Sexual selection in the sex-role reversed Eurasian dotterel

*Charadrius morinellus*

Thesis submitted for the degree of Doctor of Philosophy at the University of Leicester

by

Ian Peter Farrar Owens B.Sc.
Department of Zoology
University of Leicester

November 1991
To my parents
'There is only one first time. It was June 1933 - a sunny morning with a strong southerly breeze - and a pair of dotterels were running over a great mossy lump of hill in the Grampians. As I lay watching them I could almost hear the warm voice of the old Irish Naturalist saying that he envied me because I had not yet met dotterels on the hill.....

...1934 was my honeymoon year with the dotterels. I only wish that I now understood as much about them as I then thought that I did! The first year of a new field project is particularly rewarding. Each week - almost every day - you learn fresh and unexpected facts. Everything seems so easy and fulfilling. But understanding and interpreting takes much longer. Much longer. Each problem solved reveals more, usually more complex and equally intriguing. That is what research is about and that is why we do it. Eager young dotterel watchers will thus continue to discover new slants and new meanings. We have not yet reached the end of the beginning.'

ABSTRACT

Sexual selection in the sex-role reversed Eurasian dotterel,
Charadrius morinellus.

Ian P F Owens. Department of Zoology, University of Leicester, Leicester LE1 7RH, UK.

Current theory concerning the evolution of parental care posits that one or both of the sexes may reduce parental care when the fitness gained from alternative reproductive opportunities exceeds that from continuing with parental care. If this situation leads to a difference between the sexes in potential rate of reproduction, intra-sexual competition for mates will occur in the sex with the higher potential reproductive rate, and the other sex will display mate choice (called inter-sexual selection).

In the majority of avian species biparental care is the most common form of parental care. Polygyny is the most common consequence of polygamy; males compete for access to females and females exercise mate choice. Sex-role reversal is rare (ca. 3% of species in the world) but presents an opportunity to test the basis of theories of the evolution of parental care and sexual selection.

This thesis presents the results of a three-year study of sexual selection and sex-role reversal in a breeding population of the Eurasian dotterel, Charadrius morinellus, in the Cairngorm region of Scotland. In this species, the female is the competitive sex and the male usually provides all of the parental care; females are sequentially polyandrous.

Dotterel are dependent on a widely dispersed breeding habitat. Rather than defending territories, females compete for access to males on mating arenas (Chapter 2). After producing a clutch, females return to the arenas in order to compete for further males, this leads to a female-biased skew in the operational sex ratio (Chapter 3). The proximate factors which produces the skew in the sex ratio predict the temporal variation in the potential for sexual selection (Chapter 3). There is considerable intra-sexual plumage variation which is correlated with behavioural variability (Chapter 4). Bright females are more aggressive than dull females and thus initiate and win more fights (Chapter 4). Bright females also perform more courtship than do dull females and therefore get mates earlier in the season, as, via assortative mating, do bright males (Chapter 4). Females are, however, also the more choosy sex; females prefer to court bright males which are, in turn, likely to be in better physical condition than duller males (Chapter 4). Bright males are less likely to desert the clutch in bad weather conditions (Chapter 5). Females therefore appear to choose males on the basis of their ability to incubate their clutch. Male dotterel, because of their high level of parental care and relatively low potential rate of reproduction, are expected to exhibit behaviour which has been selected to protect their paternity. This prediction is upheld; male dotterel assure paternity of the brood for which they care through a combined strategy of prolonged, close mate-guarding and strategically timing copulations to the few days immediately before egg-laying (Chapter 6).

Active female choice for male quality related to phenotypic traits which are also influenced by the environment is contrary to the predictions of the conventional theory of mate choice. In sex-role reversed species, because the potential reproductive rate of the male is lower, male choice is expected. A new model of mate choice is introduced and used to study the effects of differences between the sexes in both the relative potential reproductive rate and relative variation in mate quality (Chapter 7). This model is successful in predicting the form of mate choice observed for all permutations of variation in potential reproductive rate and mate quality. Finally, sex-role reversed mating arenas are compared with polygynous lekking (Chapters 3, 4, 7). Constraints on the potential reproductive rate of females determine that the direction of mate choice will only rarely be reversed in non-territorial sex-role reversed species (Chapter 7). Therefore, although the mating arenas of dotterel resemble leks, an important component of true lekking, active mate choice by the non-competitive sex, is absent.
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This project was supported financially by a CASE award from the Natural Environment Research Council and the Nature Conservancy Council for Scotland. I am grateful to Prof. H. C. MacGregor and the Department of Zoology at Leicester for providing excellent facilities during the winters and whilst I was writing up and the NCCS for allowing me to be part of their 'Mountain Plateau Ecology Project', to use their equipment and for providing me with a vehicle for field work during the summers. I am also very grateful to Mr. J. Dibbins, the owner of Glenfeshie Estates, who generously allowed me to work and camp on his land, and to his head stalker, Aide Dempster, and family who frequently went out of their way to allow me to watch dotterel and always had a Scottish word for me.

The idea to work on dotterel was (mis)conceived by my two supervisors, Terry Burke and Des Thompson. During the gestation of this thesis they have, in their very different ways, taught me an immense amount about subjects as diverse as exploding (“but bloody efficient!”) petrol stoves to pre-historic heaps of greenshank pellets. It is rare that they have not got an opinion on a subject and they always enjoy an argument. Most importantly though, they have provided a lively atmosphere within which to learn. I am also grateful to them for their efforts in deciphering previous drafts of this thesis. The remaining prejudices and mistakes are my own.

The field work would, literally, not have been possible without the enormous help that the NCCS's 'dotterel team' gave me in the summers of 1988 to 1991. Keith Duncan, Rik Smith, Phil Whitfield, Sue Holt, Hector Galbraith, Stuart Murray, Stuart Rae and Torstein Solhoy have spent days talking to me about dotterel and montane ecology. It is no overestimate to say that in the summer of 1988, which was a preliminary field season, Keith taught me the majority of what I now like to think I know about dotterel. In the subsequent three years he also taught me nearly all I know about vegetation and, in partnership with Rik, everything I will ever need to know about 'Jocks'. I was also lucky enough to have a number of field assistants during the summers. Ian Henderson and Dave Currie were inexhaustible aids at crucial times in the 1989 and 1990 seasons, respectively. David Thomson didn't learn so quickly and stayed with me for the most of both the 1989 and 1990 field seasons; he and Anna Sørenson contributed enthusiastically to my data collection, ideas, prejudices and general lunacy. Thanks for your help Dave.

Back in Leicester, and during travels from there, I have benefitted from the ideas of an enormous number of people. Amongst these Ian Hartley, Ian Henderson, Sean O'Malley, Mike Bruford, Dave Currie, Andy Dixon, Mike Ritchie, Ken Norris, Andrew Pomiankowski, Geoff Parker, Pim Arntzen, Olivier Hanotte, Phil Whitfield, Fiona Hunter, Ben Sheldon, Anders Møller, John Atle Kålås, Rauno Alatalo, Lew Oring, Dov Lank, Graham Rowe, Iris van Piljen, Paul Hart, Frank Clark, Marion Petrie, Sue McCrae,
Andrew Balmford, John Reynolds, Steve Albon, Maimie Thompson, Adam Watson and my two examiners, Tim Clutton-Brock and Robert Semeonoff, have all taken the time to personally influence the work in this thesis. Steve, Ted, Lesley, Penny, Maurice, Jean and Ian have tirelessly helped with equipment and computing. Dr. J. Watters, Dr. M. J. Phillips and Mr. B. English from the Department of Mathematics and John Beckett from the Computer Centre helped me with statistics and models without laughing (too much). The staff of the Ornithological Section (Tring) of the British Museum of Natural History welcomed me back and allowed me to root through their collection (again).

I owe a longer standing debt to all the members of the Knaresborough Ringing Station, particularly John Mather and Peter Treloar, who shared their experience with me and taught me a great deal about birds both in the hand and in the bush. This education was later augmented by John Gittens on Hilbre Island who gave generously of his time and unique humour.

I have lived in the same house as Ian Hartley for three years. We have also shared the same office - for too long. That we are still good friends, and that he has contributed probably more than anybody else to this thesis speaks volumes that his reputation is not totally deserved! Dr. Ian & Laura, Sean & Joe & Megan & Jason, Sarah & Tom, Mike & Claire, Dave, Andy & Nick & Ryan, Tim, Colin, Steph and all the other members of the department have been excellent company and great friends. These, along with Sue, have helped keep me very happy or at least told me that I ought to be. I am grateful to all of them.

At the other end of the chronological scale are my newer friends in London. The Ecology Group at the Institute of Zoology and the Department of Genetics and Biometry at University College London have provided me with excellent facilities between leaving Leicester and finally finishing this thesis. Tony Flint and Steve Albon have provided funds as well as encouragement. I am extremely grateful to Josh, Pomm, Steve, Elizabeth, Sarah, Georgina, Mel, Andrew and Anders who have helped me through - especially Josh who stopped me from wallowing. On the home front, thanks to 'Arry and Tiny who have put up with a lot of financial and emotional hassle in the last couple of months and always managed to see the humourous side. The most significant factor though in my progress has been Sally - only she knows how much she has done for me - I hope she also knows that I appreciate how fortunate I am to have her friendship.

Lastly, I am indebted to my parents, to whom this thesis is dedicated. They have been continually supportive and interested in everything I have done despite my own irritability. I am grateful not only for this, but also for their efforts to help me learn to take the opportunity to enjoy my life fully. As our ideas converge I appreciate their wisdom more and more; but will probably not admit it again.
CHAPTER 1 Introduction

1.1. SEXUAL SELECTION

The wide applicability of Darwin's theory of 'evolution through natural selection' not only allowed him to explain the vast majority of phenomena he observed in living forms, but also enabled him to focus more accurately than anyone had previously been able to on the two anomalies of evolution that required further theoretical work: sexual selection and altruism (Darwin 1859). Darwin coined the term sexual selection to explain the evolution of characters that gave an individual an advantage over other individuals of the same sex and species exclusively in relation to reproduction (Darwin 1871). Darwin recognised the importance of both intra-sexual (competition for mates) and inter-sexual (choice of mates) selection. Despite this, with only a few notable exceptions (e.g., R. A. Fisher, J. B. S. Haldane, G.C. Williams), little attention was paid to sexual selection until over one hundred years after Darwin had initially sketched out the process in *The Origin of Species*. Sexual selection has, however, more recently become a focus for many biologists interested in topics in evolution and the research field is highly productive (e.g., reviews in Bradbury & Andersson 1987; Krebs & Davies 1991).

Darwin also noted the most obvious manifestation of sexual selection - sexual dimorphism. However, despite observing the 'conventional' sex-roles in which the male is the competitive sex and the female more selective, he did not comment further on how this situation might have occurred. It was Bateman (1948) who, whilst studying the distribution of the number of matings obtained by male fruit flies *Drosophila melanogaster*, realized that anisogamy may result in competition between male gametes for female gametes. Thus, by extrapolation, he explained the competitive nature of males. Williams (1966) developed this theory to include parental care as well as gamete size. Williams realized that the relatively small amount of parental care supplied by males in many species meant that they would compete for access to females in order to increase their fitness. Similarly, the high expense of each reproductive effort to the female gives rise to females becoming selective when choosing with which male to mate.

In one of the most important papers post-Darwin on evolution, Trivers (1972) produced a new synthesis of the theory of parental care. His main breakthrough was to introduce the concept of 'parental investment' (PI) which he defined as 'any investment by a parent in an individual offspring that increases the offspring's chance of surviving at the cost of the parent's ability to invest in other offspring'. This allowed him to develop a more accurate currency for the force of sexual selection - the relative parental investment of the sexes.

This revised theory of sexual selection remained fallible, however. Trivers' synthesis copes well with the conventional situation of relatively higher female PI resulting in male-
male competition and female choice, but stumbles when relative male : female PI nears parity or male PI exceeds that of the female. Trivers (1972) predicted that 'where male parental investment strongly exceeds that of the female (regardless of which sex invests more in the sex cells) one would expect females to compete among themselves for males and for males to be selective about whom they accept as a mate'. However, in species such as the three-spined stickleback, Gasterosteus aculeatus, and greater rhea, Rhea americana, males supply the majority of parental care once the eggs have been laid, and, so it may be argued that relative paternal investment is greater than maternal investment. If this is actually the case, the elegance of Trivers' model is dulled because in both these species the male remains the competitive sex.

In 1977, Emlen and Oring published a paper in which they suggested that it was the availability of alternative reproductive opportunities that was the crucial factor in determining the form of sexual selection. This theory was supported in two extensive theoretical reviews by Sutherland (1985a, 1987) catalysed by his reanalysis of Bateman's data on fruit flies (Sutherland 1985b). The theory was further investigated by Clutton-Brock and Vincent (1991) who, noting that relative PI was often difficult to measure in nature, specifically identified 'potential reproductive rate' as the crucial factor in determining which sex is the competitive sex. This argument is consistent with the observations of (i) male competition in species with conventional sex-roles, (ii) male competition in pseudo-sex-role reversed species such as the three-spined stickleback and American rhea mentioned above, and (iii) female competition in sex-role reversed species of pipefish (Sygnathidae), phalaropes (Phalaropus), and the spotted sandpiper, Actitis macularia, and Eurasian dotterel, Charadrius morinellus.

1.2. SEX-ROLE REVERSAL

Over 80% of bird species show monogamous, bi-parental care (Lack 1968). Even in species in which polygamy occurs regularly (see Oring 1982; Davies 1991 for definition), most individuals may actually be monogamous with respect to parental care (Mock 1983; Gowaty 1985). The evolution of polygamy has been traditionally analysed in terms of the costs and benefits of desertion (Dawkins 1976). Desertion by one or both sexes is expected to occur when the fitness gained from alternative reproductive opportunities exceeds the expected reduction in fitness gained from the present brood that would result from reduced parental care (Emlen & Oring 1977; Maynard-Smith 1977).

Sex-role reversal occurs in less than 5% of all bird species (Lack 1968; Oring 1982; Clutton-Brock 1991). Nevertheless, many workers have realized the potential of both reversed sex-roles and polyandry for testing hypotheses on the evolution of mate desertion. Non-cooperative polyandry is typically associated with uniparental male care of the offspring. The evolution of male-only care is fundamental to the understanding of sex-role
reversal. Seven general hypotheses have been suggested to account for the evolution of male-only care and female desertion (reviewed by Erckmann 1983; Lennington 1984; Kâlâs 1987; Oring 1985; Clutton-Brock 1991). These are now listed.

