to explain male display (see Mayr 1972; Selander 1972), he doubted that females could or would adaptively discriminate between slight variations in male plumage (1889:285-287). He also cautioned against using female mate rejection to infer the existence of mate choice, as in Darwin's (1871) examples of silver pheasant and "widow-finch" (presumably Vidua or Euplectes) males which had lost their ornamental plumes and were rejected as mates. Wallace (1889:286) rightly pointed out that to females, breeding plumage indicates physiological readiness to breed. Ironically, only a century later are Wallace's points earning widespread support among contemporary biologists (Trivers 1972; Partridge & Halliday 1984; but cf. chapters in Bateson 1983).

It remains doubtful whether females can accrue genetic benefits for their offspring through sexual discretion (e.g. O'Donald 1962; Partridge 1980; Boake 1985), rather than gain only immediate ecological resources, or no adaptive advantage at all (e.g. Halliday 1983; Partridge & Halliday 1984). A popular example of apparent female choice of extreme male phenotypes is the already-classic field experiment of Andersson (1982a), who manipulated the tail length of male long-tailed widows *Euplectes progne*, and showed that the territories of tail-lengthened males subsequently had an increased density of nesting females. Tail manipulation apparently did not affect a male's effectiveness at territorial defense. Andersson (1982b) then developed a theoretical model which suggested a link between sexually-selected characters and general phenotypic quality (the "condition-dependent hypothesis;" see also Parker 1982), thus tacitly invoking genetic benefits to offspring of ornamented males. Andersson's (1982a) elegant paper has thus become a textbook example of adaptive female choice, but his conclusions are not thoroughly substantiated by field data, and may therefore be premature.

For example, Andersson (1982a) measured male territorial defense and display rates before and after tail manipulation in single observation periods of only 0.5 h each. Comparisons drawn from these brief periods are unlikely to be meaningful (Morrison 1988; Barnard unpubl. data), even if efforts were made to control for weather and time of day, as they apparently were not. There may also be natural seasonal declines in territorial behaviour as the nesting cycle progresses, a possibility which Andersson does not address. Furthermore, we are told only that test males had "similar" initial tail length and territory quality; no data are presented on these variables, nor on prior mating success. These and other weaknesses (see also Baker & Parker 1983) may be due in part to the enforced brevity of Andersson's *Nature* article; his undeniable ingenuity makes it difficult to criticize seriously his methodology. However, even the best field experiments cannot escape uncontrollable variables; for this reason it is essential to attempt to validate field conclusions in more controlled settings.

Birds that are both promiscuous and nonparental lend themselves particularly well to experiments on the role of sexual selection in the elaboration of male phenotypic traits. First, such animals avoid the potentially complicating effect of prolonged, exclusive sexual associations on their subsequent mating patterns. Because individuals have no direct knowledge of another's previous reproductive success, their mate choice cannot be influenced by the partner's past breeding performance, as it is in monogamous species (Coulson & Thomas 1983; Rowley 1983; Freed 1987).

Second, males and females of nonparental species are characterized by an unusually similar, and minimal, input into reproduction. In brood parasites, maternal investment is limited to egg production and deposition in a suitable host nest, while male investment ceases at mating. We can therefore expect that females are minimally influenced by male-controlled resources (including paternal ability: Searcy 1982; Searcy & Yasukawa 1983; Payne 1984; Simmons 1988), and maximally affected by phenotypic traits of the male himself (Dufty 1986). Also, while the seasonal costs of egg production for female brood parasites should be high, due to the greater egg numbers produced (Payne 1973a, 1976, 1977a; Scott & Ankney 1983), the per-offspring parental investment of female parasites is much less than that of nesting females, and more equal to that of their copulation partners.

These parental investment ratios should significantly influence mating systems and the basis of mate choice (Trivers 1972; Burley 1977), since reproductive discretion is correlated with relative effort. Yet empirical studies of sexual selection in vertebrates normally employ species in which only one sex, usually the female, has an extensive post-fertilization investment in parental care (Payne 1979b, 1984; Arnold & Wade 1984a,b). In lekking species, which have been the focus of much attention (e.g. Bradbury 1981; Bradbury & Gibson 1983; Payne 1984), males contribute only gametes to offspring (Wittenberger 1981) or inseminations to ovulating females (Chapter 3), while females normally bear the cost of raising a brood. By contrast, of the few studies in which investment is more equal between the sexes, most involve monogamous species with biparental care (Burley 1977, 1981,

1986; Burley & Moran 1979; ten Cate & Mug 1984). The relatively low and even reproductive effort in brood parasites may, therefore, provide an unusual counterpoint to our understanding of sexual selection in parental species.

To my knowledge, mating systems and sexual selection have previously been studied with only three homeotherms in which neither sex has a substantial parental investment (see Arak 1983 for anurans; Blum & Blum 1979 and Breed et al. 1980 for invertebrates). All are avian brood parasites: the brown-headed cowbird *Molothrus ater* (West et al. 1981; Dufty 1986; Teather & Robertson 1986; Yokel 1986), the orange-rumped honeyguide *Indicator xanthonotus* (Cronin & Sherman 1977), and the steel-blue widowfinch *Vidua chalybeata* (Payne 1983, 1984; Payne & Payne 1977; Payne & Groschupf 1984). Widowfinches and other viduines exhibit more pronounced sexual dichromatism than other obligate brood parasites, although their size dimorphism is moderate (Payne 1977b, 1984; Chapter 4). While females are sparrowy and inconspicuous, males in breeding plumage have iridescent or brightly colored plumage, some with long, ornamental rectrices. The long-tailed species, such as the pin-tailed (*V. macroura*), shaft-tailed (*V. regia*), and paradise whydahs (*V. paradisaea*), are ideal subjects for sexual selection research. Males are aggressive, have an energy-expensive courtship display, and their plumage ornaments can be easily manipulated for experimentation on the roles of intra- and intersexual selection.

In an effort to pursue Andersson's (1982a) experimental methods further using carefully-controlled aviary conditions, I analysed female responses to super- and subnormal tail lengths in the parasitic shaft-tailed whydah. The tails of breeding male shaft-tailed whydahs are slim and spatulate ($\bar{x}$ = 235 mm, c.v. = 5.7%, N = 12; see Frontispiece). They are proportionally slightly shorter than those of Andersson's (1982a) long-tailed widows (approximately two times body length), but are easier to manipulate in experimental conditions. Furthermore, the whydah's parasitism and promiscuity simplify assumptions about the quality of male-controlled resources, including paternal care.

METHODS

To test the sexual responses of females to experimentally-induced phenotypic variation in breeding males, I conducted aviary trials in which hormone-treated females were presented with a choice pair (Burley & Moran 1979) of identically caged breeding males. Males differed in the length of their tails, which had been artificially lengthened, shortened, or "sham-treated" by standard amounts. Female solicitation responses to these males were scored as an index of differential receptivity to experimental males.

Preliminary experiments

In late April and early May 1985, I ran preliminary trials with a female and four breeding males to judge their responses to captivity and their aggressive/sexual responses to each other. I also established a suitable experimental design for the following year's trials. These birds were released on 5 - 6 May, and a new set of shaft-tailed whydahs was trapped in 1986 for the main experiments.