1. **The exhausted female hypothesis.** Males are able to care for the clutch but females cannot do so because they are nutritionally stressed as a consequence of egg-laying (Nethersole-Thompson 1973; Graul et al. 1977; Maynard-Smith 1977; Oring & Lank 1984). There is, however, no evidence indicating that polyandrous species of waders are more heavily stressed by egg-laying than monogamous waders (Erckmann 1981, 1983; Reynolds 1987) or that polyandrous waders occupy particularly unproductive ecosystems (Erckmann 1983). Further, there is no clear evidence of stress post-egg laying (Clutton-Brock 1991).

2. **High nest failure.** High nest loss favours the emancipation of the female partner to produce a replacement clutch as necessary (Jenni 1974; Pienkowski & Greenwood 1979; Ridley 1980; Oring 1982; Kâlâs 1982; Kâlâs & Byrkjedal 1984). Erckmann (1983) found no evidence of higher nest predation in polyandrous wader species than in monogamous species.

3. **Fluctuating food.** Emancipation of the female is favoured in order that the pair can take advantage of food when it is abundant and produce a second brood (Parmelee & Payne 1973; Graul 1973). Polyandrous species of waders do not, however, experience unusually widely fluctuating food conditions, and do not produce an unusually wide range of broods per season (Erckmann 1983).

4. **Male-biased operational sex ratio.** Causes female-biased benefits to desertion (Jenni 1974; Ridley 1980). Erckmann (1983) found a wide variety of sex-ratios in polyandrous species of waders, and most were close to unity. This has been confirmed by more recent studies (e.g., Lank et al. 1985; Colwell & Oring 1988; Whitfield 1990; Chapter III).

5. **Short breeding season.** Favours male parental care as secondary matings are unlikely for males (Wittenberger 1979; 1981). However, polygyny is found more commonly than polyandry in ecosystems with a short season, and polyandry does occur in the tropics (Pitelka et al. 1974; Erckmann 1983).

6. **Assessment of reproductive state.** It is less crucial for females to be able to judge the reproductive condition of the male than vice versa because it is the female which must produce the clutch, females may therefore gain secondary mating opportunities more easily and are more likely to desert (Oring 1986). This is, however, true of all avian species and does not, alone, explain the occurrence of polyandry.
7. **Stepping stone model.** Polyandry evolved from the double-clutching found in other species (Jenni 1974; Pitelka et al 1974; Pienkowski & Greenwood 1979; Ridley 1980). In double-clutching species the female lays two clutches, the first of which is cared for by the male and the second of which the female cares for herself. If the male is the father of both clutches he may benefit from this system, however, in some cases it is known that the female seeks other males before producing the second clutch (Hildén 1975). If these other males are not already incubating a clutch it is easy to see how sequential polyandry may evolve. However, Erckmann (1983) considered that many polyandrous species of waders are only distantly related to double-clutching species and the patterns of incubation and breeding ecology between the two groups are very different (Nethersole-Thompson & Nethersole-Thompson 1986).

Therefore, despite the abundance of theoretical work, no satisfactory explanation for the evolution of polyandry has yet been produced. Following his exhaustive review, Erckmann (1983) concluded that "no single model is sufficient to explain all cases of polyandry in shorebirds, but several models in modified form may apply under particular circumstances." More recently, Clutton-Brock (1991) concluded that "the evolution and distribution of polyandry and uniparental male care remains a puzzle".

Theoretical and experimental work addressing the occurrence of polygamy (be it polyandry or polygyny) across species has tended to focus on variation in the costs of desertion rather than the benefits. Lack's (1968) classic review noted that long periods of incubation and chick care were associated with obligate monogamy in many seabird species. In general, he believed that the high costs of desertion were the primary reason for monogamy being the predominant avian mating system: "each male and each female will, on average, leave most descendants if they share in raising a brood" (Lack 1968). This hypothesis has been tested by the experimental removal of male partners in species where the male usually participates in parental care. In summary, experiments of this nature demonstrate that when the male is removed the female compensates but does not, or cannot, do so completely (reviewed in Wolf et al 1988; Bart & Tornes 1989; Mock & Fujioka 1990; Clutton-Brock 1991; Davies 1991). The precise effects of male removal upon realized offspring fitness in these experiments are difficult to judge as chicks are rarely followed to independence. In three studies which have followed offspring to independence, male removal reduced the number of young successfully reaching independence by between 38% and 66% (Smith et al 1982; Greenlaw & Post 1985; Wolf et al 1988). Male care, therefore, seems to *increase* reproductive success, but it is not necessarily essential for the production of independent young.

How, then, does the cost of male desertion correlate with the evolution of polygyny? Webster (1991) compared the effects of male removal experiments upon fledging success in monogamous versus polygynous species. He suggested that, if the costs of male...
desertion were of primary importance in leading to the evolution of polygyny, reproductive success should be less affected by male-removal in polygamous species than in monogamous species. No significant difference was found. Additionally, in some precocial species, where post-hatching parental care consists simply of guarding the young against predators, the experimental removal of males causes little reduction in reproductive success, yet the male stays with the female throughout the breeding season (Martin & Cooke 1987; Martin et al 1985).

Smith and co-workers (Smith et al 1982) and Hannon (1984) attempted to manipulate the benefits, as opposed to the costs, of desertion. They removed territory-holding males and observed the consequential behaviour of the remaining males. Both desertion and polygyny were found to increase with the availability of additional females, indicating that the availability of secondary mates may limit potential polygamy. Burley's work on zebra finches, *Taeniopygia guttata*, provides a fascinating intra-specific example of the importance of the availability of alternative reproductive opportunities in predicting mate desertion. Experiments, both in the laboratory and in the wild, indicate that female zebra finches prefer males with colour rings of certain 'attractive' colours (Burley 1985, 1986c). In aviary experiments, males with 'attractively-coloured' rings were found to be more likely to desert their mate than males with 'non-attractively-coloured' rings because the benefits of desertion were greater for attractive males (Burley 1988). These results suggest that in some avian species monogamy is stable, not because of prohibitive costs of desertion, but because the availability of alternative reproductive opportunities is often limited.

This argument may be continued to suggest that, all other things being equal, it is the sex which has most to gain from desertion that will desert the other. The key question to the understanding of sex-role reversed parental care now becomes: what are the female-specific benefits of desertion in those species with role-reversed mating and parental care systems? Wittenberger (1980) considered this point but could not find any single factor which was common to the sex-role reversed species of bird but not found in other groups. In my own opinion this area represents the most fertile for future work on the evolution of sex-role reversal.

1.3. ORGANIZATION OF THE THESIS

This thesis is divided into two parts. *Part One* examines sexual selection and sex-role reversal within one species of sex-role reversed bird, the Eurasian dotterel, to assess the implications of role-reversal for both intra-sexual competition for mates and inter-sexual mate choice. The dotterel is a plover (Charadriidae; Charadriiformes) which breeds on arctic-alpine tundra throughout northern Scandinavia into central USSR. Dotterel over-winter in northern Africa and the Middle East. This research was performed during the
summers of 1989 and 1990 on a group of hills in the Central Highland within the range of
the small Scottish breeding population. Female dotterel compete for access to males, but
after laying the clutch, the female deserts the male and attempts to pair with further males.
Males perform the majority, usually all, of the parental care. (Nethersole-Thompson 1973;

Chapters 2 and 3 describe the non-territorial, sex-role reversed mating system of the
dotterel. The dotterel mating arenas, which are the sites of intense female-female
competition for access to males, are compared with the analogous phenomenon of lekking
in polygynous species. Additionally, the importance of the operational sex ratio and more
proximate measures of mate availability in predicting temporal variation in the potential for
sexual selection are studied, and a good reason is given to 'measure sexual selection'
(compare Grafen 1987).

Chapter 4 examines the exact nature of female-female competition on the mating arenas.
Considerable inter-female plumage variation is correlated with behavioural differences
between females. Bright females are more aggressive and have a potentially higher
reproductive rate. However, evidence for mate choice by males, as predicted by Trivers
(1972), is not found. Instead, female choice operates; females prefer to court brightly
coloured males which may be in good physical condition. The possible reasons for female
choice are investigated in Chapter 5, which concludes that males in good condition are
more likely to successfully complete incubation. Chapter 6 investigates the possibility of
the existence of alternative reproductive tactics leading to male-cuckoldry in dotterel. The
evidence presented in this study suggests that male dotterel adopt a strategy likely to ensure
their own paternity of the brood for which they care.

Part Two discusses the effect of the sex-roles upon the direction of, and strength of
selection for, mate choice. In particular the case of the dotterel is used to draw together
previous theories of mate choice into a consistent framework. This section also acts as a
conclusion by tying together the patterns found in the rest of the thesis. Chapter 7 presents
a new model of mate choice which accounts for the direction of, and strength of selection
for, mate choice for all permutations of relative reproductive rate and relative variation in
mate quality. This synthesis is found to account for the full range of competitive and coy
behaviours brought to our attention by Darwin's recognition of sexual selection.
PART ONE

Sexual selection and sex-role reversal

in the dotterel
CHAPTER 2 Habitat use and non-territorial mate competition

Abstract.- It is usually assumed that, in species exhibiting sex-role reversal, female reproductive rate is limited by access to males, and male reproductive rate is limited by the availability of nutrients. When the resources important to males are temporally and spatially aggregated, females should defend territories in order to obtain exclusive access to a maximum number of males. When resources cannot be defended in this way females do not defend territories and should, instead, compete directly for access to males. The sex-roles are reversed in the Eurasian dotterel, Charadrius morinellus, which displays uniparental male care and sequential polyandry. Conflicting evidence exists in the literature that males and/or females defend territories and that females compete for access to males. In this study, the habitat preferences of dotterel were examined in detail throughout the breeding cycle. Dotterel were found to preferentially use Racomitrium lanuginosum heath upon arrival and for nesting but moved their broods into blanket bog and the Nardus stricta/R.lanuginosum mosaics. Nest sites were chosen to be near to a source of nest lining material and to provide shelter, especially from the prevailing wind, whilst maintaining all-round vision. No evidence of competition for nutrient resources was found in an analysis of the distribution of individuals in pre-breeding flocks or pairs, or among incubating males or among broods. Dotterel therefore appear to be distributed in a random fashion with respect to previously settled dotterel. Dotterel breed at low density and the plant communities upon which they are dependent are widely scattered. It is, therefore, suggested that territory defence may not be a viable option for female dotterel. Reasons for mate-access polyandry being a result of this are discussed.

2.1. INTRODUCTION

The strength of selection promoting the evolution of polygamy, and the stability of the resulting mating system, is dependent on the costs and benefits of desertion by one or both sexes (Emlen & Oring 1977; Maynard-Smith 1977). The costs of desertion are determined by variance in the extent of the reduction in fitness gain from the present reproductive effort when parental care is reduced (Wolf et al 1988; Bart & Tornes 1989; Webster 1991). The benefits of desertion are dependent upon the availability of alternative reproductive opportunities. The availability of alternative reproductive opportunities is, in turn, dependent upon the absolute number of mates available and an individual’s ability to gain exclusive access to those mates. The ability to gain access to mates will vary with operational sex ratio and the temporal and spatial distribution of mates (Emlen & Oring 1977; Chapter 3). Finally, the spatial distribution of mates will be a consequence of the distribution of limiting resources. The spatial distribution of individuals and the extent of
interference between subsequently settling individuals is therefore an intrinsic, if rather
neglected, aspect of the evolution and stability of mating systems.

Classical studies on mating systems, both theoretical and empirical, have been undertaken
on polygynous birds. These studies usually assume that access to females is the limiting
factor on male reproductive rate but access to nutrient resources is the limiting factor on
female reproductive rate (Bateman 1948; Williams 1966; Trivers 1972; Bradbury &
Vehrencamp 1977; Emlen & Oring 1977). Males seeking to gain exclusive access to
females may therefore do so either directly by competing for access to females, or indirectly
by defending resources scarce to the female and thereby predicting the settlement pattern of
females (Davies 1991). When males can monopolize a significant proportion of the
resources required by the female, male competition usually takes the form of territory
defence. When males cannot defend the resources required by the female, however, males
can compete for access to mates either on a lek or by defending a harem (reviewed in

A complementary classification is also used for polyandrous mating systems (Oring 1982,
1985). In the Jacanidae the sex roles are reversed and females defend territories on ponds
which the males use to raise the brood (Jenni & Collier 1972; Jenni & Betts 1978). A
similar pattern is seen in the spotted sandpiper Actitis macularia, where a female may attract
up to four males to her territory, which consists of a strip of shoreline of a lake (Oring &
Knudsen 1972; Oring & Lank 1984; Oring et al 1991a, b). Both of these examples are
termed 'resource defence polyandry' (Oring 1982). In contrast, female phalaropes
Phalaropus spp. do not defend resources but, instead, compete between themselves for
access to males on small pools; this is 'female access polyandry' (Hildén & Vuolanto 1972;
Schamel & Tracy 1977; Reynolds 1987; Colwell & Oring 1988; Whitfield 1990).

The Eurasian dotterel Charadrius morinellus exhibits sex-role reversal and sequential
are known to compete for males on mating arenas (Nethersole-Thompson 1973). There is,
however, conflicting evidence regarding the existence of territory defence by females and/or
males (Nethersole-Thompson 1973; but see also Kålås & Byrkjedal 1984; reviewed in
Nethersole-Thompson & Nethersole-Thompson 1986). Dotterel breed at low densities on
arctic-alpine tundra and little is known of their exact habitat requirements, the extent of
nutrient requirements or limitation in males, or the opportunity for resource defence by
females. These factors are fundamental to an understanding of the evolution of sex-role
reversed mating systems and for identifying patterns in common with the analogous cases
of polygyny in other groups.

Winter habitat use in waders is well documented and has been the focus of a large body of
research concentrating upon the adaptive benefits of flocking (reviewed in Pulliam &
Caraco 1984; Barnard & Thompson 1985). However, the majority of research conducted on waders during the breeding season has concentrated upon their breeding success or mating system (e.g., Graul 1973; Nethersole-Thompson 1973; Hildén 1975; Evans & Pienkowski 1984; Kåås & Byrkjedal 1984; Oring & Lank 1984; Reynolds 1987; Höglund et al 1990). Few studies have examined the habitat requirements of waders during their breeding season (but see Haworth & Thompson 1990; Thompson & Thompson 1991). A recent study by Galbraith et al (1992) identified associations between habitat use and invertebrate abundance in dotterel. However, their analysis, in common with all others on waders during the breeding season, did not investigate the effect of intraspecific competition for resources. The relative importance of prey availability and territorial behaviour could not, therefore, be investigated.

In this study the effect of intraspecific competition is examined by comparing the distribution of individual dotterel whose breeding chronologies overlap with the distribution of dotterel whose breeding chronologies do not overlap. If competition or another form of disruptive settlement occurs, the degree of dispersal between potential 'competitors' should be greater than that between 'non-competitors'.

The aims of this study are to (i) determine habitat preferences of dotterel through their breeding chronology, and (ii) test for the presence of intra-specific competition through the breeding season.

2.2. METHODS

The study was carried out between May 3rd and August 31st of 1989 and 1990. The study site is a 13 km² area of montane-zone plateau in the central Cairngorm region of Scotland. The maximum north-south distance is 5km and the maximum east-west distance 3.5 km. The plateau is entirely within the study area and lies at approximately 960m above sea-level. The study site, therefore, represents a non-enclosed sample of the dotterel breeding population in Scotland. The site is not named to protect the location of this concentration of breeding dotterel. Although many individuals arrive, pair and subsequently breed within the study area (personal observation of marked birds), others are known to move within a breeding season to other upland areas within Scotland (NCCS unpublished data) as well as to Norway (Thomas et al 1989).

2.2.1 Breeding habitat

A vegetation map of the study site was produced based on Birks and Ratcliffe's (1980) classification of upland vegetation types (see also Appendix 1 in Thompson & Brown 1992). A 125 m-square grid based on topographical features in the field was used and the dominant vegetation type within each square recorded. This method tends to under-
represent the relative cover of rare communities and over-estimate the common communities but was satisfactory here because an index of gross availability, rather than a species list, was required. If the rare communities were used frequently by dotterel this would become evident when habitat use was compared with habitat availability. Work by Galbraith et al (1992) has, however, already shown that monitoring vegetation types provides a sufficient level of detail for measuring habitat use.

The dominant plant community within the area of 50 m radius around each nest was recorded. The relative cover of each plant community observed surrounding nests was compared to that expected from the vegetation map of the entire study site (expected by random selection) using a G-test (Sokal & Rohlf 1981).

2.2.2 Habitat use

The dominant vegetation community type within 2 m radius of the individual dotterel(s) was recorded. The vegetation classes used, based on Birks & Ratcliffe (1980), were: (1) Species-rich Racomitrium heath; R. lanuginosum dominated (≥ 75% cover) heath with at least three other plant or lichen species present per square metre; (2) Species-poor Racomitrium heath; R. lanuginosum dominated (≥ 75% cover) heath with less than three other plant or lichen species present per square metre; (3) Broken species-rich Racomitrium heath throughout; R. lanuginosum dominated (≥ 75% plant cover) heath with at least 25% bare ground; (4) Racomitrium / Nardus complex; R. lanuginosum (≥ 50% cover) and N. stricta (≥ 25% cover); (5) Nardus / Racomitrium complex; N. Stricta (≥ 50% cover) and R. lanuginosum (≥ 25% cover); (6) Nardus snow bed; N. stricta ≥ 75% cover; (7) Eriophorum blanket mire; E. vaginatum and eroded peat ≥ 50% cover; (8) Spring flush; Philonotis fontana / Saxifraga stellaris ≥ 50% cover; (9) Calluna heath; C. vulgaris ≥ 75% cover; and (10) Bare ground; at least 75% of ground has no plant or lichen cover. As Thompson & Brown (1992) make clear, these classes are discrete. Thus whilst classes 1-3 are chionophobous (snow-avoiding), class 6 is chionophilous whilst class 7 forms under ombrotrophic conditions.

Observations were made for individuals or groups of dotterel (cf., Galbraith et al 1992) as follows.

2.2.2.1 Pre-breeding flocks.

Dotterel form pre-breeding flocks on the higher parts of the study area which constitute mating arenas on which females compete for access to males (Nethersole-Thompson 1973). The dominant vegetation class occupied by undisturbed members of a pre-breeding flock was recorded at a random moment on each day that such an aggregation was encountered at a location.
2.2.2.2 Pairs.
The dominant vegetation class occupied by undisturbed members of a pair was recorded at a random moment on each day that a pair was encountered at a location.

2.2.2.3 Foraging bouts of incubating males.
The dominant vegetation class occupied by an undisturbed breeding male at a random moment during a foraging bout was recorded on each day an incubating male was recorded at a location.

2.2.2.4 Males with broods.
The dominant vegetation class occupied by an undisturbed male with a brood was recorded at a random moment on each day a male with brood was encountered at a location.

2.2.3 Nest site selection

2.2.3.1 Selection within 50 m radius.
A detailed vegetation map using Birks and Ratcliffe's (1980) classification was drawn for the area of 50 m radius around each nest. From these maps the proportional area of each plant community was determined for an area of 10 m radius around each nest. Also, from each nest-site map, the proportion of each vegetation class within ten random areas of 10 m radius was determined.

2.2.3.2 Selection within 10 m radius.
The species of plant or lichen encountered at 32 random positions within an area of 1 m radius around each nest was determined using a point-vegetation-sampler. Only the uppermost contact on the point was recorded because the physiognomy of the vegetation was of primary interest. The proportional representation of each plant species in the area of 1 m radius around the nest was then calculated. The proportional representation of each plant species in the area of 10 m radius around the nest was similarly calculated by repeating this process around five random points within an area of 10 m radius from the nest.

2.2.3.3 Selection within 1 m radius.
The species of plant or lichen encountered at 32 random positions within an area of 0.1 m radius around each nest was determined using a point-vegetation-sampler. Only the uppermost contact on the point was recorded. The proportional representation of each plant species in the area of 0.1 m radius around the nest was then calculated. The proportional representation of each plant species in the area of 1 m radius around the nest was similarly calculated by repeating this process around five random points within an area of 1 m radius of the nest.
2.2.3.4 Nest site position.

The position of each nest was recorded in relation to the micro-topography of the study area. Each nest's position was recorded according to whether it was (i) on level ground, (ii) on top of a hummock, (iii) in a dip between hummocks, or (iv) on the side of a hummock, in which case the direction of the slope was recorded using the eight sub-points of the compass. The same classification system was also used to record the position of ten random sites within an area of 1 m radius around each nest site. The observed distribution of nest positions was compared with that expected from the random samples using a G-test.

The maximum height of vegetation (potential cover) above the edge of the nest cup within 0.05 m of the perimeter of the nest was measured at the eight sub-points of the compass around each nest. The same measurements were also taken around ten random points within an area of 1 m radius around the nest. For each nest site the nest measurements and mean of the ten random measurements were recorded. The distribution of heights from around nests was compared with the distribution of mean heights around the random positions, at each sub-point of the compass, using a two-tailed Wilcoxon-Mann-Whitney test.

The wind direction was recorded at intervals of at least six hours between first egg date and last hatching date in both years. These data were combined between years. The proportion of time that the wind came from each sub-point of the compass was compared with the mean height of cover around nests and the mean height of cover around random points at each sub-point of the compass by calculating the two-tailed Spearman rank correlation coefficient (Siegel & Castellan 1988) for each pairwise comparison in order to see whether or not birds chose to nest in the lee, or otherwise, of vegetation.

The distance to the nearest boulder (> 0.1 m maximum visible chord) from each nest site was recorded. The distances from 10 random sites, within an area of 10 m radius around each nest, to the nearest boulder were also recorded. The distribution of the observed distances to the nearest boulder from nest sites was compared with that expected from mean distances from the random positions using a two-tailed Wilcoxon-Mann-Whitney test. The analysis was repeated within 10 m areas using a two-tailed paired Wilcoxon signed ranks test.
2.2.4 Competition for resources

Competition for nutrient resources between either females or males should be manifest as a non-random spatial distribution of potential competitors. This is because competing individuals should either disrupt the settlement of one another, or avoid one another. Therefore, competitors should be further apart than would be expected by chance. I tested this hypothesis by comparing the nearest-neighbour distances between dotterel which were at the same stage of their breeding chronology with the nearest-neighbour distances between dotterel whose breeding chronologies did not overlap. This analysis was performed on dotterel during the pre-breeding, pairing, nesting and pre-fledging stages.

2.2.4.1 Pre-breeding flocks.
The exact position of all pre-breeding flocks of dotterel seen between 17th May and 26th May 1990 inclusive was recorded on a 1: 25,000 scale map and the date of observation noted. Each flock was recorded only on the first time it was seen each day. These maps were used to calculate the minimum distances between pre-breeding flocks on the same day. For each day's observations the total number of flocks seen was noted and an equal number of randomly selected flock positions recorded on other days within the 10-day period was noted on the same map. This map was then used to calculate the minimum between-flock distance on a different days. It is necessary to control for the number of observations within a day to ensure that the sampling density is constant within and across days. The distributions of within-day and across-day minimum distances were compared using a two-tailed two sample Kolmogorov Smirnov test for small samples (Siegel & Castellan 1988).

2.2.4.2 Pairs.
The exact position of all pairs of dotterel seen between 17th May and 26th May 1990 inclusive was recorded on a 1: 25,000 scale map and the date of observation noted. Each pair was recorded only on the first occasion that it was seen during the 10-day period. These maps were used to calculate the minimum distance, from each pair, to another pair on the same day. For each day's observations the total number of pairs seen was noted and an equal number of randomly chosen pair positions from other days within the 10-day period were noted on the same map. This map was then used to calculate the minimum distance, from each pair, to the position of another pair on a different day. It was again necessary to control for the number of observations within a day to ensure that the sampling density is constant within and across days. The distribution of within-day and across-day minimum distances were compared using a two-tailed two sample Kolmogorov-Smirnov test for small samples.
2.2.4.3 Nests.
In both 1989 and 1990 the distribution of first egg dates of nests on the study site was bimodal and resulted in a high degree of overlap in breeding chronology between nests (Chapter 3). Fifteen nests, whose first egg dates were within 15 days of each other, were randomly selected from each year. The incubation period of dotterel varies between 21 and 30 days (Nethersole-Thompson 1976; Chapter 3). Therefore, some overlap in the incubation phase occurred between all of the selected nests within a year. The precise positions of these nests were transposed onto a 1:25,000 scale map. Using this map, the minimum within-year and across-year distances to another nest were measured for each nest. As 15 nests were used from both years, sampling density was automatically controlled for. The distribution of within-year and across-year minimum distances were compared using a two-tailed two sample Kolmogorov-Smirnov test for small samples.

2.2.4.4 Broods.
In both 1989 and 1990, nine broods were selected randomly from those which hatched within a single 5-day period. The precise positions of these broods on the first day seen within the 5-day period were transposed onto a 1:25,000 scale map. This map was used to estimate the minimum within-year and across-year distances to another brood. As nine broods were used from both years, sampling density was automatically controlled for. The distributions of within-year and across-year minimum distances were compared using a two-tailed two sample Kolmogorov-Smirnov test for small samples.

2.3. RESULTS

2.3.1 Breeding habitat

The proportional cover of each vegetation class on the study site is shown in Fig 2.1a. Again, the vegetation map is not shown to protect the breeding sites of the dotterel. The proportional cover of each vegetation class within the nesting areas is shown in Fig 2.1b.

Habitat use of each vegetation class by dotterel was compared with that expected from the proportional cover of each plant community on the vegetation map of the study site, during each phase of the breeding chronology independently, using a G-test. The proportional use by dotterel of each plant community was also compared with that expected from the mean proportional cover of each plant community within an area 50m radius around each nest using a G-test. Here, G-tests have an advantage over conventional Chi-square tests because the independent pairwise comparisons for each community can also be analyzed meaningfully independently because sub-partitioned G statistics are simply summed to give the overall G-statistic (Sokal & Rohlf 1981).
These distributions are significantly different from one another (G-test N = 71, df = 3, G = 24.586, p < 0.001). The details of this test are shown in Table 2.1. Nesting areas contain greater areas of R. lanuginosum heath and less Eriophorum spp. - Empetrum spp. dominated blanket bog than expected if the birds nested at random across the study site.

2.3.2 Habitat use

The habitat used by dotterel in the pre-breeding, paired, nesting and pre-fledging phases of their breeding chronology were compared with habitat availability (i) on the entire study site, and (ii) immediately (< 50m radius) around the nest sites. These two comparisons were used to establish (i) whether dotterel show habitat preferences on a coarse-grain, and (ii) whether the habitat chosen for nesting reflects homogeneous habitat requirements throughout the breeding chronology.

2.3.2.1 Pre-breeding flocks.

The observed relative use of each plant community by pre-breeding flocks was compared with that expected from the relative cover across the entire study site and that predicted from the relative cover in the nesting areas and is shown in Figs 2.2a and 2.2b, respectively. The observed distribution is significantly different from that predicted from the vegetation map of the study site (N = 216, df = 5, G = 241.871, p < 0.001) and that predicted from the nesting areas (N = 216, df = 5, G = 80.576, p < 0.001). The details of these tests are shown in Tables 2.2 and 2.3 respectively.

Pre-breeding flocks of dotterel used Racomitrium heath and Philonotis / Saxifraga flushes (the main component of the 'other' category for flocks) more than expected from the overall abundance of such communities or their abundance around nesting areas. Nardus snowbed, Nardus / Racomitrium heath and blanket bog were avoided.

2.3.2.2 Pairs.

The observed relative use of each plant community by pairs was compared with that expected from the relative cover across the entire study site and that expected from the relative cover in the nesting areas and is shown in Figs 2.3a and 2.3b respectively. The observed distribution is significantly different from that predicted from the vegetation map of the study site (N = 168, df = 5, G = 164.187, p < 0.001) and that predicted from the nesting areas (N = 168, df = 5, G = 94.800, p < 0.001). The details of these tests are shown in Tables 2.4 and 2.5 respectively.

Pairs also use Racomitrium heath more than expected from the overall pattern of community abundance or the abundance around nesting areas. Nardus snowbed, Nardus...
Figure 2.1 Mean proportional abundance of plant communities (a) on the whole study plateau, and (b) within an area of 50m radius around the nest sites. Abbreviations: R (R. lanuginosum heath), N (N.stricta snowbed), Bb (Blanket bog), and Bg (Bare ground).
Table 2.1. Comparison between the observed proportion of each plant community category in dotterel nesting areas and that expected from the proportional cover over the whole study plateau.