Main experiments

(a) Test facilities and maintenance of subjects: I conducted 44 trials in March/April 1986, during the height of the local breeding season, in an outdoor aviary (6.0 x 2.8 x 2.2 m) set in Acacia savanna breeding habitat at the Mosdene study site. Four breeding males and four adult females were trapped from call-sites 12 - 18 km from the aviary. As I could not obtain birds known to be unrelated and unfamiliar with each other from distant points outside the study area, I attempted to standardize the degree of likely familiarity by trapping all the birds from the same 8-km stretch of road. Female and male whydahs visit call-sites within a home range of several square kilometres (Chapter 2; see also Payne & Payne 1977; Shaw 1984; Chapter 3), so it is quite possible that individuals in the trials had encountered each other before. However, this would not introduce any systematic bias in the randomized design of the trials, and indeed no female preference for individual males was found (see Results).

Females were housed together in an outdoor holding aviary (1.3 x 0.6 x 0.6 m), and males housed singly in visually isolated, identical experimental cages (1.1 x 0.8 x 0.8 m) within the main aviary. During the experiments, the two males not involved in any one trial were held singly in a quiet outbuilding. Birds were continually supplied with fresh water, millet, the green inflorescences of preferred grasses, termites, and ground cuttlebone. All were acclimated for 17 - 29 days before trials began and adapted quickly to captivity. Colour rings were removed for the duration of the experiments.

(b) Female and male treatments: Females received subcutaneous silicone tubing implants of 17-β-oestradiol (12 mm long, inner diameter 1.6 mm, outer diameter 2.3 mm) along the flank five days before trials began, following Searcy (1984) and Catchpole et al. (1984). On each day males were randomly allocated to one of four treatment groups: tail lengthening, tail shortening, and two sham-treated (cut and reglued) controls. One control bird was used in the day's trials while the other was rested. By chance, some males experienced certain tail treatments more frequently than others, and were involved in more trials. Manipulation procedures followed Andersson (1982a); shortening modified tail length to 125 mm (47% decrease), sham-treatment to 232 mm (1% decrease), and lengthening to 330 mm (40% increase). Male treatments changed daily, so that a tail-lengthened male could be either tail-shortened, sham-treated, or again tail-lengthened the following day. Males were visually isolated at all times.

(c) Trial procedures: In each trial, a randomly selected female was introduced for 100 min into the main aviary with a choice pair of separately caged, tail-manipulated males. I watched trials with binoculars from a darkened hide 14.5 m away, and scored female solicitations (Shaw 1984:Fig. 3a) for classification of trials as "choice" or "no-choice" situations. Criteria for determining a choice were particularly strict. A female had to solicit copulation while perched on one of two perches immediately adjacent to a male; activity on "neutral" perches was disregarded. Simple association with a test male, considered by many other researchers to indicate mate choice (e.g. Burley & Moran 1979; Bischoff et al. 1985; Kodric-Brown 1985;



Plate 6. Female and male (with sham-treated "control" tail) shaft-tailed whydahs in the experimental aviary, showing housing of the male within a test cage, and position of the perch from which a soliciting female was considered to have made a definitive choice. The second test male occupied an identical cage immediately to the left of the picture.

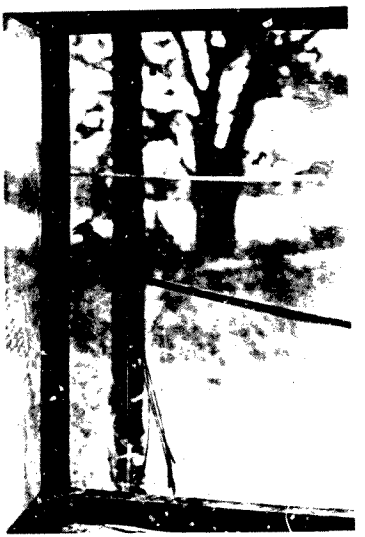


Plate 7. Male shaft-tailed whydah with experimentally lengthened rectrices.

Burley 1986; Shapiro & Dewsbury 1986), was not sufficient. One female was removed when she had not responded to oestradiol treatment after 16 trials, and her data were omitted from all analyses. Subsequent trials were randomized among the remaining females, as insufficient time was available to trap, acclimatize and hormone-treat another.

To analyse sexual display and other activity during trials, I spot-sampled behaviour of the test birds at 1-min intervals (Altmann 1974). Cumulative scores for aggressive flights, sexual displays, vocalizations, and neutral activities (perching, preening, feeding, roosting) were compared for males. During analysis, I knew birds only by a number to minimize any unconscious bias.

RESULTS

Do females choose males with long tails?

Of the 44 trials (Table 5.1), females performed solicitation displays to a single male in 54.5% ("single-choice trials"), to both males in [illegible] ("dual-choice trials"), and to neither male in 36.4% ("no-choice trials"). In single-choice trials, taking trials as independent data points for the moment, females always chose the longer-tailed male of a choice pair (χ^2 = 22.04, df = 1, P < 0.0001). It is, however, more prudent to regard individual females as sample units. The expected cell values for individual females are too small to treat statistically, but the results are extremely clearcut (Table 5.1). When a single choice was made, the longer-tailed male was always chosen. Furthermore, in each trial where a female solicited both males (dual choice), the longer-tailed male was always solicited first and more frequently. Each female followed this general pattern, although a single female (♀ AB18350) was involved in all four dual-choice trials. Females showed neither "side preference" for male position in the aviary (χ^2 tests; n.s.) nor preference for individual males (n.s.), and both male position and tail treatment were fully randomized in any case. Therefore, tail length appeared to have a strong influence on female solicitation patterns, and supernormal tails were preferred to controls of normal length (cf. Andersson 1982a; Møller 1988).

Table 5.1. Individual female sexual responses to tail-manipulated males in choice-pair trials.

Female	Total no. of trials	Choice for: Longer-tailed male	Shorter-tailed male	Neither male	Both males
AB18350	14	6	0	4	4
AB18354	14	11	0	3	0
AB18355	12	7	0	5	0
AA88882*	4	0	0	4	0
Total	44	24	0	16	4

*removed from subsequent experiments due to lack of sexual behaviour; data omitted from analyses

Does tail length influence male display intensity?

However, these results are more complex than they might seem. Individual males given longer tails displayed and vocalized significantly more than their shorter-tailed pairmates, whether control or short-tailed males (Fig. 5.1; Wilcoxon two-sample rank tests using normal approximation with continuity correction of 0.5). This was true even though males were visually isolated and tail treatments changed daily. Taking males individually (Table 5.2), three of four males were significantly more aggressive and active when they had a longer tail than their unseen pairmate, and all males displayed sexually and vocalized more at these times. When shorter-tailed than a pairmate, males spent more time perching, preening, and even roosting. Indeed, some shorter-tailed males appeared to sleep up to 26 mins at a

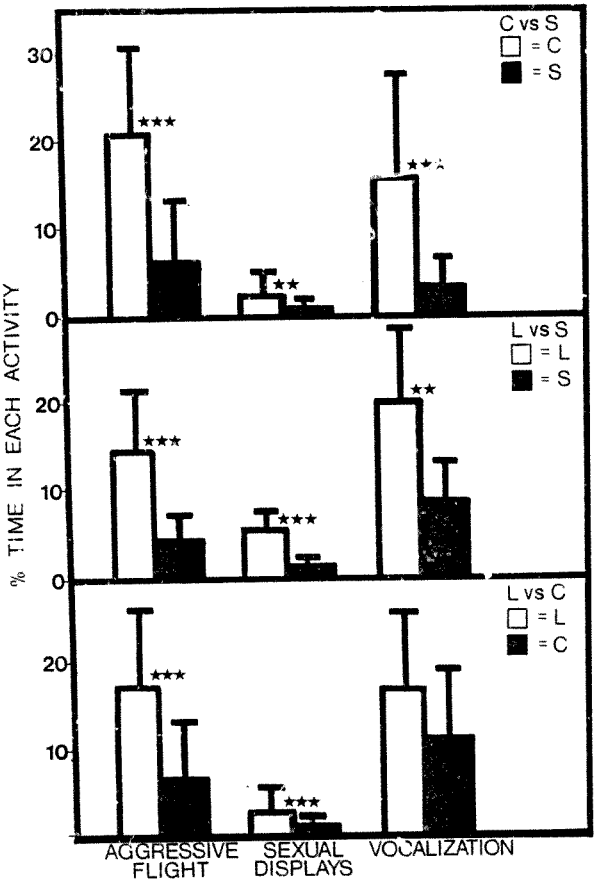


Figure 5.1. Aggressive flights, sexual displays and vocal activity by experimental male shaft-tailed whydahs subjected to different tail treatments.

time during the 100 min trials; longer-tailed males never roosted when a female was present. The behaviour of longer-tailed males was thus characterized by more sexual display, aggression, vocalization, and overall activity.