<table>
<thead>
<tr>
<th>Plant Community</th>
<th>Observed number</th>
<th>Proportion on plateau</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>43</td>
<td>0.433</td>
<td>30.74</td>
<td>28.837</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>20</td>
<td>0.283</td>
<td>20.09</td>
<td>-0.180</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>4</td>
<td>0.264</td>
<td>18.74</td>
<td>-12.357</td>
</tr>
<tr>
<td>Other</td>
<td>4</td>
<td>0.020</td>
<td>1.42</td>
<td>8.285</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>71</strong></td>
<td></td>
<td></td>
<td><strong>24.586</strong></td>
</tr>
</tbody>
</table>

*(p < 0.001)*
Figure 2.2 Comparison between the proportional habitat use of each plant community by dotterel in pre-breeding flocks and the mean proportional abundance of the plant communities (a) on the plateau, and (b) within an area of 50m radius around the nest sites. Abbreviations: R (R. lanuginosum heath), R/N (R. lanuginosum / N. stricta heath), N/R (N. stricta / R. lanuginosum heath), N (N. stricta snowbed) and Bb (Blanket bog).
Table 2.2. Comparison between the observed proportional use of each plant community category by pre-breeding flocks and that expected from the proportional cover over the whole study plateau.

<table>
<thead>
<tr>
<th>Plant Community Category</th>
<th>Observed Number</th>
<th>Proportion on Plateau</th>
<th>Expected Number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>115</td>
<td>0.275</td>
<td>59.40</td>
<td>151.947</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>35</td>
<td>0.158</td>
<td>34.10</td>
<td>1.824</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>26</td>
<td>0.186</td>
<td>40.20</td>
<td>-22.660</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>7</td>
<td>0.097</td>
<td>20.95</td>
<td>-15.347</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>1</td>
<td>0.264</td>
<td>57.02</td>
<td>-8.087</td>
</tr>
<tr>
<td>Other</td>
<td>33</td>
<td>0.020</td>
<td>4.32</td>
<td>134.195</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>216</strong></td>
<td></td>
<td><strong>241.871</strong></td>
<td></td>
</tr>
</tbody>
</table>

\( p < 0.001 \)

Table 2.3. Comparison between the observed proportional use of each plant community category by pre-breeding flocks and that expected from the mean proportional cover within the nesting areas.

<table>
<thead>
<tr>
<th>Plant Community Category</th>
<th>Observed Number</th>
<th>Proportion in Nesting Areas</th>
<th>Expected Number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>115</td>
<td>0.366</td>
<td>79.01</td>
<td>86.323</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>35</td>
<td>0.240</td>
<td>51.84</td>
<td>-27.497</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>26</td>
<td>0.240</td>
<td>51.84</td>
<td>-35.838</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>7</td>
<td>0.042</td>
<td>9.07</td>
<td>-3.630</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>1</td>
<td>0.056</td>
<td>12.10</td>
<td>-4.986</td>
</tr>
<tr>
<td>Other</td>
<td>33</td>
<td>0.056</td>
<td>12.10</td>
<td>66.240</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>216</strong></td>
<td></td>
<td><strong>80.576</strong></td>
<td></td>
</tr>
</tbody>
</table>

\( p < 0.001 \)
Figure 2.3 Comparison between the proportional habitat use of each plant community by dotterel in pairs and the mean proportional abundance of the plant communities (a) on the plateau, and (b) within an area of 50m radius around the nest sites.

Abbreviations: R (R.lanuginosum heath), R/N (R.lanuginosum / N.stricta heath), N/R (N.stricta / R.lanuginosum heath), N (N. stricta snowbed) and Bb (Blanket bog).
### Table 2.4. Comparison between the observed proportional use of each plant community category by pairs and that expected from the proportional cover over the whole study plateau.

<table>
<thead>
<tr>
<th>Plant Community</th>
<th>Observed number</th>
<th>Proportion on plateau</th>
<th>Expected number (G-statistic)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>97</td>
<td>0.275</td>
<td>46.20 (209.749)</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>26</td>
<td>0.158</td>
<td>26.54 (-1.077)</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>25</td>
<td>0.186</td>
<td>31.25 (-11.154)</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>11</td>
<td>0.097</td>
<td>16.30 (-8.647)</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>6</td>
<td>0.264</td>
<td>44.35 (-24.005)</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>0.020</td>
<td>3.36 (-0.680)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>168</strong></td>
<td></td>
<td><strong>164.187</strong>(p &lt; 0.001)</td>
</tr>
</tbody>
</table>

### Table 2.5. Comparison between the observed proportional use of each plant community category by pairs and that expected from the mean proportional cover within the nesting areas.

<table>
<thead>
<tr>
<th>Plant Community</th>
<th>Observed number</th>
<th>Proportion in nesting areas</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>97</td>
<td>0.366</td>
<td>61.49</td>
<td>144.001</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>26</td>
<td>0.240</td>
<td>40.32</td>
<td>-22.815</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>25</td>
<td>0.240</td>
<td>40.32</td>
<td>-23.899</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>11</td>
<td>0.042</td>
<td>7.06</td>
<td>9.768</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>6</td>
<td>0.056</td>
<td>9.41</td>
<td>-5.398</td>
</tr>
<tr>
<td>Other</td>
<td>3</td>
<td>0.056</td>
<td>9.41</td>
<td>-6.858</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>168</strong></td>
<td></td>
<td><strong>94.8</strong></td>
<td></td>
</tr>
</tbody>
</table>

*(p < 0.001)*
Racomitrium mosaics and blanket bog were avoided. However, pair-use of Nardus snowbed was more frequent than expected from its abundance within nesting areas.

2.3.2.3 Foraging bouts of incubating males.
The observed relative use of each plant community by incubating males during foraging bouts was compared with that expected from the relative cover across the entire study site and that expected from the proportional cover in the nesting areas and is shown in Figs 2.4a and 2.4b respectively. The observed distribution was significantly different from that predicted from the vegetation map of the study site (N = 153, df = 5, G = 77.764, p < 0.001) and that predicted from the assay of nesting areas (N = 153, df = 5, G = 59.322, p < 0.001). The details of these tests are shown in Tables 2.6 and 2.7 respectively.

Incubating males used Nardus / Racomitrium heath less than expected from the distribution around nests. Racomitrium heath was used more than expected from the abundance around nests, as was blanket bog. The use of blanket bog was, however, not as great as would be expected from its overall abundance on the plateau.

2.3.2.4 Males with broods.
The observed relative use of each plant community by males with broods was compared with that expected from the relative cover across the entire study site and that expected from the relative cover in the nesting areas and is shown in Figs 2.5a and 2.5b respectively. The observed distribution was significantly different from that expected from the vegetation map of the study site (N = 149, df = 4, G = 18.163, p < 0.01) and that expected from the assay of nesting areas (N = 149, df = 4, G = 127.147, p < 0.001). The details of these tests are shown in Tables 2.8 and 2.9 respectively.

Males with broods show a very different set of habitat preferences to dotterel at other stages of their breeding chronology. Broods used blanket bog and Nardus snowbed more than expected from the abundance around nests. The use of blanket bog was so high that it did not differ significantly from that expected from the prevalence of bog on the plateau as a whole. Racomitrium heath and Nardus / Racomitrium mosaics were used less than expected from their overall abundance on the plateau or that in the nesting areas.

2.3.3 Nest site selection

2.3.3.1 Selection within 50 m radius.
The observed mean relative cover of each plant community in the area of 10 m radius around the nest and in random positions within an area of 50 m radius around the nest are shown in Figs 2.6a and 2.6b respectively.
Figure 2.4 Comparison between the proportional habitat use of each plant community by incubating male dotterel and the mean proportional abundance of the plant communities (a) on the plateau, and (b) within an area of 50m radius around the nest sites. Abbreviations: R (R. lanuginosum heath), R/N (R. lanuginosum / N. stricta heath), N/R (N. stricta / R. lanuginosum heath), N (N. stricta snowbed) and Bb (Blanket bog).
Table 2.6. Comparison between the observed proportional use of each plant community category by incubating males and that expected from the proportional cover over the whole study plateau.

<table>
<thead>
<tr>
<th>Plant Community Category</th>
<th>Observed number</th>
<th>Proportion on plateau</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>77</td>
<td>0.275</td>
<td>42.08</td>
<td>93.070</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>38</td>
<td>0.158</td>
<td>24.17</td>
<td>34.375</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>9</td>
<td>0.186</td>
<td>28.46</td>
<td>-20.722</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>16</td>
<td>0.097</td>
<td>14.84</td>
<td>2.406</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>12</td>
<td>0.264</td>
<td>40.39</td>
<td>-29.129</td>
</tr>
<tr>
<td>Other</td>
<td>1</td>
<td>0.020</td>
<td>3.06</td>
<td>-2.237</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>153</strong></td>
<td></td>
<td></td>
<td><strong>77.764</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>(p &lt; 0.001)</em></td>
</tr>
</tbody>
</table>

Table 2.7. Comparison between the observed proportional use of each plant community category by incubating males and that expected from the mean proportional cover within the nesting areas.

<table>
<thead>
<tr>
<th>Plant Community Category</th>
<th>Observed number</th>
<th>Proportion in nesting areas</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>77</td>
<td>0.366</td>
<td>56.00</td>
<td>49.047</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>38</td>
<td>0.240</td>
<td>36.72</td>
<td>2.604</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>9</td>
<td>0.240</td>
<td>36.72</td>
<td>-25.310</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>16</td>
<td>0.042</td>
<td>6.43</td>
<td>29.192</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>12</td>
<td>0.056</td>
<td>8.57</td>
<td>8.085</td>
</tr>
<tr>
<td>Other</td>
<td>1</td>
<td>0.056</td>
<td>8.57</td>
<td>-4.296</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>153</strong></td>
<td></td>
<td></td>
<td><strong>59.322</strong></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td><em>(p &lt; 0.001)</em></td>
</tr>
</tbody>
</table>
Figure 2.5 Comparison between the proportional habitat use of each plant community by dotterel broods and the mean proportional abundance of the plant communities (a) on the plateau, and (b) within an area of 50m radius around the nest sites. Abbreviations: R (R. lanuginosum heath), R/N (R. lanuginosum / N. stricta heath), N/R (N. stricta / R. lanuginosum heath), N (N. stricta snowbed) and Bb (Blanket bog).
Table 2.8. Comparison between the observed proportional use of each plant community category by broods and that expected from the proportional cover over the whole study plateau.

<table>
<thead>
<tr>
<th>Category</th>
<th>Observed number</th>
<th>Proportion on plateau</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>28</td>
<td>0.275</td>
<td>40.97</td>
<td>-21.322</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>31</td>
<td>0.158</td>
<td>23.54</td>
<td>17.062</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>26</td>
<td>0.186</td>
<td>27.71</td>
<td>-3.320</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>24</td>
<td>0.097</td>
<td>14.45</td>
<td>24.403</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>40</td>
<td>0.264</td>
<td>39.34</td>
<td>1.339</td>
</tr>
<tr>
<td>Other</td>
<td>0</td>
<td>0.020</td>
<td>2.98</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>149</td>
<td></td>
<td></td>
<td>18.163</td>
</tr>
</tbody>
</table>

\( p < 0.01 \)

Table 2.9. Comparison between the observed proportional use of each plant community category by broods and that expected from the mean proportional cover within the nesting areas.

<table>
<thead>
<tr>
<th>Category</th>
<th>Observed number</th>
<th>Proportion in nesting areas</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Racomitrium heath</td>
<td>28</td>
<td>0.366</td>
<td>54.34</td>
<td>-37.331</td>
</tr>
<tr>
<td>Racomitrium / Nardus heath</td>
<td>31</td>
<td>0.240</td>
<td>35.76</td>
<td>-8.856</td>
</tr>
<tr>
<td>Nardus / Racomitrium heath</td>
<td>26</td>
<td>0.240</td>
<td>35.76</td>
<td>-16.574</td>
</tr>
<tr>
<td>Nardus snow bed</td>
<td>24</td>
<td>0.042</td>
<td>6.26</td>
<td>64.521</td>
</tr>
<tr>
<td>Eriophorum blanket bog</td>
<td>40</td>
<td>0.056</td>
<td>8.34</td>
<td>125.387</td>
</tr>
<tr>
<td>Other</td>
<td>0</td>
<td>0.056</td>
<td>8.34</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td>149</td>
<td></td>
<td></td>
<td>127.147</td>
</tr>
</tbody>
</table>

\( p < 0.001 \)
Figure 2.6 The mean proportional abundance of plant communities (a) observed within an area of radius 10m around nest sites, compared with (b) that expected from the distribution of communities within an area of 50m radius around the nest sites. Abbreviations: R (R. lanuginosum heath), N (N. stricta heath), Bb (Blanket bog), Bg (Bare ground) and Jt (J. trifidus heath).
For each plant community, the distribution of proportions of cover around nests was compared to the distribution of proportions of cover around the random positions using a two-tailed Wilcoxon-Mann-Whitney test on the combined data between nests. Within-nesting-area comparisons were also made for the most common vegetation classes using a two-tailed paired Wilcoxon signed ranks test for small and large samples, as appropriate (less common classes were not used because the sample size would have been prohibitively small) (Siegel & Castellan 1988).

**Racomitrium** heath (Wilcoxon-Mann-Whitney test $N = 63$, converted $z = 2.323$, $p < 0.05$: paired Wilcoxon signed ranks test $N = 49$, converted $z = 3.488$, $p < 0.001$) and *Juncus trifidus* heath ( $N = 63$, $z = 2.900$, $p < 0.01$: $N = 7$, $T^+ = 18$, $p > 0.20$) constituted significantly greater proportions of cover within an area of 10 m around the nest than expected. *Nardus* heath constituted a significantly smaller proportion of cover than expected ($N = 63$, $z = 2.900$, $p < 0.01$: $N = 44$, $z = 3.861$, $p < 0.001$). There was no significant difference in the proportional cover of *Eriophorum* blanket bog ($N = 63$, $z = 1.574$, $p > 0.10$) or bare ground ($N = 63$, $z = 1.876$, $p > 0.05$).

**2.3.3.2 Selection within 10 m radius.**

The observed mean relative cover of each species of plant and lichen in the area of 1 m radius around the nest and in random positions within an area of 10 m radius around the nest are shown in Figs 2.7a and 2.7b respectively.

The relative proportions of cover around nests was compared with that predicted on the basis of random positions within a 10 m radius using a two-tailed Wilcoxon-Mann-Whitney test on the combined data between nests. Within-10m-area comparisons were also made for the most common plant species using a two-tailed paired Wilcoxon signed ranks test for small and large samples as appropriate.

*N. stricta* ($N = 64$, converted $z = 2.532$, $p < 0.05$: $N = 32$, converted $z = 1.123$, $p > 0.20$), *Carex bigelowii* ($N = 64$, $z = 2.946$, $p < 0.01$: $N = 27$, $z = 3.307$, $p < 0.001$), *Agrostis canina* ($N = 64$, $z = 2.893$, $p < 0.01$: $N = 31$, $z = 2.168$, $p < 0.05$) and *Dicranum* spp. ($N = 64$, $z = 3.731$, $p < 0.001$) were less represented than in random positions. There were, however, no significant differences in the relative cover of *R. lanuginosum* ($N = 64$, $z = 0.861$, $p > 0.20$), *L. trifidus* ($N = 64$, $z = 0.797$, $p > 0.20$), *Cladonia* spp. ($N = 64$, $z = 0.088$, $p > 0.20$) or bare ground ($N = 64$, $z = 0.992$, $p > 0.20$).
Figure 2.7 The mean proportional abundance of plant species (a) observed within an area of radius 1m around nest sites, compared with (b) that expected from the distribution of plant species within an area of 10m radius around the nest sites. Abbreviations: Rl (R. lanuginosum), Ns (N. stricta), Bg (Bare ground), Jt (J. trifidus heath), Cb (C. bigelovii), A (Agrostis spp.), C (Cladonia spp.) and D (Dicranum spp.).
2.3.3.3 Selection within 1 m radius.
The observed mean relative cover of each species of plant and lichen in the area of 0.1 m radius around the nest and in random positions within an area of 1 m radius around the nest are shown in Figs 2.8a and 2.8b respectively.

The relative proportions of cover around nests were compared with those expected from random positions within 1 m radius using a two-tailed Wilcoxon-Mann-Whitney test on the combined data between nests. Within-1m-radius comparisons were also made for the most common plant species using a two-tailed paired Wilcoxon signed ranks test for small and large samples as appropriate.

Cladonia spp. (N = 64, converted z = 3.731, p < 0.01) were more prevalent in the area immediately around the nest sites than expected from the random positions. There were, however, no significant differences in the proportional cover of R. lanuginosum (N = 64, z = 1.081, p > 0.20), N. stricta (N = 64, z = 1.801, p > 0.05), Carex bigelowii (N = 64, z = 0.158, p > 0.20), Agrostis canina (N = 64, z = 0.989, p > 0.20), Dicranum spp. (N = 64, z = 0.367, p > 0.20) or bare ground (N = 64, z = 1.415, p > 0.20).

2.3.3.4 Nest site position.
The observed and expected distributions of nest sites with respect to micro-topography are shown in Figs 2.9a and 2.9b respectively. These distributions are significantly different (G test N = 63, df = 4, G = 73.697, p < 0.001). The details of this test are shown in Table 2.10.

Dotterel are more likely to nest on top of a hummock or on the lee side of a hummock than expected from random, and less likely to nest in a dip between hummocks or on flat ground.

The observed mean potential cover immediately around nest sites is shown in Fig 2.10a and the expected distribution from the random sites around nests is shown in Fig 2.10b. These distributions are significantly different as shown in Table 2.11. The proportion of time that the wind comes from each sub-point of the compass is shown in Fig 2.10c. The correlation coefficient between the prevailing wind direction and the observed and expected distribution of cover is shown in Table 2.11. Accordingly, dotterel select nest sites whose micro-topography provide protection from the prevailing wind.

The observed mean height of potential cover around nests was compared with that expected from random samples for each sub-point of the compass independently using the Wilcoxon-Mann-Whitney test for large samples. There is a significant positive correlation between the mean height of potential cover around the nest and the frequency of wind directions (Spearman rank correlation coefficient N = 8, rs = 0.905, p < 0.01).
Figure 2.8 The mean proportional abundance of plant species (a) observed within an area of radius 0.1m around nest sites, compared with (b) that expected from the distribution of plant species within an area of 1m radius around the nest sites.

Abbreviations: Rl (R. lanuginosum), Ns (N. stricta), Bg (Bare ground), Jt (J. trifidus heath), Cb (C. bigelowii), A (Agrostis spp.), C (Cladonia spp.) and D (Dicranum spp.).
Figure 2.9 The distribution, with respect to local topography, of (a) nest sites, and (b) random positions within an area of 1m radius around the nest sites.
Table 2.10. Comparisons between the observed distribution of nest positions with respect to local topography and that expected from the distribution of random points sampling.

<table>
<thead>
<tr>
<th>Observed number</th>
<th>Proportion at random points</th>
<th>Expected number</th>
<th>G-statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flat ground</td>
<td>10</td>
<td>0.416</td>
<td>26.20</td>
</tr>
<tr>
<td>Top of hummock</td>
<td>25</td>
<td>0.135</td>
<td>8.37</td>
</tr>
<tr>
<td>On slope in lee of prevailing wind*</td>
<td>25</td>
<td>0.163</td>
<td>10.24</td>
</tr>
<tr>
<td>(N, NE, E and SE slopes)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>On slope facing prevailing wind*</td>
<td>2</td>
<td>0.156</td>
<td>9.80</td>
</tr>
<tr>
<td>(S, SW, W and NW slopes)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>In dip between hummocks</td>
<td>1</td>
<td>0.133</td>
<td>8.370</td>
</tr>
<tr>
<td>Total</td>
<td>63</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The direction of the prevailing wind is inferred from the data shown in Table 2.11.
The distribution, with respect to the points of the compass, of (a) mean potential cover around the nest sites, compared with (b) the mean potential cover around random points within an area of 10m radius around the nest sites, and (c) the proportional direction of the source of the wind.
Table 2.11. Comparisons between the observed distribution of potential cover around nest sites with respect to wind direction and that expected from the distribution around random points.

<table>
<thead>
<tr>
<th>Wind Direction</th>
<th>Mean observed cover (mm)</th>
<th>Mean expected cover (mm)</th>
<th>U test (N = 63)</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>North</td>
<td>20.12</td>
<td>3.21</td>
<td>5.590</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>North East</td>
<td>14.59</td>
<td>2.01</td>
<td>5.153</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>East</td>
<td>15.90</td>
<td>3.07</td>
<td>4.261</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>South East</td>
<td>16.07</td>
<td>4.14</td>
<td>6.415</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>South</td>
<td>25.08</td>
<td>3.13</td>
<td>8.105</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>South West</td>
<td>34.92</td>
<td>3.59</td>
<td>8.212</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>West</td>
<td>31.97</td>
<td>3.69</td>
<td>8.212</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>North West</td>
<td>27.70</td>
<td>3.66</td>
<td>7.506</td>
<td>p &lt; 0.001</td>
</tr>
</tbody>
</table>
There is no significant positive correlation between the mean height of potential cover around random points and the frequency of wind directions ($N = 8, r_s = 0.476, p > 0.20$).

The nearest-boulder-distances from nests and from random sites are shown in Figs 2.11a and 2.11b, respectively. These distributions do not differ significantly (Wilcoxon-Mann-Whitney test $N = 52$, converted $z = 0.556, p > 0.20$; paired Wilcoxon ranked sign test $N = 53$, converted $z = 1.258, p > 0.20$).

2.3.4 Competition for resources

2.3.4.1 Pre-breading flocks.
The distributions of within-day and across-day minimum inter-flock distances are shown in Figs 2.12a and 2.12b respectively. These distributions are not significantly different (two sample Kolmogorov Smirnov test $m = 30, n = 30, D = 0.200, p > 0.40$).

2.3.4.2 Pairs.
The distributions of within-day and across-day minimum inter-pair distances are shown in Figs 2.13a and 2.13b respectively. These distributions are not significantly different ($m = 26, n = 26, D = 0.231, p > 0.40$).

2.3.4.3 Nests.
The distributions of within-year and across-year minimum inter-nest distances are shown in Figs 2.14a and 2.14b respectively. These distributions are not significantly different ($m = 30, n = 30, D = 0.300, p > 0.20$).

2.3.4.4 Broods.
The distributions of within-year and across-year minimum inter-brood distances are shown in Figs 2.15a and 2.15b respectively. These distributions are not significantly different ($m = 18, n = 18, D = 0.300, p > 0.20$).

2.4. DISCUSSION

2.4.1 Breeding habitat and habitat use

The plateau is dominated by species-rich *R. lanuginosum* heath juxtaposed with *N. stricta* snowbeds on the higher areas and *Eriophorum* spp. blanket bog throughout the wetter areas (Fig 2.1a). Heather, *C. vulgaris*, dominated moorland and rocky corries surround the site to the east, south and west. This vegetation composition is typical of that inhabited by dotterel on schist bed rock in the Cairngorm region (D. A. Ratcliffe in Nethersole-Thompson 1973; Nethersole-Thompson & Nethersole-Thompson 1986;
Figure 2.11 The distribution of the minimum distance to a stone or boulder (a) observed from nest sites, and (b) expected from the distribution around random positions within an area of 10m radius around the nest sites.
Figure 2.12 The distribution of minimum inter-flock distances (a) observed within a day, and (b) expected from the distribution across days.
Figure 2.13 The distribution of minimum inter-pair distances (a) observed within a day, and (b) expected from the distribution across days.
Figure 2.14 The distribution of minimum inter-nest distances (a) observed within a year, and (b) expected from the distribution across years.
Figure 2.15 The distribution of minimum inter-brood distances (a) observed within a year, and (b) expected from the distribution across years.
Habitat use, however, was not uniform with respect to either availability, or breeding chronology. Dotterel tended to nest predominantly on the *R. lanuginosum* heath or *R. lanuginosum / N. stricta* mosaics and avoided montaine *C. vulgaris* heath, bare ground and blanket bog (Table 2.1; Fig 2.1).

Galbraith et al (1992) and Thompson and Brown (1992) contrast habitat use by dotterel on three Scottish sites. Their findings are in accordance with those presented here. Furthermore, these studies suggest that broods, compared with dotterel during the rest of the breeding season, prefer blanket bog mosaics in some areas because they meet the feeding requirements of both the males and their chicks. As Thompson and Brown (1992) show, the relative abundance of invertebrates varies across vegetation types. *R. lanuginosum* heath has the highest densities of tipulids (*Tipula montana*) and beetles (*Byrrhus spp.*, *Otiorhynchus spp.*) which are important in the diet of adults but such heath does not contain sawflies (*Symphyta spp.*) which are a major component in the diet of chicks (Galbraith et al 1992). These sawflies are most prevalent in wetter, bog-dominated areas, and Galbraith et al (1992) suggest that *R. lanuginosum* - bog mosaics meet the ideal joint feeding requirements of adults and their chicks. On the study site upon which my study was carried out I found that dotterel did not nest in a fine-grain heath-bog mosaic, despite the fact that *R. lanuginosum* and bog were frequently found juxtaposed, but rather nested in heath and then moved their chicks into the bog. This system is probably facilitated by the course-grain heath-bog mosaic across the plateau as a whole.

### 2.4.2 Nest site selection

The detailed analysis of nest position within an area of radius 10m around the nest, compared with the mean cover within an area of 50m radius around the nest, confirmed the impression from the gross analysis based on Fig 2.1 that dotterel avoid heaths with a lot of *N. stricta* and prefer the higher altitude areas consisting of species-rich *R. lanuginosum* heath or *J. trifidus* heath (Fig 2.6). On a finer scale, dotterel avoid the presence of grasses such as *N. stricta* and *A. canina*, the sedge *C. bigelowii* and mosses (i.e., *Dicranum spp.*) in the near (< 1m radius) vicinity of the nest (Fig 2.7). Once these requirements have been met, however, the only feature of vegetation which appears to influence the exact position of the nest is the local abundance of lichen (*Cladonia spp.*) species (Fig 2.8). Dotterel use lichens to line their nests (Nethersole-Thompson 1973) and this is probably the reason that they tend to use areas rich in *Cladonia spp.* Interestingly, *Cladonia uncialis* is also the most tubular lichen found in upland ecosystems; it may therefore provide the best thermal insulating material available.

The exact positioning of the nest site is also significantly influenced by micro-topographical factors. Dotterel tend to nest on the top or on the lee slope of hummocks with respect to the prevailing wind (Fig 2.9; Table 2.10). The dips between hummocks are rarely used and
not nearly as often as expected. The use of the lee side of hummocks presumably reduces the effect of wind-chill on both the male and the eggs whilst maintaining a wide field of view for predators and minimizing the risk of being covered by snow due to drift. The nest is usually also protected from the direction of the prevailing wind by local vegetation and raised ground around the nest (Table Fig 2.10; 2.11). Contrary to observations of dotterel on their Norwegian breeding grounds (I. Byrkjedal and J. A. Kålås personal communication), no evidence was found to suggest that dotterel nest near to stones or boulders (Fig 2.11). In habitats without solifluction hummocks, however, stones and boulders may indeed be used to achieve the type of sheltered nest site which was found to be preferred in this study. Ingvar Byrkjedal (personal communication) has suggested that nesting near to stones helps dotterel to find their nest in foggy weather. Since fog cover is more frequent in Norway than in Scotland (J. A. Kålås personal communication), this may be another reason why dotterel are more likely to nest next to boulders in Norway than in Scotland.

2.4.3 Competition for resources

This study has demonstrated that dotterel are not randomly distributed over their breeding habitat. Significant preferences and aversions are shown at each stage of the breeding chronology for, and against, specific plant communities. Such communities are limited in their abundance and aggregated in distribution. If the breeding density of dotterel was sufficiently high, therefore, with respect to the distribution of resources, competition should result.

If competition for nutrient resources between dotterel was high we would expect dotterel to be further apart when their breeding chronologies overlap than when they do not. Therefore, there should be greater spatial dispersion between individuals which might compete compared to that between individuals which do not compete. Competition between pre-breeding flocks and pairs was analysed between days within the same year and competition between incubating males (nests) and broods was analysed between years within 15-day and 5-day periods respectively.