Table 5.2. Univariate F-ratios summarizing influence of tail length on male behaviour during mate choice trials.

Male	AB18349	AB18353	BB57149	AB18351
Sexual display	8.37**	17.41***	11.90***	4.73*
Aggressive flight	10.04**	1.80	7.70**	6.82**
Vocalization	5.94*	13.92***	7.03**	23.58***
Hopping	0.29	3.63*	1.99	3.53
Total activity score	13.00***	0.57	6.71**	17.81***
Feeding	4.10*	0.41	0.36	0.62
Perching	0.97	0.30	4.15*	4.67*
Preening	0.28	0.02	2.64	2.26
Total inactivity score	7.82**	0.43	4.57*	8.08**
df	2,13	2,21	2,21	2,17

*P < 0.05; **P < 0.01; ***P < 0.001; one-way ANOVA

Do females respond to tail length or display intensity?

Although further time was unavailable, I sought to control male display activity in a short series of four trials by presenting test females with a long-tailed, freshly mounted decoy and a short-tailed live male. The decoy had previously elicited extremely strong aggression from territorial males in the field; from the hide it could not be distinguished from a perched, inactive pairmate. In none of the

four trials did the test female solicit copulation. However, females spent almost three times more time next to the short-tailed live male (χ^2 = 28.08, df = 1, P <0.0001).

DISCUSSION

When given a longer tail than their unseen pairmate, male shaft-tailed whydahs displayed sexually, flew aggressively and vocalized much more than their pairmates, even though tail treatments changed daily and males never saw each other. Whether this is due to male "self-awareness" or feedback via females is unclear, but it should be a simple matter to compare male behaviour in the absence of females. It was apparent during the trials that the presence of a female was a necessary stimulus for male sexual display. In both field and aviary situations, however, males appear readily intimidated by other males, even if the latter can only be heard and not seen (Barnard, unpubl. data; see also studies by Siegfried 1985; Bruce et al. 1988).

Female whydahs in the choice pair tests directed their copulation solicitation displays at vigorously displaying, longer-tailed males. When confronted with a tail-shortened live male and a tail-lengthened decoy, females solicited neither but spent significantly more time near the active, live one. Similar experiments, using males treated with testosterone or mild anaesthetic drugs, should clarify whether display activity or ornament length is more important to females. However, these preliminary data suggest that sexual display activity strongly influences female solicitation patterns, as is the case in fish (Farr 1980; Thresher & Moyer 1983; Bischoff et al. 1985), spiders (Jackson 1981), and other birds (Garson et al. 1980; Bossema & Kruijt 1982; Kruijt et al. 1982; Searcy 1984; Simmons 1988). At the proximate level (Sullivan 1989), this may be due to a differential neuroendocrinological stimulation of females (e.g. Dyson & Passmore 1988).

Female choice and mate recognition

Models of intersexual selection which propose genetic benefits to "choosy" females, via offspring quality (O'Donald 1963; Zahavi 1975;

Borgia 1979; Weatherhead and Robertson 1979; chapters in Thornhill and Alcock 1983), seem intuitively appealing to those of us raised in the adaptationist school. However, current consensus (Searcy 1982; Bateson 1983) points to serious theoretical flaws in "good genes" arguments, chiefly but not exclusively the low heritability of fitness factors, and the dearth of empirical support (cf. Partridge and Harvey 1986). As Wade (1984) says, there is every reason to expect that female mating preferences can be based on entirely arbitrary male traits.

Before the recent spurt of growth in behavioural ecology, articulated by Krebs and Davies (1978), the elaboration of male epigamic features was seen primarily in the context of intermale competition. Mate choice, correspondingly, was viewed by the proponents of the Modern Synthesis (Dobzhansky 1937; Huxley 1938; Mayr 1942, 1972) as a mere byproduct of "selection for interspecific isolating mechanisms" (Kirkpatrick 1984). The concept is now unfashionable, a fact lamented by Partridge and Harvey (1986). Part of the problem appears to be based in the emphasis on "isolation." Partridge and Harvey (1986) remark, "Cases of premating isolation between species that have never met cannot be explained by selection for reproductive isolation." However, a species concept with emphasis on positive recognition of potential mates (e.g. Lambert et al. 1982; Paterson 1985), rather than negative avoidance of hybridization, overcomes this concern. If arbitrary, species-specific sexual traits are important in **facilitating** conspecific reproduction rather than **preventing** gamete wastage (Masters et al. 1987), sympatric or allopatric species are largely irrelevant to the evolution of sexual traits.

In concept, the evolution of arbitrary, species-specific male sexual traits is a relatively simple matter. The subsequent elaboration of these traits, be they ornamental plumage, complex song repertoires or large bodies, is more problematic, as the vast literature attests. However, there is little compelling evidence for the idea that female "choice" is anything more than species recognition and discrimination of reproductively-capable males (Trivers 1972) whose dominance or ability to control resources have been established through intrasexual selection (Beehler & Foster 1988). This parsimonious approach views

male ornaments as primarily male-focused, functioning in territorial defence and mutual intimidation through dominance (e.g Lyon & Montgomerie 1985).

Ornament acquisition and mate choice for high fertility

If there is any adaptive reason why whydah females should actively discriminate against shorter-tailed males when seeking copulations, it is simply that the tails of such males may reflect low fertility and an incomplete physiological readiness to breed. As demonstrated in Chapter 4, adult male whydahs do not all acquire breeding plumage at the same time. Some males are still in prenuptial body moult well into the breeding season, belatedly growing ornamental plumes. These males appear unable to control an established call-site under normal circumstances (see also Chapter 2), and behave submissively in the presence of longer-tailed males. It is likely that these males were the subordinates driven out of a flock in the early breeding season by the dominant, first-moulting male, and that their low dominance status contributed to the delay in moult through social suppression of hormonal development (see also Siegfried 1985). In the mid-breeding season, they may have lower (but increasing) levels of circulating androgens such as testosterone, and possibly smaller testes (see also Møller & Erritzøe 1988). If so, short-tailed males may be discriminated against by females simply because they are not yet fully fertile.

Female parasites such as whydahs are under severe temporal constraints during the breeding season, due to problems involved in synchronizing egg-laying with that of a host pair (see Payne 1977a; Chapter 3). While this should not promote indiscriminate promiscuity, it does suggest that females should be less interested, evolutionarily, in males offering abstract genetic "quality" than in males which can fertilize them rapidly. Intuitively we may suppose that the two are correlated (Andersson 1982b, 1986), but this still awaits empirical confirmation. Both a long tail and a vigorous display should, however, be reliable indicators of prime breeding condition and high fertility to females.