No significant difference was found in the dispersal pattern of flocks, pairs, nests or broods within-period observations compared to that found across-period observations (Figs 2.12, 2.13, 2.14 & 2.15). Competition for nutrient resources does not, therefore, appear to be a significant factor in determining the spatial dispersion of breeding dotterel. This is perhaps because dotterel breeding density is too low with respect to the availability of resources for competition to occur. This may be the factor which precludes females from adopting a territory-holding strategy in order to obtaining multiple mates. Territory-holding would not be profitable as territories would either be too small, and thus insufficient to allow birds to monopolize the resource, or they would be too large for it to be possible to
maintain exclusive access within them. The obvious strategy open to females in order to increase their potential reproductive rate, therefore, is to gain direct access to a high number of males. Female-female competition for access to mates may therefore become manifest as competition on mating arenas in an analogous manner to the competition between males observed on polygynous leks (Chapter 4; Chapter 7) rather than through resource-defence which is analagous to territorial polygyny.

There are, however, two alternative interpretations of this data. I will now consider these separately now and explain why I do not think that they are as satisfactory as the one presented above.

The first concerns the evolution of female mating arenas. In this chapter I have emphasized that competing for direct access to males may be the only option left to females which cannot profitably defend territories. But there may be other, independent, reasons why females aggregate for display (reviewed in Kirkpatrick & Ryan 1991). One of the most intriguing suggestions is that females aggregate at 'hot spots' - areas where males feed early in the season (reviewed in Bradbury et al. 1986). This is consistent with the observation that mating arenas usually occur at chionophobic sites early in the season. Thereby, females may maximize the opportunity to (i) encounter males, and (ii) select a good quality male. I suggest that these may be important factors in the evolution of aggregated female displays. However, the fact that neither female nor males defend territories, even when there is no snow on the plateau, indicates that they are not the principle components. Also, immediately upon pairing the male and female leave the mating arenas and settle elsewhere on the plateau. If a female could defend a large area of suitable nesting habitat she might secure males even earlier in the season. To conclude, territory defence should be a profitable tactic for females if nutrient defence was feasible. The social benefits of female aggregations do not, therefore, adequately describe the evolution of mate access polyandry in dotterel.

The second alternative hypothesis concerns the adaptive benefit of spacing behaviour in the context of predator avoidance. The argument is that dotterel may space themselves out, not because of intra-specific competition for resources, but in order to minimize the probability of attracting the attention of predators. Under this hypothesis, dotterel whose breeding chronologies overlap should be further apart than those whose chronologies do not overlap. But this is the same prediction as for the 'resource competition' hypothesis. However, in the case of this particular study, this lack of a diagnostic prediction is not a problem. This is because the results presented in this chapter indicate that the presence of other dotterel does not influence the subsequent settlement pattern of individuals. The anti-predation hypothesis does not therefore adequately describe the distribution of dotterel.
The main conclusion of this part of the study therefore holds; dotterel settle randomly with respect to other dotterel. This suggests that intra-specific competition for resources is low and it seems likely that this may be a primary factor in the evolution of mate-access polyandry in the dotterel with the 'hot-spot' hypothesis explaining the exact location of the mating arenas.
CHAPTER 3 Female mating arenas and the potential for sexual selection

Abstract.- The sex-roles are reversed in the Eurasian dotterel Charadrius morinellus. Males provide uniparental care in many populations and females compete for access to males on a mating arena. Immediately after producing a clutch the female deserts the male who then incubates and cares for the brood, whilst the female may compete with other females to become polyandrous. This study describes the mating system in detail and draws attention to the parallel example of lekking in polygynous species. The potential for, and temporal variation in, sexual selection acting within the study population over two years was studied by observing indices of intra-sexual and inter-sexual display. Theory predicts that the amount of intra-sexual competition and courtship should be positively correlated with the extent of bias towards the competitive sex in the operational sex ratio (OSR). Female bias in OSR was, however, negatively correlated with both agonistic and courtship events. More proximate predictors of the availability of alternative reproductive opportunities were also introduced into the model. Of these predictors, the absolute numbers of males and females present on the plateau were more successful than OSR in describing the variance in courtship activity. These results suggest that, although the aims of OSR measurement are valid, in this species, which breeds at very low density, the absolute availability of mates is more important than the OSR in describing the strategy adopted by individuals. It is also emphasized that the skew in OSR observed in the study population is a consequence of this extreme mating system and is not its cause.

3.1. Introduction

Sex-role reversal, where females compete for males which provide most of the parental care, is very unusual in birds (Lack 1968; Ridley 1978; Oring 1982; Clutton-Brock 1991). In role-reversed mating systems females are potentially polyandrous. It is the mechanism by which females may acquire more than one male that is used to classify sex-role reversed avian mating systems (Oring 1982, 1985; Clutton-Brock 1991; Davies 1991). In resource defence polyandry the females defend a resource which the males require in order to breed. Females compete to hold the resource, usually a nesting territory, and males are expected to choose females primarily on the quality of resource held. Kålås (1987) predicted that, in resource defence polyandry, intra-sexual competition between females should be high, but inter-sexual selection may be of less importance because males choose between females on the basis of territory quality, which may be determined by the female dominance hierarchy. RDP has been studied in the Jacanidae and Scolopacidae (Jenni & Collier 1972; Oring & Knudson 1972; Graul et al 1977; Jenni & Betts 1978; Oring & Maxon 1978; Oring et al 1991a, b; Lank et al 1985). Female access polyandry describes a system where the females
do not defend resources but compete amongst themselves for access to males. Kålås
(1987) therefore predicted that in female access polyandry inter-sexual selection should be
more important than intra-sexual competition because males choose females on the basis of
female phenotype and females do not fight to defend resources. Female access polyandry
has been studied in the Charadriidae and Scolopacidae (Nethersole-Thompson 1973;
Erckman 1983; Kålås & Byrkjedal 1984; Reynolds et al. 1986; Reynolds 1987; Colwell &

The Eurasian dotterel, *Charadrius morinellus*, exhibits female access polyandry
(Nethersole-Thompson 1973; Kålås & Byrkjedal 1984). The breeding areas are typically
large, relatively homogenous and structurally simple; females do not defend an exclusive
territory (Chapter 2). Females are known to compete for males, desert the clutch upon
completion and be sequentially polyandrous (Nethersole-Thompson 1973; Kålås 1987).

In this study, the mating system of the Eurasian dotterel is used to test empirical measures
of the potential for sexual selection. Darwin (1871) coined the term sexual selection to
explain the occurrence of characters whose evolution "depends on the advantage which
certain individuals have over other individuals of the same sex and species, in exclusive
relation to reproduction". A good measure of the potential for sexual selection was sought
in order to provide a comparative framework in which to study the evolution of secondary
sexual traits and mating systems. Following Bateman (1948), several authors have
ominated the degree of intra-sexual variance in number of mates as a suitable index of the
potential for sexual selection (e.g., Payne 1979; Wade 1979; Wade and Arnold 1980; Finke
1982; Arnold 1983; McCauley 1983; Arnold & Wade 1984a, b; Partridge & Halliday 1984;
Price 1984). Emlen & Oring (1977) proposed that the operational sex ratio (OSR) was
more likely to be a good index of the potential for sexual selection. The OSR is defined as
"the ratio of fertilizable females to sexually active males" (Emlen & Oring 1977). In two
review papers, Sutherland (1985a, 1987; see also Koenig & Albano 1986) exposed the
weakness of using potential intra-sexual variance in reproductive fitness as a measure of the
potential for sexual selection and supported the OSR approach. This conclusion was in
agreement with that published a few years before by Lande and Arnold (1983) and Clutton-
Brock (1983) who indicated that measures of variance in the number of mates obtained did
not necessarily predict the strength of sexual selection but may approximate to the potential
for sexual selection in some cases. Despite this sound groundwork and an increased
awareness of the potential importance of OSR (Parker 1984a; Mock 1985; Gowaty 1985),
few studies have succeeded in comparing empirical measures of OSR with direct
observations of intra-sexual competition. The most notable exception is Colwell & Oring's

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Complete female desertion and male-only care in species exhibiting female access polyandry leads to a large skew in the OSR. The comparable polygynous groups in the western Palearctic are those with male desertion and female only care; i.e., members of the Anatidae and the lekking Tetraonidae, Pheasianidae and Otididae. In other avian groups, biparental care is usually adopted with a reduction in the male's contribution with polygyny (Lack 1968); thus the potential bias in the OSR is not as large. The sex-role reversed waders are therefore an interesting group when studying the effects of biased OSRs. Colwell & Oring (1988) found a positive correlation between indices of OSR and estimates of intra-sexual competition. They summarized that "OSR may provide a useful estimate of the opportunity for sexual selection, especially in species with mate defence mating systems", although this approach has been criticized (by Colwell and Oring, 1988, among others) because OSR is necessarily an indirect measure of proximate factors controlling mate availability, namely breeding synchrony, male density and female density.

The aims of this study were to (i) compare the sex-role reversed mating system of the dotterel with the synonymous example of lekking found in polygynous species, and (ii) explore the utility of using OSR and more proximate measures of mate availability as an index of the potential for sexual selection when controlling for other sources of temporal and individual variation.

3.2. METHODS

This study was carried out in the summers (May to August) of 1989 and 1990 on a montane zone, high level plateau in the South-East Cairngorm region of Scotland. The study site consisted of *Racomitrium lanuginosum*-dominated heath and alpine-arctic tundra on schist bed rock at ca.1000 m above sea level and is described in detail elsewhere (Chapter 2).

Observations began when the dotterel arrived on the study site in early May and continued until the end of July. Data are presented here from 1st May to 7th July for 1989 and 8th May to 7th July for 1990. Approximately 65 and 45 breeding attempts were made in 1989 and 1990 respectively (Chapter 2). A vehicle was used as a hide for behavioural observations; 54 and 50 workable days were spent on the plateau in 1989 and 1990 respectively. The majority of nights were spent on the plateau enabling observations between 08.00 and 23.00 hours.

3.2.1 Breeding chronology

Approximately half the study site was censused each day on foot by repeatedly walking approximately 100 m, stopping and scanning through 360° with 8x or 10x binoculars.
Narrow strips of suitable habitat were censused in a zig-zag fashion, broader areas of suitable habitat in parallel tracts approximately 50 m apart. The sex (for criteria see Kålås 1988; Chapter 4), flock sex ratio and flock size were recorded for all dotterel encountered. Census data was not duplicated when areas were revisited within the same day.

First egg dates were back calculated where necessary from hatching date by using the mean incubation period within a year (1989 = 23 days, 1990 = 27 days).

During song flights, female dotterel fly high over the breeding area and produce a series of shrill calls for a period of approximately 10 seconds (Nethersole-Thompson 1973; Kålås & Byrkjedal 1984). The displays are easy to hear and the flying bird can usually be observed. I noted the time, precipitation, wind speed and cloud cover during each song flight. Weather notes were also made at random intervals during days on which song flights were heard. These random observations were compared with those recorded at the time of a song flight using logistic regression (Sokal & Rohlf 1981).

3.2.2 Operational and site sex ratios

Most individuals were not individually marked at the beginning of the season. Daily observations of sex ratios and census data were therefore not independent. The daily census figures were therefore summed over 5-day periods from 3 May to 28 May and 10-day periods from 29 May through to the end of the season in each year. A minimum of five days was used for the observation period because individuals pair quickly upon joining a mating arena (personal observation of marked birds), therefore the chance of including an individual in more than one period is minimized as far as possible. Ten-day periods were used later in the season as fewer individuals could be found away from nests on the plateau during this stage. This resulted in 10 observation periods per year. The number of dotterel seen on the plateau each day and the proportion of these in pairs was recorded and summed within each observation period. The total count of dotterel away from nests within the ten observation periods in 1989 was 80, 57, 68, 56, 54, 51, 43, 77, 56 and 41; in 1990 the counts were 0, 115, 101, 128, 128, 52, 50, 24, 50 and 87, respectively. The two-tailed paired Wilcoxon signed rank test (Siegel & Castellan 1988) was used to test for significant deviation from 1 : 1 sex ratio through the season. Summing the daily data will not add power to this test because each 5- or 10-day period was taken as an event rather than each individual (this test utilizes the direction and ranked scale, but not the absolute magnitude, of a skew). Hence, an artificial inflation of the number of degrees of freedom (pseudoreplication) is avoided. This problem was not solved in any of the previous studies of sex ratios in sex-role reversed species (see Lank et al 1985; Reynolds 1987; Colwell & Oring 1988).
Site sex ratio (SSR) for each 5- or 10-day period was calculated from \[
\frac{\text{sum of daily counts of females}}{\text{[(sum of daily counts of males) + (sum of number of males known to have a nest and not seen away from it, per day)]}}
\]. The number of males on nests was adjusted in retrospect each day to account for new nests and desertions, and only included nests within the area searched for flocks. Operational sex ratio was calculated from \[
\frac{\text{sum of daily counts of females}}{\text{sum of daily counts of males not known to have a nest}}
\].

3.2.3 Potential for sexual selection

The rate of occurrence of agonistic encounters on the mating arenas was taken as an index of intra-sexual competition. Courtship display by females on the arenas and song flights over the breeding plateau were used as indices of inter-sexual courtship (cf., Colwell & Oring 1988).

Focal individual, one-minute interval one-zero activity budgets (Altmann 1974) were taken for 30-minute periods throughout the breeding season. Focal individuals were female according to plumage score and behaviour (Chapter 4). The effect of non-independence of data originating from the same individual(s) was minimized by collecting data infrequently but over a long period of time. Precipitation (0,1), percentage cloud cover and wind speed (0 = Beaufort scale 0 to 1, 1 = Beaufort 2 to 3, 2 = Beaufort 4 to 5, 3 = Beaufort 5 plus), the number of birds in the flock and flock sex ratio were noted at the beginning of the budget. At the end of each minute those activities which had been performed by the focal individual in the previous minute and the nearest neighbour distance estimated to the nearest five metres were recorded. Behavioural categories were: I = no visible activity during entire minute (inactive), F = feeding, W = walking, A = agonistic, C = courtship. Data from each 30-minute budget was summarized as the proportion of fully observed minutes in which each activity occurred and the mean nearest-neighbour distance at the end of the minute intervals.

The effects of the selection variables - OSR and proximate measures of the availability of mates (absolute number of males available on the plateau and absolute number of females available on the plateau; available birds were not in pairs or on nests) - upon behaviour were investigated when the effects of the control variables - individual plumage score, date, flock sex ratio, flock size, precipitation, wind speed and cloud cover - were controlled for. Mean 5- or 10-day period values were used for OSR, SSR, number of males available on plateau and number of females present on plateau. Initially, multiple linear regression analysis was used on the raw data but the resulting residual values were highly skewed (see discussion in Lande & Arnold 1983; Mitchell-Olds & Shaw 1987). The data for the independent X variables and the Y variables I, F, W and mean nearest neighbour distance were skewed to the left. These data were therefore rank transformed to reduce this skew (M. J. Phillips & B. English personal communication). The data for Y variables A and C
were logistically transformed because this data was distributed in a manner similar to the Poisson distribution (rare events). The regression analysis was repeated using a stepwise procedure. The residual values were normally distributed (p < 0.300) (Sokal & Rohlf 1981). The stepwise regression did not introduce spurious X variables into the model because an 'F to enter value' (threshold F-value for a variable to enter the final model) equivalent to p < 0.10 for simple regression was used as the criterion for introduction (Sokal & Rohlf 1981). Relevant control variables (see table 3.1) were forced into the model before any significant selection variables were allowed to enter.

The effects of OSR and proximate measures of the availability of mates upon the number of song flights heard each day were also investigated. Rank number of song flights per day was put into a stepwise multiple regression against OSR, number of males available on the plateau and number of females available on the plateau when controlling for date, SSR, number of nests on the plateau, proportion of males on the plateau which were paired and proportion of females on the plateau which were paired. Mean 5- or 10- day period values were used for OSR, SSR, number of males on the plateau, number of females on the plateau, proportion of males on the plateau which were paired and proportion of females on the plateau which were paired.

3.3. RESULTS

3.3.1 Breeding chronology

First egg dates grouped with respect to the 5- or 10-day periods are shown in Fig 3.1a & 3.1b for 1989 and 1990 respectively. Nest desertions grouped with respect to the 5- or 10-day periods are shown in Fig 3.2a & 3.2b for 1989 and 1990 respectively. Mean daily counts of total number of females, males not nesting, males on nests and total number of males are shown for each 5- or 10- day period in Fig 3.3a (1989) and Fig 3.3b (1990).

3.3.2 Operational and site sex ratios

The proportion of each sex paired through the season is shown in Fig 3.4a (1989) and Fig 3.4b (1990). Assuming each 5- or 10- day period is an independent observation, males were significantly more likely to be paired throughout the season than were females in both 1989 (two-tailed paired Wilcoxon signed rank test, T+ = 45, N = 9, p < 0.01) and 1990 (T+ = 31.5, N = 8, p < 0.10).

The observed OSRs and SSRs are shown in Fig 3.5a (1989) and Fig 3.5b (1990). The OSR is significantly female-biased in 1989 (T+ = 45, N = 9, p < 0.01) but not consistently so in 1990 (T+ = 22, N = 8, p > 0.20). The SSR is male-biased for the last 55 days of the 1989 season and last 60 days of the 1990 season (T+ = 41, N = 9, p < 0.05).
Figure 3.1 Number of nests initiated during each 5- or 10- day period in (a) 1989 and (b) 1990.
Figure 3.2 Number of nest desertions occurring during each 5- or 10-day period in (a) 1989 and (b) 1990.
Figure 3.3 Temporal variation in the average number of males and females observed on the study site per day in (a) 1989 and (b) 1990.
Figure 3.4 Temporal variation in the proportions of non-incubating males and females on the study site which were paired at any moment in (a) 1989 and (b) 1990.
Figure 3.5 Temporal variation in operational sex ratio (OSR) and site sex ratio (SSR) on the study site in: (a) 1989 and (b) 1990.
3.3.3 Potential for sexual selection

The F values, sign of correlation and associated probabilities of stepwise regression between behavioural components and potential determinants of selection are shown in Table 3.1. The F-to-remove values (F values resulting from final model) are given for those variables which were included in the final model. The F-to-enter values are given for the other variables which did not enter the final model (Sokal & Rohlf 1981).

Table 3.2 shows the F values, sign of correlation and associated probabilities of stepwise regression between the number of song flights observed and potential determinants of the potential for selection. The occurrence of song flight displays was found to be negatively associated with cloud cover (converted Kendall correlation coefficient T value corrected for ties, N = 102, z = -2.998, p < 0.01), precipitation (N = 102, z = -2.151, p < 0.05) and wind speed (N = 102, z = -2.844, p < 0.01).

Stepwise models were tested against non-stepwise multiple regression analysis and the factors isolated by principle component analysis. These methods gave qualitatively the same results but were invalid because of the forced inclusion of unimportant X variables and violation of the assumptions of the normal distribution by the untransformed data. However, this agreement is perhaps not surprising as principle component analysis and linear regression use a similar mathematical mechanism to achieve partial correlation coefficients.

3.4. DISCUSSION

3.4.1 Breeding chronology

A schematic representation of the breeding chronology of the dotterel in Scotland is given in Fig 3.6. The birds arrive back from North Africa in early May and immediately form aggregations at the higher points of the plateau (Chapter 2). These aggregations serve as mating arenas where females compete for access to males in order to form pairs (Nethersole-Thompson 1973). Females gain exclusive access to a male by isolating him from the rest of the flock. Mating arenas may hold up to 28 dotterel, which is more than in Nethersole-Thompson's time:

*Dotterels usually mate [form pairs] on flats and plateaux. These small groups are often extremely tame. Hens raise their wings as they chase and try to isolate the cocks. A hen also runs ahead and sits down as if brooding and then runs on again. In the Cairngorms and Grampians, mating groups have consisted of five*
Table 3.1  Variation in behavioural components explained by the OSR and proximate measures of the potential for sexual selection when the effects of control variables are removed.

<table>
<thead>
<tr>
<th>Behaviour (Y1 to Y7)</th>
<th>A</th>
<th>C</th>
<th>I</th>
<th>F</th>
<th>W</th>
<th>N-N</th>
</tr>
</thead>
<tbody>
<tr>
<td>F(V2,V1)</td>
<td>F(56,3)</td>
<td>F(56,2)</td>
<td>F(56,2)</td>
<td>F(56,1)</td>
<td>F(56,3)</td>
<td>F(56,1)</td>
</tr>
</tbody>
</table>

**Selection variables (X1 to X5)**

- OSR  
  -0.55 -0.01 +0.94 -1.02 -0.95 -0.14 
- FSR  
-0.65 -2.90 +0.20 +2.06 -0.14 +8.18** 
- Flock size  
+1.31 +1.18 -0.13 -0.09 +0.24 -1.36 
- Number of males  
+4.87** +22.60*** -0.12 +0.08 +8.09*** -0.71 
- Number of females  
-2.50 +0.34 -0.41 +0.63 -0.33 -0.54 

**Control variables (X6 to X11)**

- Date  
  +0.89 +0.01 -19.32*** +21.95*** +17.81*** +2.82 
- Time  
  -1.14 -1.78 +0.65 -2.40 -0.24 +0.02 
- Cloud cover  
  -11.03*** -0.09 -0.62 +0.27 +0.20 +1.19 
- Precipitation  
  +0.64 -3.02 -0.43 -0.01 +0.33 +0.73 
- Wind speed  
  +0.63 -1.52 +0.02 -3.18 -1.73 +0.13 
- Individual  
  +5.28** +14.90*** -8.60** +0.16 +6.11** +2.39 

Columns show F values and sign of correlation resulting from stepwise multiple regression between each Y variable and the X variables (F-to-enter for X variables not in the final model and F-to-remove for X variables introduced into the final model). X variables indicated with one or more asterisk explained a significant (* p<0.05; ** p<0.01; *** p<0.001) amount of the variation in the Y variable in the final model. In each case, all variables introduced into the final model described a significant amount of the variation in the Y variable. The relevant control variables were introduced into the final model before any selection variables. V1 = Number of X variables introduced into the final model. V2 = (Number of observation periods - 2). Y variables are agonistic encounter (A), courtship (C), inactivity (I), feeding (F), walking (W) and mean nearest-neighbour distance (N-N). X variable abbreviations include plumage score of focal individual (individual), operational sex ratio (OSR), flock sex ratio (FSR), mean number of males present on study site per day (Number of males), mean number of females present on study site per day (Number of females).
Table 3.2 Variation in number of song flight displays explained by OSR and proximate measures of the potential for sexual selection when the effects of control variables are removed.

<table>
<thead>
<tr>
<th>X variables</th>
<th>F(98,5)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Selection variables (X1 to X3)</td>
<td></td>
</tr>
<tr>
<td>OSR</td>
<td>-2.15</td>
</tr>
<tr>
<td>Number of males</td>
<td>-10.58***</td>
</tr>
<tr>
<td>Number of females</td>
<td>+3.86**</td>
</tr>
<tr>
<td>Control variables (X4 to X8)</td>
<td></td>
</tr>
<tr>
<td>Date</td>
<td>-26.15***</td>
</tr>
<tr>
<td>SSR</td>
<td>-12.73***</td>
</tr>
<tr>
<td>No. of Nests</td>
<td>+2.40</td>
</tr>
<tr>
<td>Proportion of males paired</td>
<td>+0.26</td>
</tr>
<tr>
<td>Proportion of females paired</td>
<td>-4.58**</td>
</tr>
</tbody>
</table>

F values and sign of correlation resulting from stepwise multiple regression between the Y variable (number of song flight displays) and the X variables (F-to-enter for X variables not in the final model and F-to remove for the X variables not introduced into the final model). All variables introduced into the final model explained a significant amount of the variance in the Y variable. X variables indicated with one or more asterisk explained a significant amount of the variation in the Y variable in the final model (* p<0.05; ** p<0.01; *** p<0.001). X variable abbreviations are the same as in Table 3.1. 'Proportion of males paired' and 'Proportion of females paired' refer to the mean proportions of non-incubating males and females on the study site which are paired during the relevant 5- or 10-day period, respectively.
Fig 3.6 Breeding chronology of the Eurasian dotterel in Scotland
to eight birds. For example, on the 12th May, 1942 I watched a group of four hens and three cocks on a Cairngorm top. Time after time, the hens raised their wings and shut them again. Then one suddenly ran forward, squatting and apparently brooding. When no cock followed her she returned to the group, raised her wings and soon afterwards again ran and squatted. Finally, all seven dotterels, whirring noisily flew away and resumed display on a flat about three hundred yards ahead. In the Grampians, on 25th May, 1967, Colin Murdoch watched another group of seven, of three or four hens and probably three cocks. A cock and hen left the group, the hen started to scrape and then ran a few yards forward. In the group two hens raised their wings and ran at one another like blackcocks at a lek.

Nethersole-Thompson (1973)

Once paired, the birds leave the mating arena and settle elsewhere on the plateau (Nethersole-Thompson 1973; Chapter 2). After the female has laid a clutch of 3 eggs she deserts the male and competes with other females for access to males. A second period of intense courtship ensues during which some females succeed in becoming polyandrous (Nethersole-Thompson 1973; Nethersole-Thompson & Nethersole-Thompson 1986 and references therein; personal observation of marked females). Any male whose clutch fails may also return to the mating arena (personal observation of marked males). Males become paired rapidly but females must compete for access to males (Fig 3.4). In 1989 several nest failures occurred at the end of the season; these were due predominantly to trampling by red deer Cervus elephus (Fig 3.2a). Trampling also occurred in 1990 but a large number of nest failures also occurred in mid-June; these were due to heavy falls of snow (Fig 3.2b). Subsequent to this, approximately half the nests active at the time of the major snow fall on the plateau failed and a large number of males re-paired within a couple of days (see also Chapter 5). The resulting nests observed in Fig 3.1b are possibly an underestimate of the true number initiated at this time because little emphasis was placed on finding new nests at this stage of the breeding season.

3.4.2 Operational and site sex ratios

Although the sex ratio appears to be 1 : 1 at the beginning of the season, the mating system of the dotterel leads to a female biased OSR with an abundance of reproductively viable females throughout much of the season (Fig 3.5). The SSR, however, soon becomes male-biased as many females appear to leave the plateau after the initial wave of nests (Fig 3.3). It is unlikely that these females are simply in other areas of Scotland as similar work on other hills provides the same observation (NCCS unpublished data). Also, during the late snow in 1990 the OSR became temporarily male-biased as many males were forced to desert their nests. If females were simply more difficult to see when not actively displaying on the arenas we would expect to have seen the females back on the arenas and the OSR to
remain female-biased throughout this period. It therefore appears that some females leave the Scottish breeding grounds prior to the first clutches hatching. Such females may simply move to other feeding/breeding grounds, the possibility exists though that they move to breeding grounds further east where the first nests of the year will not yet have been laid (Thomas et al. 1989).

The breeding chronology described here is broadly similar to that previously described in Scotland (Nethersole-Thompson 1973; Watson 1989) and that observed in Scandinavian populations (Kålås & Byrkjedal 1984; Kålås 1987). The major differences between the breeding biologies of the Scottish and Scandinavian populations are that (i) the birds arrive back from their wintering quarters already paired in Scandinavia and thus mating arenas are rarely seen, and (ii) a greater proportion of females help with incubation and chick rearing in Scandinavia (Kålås & Byrkjedal 1984; Kålås 1986, 1987). The season in Scandinavia is also up to a month later than in Scotland (Nethersole-Thompson 1973; Cramp & Simmons 1983), presumably because of longer snow lie at more northern latitudes. Scandinavian birds presumably become paired during migration and mating arenas have indeed been observed in Denmark during mid-May (A. P. Möller, personal communication). Similarly, the shorter season in Scandinavia will reduce the probability of females successfully finding subsequent partners and becoming polyandrous. Also, the mean breeding density of the Scandinavian populations is much lower than that in many areas of Scotland (J. A. Kålås, I. Byrkjedal, D. B. A. Thompson, D. P. Whitfield, unpublished data). The likelihood of females finding available mates is therefore possibly lower in Scandinavia than Scotland. Therefore, in the Scandinavian populations, females may increase their fitness more by helping a mate in parental duties rather than by deserting to find another male.

Allowing for the reversal in sex-roles, the similarities between the mating system of the Eurasian dotterel and conventional lekking are striking:

1. Females compete for access to males at a geographically predictable, non-resource based site.
2. Male breeding attempts are non-synchronous and females remain reproductively active throughout the male breeding season.
3. The female reproductive time unit per clutch is much shorter than that of the male.
4. Potential variation in female reproductive success is high.
5. The OSR is highly female-biased.