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Ornament acquisition and mate choice for high fertility

If there is any adaptive reason why whydah females should actively discriminate against shorter-tailed males when seeking copulations, it is simply that the tails of such males may reflect low fertility and an incomplete physiological readiness to breed. As demonstrated in Chapter 4, adult male whydahs do not all acquire breeding plumage at the same time. Some males are still in prenuptial body moult well into the breeding season, belatedly growing ornamental plumes. These males appear unable to control an established call-site under normal circumstances (see also Chapter 2), and behave submissively in the presence of longer-tailed males. It is likely that these males were the subordinates driven out of a flock in the early breeding season by the dominant, first-moulting male, and that their low dominance status contributed to the delay in moult through social suppression of hormonal development (see also Siegfried 1985). In the mid-breeding season, they may have lower (but increasing) levels of circulating androgens such as testosterone, and possibly smaller testes (see also Møller & Erritzøe 1988). If so, short-tailed males may be discriminated against by females simply because they are not yet fully fertile.

Female parasites such as whydahs are under severe temporal constraints during the breeding season, due to problems involved in synchronizing egg-laying with that of a host pair (see Payne 1977a; Chapter 3). While this should not promote indiscriminate promiscuity, it does suggest that females should be less interested, evolutionarily, in males offering abstract genetic "quality" than in males which can fertilize them rapidly. Intuitively we may suppose that the two are correlated (Andersson 1982b, 1986), but this still awaits empirical confirmation. Both a long tail and a vigorous display should, however, be reliable indicators of prime breeding condition and high fertility to females.

Breeding shaft-tailed whydahs possess a suite of sexual characters which intimidate conspecific and congeneric males in the field, which appear to influence their self-concept of status (this study: also Hamerstrom 1981), and which also attract and stimulate receptive females. I have argued that female solicitation responses may reflect differential stimulation by vigorous male display, and not necessarily female preference for large ornaments per se (Sullivan 1989 discusses proximate and ultimate explanations of mate choice). There is growing evidence that females respond differentially to males with intense or elaborate displays (e.g. Farr 1980; Jackson 1981; Bossema & Kruijt 1982; Kruijt et al. 1982; Thresher & Moyer 1983; Searcy 1984; Bischoff et al. 1985). This does not mean that ornaments themselves do not have an additive stimulatory effect on females (Brodsky 1988). After all, at the proximate level full-length tails are more conspicuous than short ones, and at the ultimate level these should normally indicate high fertility, as well as the correct species. In nonparental species such as the shaft-tailed whydah, if a male is sexually mature and fertile, possesses the appropriate suite of species-specific traits, and can rapidly stimulate female solicitation, why need we invoke more elaborate adaptive arguments?

CHAPTER 6. SYNTHESIS AND CONCLUSIONS

As might be apparent to the cynical reader, the subject of sexual behaviour and sexual selection in the whydahs affords a look into some of the problems of scientific methodology raised in Chapter 1. While perhaps no scientific enquiry can be entirely free of these problems, research into the evolution of behaviour is especially prone to arguments about causation, the biases of different evolutionary paradigms, and the appropriate levels of analysis. In this concluding chapter, I take a brief look at each of these in turn in the context of this thesis.

Universal causation

Sexual behaviour, more than many other form of behaviour, represents a set of complex interactions between individuals. Some of these reflect adaptive compromises; others reflect constraints on one or more of the participants. Some are genuinely cooperative ventures, such as monogamous breeding in otherwise polygynous taxa (e.g. foxes, Alcock 1979:244), while others still show the "ragged edge" of conflict (e.g. egg-destruction in communally breeding birds, Mumme et al. 1983). There are, plainly, a number of forces at work in the evolution of sexual behaviour in any vertebrate. Why, then, should we assume that specific aspects of a species' sexual repertoire are necessarily attributable to a single evolutionary pressure?

The most obvious example here is the evolution of elaborate male ornaments (Chapters 4 and 5). As with other traits ascribed to sexual selection, ornaments have recently been the focus of prolonged debate. Are they due to the action of female choice (e.g. Zahavi 1975; Andersson 1982a; Møller 1988)? Competition among rival males (reviewed by Searcy 1982)? Advertisement of unprofitability to potential predators (Baker & Parker 1979, 1983; Baker & Hounsome 1983; Baker 1985; cf. Andersson 1983a,b; Lyon & Montgomerie 1985)? Simple species recognition (Lambert et al. 1982; see also Kirkpatrick 1984; Partridge & Harvey 1986)? Even Malte Andersson (1982a,b, 1986), who

is well-known for promoting female choice as a driving force behind ornaments, cautions against simplistic assignment of traits to single causes. In testing Baker & Parker's (1979) hypothesis for the evolution of conspicuous seasonal plumages in birds, he writes (Andersson 1983b):

> "In light of the wide range of life histories and ecology among birds, it seems unlikely that all variation in their coloration is caused by a single major selective pressure. Conspicuous coloration has probably evolved for several reasons, not only those related to predation. As in many other areas of evolutionary biology..., multiple causation may often be important in the evolution of conspicuous coloration, since *risk of predation, hybridization and competition for mates are* not mutually exclusive selection pressures..."

Whydah females are without doubt sexually stimulated by male ornaments, as we saw in Chapters 3 and 5. After all (if for no other reason), the ornament forms an integral part of the visible phenotype of an appropriately mature, conspecific male. But the breeding plumes of viduines may not have evolved through a single mechanism, whether it be the selective action of choosy females, of intimidated rivals, of wary predators, or of conspecific mate recognition. Even if they did, these ornaments may now serve additional functions, complicating the testing of competing hypotheses. This is not to say that study of the evolution of sexual traits is a waste of time. Rather, the distinction between the first two processes, mate choice and sexual competition, remains largely semantic because there are few ways to separate them clearly in the field. In many respects it is fruitless to debate the issue as though the two forces operate in isolation.

Paradigm bias

However, I cannot pretend to remain entirely noncommittal about the mechanisms of sexual selection acting on whydahs, and indeed no-one who has spent thousands of hours in the field watching viduines could. Of the two mechanisms, I have belatedly come to regard male sexual

competition (via intimidating plumage ornaments) to be much more important in whydah mating systems, since male dominance interactions appear to determine control of call-sites, where females encounter mates (see also Payne & Payne 1977; Halliday 1983; Beehler & Foster 1988). [There is yet no evidence that male "floaters" or "sneakers" gain many, if any, copulation opportunities through such a strategy.] Rohwer's experimental work on dominance in sparrows (Rohwer 1977, 1982, 1985, Rohwer & Ewald 1981, Rohwer et al. 1981) has stimulated a series of investigations into the nature and importance of intimidating plumages in birds (e.g. Møller 1987a,b). These imply that dominance interactions are at least as important as female sexual preferences in the evolution of certain types of plumage. In species where badge size or colour alters with age or breeding condition, male badges can be a potent threat to young or subordinate males (Beehler 1988).

Without a call-site, a male whydah is unlikely to breed at all; even with a site he may not copulate more than a few times in his lifetime. The control of a well-watered, grassy and fairly central call-site is most desirable for males, and those with less favourable circumstances must continuously seek better opportunities (Chapter 2) by monitoring the occupancy of preferred sites (see also Payne 1973a; Payne & Payne 1977; Shaw 1984). Males which are in peak breeding condition, aggressive and energetic, stand the best chance of ousting rivals from preferred sites, although it is true that even immature males may temporarily sing and court females from a call-site during the owner's absence. To succeed reproductively in a whydah's world, a male must be pugnacious, sleek and bold, and indeed these words are the most often used by garden birdwatchers to decribe the male pin-tailed whydah.

In the realm of female choice, however, male plumages probably do play a certain role. Two lines of evidence suggest this possibility to me. First, as we saw in Chapter 4, there is substantial variation in the timing of ornament acquisition in pin-tailed whydahs. Shaft-tailed whydah males similarly appear to grow tail ornaments at different times, and in both species this reflects variation in the timing of

overall body moult into nuptial plumage. Early-moulting males seem to acquire the first (and at least in some cases the best) local call-sites, and drive off the later-developing subordinates. Second, there are temporal constraints on breeding females (Chapter 3), so that rapid and assured fertilization is an advantage. Therefore, females copulating with the longest-tailed male in the vicinity are most likely to have chosen a dominant, fully fertile mate. There is, as yet, no need to invoke "good genes" arguments to explain a mating advantage for long-tailed males (see below). I remain open to the possibility of genetic considerations in mate choice but, as stated long ago by Trivers (1972), female choice seems to be adequately explained by choice for the right sex, the right species and sexual maturity. I suspect, however, that females do gain in some situations by choosing dominant males; whether this benefit accrues to themselves or their offspring is still unclear (e.g. Searcy 1982).

Levels of analysis

Brian Sullivan (1989) has recently made the point that ascribing female copulation patterns to "differential stimulation" (Chapter 5; Arak 1988; Dyson & Passmore 1988) is not sufficient reason to discount the action of female choice. In his view, differential stimulation (passive choice) explanations address only the proximate level and not the ultimate evolutionary significance of the sexual response. I strongly agree with Sullivan that the two levels should not be confused, since they address different questions: ultimate causation being found in the realm of evolutionary origins and significance, and proximate causation in the realm of physiological mechanisms and ontogenetic processes. In many ways Sullivan's (1989) comments are analogous to the debate between Jamieson (1989) and Sherman (1989) on whether adaptationist and nonadaptationist hypotheses should be regarded as competing or complementary. The idea that female whydahs choose long-tailed males because they are dominant, fertile, genetically superior, or the correct species (for example), would be an adaptationist hypothesis. Such a choice (if the link could be made) would clearly be adaptive for females. The possibility that females choose long-tailed males because the tails are more scintillating

(e.g. supernormal stimuli) is, by contrast, explicable at the psychological, proximate level. However, as Sullivan (1989) points out, the ultimate reason for such a sensory mechanism must still be addressed.

Intimidation and scintillation: the ornamental plumes of whydahs

Intense sexual display, which is energetically costly for male whydahs, stimulated female solicitation in both field (Chapter 3) and aviary settings (Chapter 5). However, although females solicited tail-lengthened males preferentially to controls and tail-shortened males in the aviary, there was no relationship between ornament length and male mating success in the field. How can these apparently conflicting last two results be reconciled?

First, although there is great variation in ornament length in the field (Chapter 4), the field studies are of males with the natural range of ornaments, while the aviary studies manipulated tail ornaments to an abnormally long and abnormally short length. This situation was purposely contrived to clarify female responses to relatively unsubtle phenotypic differences. Further experiments which I hope to do will, among other things, gradually narrow the differences and increase the number of males presented to females. However, laboratory and field studies can easily generate conflicting results due to the necessarily simplified laboratory environment. After all, the purpose of laboratory work is to isolate otherwise interacting environmental forces, and it is not surprising if this isolation stimulates behaviour that would not occur in the same form in the wild.

One completely unexpected aspect of my aviary work was the finding that manipulating a male's tail affects his perception of his own dominance status. This was true even though males could only hear their rivals, and not see them. To me, this suggested a strong role for male ornaments in intrasexual competition. At the psychological (proximate) level, long ornaments are intimidating to other males, at least as much as they are scintillating to females. If there is a way

of meaningfully comparing the responses of males and females to variation in male ornaments (for example, by comparing percentage change in plasma hormone profiles of males and females exposed to supernormal ornaments), it may be possible to infer the relative importance of intra- and intersexual selection in the evolution of ornaments.

Female choice for male fertility and dominance

Halliday's (1983) review distinguished six forms of mate choice: choice for 1) high fecundity or fertility; 2) immediate gains and parental abilities; 3) resources and high male status; 4) mate complementarity; 5) good physical condition, and 6) the most effective courtship displays. As he notes, few of these forms are mutually exclusive, and prospective breeders may use one or more forms as cues to another (Andersson 1982b). Also, "most effective courtship displays" and to some extent "mate complementarity" lie within the proximate domain, as discussed above (Sullivan (1989). However, Halliday found the evidence persuasive in favour of immediate gains for females, including male characters such as defended resources, effective courtship displays, and high fecundity. By contrast, the invocation of genetic benefits as well as material gains to females (e.g. Thornhill 1980) seems redundant and tenuous (Halliday 1983), in view of the demonstrable and substantial benefits of the latter.

As discussed in Chapter 3, female whydahs face temporal constraints during the breeding season, due to problems involved in synchronizing egg-laying with that of a suitable host. There is thus every reason to expect that female choice should foster fertile, responsive and vigorously displaying males. If a female can simultaneously meet her immediate food and water needs when she visits a call-site, and if possible locate breeding hosts (Chapter 2), her time will be spent economically.

Like an incomplete tail ornament, an incomplete song repertoire (e.g. Searcy 1984) may warn females that a male may be less successful in fertilizing their eggs than a fully-developed breeder. Such cues to

physiological status seem to me much more persuasive, and parsimonious, explanations for female mating patterns than arguments based on hypothetical genetic advantages to the offspring of choosy females (see also Trivers 1972). There is currently no reason to suppose that breeding tail length is strictly genetically controlled, nor that females themselves should benefit even if it is (Halliday 1983). Further data on heritability of plumage characters and relative success of males would be needed before such an assumption could legitimately be made. However, if male physiological responsiveness to environmental cues is genetically based, and if early-developing males acquire choice call-sites through dominance, then the high mating success of males with good call-sites may indeed reflect systematic genetic variation. Female choice of these males as copulation partners may, therefore, have genetic consequences, apparently due to male dominance or tail length.

My studies of whydahs, while frustratingly patchy in many places, have described important, topical, and (to me at least) exciting angles of their sexual behaviour. However, one of my ulterior aims in the drafting of this thesis was to point out that the study of single sexual traits in isolation is never as simple, nor as informative, as it might at first seem. While the experimental isolation of traits is of undoubted utility as a first step, it should not blind us to the complex interactions involved in the evolution of mating systems. We tend to assume that the animal behaviour can be best understood by teasing apart and resolving its component "parts," but we should not then forget that these parts interact additively to form a whole which is normally much greater than the sum. I hope that the material presented and questions raised in this thesis are provocative, and that others will be prompted to join me in the study of this striking and fascinating group of birds.

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Appendix 1. Ecological and spatial characteristics of pin-tailed whydah call-sites in the Cape in 1984.

Call-site[1]	PAMPERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNE/SHB
G 84	1	nd	*Pinus* sp.	4.6	disturbed	*Cynodon*	(1)	nd	nd	nd
			gravestones	1.2	wetland dune	*Eragrostis*				
T 84	3	nd[2]	*Acacia pearsii*	3.2	rural garden near lake	*Cynodon*	(4)	nd	nd	nd
W 84	3	nd[2]	*Acacia pearsii*	nd	rural garden near lake	*Cynodon* artificial	(5)	nd	nd	nd

[1] G = Graveyard; T = Tandy; W = Wilderness

[2] Homestead water, usually freely available

Append x 2. Ecological and spatial characteristics of pin-tailed whydah call-sites in the Cape in 1985.

Call-site[1]	PANPERC	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNEIGHB
G 85	1	nd	*Ficus* sp.	4.6	disturbed	*Cynodon*	(1)	1.61	0.35	BC 85
			gravestones	1.2	wetland dune				1.26	MI 85
H 85	3	nd[2]	*Ficus* sp.	5.0	garden near	artificial	(5)	0.10	0.03	Hb[3]85
			wire	3.6	wetland				0.07	Hc[3]85
HB 85	3	nd[2]	nd	nd	rural garden near river	nd	nd	nd	nd	nd
BS 85	nd	nd[2]	wire	4.0	disturbed wetland dune	nd	nd	nd	0.54	RV 85
									1.24	R 85
R 85	3	nd[2]	wire	4.0	disturbed wetland dune	*Cynodon* *Panicum* composite buds	(3)	4.35	2.05	RV 85
									2.30	BS 85
BC 85	?	nd[2]	wire	4.0	disturbed wetland dune	nd	nd	1.67	0.35	G 85
									1.32	MI 85
MI 85	nd	nd[2]	wire	4.0	disturbed wetland dune	nd	nd	2.58	1.26	G 85
									1.32	BC 85
RV 85	nd	nd	fence	1.4	disturbed wetland dune	nd	nd	2.59	0.54	BS 85
									2.05	R 85

[1] G = Graveyard; H = Hartley; HD = Herd; BS = Bolangvlei Southeast; R = Rondevlei; BC = Bolangvlei Channel; MI = Hexagons; RV = Rondevlei Village

[2] homestead water, usually freely available

[3] three males at this site occupied different corners of a suburban garden; one (Ha) was behaviourally dominant

Appendix 3. Ecological and spatial characteristics of pin-tailed whydah call-sites in the Cape in 1986.

Call-site[1]	PAMPERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNEIGHB
G 86	1	nd	gravestones	1.2	disturbed	*Cynodon*	(1)	3.60	0.35	BC 86
			wire	4.0	wetland dune	*Eragrostis*			3.25	BS 86
						Digitaria				
T 86	3	nd[2]	*Acacia karroo*	nd	rural garden	*Cynodon*	nd	3.50	1.68	U 86
					near lake				1.82	HF 86
H 86	3	nd[2]	*Ficus* sp.	5.0	ga den near	artificial	(5)	nd	nd	nd
			wire	3.6	wetland					
BS 86	nd	nd[2]	wire	4.0	disturbed	nd	nd	5.71	2.45	D 86
					wetland dune				3.26	G 86
D 86	3	nd[2]	nd	nd	pasture	nd	nd	nd	nd	nd
GV 86	nd	nd	wire	4.0	disturbed	nd	nd	nd	nd	nd
					wetland dune					
BC 86	3	nd[2]	nd	nd	disturbed	nd	nd	3.70	0.35	G 86
					wetland dune				3.35	BS 86
HF 86	nd	nd	vine wire	nd	hop fore near	nd	nd	nd	1.30	U 86
					wetland				nd	nd
U 86	3	0.20[2]	fence	1.6	rural garden	*Cynodon*	(5)	2.98	1.30	HF 86
			clothesline	2.0	near wetland	artificial			1.68	T 86

[1] G = Graveyard; T = Tandy; H = Hartley; BS = Bolangvlei Southeast; D = Dathurst; GV = Groenvlei; BC = Bolangvlei Channel; HF = Hopfields; U = uJobela

[2] homestead water, usually freely available

Appendix 4 Ecological and spatial characteristics of pin-tailed whydah call-sites in the Transvaal in 1985.

Call-site[1]	PAN-PERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRST S	GRSAVAIL	COMPOSIT	NND	NME GHB	METPOSIT
NC 85	nd	910	wire	4.0	open floodplain tarred road	*Panicum* *Eragrostis*	5	1.41	0.49	CP 85	2.88
CP 85	3	864	*Rhus pyroides* wire	2.8 4.0	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis*	5	1.16	0.48	NC 85	2.77
CF 85	2	surface	fence wire	1.4 4.0	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis*	5	1.11	0.51	CP 85	3.14
H 85	2	surface	wire	4.0	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis*	5	1.69	0.61	CF 85	4.35
B 85	2	546	wire fence	4.0 1.4	open floodplain tarred road	*Panicum* *Urochlua* *Eragrostis*	5	4.05	1.75	H 85	2.65
EP 85	2	1414	*Rhus pyroides* *A. tortilis*	5.0 3.8	open floodplain	*Panicum* *Urochloa*	(4)	1.59	0.50	N2 85	3.65
H1 85	2	1414	*Rhus pyroides*	4.2	open floodplain	*Eragrostis* *Urac* + *Panicum*	(4)	1.20	0.22	N2 85	4.12
N2 85	3	1852	*A. tortilis* *Rhus pyroides*	3.8 3.6	open floodplain	*Panicum* *Urochloa* *Cynodon*	(5)	0.72	0.22	N1 85	4.43
RP 85	3	1852	*A. tortilis*	3.6	open floodplain	*Panicum* *Eragrostis*	(4)	0.90	0.20	CG 85	4.50
CF 85	2	464	fence *Rhus pyroides*	1.4 nd	open floodplain	*Panicum* *Eragrostis*	(5)	1.18	0.20	RP 85	4.91
GD 85	2	550	*D. cinerea*	3.1 3.2	floodplain-woodland margin	*Eragrostis* *Digitaria* *Panicum*	(5)	5.81	2.90	N2 85	9.38
N 85	1	nd	*A. nilotica* wire	4.2 4.0	agricultural gravel road	*Panicum* *Eneagrogon*	4	nd	1.41	RQ 85	1.51
RQ 85	3	nd	*A. karroo* *A. nilotica*	3.4 3.2	2° *A. karroo* woodland	*Digitar...* *Urochlua*	(2)	nd	1.41	N 85	1.51

(continued)

Appendix 4 (continued).

Call-site[1]	PERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	MND	NNEIGHB	NETPOSIT
VB 85	nd	nd[2]	*A. nellifera*	2.8	*A. karroo* wood-	*Panicum*	nd	3.36	0.95	VE 85	11.20
			fence	2.2	land, dirt road	*Cenchrus*					
						Setaria					
VE 85	nd	nd	fence	1.4	open floodplain	*Panicum*	(5)	2.83	0.95	VB 85	11.45
					dirt road	*Urochloa*					
VW 85	nd	nd	fence	1.4	open floodplain	nd	nd	2.96	1.25	C 85	11.07
					dirt road						
C 85	2	surface	fence	2.2	open floodplain	*Panicum*	(5)	3.08	1.25	VW 85	11.00
						Eragrostis					
PG 85	nd	nd	fence	1.4	disturbed *Termi-*	nd	nd	4.61	1.71	VW 85	nd
					nalia woodland						
PS 85	nd	nd[2]	fence	1.4	agricultural	nd	nd	nd	nd	nd	nd
					dirt road						
NV 85	nd	nd	fence	2.2	open floodplain	nd	(5)	nd	nd	nd	nd
					dirt road						
SC 85	3	0.48	*A. grioloba*	2.8	rural garden	artificial	(5)	nd	nd	nd	nd
			A. nellifera	2.6	near floodplain	*Panicum*					
SS 85	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					tarred road						
MA 85	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					tarred road						
NR 85	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					tarred road						
DW 85	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					tarred road						

[1] NC = Northwest Corner; CP = Central Pan; CF = Central Fence; H = Highway, B = Borrow Pits; EP = East Pan; N1 = Nyl Pan 1; N2 = Nyl Pan 2; BP = Big Pan; CG = Cargnelutti; GB = Graham Dam; N = Nilotica; RQ = Rauch's Quarry; VB = Vogelfontein Bush; VE = Vogelfontein East; VW = Vogelfontein West; C = Cobra; PG = Power Grid; PS = Farm Stall; NV = Nylsvley; SC = Sericea; SS = Silos; MA = MacAdam; NR = Nylstroom Road; DW = David's Widows

[2] homestead water, usually freely available

Appendix 5. Ecological and spatial characteristics of pin-tailed whydah call-sites in the Transvaal in 1996.

Call-site[1]	PANPERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	WND	NNEIGHB	NETPOSIT
GV 86	2	378	*wire*	4.0	2° *Acacia* woodland	*Urochloa* *Eragrostis*	nd	nd	nd	nd	nd
JP 86	3	1400	*Rhus erroides*	2.8	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis* *Cynodon*	3	1.16	0.48	NC 86	7.64
H 86	2	surface	*wire*	4.0	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis*	3	1.69	0.64	CF 86	5.89
MW 86	nd	nd	*wire* *Rhus* sp.	4.0 3.4	open floodplain tarred road	*Panicum* *Eragrostis* *Urochloa*	3	1.85	0.80	B 86	3.97
B 86	2	546	*wire* fence	4.0 1.4	open floodplain tarred road	*Panicum* *Urochloa* *Eragrostis* *Cenchrus*	3	2.55	0.80	MW 86	2.65
EP 86	2	1022	*Rhus erroides* *A. tortilis*	5.0 3.8	open floodplain	*Panicum* *Urochloa*	(5)	0.74	0.24	M1 86	8.69
M1 86	2	392	*Rhus erroides*	4.2	open floodplain	*Eragrostis* *Urochloa* *Panicum* *Cynodon*	(4)	0.46	0.22	M2 86	9.05
M2 86	3	400	*A. tortilis* *Rhus erroides*	3.8 3.6	open floodplain	*Panicum* *Urochloa* *Cynodon*	(5)	0.61 (0.89)[2]	0.22 (0.39)	M1 86 (BP 86)	9.39
BP 86	3	1452	*A. tortilis*	3.6	open floodplain	*Panicum* *Eragrostis*	(5)	0.59	0.20	CG 86	9.25
CG 86	2	464	fence	1.4	open floodplain	*Panicum* *Eragrostis*	(5)	0.79	0.20	BP 86	9.50
GB 86	2	550	*A. cibersa* *A. karroo*	3.1	floodplain-woodland margin	*Eragrostis* *Digitaria* *Panicum*	(4)	3.99	1.09	BD 86	11.91

(continued)

Appendix 5 (continued).

Call-site[1]	PAN-PERM	PANSIZE	CSTYPE	CSWEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	WND	NWEIGHB	NETPOSIT
BL AK	3	457	*A. fortilis*	3.0	floodplain-woodland margin	*Panicum*	(2)	3.04	1.09	GD 86	10.21
			A. farroo	6.4		*Eragrostis*					
						Urochloa					
SF 86	nd	nd[2]	*wire*	4.0	agricultural dirt road	*Panicum*	(4)	7.85	3.40	N 86	1.09
						Urochloa					
N 86	nd	nd	*A. nilotica*	4.2	agricultural	*Panicum*	4	4.81	1.41	RQ 86	1.51
			wire	4.0	tarred road	*Cenchrus*					
RQ 86	3	nd	*wire*	4.0	2[3] *A. farroo*	*Digitaria*	nd	5.86	1.41	N 86	1.51
					woodland	*Urochloa*					
SC 86	3	0.48[2]	*A. mellifera*	nd	rural garden	artificial	(5)	nd	nd	nd	nd
			A. eriloba	nd	near floodplain	*Panicum*					
						Cenchrus					

[1] GV = Great Valley; CP = Central Pan; H = Highway; Mi = Midway, B = Borrow Pits; EP = East Pan; N1 = Nyl Pan 1; N2 = Nyl Pan 2; BP = Big Pan; CA = Cargnelluttis; GS = Graham Dam; BD = Bypass Dam; SF = Small Farm; N = Nilotica; RQ = Rauch's Quarry; SC = Sericea

[2] ( ) = corresponding values after the takeover of N2 call-site in mid-season by o DGYY (previous owner of N1 site)

[3] homestead water, usually freely available

Appendix 6. Ecological and spatial characteristics of shaft-tailed whydah call-sites in the Transvaal in 1985

Call-site[1]	PAN-PROX	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNFISHB	NETFOSIT
RC 85		[2]	nd	nd	2° *Acacia* woodland, tarred road	*Eragrostis*	nd	nd	nd	nd	1.58
MD 85	3	[2]	wire	3.8	homestead/ cattle kraal	*Urochloa* *Panicum*	nd	nd	nd	nd	2.21
RG 85	nd	nd	nd	nd	2° *Terminalia* woodland/farm	*Urochloa*	(2)	nd	nd	nd	nd
V 85	nd	nd	wire	4.0	agricultural dirt road	nd	nd	4.36	1.84	AP 85	1.60
AP 85	3	nd	*A. nilotica* wire	4.6 4.0	open 2° *Acacia* woodland gravel road	*Eragrostis* *Digitaria* *Cenchrus*	4	2.55	0.71	FP 85	0.60
FP 85	nd	nd	wire	4.0	agricultural gravel road	*Eragrostis* *Cenchrus* *Panicum*	nd	3.22	0.71	AP 85	0.80
F 85	nd	nd	*A. nilotica*	6.3 5.8	2° *Acacia* woodland gravel road	*Eragrostis* *Urochloa* *Panicum*	3	3.78	1.36	GG 85	0.30
GG 85	3	nd	*A. karroo* wire	5.0 4.0	2° *Acacia* woodland, gravel rd	*Digitaria* *Brocalos*	4	3.91	1.36	F 85	0.79
L 85	nd	nd	*A. nilotica* *A. karroo*	4.4 4.2	open 2° *Acacia* woodland gravel road	*Eragrostis* *Urochloa* *Cenchrus*	4	6.41	2.55	GG 85	2.66
CD 85	nd	nd	wire	4.0	agricultural tarred road	nd	nd	nd	nd	nd	nd
CC 85	nd	nd	wire	4.0	agricultural tarred road	nd	nd	nd	nd	nd	nd
JN 85	nd	nd	wire	4.0	open 2° *Acacia* woodland	nd	nd	nd	nd	nd	nd
LS 85	3	nd	wire	4.0	agricultural tarred road	nd	nd	nd	nd	nd	nd

(continued)

Appendix 6 (continued).

Call-site[1]	PAN-PERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	WND	WNEIGHB	NETPOSIT
FY 05	nd	nd	nd	nd	agricultural dirt road	nd	nd	nd	nd	nd	nd
JB 05	nd	nd	wire	4.0	agricultural dirt road	nd	nd	nd	nd	nd	nd

[1] RS = RS19 Highway; RD = Rosdene Drive; RG = Rocky Gate; V = Village; AP = Abandoned Pasture; FP = Fallow Pasture; F = Fork; GG = Gravel Gate; L = Locatie; CB = Cornfield; CC = Cisticola Corner; JN = Junction; LS = Lake Superior; FY = Flyer; JB = Jabula

[2] homestead water; usually freely available

Appendix 7. Ecological and spatial characteristics of shaft-tailed whydah call-sites in the Transvaal in 1986.

Call-site[1]	PAN-PERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNEIGHB	NETPOSIT
SF B6	nd	nd[2]	*A. karroo*	3.8	agricultural dirt road	*Panicum* *Urochloa* *Eragrostis*	(4)	4.31	0.83	AP B6	0.89
AP B6	3	nd	*A. nilotica* wire	4.6 4.0	open 2° *Acacia* woodland gravel road	*Eragrostis* *Digitaria* *Cenchrus*	3	3.93	0.83	SF B6	0.75
F B6	nd	nd	*A. nilotica*	6.3 5.8	2° *Acacia* woodland gravel road	*Eragrostis* *Urochloa* *Panicum*	3	4.46	1.36	GG B6	0.30
GG B6	3	nd	wire *A. nilotica*	4.0	2° *Acacia* woodland, gravel rd	*Digitaria* *Urochloa*	4	3.91	1.36	F B6	0.29
L B6	nd	nd	*A. nilotica* *A. karroo*	4.4 4.2	open 2° *Acacia* woodland gravel road	*Eragrostis* *Urochloa* *Cenchrus*	nd	6.41	2.55	GG B6	2.66
DT B6	nd	nd	wire	4.0	agricultural/ *Combretum* woodland, dirt road	nd	nd	nd	nd	nd	nd
CD B6	nd	nd	wire *A. karroo*	4.0 nd	agricultural tarred road	nd	nd	nd	nd	nd	nd

[1] SF = Small Farm; AP = Abandoned Pasture; F = Fort; GG = Gravel Gate; L = Locatie; DT = Detour; CD = Cornfield

[2] homestead water, usually freely available

Appendix B. Ecological and spatial characteristics of paradise whydah call-sites in the Transvaal in 1985.

Call-site[1]	PAN-PERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNEIGHB	NETPOSIT
GV 85	2	3	nd	nd	2° *Acacia* woodland, tarred road	*Brachiaria* *Eragrostis*	nd	nd	nd	nd	nd
E 85	1	73.5	no	nd	floodplain-woodland margin	*Panicum* *Eragrostis*	(2)	6.00	2.79	MP 85	2.84
MD 85	3	nd	nd	nd	homestead/cattle kraal	*Brachiaria* *Panicum*	(3)	4.40	2.00	MR 85	3.20
MP 85	3	nd	wire *A. karroo*	4.0 nd	2° *Acacia* woodland, tarred road	*Brachiaria* *Eragrostis*	(3)	2.98	0.58	MR 85	3.64
MR 85	nd	nd	wire	4.0	2° *Acacia* woodland, dirt road	nd	nd	2.58	0.58	MP 85	3.75
S 85	nd	nd	wire fence	4.0 1.4	agricultural dirt road	*Coleria* *Brachiaria* *Cenchrus*	(4)	5.01	2.50	MR 85	6.56
V 85	nd	nd	wire	4.0	agricultural gravel road	nd	nd	3.89	1.51	AP 85	1.87
D 85	nd	nd[2]	wire	4.0	homestead dirt road	nd	nd	nd	nd	nd	nd
AP 85	3	nd	wire *A. nilotica*	4.0	open 2° *Acacia* woodland gravel road	*Eragrostis* *Digitaria* *Cenchrus*	4	2.21	0.60	FP 85	0.92
FP 85	nd	nd	wire	4.0	agricultural gravel road	*Eragrostis* *Brachiaria* *Cenchrus*	nd	1.54	0.60	AP 85	0.60
BT 85	nd	nd	wire	4.0	agricultural gravel road	nd	(2)	2.61	0.91	FP 85	2.30
F 85	nd	nd	*A. nilotica*	5.0	2° *Acacia* woodland gravel road	*Eragrostis* *Brachiaria* *Digitaria*	3	2.81	1.00	GG 85	0.41
GG 85	3	nd	wire *A. karroo*	4.0 5.0	2° *Acacia* woodland, gravel rd	*Digitaria* *Brachiaria*	4	3.59	1.00	F 85	0.30

(continued)

Appendix 8 (continued).

Collsite[1]	PANPERM	PANSIZE	CSTYPE	CSHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	MND	MNEIGHB	METPOSIT
L 85	nd	nd	wire	4.0	open 2° *Acacia* woodland gravel road	*Eragrostis Brachiar Cenchrus*	4	6.14	2.59	GG 85	2.40
N4 85	nd	nd	nd	nd	agricultural tarred road	nd	nd	nd	nd	nd	nd
NR 85	nd	nd	wire	4.0	agricultural tarred road	nd	nd	nd	nd	nd	nd
HL 85	nd	nd[2]	*Acacia* sp.	nd	2° *Acacia* woodland, homestead	nd	(2)	nd	nd	nd	nd

[1] GV = Great Valley; E = Everglades; MD = Mosdene Drive; MP = Mud Pools; MR = Mosdene Road; S = Sunflowers; V = Village; D= Depot; AP = Abandoned Pasture; FP= Fallow Pasture; BT = Black Turf; F = Fork; GG = Gravel Gate; L = Locatie; N4 = Nylstroom 40; NR = Nylstroom Road; HL = Hamlet

[2] homestead water, *usually freely available*

Appendix 9. Ecological and spatial characteristics of paradise whydah call-sites in the Transvaal in 1986.

Call-site[1]	PERM	PANSIZE	CSTYPE	COVHEIGHT	HABITAT	GRSTYPES	GRSAVAIL	COMPOSIT	NND	NNEIGHB	NETPOSIT
MP 86	3	nd	wire	4.0	2° *Acacia* wood-	*Urochloa*	nd	3.50	0.58	MR 86	3.50
			A. karroo	nd	land, tarred road	*Eragrostis*					
MR 86	nd	nd	wire	4.0	2° *Acacia* wood-	nd	nd	3.08	0.58	MP 86	3.82
					land, dirt road						
S 86	nd	nd	wire	4.0	agricultural	*Chloris*	(4)	5.42	2.50	MR 86	8.55
			fence	1.4	dirt road	*Urochloa*					
						Cenchrus					
H 86	nd	nd	wire	4.0	agricultural	nd	nd	6.30	2.80	AP 86	6.61
					gravel road						
AP 86	3	nd	wire	4.0	open 2° *Acacia*	*Eragrostis*	3	4.30	0.76	SF 86	0.89
			A. nilotica	4.6	woodland	*Digitaria*					
					gravel road	*Cenchrus*					
SF 86	nd	nd[2]	wire	4.0	agricultural	*Panicum*	4	4.18	0.76	AP 86	0.75
					gravel road	*Eragrostis*					
F 86	nd	nd	*A. nilotica*	5.0	2° *Acacia*	*Eragrostis*	3	4.54	1.00	GG 86	0.41
					woodland	*Urochloa*					
					gravel road	*Digitaria*					
GG 86	3	nd	wire	4.0	2° *Acacia* wood-	*Digitaria*	4	3.59	1.00	F 86	0.30
			A. nilotica	nd	land, gravel rd	*Urochloa*					
L 86	nd	nd	wire	4.0	open 2° *Acacia*	*Eragrostis*	nd	6.14	2.59	GG 86	2.46
					woodland	*Urochloa*					
					gravel road	*Cenchrus*					
SW 86	nd	nd	wire	4.0	*Terminalia* wood-	nd	nd	nd	nd	nd	nd
					land, gravel rd						
BU 86	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					gravel road						
I 86	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					gravel road						
PS 86	nd	nd	wire	4.0	agricultural	nd	nd	nd	nd	nd	nd
					gravel road						

[1] MP = Mud Pools; MR = Mosdene Road; S = Sunflowers; H = Harolong; AP = Abandoned Pasture; SF = Small Farm; F = Fork; GG = Gravel Gate; L = Location; SW = Singlewood; BU = Built; I = Zeekoe; PS = Parys

[2] homestead water, usually freely available

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