These similarities, and arising anomalies, are discussed in the companion chapter (Chapter 4) which concludes that, despite these similarities, dotterel do not in fact truly lek. This is because, contrary to the predictions of the theory of sexual selection, the direction of mate choice is not reversed and therefore an important component of lekking is missing. The
phenomenon of sexual selection and mate choice in sex role reversed avian species will be more widely discussed in Chapter 7.

3.4.3 Potential for sexual selection

The large female-biased skew in the OSR observed in this population is probably unusual among avian species (Sundberg 1988). In most avian mating systems both sexes provide at least some parental care and therefore the OSR usually remains close to unity (Lack 1968). The large skew in the OSR observed here is facilitated by complete female desertion. The opposite directions of the skews in OSR and SSR are also unusual (Sundberg 1988). The mating system of the dotterel therefore provides an excellent test of the fundamental feature of the OSR hypothesis; it is the availability of each sex for reproduction that influences the form of, and potential for, sexual selection (Emlen & Oring 1977; Sutherland 1985a).

In this study, the OSR did not prove to account for a significant amount of the variance in agonistic behaviour once individual variation correlated with plumage brightness was removed (Table 3.1). This observation is contrary to Emlen & Oring's (1977) hypothesis of the way in which OSR will be correlated with the potential for sexual selection; females should have fought more when the OSR was more female-biased. I suggest that this was not found in this study because of the nature of competition on the mating arena. Females do not hold territories on the arena. They therefore only fight over access to males. Variation in the rate of occurrence of agonistic behaviour was better explained by the absolute number of unpaired males available on the plateau at the time. Females fight more when there are a large number of males available on the plateau (Table 3.1). Hence, female aggression is linked more closely to the presence of males for which to fight than to the presence of females with which to fight.

Similarly, the OSR itself was not a good predictor of the occurrence of display flights or courtship behaviour on the mating arena, although the absolute number of males available on the plateau was. The OSR did not explain a significant proportion of the variance in courtship behaviour on the mating arena (Table 3.1). Females were involved in more courtship events when the absolute number of males on the plateau was high (Table 3.1). Females performed more song flights when there were few males available for mating (Table 3.2). This relationship is independent of the fact that the number of song flights increases as the number of females increases (if the order of introduction of the two significant selection variables is reversed the absolute number of males still describes a significant amount of the variation in the number of song flights; F(98,4) = 5.905, p < 0.001). Again, these findings are contrary to the direct predictions of Emlen & Oring's (1977) OSR hypothesis.
These results are particularly pertinent when it is remembered that Colwell & Oring (1988) concluded that OSR would be a robust measure of sexual selection, 'especially in species with mate defence mating systems'. This apparently describes many species which show FAP. The mating arenas of dotterel are not, however, areas where mate defence takes place. Females acquire a male by separating him from the rest of the arena. 'Mate defence' takes place, if at all, elsewhere on the plateau. The subject of mate defence in dotterel is discussed in greater detail in Chapter 6.

The lack of success of OSR in predicting the temporal pattern of competition and courtship in dotterel emphasizes the importance of the exact spatial and temporal distribution of each sex in determining the form of sexual selection. Female dotterel compete for, and court, males which represent a scarce resource. Males are not just rare because they limit a female's potential reproductive success. Males are also distributed at very low density. Thus, ratios have little effect upon the strength of competition compared to absolute density of males. Females only compete with one another when males are present. Therefore, when a lot of males are present the females fight frequently. An increase in the number of females present does not increase the incidence of fighting or courtship because, typically, only two or three females are involved in an aggressive encounter. Hence, even when only two females are present they may spend a lot of time fighting and if more females were present it would probably be only the brightest ones (see Chapter 4) which would fight. Females even fight when there is an apparent surplus of males in the flock. This may be because the females compete to acquire a 'good quality' male. This question, of mate choice, is studied in more detail for dotterel in Chapter 4 and the wider topic of mate choice in sex-role reversed species is considered in Chapter 7.

Upon first interpretation the results of this study suggests that the OSR is not an important factor in predicting the potential for sexual selection. However, the OSR was initially proposed as an empirical index of the availability of mates (Emlen & Oring 1977). This study strongly supports that theoretical framework. The OSR does attempt to measure the crucial factor: availability of alternative reproductive opportunities. The OSR approach may well be successful in populations of species breeding at higher density.

'Measuring sexual selection: why bother?' This was the title of an invited paper by Alan Grafen presented at the Dahlem workshop on sexual selection (Bradbury & Andersson 1987). In this intriguing essay Grafen plays the Devil's advocate to the studies of Bateman (1948) and others: not only is the intra-sexual variation in the number of mates obtained the wrong way to measure sexual selection, but the whole idea of numerical measurement is not even interesting! Grafen summarized,

*Reading discussions of exactly how sexual selection should be measured (e.g., Payne 1979; Wade 1979; Wade and Arnold 1980; Arnold 1983; Arnold and Wade*
1984b; Sutherland 1985[a]) makes me imagine historians debating whether the significance of the Boston Tea Party should be assessed by the wet or the dry weight of the tea thrown overboard. It is not necessary to be numerically precise to be right.

So what is interesting about sexual selection? Grafen (1987) also considered this point and produced the following list of what he considered 'interesting questions':

1. Female choice or male competition?
2. Number or quality of females?
3. Does male competition lead to organs designed as weapons or displays?
4. Is female choice for genes or paternal care?
5. If for genes, what maintains the genetic variability among males?
6. Does sexual selection work on both sexes at once?
7. Does sexual selection do for a species more of what sex already does?

As Grafen stated, 'interesting answers would likely not be yes or no, but an account of what circumstances the answer was yes, and when no, and an explanation'. I think that I could provide a suitable set of answers to these questions concerning sexual selection in the dotterel. However, I still would not know why the sex-roles are reversed. Surely this is an interesting question? To answer this question it is necessary to know about the sex-specific costs and benefits of mate-desertion. This an implicit aim of OSR measurement (Emlen & Oring 1977; Colwell & Oring 1989). So there is a reason to understand the potential for sexual selection. But Grafen even predicted this: he reviewed five reasons for measuring sexual selection (Grafen 1987):

1. to test predictions of sexual selection theory,
2. to measure things about selective surfaces,
3. to explain rhetorical claims,
4. to provide security of argument through precision,
5. to explain sex differences.

Grafen dismissed the first four of these as, respectfully: flawed, not interesting, misleading and unnecessary. The fifth reason was, he claimed, the 'only good reason'. This was because Grafen saw the explanation of differences between the sexes as the most fundamental question in sexual selection: and the phenomenon for which Darwin invented the term.
3.4.4 Skewed OSR and the evolution of polyandry

Both male and female-biased sex ratios have been proposed as important factors in the evolution of sex-role reversal. A male-biased sex ratio provides females with potentially more than one mate, therefore females compete to secure the largest number of males (Hildén & Vuolanto 1972; Maynard Smith & Ridpath 1972; Schamel & Tracy 1977; Ridley 1978). A female-biased sex ratio promotes competition between females in order to secure a mate leading to sex-role reversal (Emlen & Oring 1977). A test of these ideas is provided by the mass desertion early in the 1990 season. During this period the OSR became highly male-biased, in contrast to the usual female bias. The sex-roles did not however become conventional. Females continued to compete for males, males were not seen to become aggressive. This observation emphasizes the limitations of using any single measure as a description of sexual selection. Proximate measures of the OSR may describe the potential for sexual selection in some systems, they do not, however, always predict its direction. This is because the skew in the OSR does not explain the origins of sex-role reversal in this system. Early spring observations indicated that the population sex ratio was at unity (Fig 3.5). The skew in the OSR is a result of the mating system and not, as has been frequently suggested, a cause of it. A momentarily male-biased OSR does not cause conventional sex roles to be adopted because (i) sex-role reversal occurs because of the sex-specific benefits to females of desertion when breeding is at low density (Chapter 7), (ii) females will still be selected to compete for males of good phenotypic quality (Chapter 4; Chapter 5; Chapter 7), and (iii) historical inertia causes the sex-roles determined by factors (i) and (ii) to be inflexible within such a short period of time.
CHAPTER 4 Individual variation and mate choice

Abstract.- The Eurasian dotterel Charadrius morinellus exhibits an extreme form of sex-role reversed mating system, analogous in many respects to lekking in polygynous species. In dotterel, females are the competitive sex and males perform all parental care. Intra-sexual plumage variation is prominent in both sexes. In this study it is demonstrated that bright females fight more and win more fights than do dull females. This is not because bright females have an intrinsically higher resource holding potential but because they initiate more fights. Bright females also do more courting than do dull females, and all females prefer to court bright males. Bright females get mates earlier in the season, as, via assortative mating, do bright males. Bright males are in better condition than dull males. This leads to the suggestion that females choose bright males because they are likely to be better parents. Active female choice for males of high phenotypic quality, which is likely to have a large environmental component, is contrary to what would be predicted if the mating system of the dotterel represented sex-role reversed lekking.

4.1. INTRODUCTION

Inter-sexual plumage dimorphism in birds is a classic example of the elaboration of secondary sexual characters via sexual selection (Darwin 1871; Fisher 1915). Males are usually brighter than females and the dimorphism is usually most pronounced in species in which the potential for sexual selection is greatest (Fisher 1930; reviewed in Harvey & Bradbury 1991). Plumage elaboration is used as a cue in both intra-sexual conflict and inter-sexual courtship. Females tend to prefer males with more showy plumage (e.g., O'Donald 1980a; Andersson 1982a; Grant & Grant 1987; Heisler et al 1987; Moller 1988a; Norris 1990a; Petrie et al 1991). The evidence that plumage is used as a signal in these contexts is convincing. Why such characters are so widely used is more intriguing (see Partridge & Harvey 1986, Maynard-Smith 1991).

Intra-sexual plumage variability is also well documented, especially amongst passerine bird species. Hypotheses aimed at describing its adaptive significance are numerous (e.g., Selander 1972; Rohwer 1975; Shields 1977; Balph et al 1979; Lyon & Montgomerie 1986; Watt 1986; Whitfield 1987; Dawkins & Guildford 1991). Evidence from empirical research on passerines suggests that plumage characters do act as signals between individuals during competition. Plumage form can signal dominance or submissiveness even within sex and age classes (reviewed in Watt 1986; Whitfield 1987; Maynard-Smith & Harper 1988; Norris MS). The plumage forms are termed 'badges of status' (Dawkins & Krebs 1978); typically a large badge signifies dominance whilst a small badge indicates submissiveness. Badges usually consist of an area of bright or dark plumage of variable size between individuals. The badges of some species are also those characters used during mate choice (e.g., Eckert
Zahavi (1987) and Grafen (1991a,b) unified the theoretical basis of sexual selection and conventional signalling. They pointed out that the phenomena were closely related; both could be expressed in terms of a signaler and a receiver. Previous studies had debated whether signals must be honest in order to be stable or if a self-reinforcing signal, equivalent to Fisher's (1930) runaway model of sexual selection powered by female choice, could work (Zahavi 1975, 1977; Maynard-Smith 1976a) . Grafen (1991b; see also Pomiankowski et al 1991; Iwasa et al 1991) pointed out that either system may be stable, but agreed with Zahavi (1987) that honest signalling seemed the most parsimonious explanation of natural signalling. Recently, Zahavi (1991) has gone further than this and has suggested that the term 'sexual selection' is of little use. He suggests that sexual selection is simply a special case of 'signal selection'. An alternative view is that signal selection is an interesting component of sexual selection but does not encompass all areas of sexual selection. For example, signal selection teaches us little about the effect of sex itself upon sexual selection, neither does signal selection encompass the subject of variation in the potential for sexual selection. Equally, sexual selection does not cover all areas of signal selection. Neither term is simply a sub-division of the other; they simply overlap in some areas. Both terms are of use; in conjunction and independently. However, whether or not Zahavi's suggestion is adopted, the critical questions in both sexual selection and conventional signalling are (i) what is being signalled?, (ii) why is the signal honoured by the receiver?, and (iii) why does cheating not occur? These questions are not independent; a precise answer to any one of them inevitably solves the remaining two.

In this study I present evidence on the importance of plumage variability in a sex-role reversed, non-passerine species, the Eurasian dotterel Charadrius morinellus. In the dotterel the female is the competitive sex (Nethersole-Thompson 1973; Kååls & Byrkjedal 1984). As would be predicted, the female is larger and more brightly coloured than the male (Kååls 1988). Females are potentially polyandrous and compete for access to males on mating arenas throughout the breeding season (Nethersole-Thompson 1973; Nethersole-Thompson & Nethersole-Thompson 1986). This extreme form of female access polyandry may be likened to the lekking found in polygynous species (Nethersole-Thompson 1973; Chapter 3; Chapter 7). Using this comparison we would predict that males should use variation in female display or morphology as criteria in active mate choice. Males should benefit from mate choice, in an analogous way to females of polygynous lekking species, by either (i) producing offspring of high genetic quality (Darwin 1871; Fisher 1938; Hamilton & Zuk 1982), (ii) producing sexy daughters (Fisher 1958; Weatherhead & Robertson 1979), (iii) avoiding sexually transmitted parasites (Freeland 1976; Hamilton
1990), or (iv) gaining a direct benefit from the female (reviewed in Kirkpatrick & Ryan 1991).

The aims of this study are to (i) study the effect of intra-sexual plumage variability on the behaviour and potential reproductive success of females, (ii) identify the direction of, and cues used in, mate choice in the dotterel, and (iii) identify the adaptive benefit of mate choice.

4.2. METHODS

The study site, a 13 km² upland plateau in the Cairngorm region of northern Scotland, is described in detail in Chapter 2. The methods used in this study are largely the same as those described in more detail in the companion chapter (Chapter 3). I describe only additional methods in detail here.

4.2.1 Plumage scores

Dotterel show sufficient sexual dimorphism in plumage to be able to separate the sexes reliably in the field (Nethersole-Thompson 1973). Females are consistently brighter than males. Females have fewer streaks on their blacker caps, more extensive and less interrupted black belly patches and less interrupted rufous colouration on the breast (Kâlâs 1988). However, intra-sexual plumage variation is also evident (Nethersole-Thompson 1973). Males range from being totally without breeding colouration to having plumage similar to a dull female. Females show a similarly wide spectrum of plumage form. These differences are very noticeable in the field. In order to quantify the variation in plumage both between and within the sexes a plumage score system was developed based on Kâlâs' (1988) inter-sexual analysis. The plumage score criteria are shown in Table 4.1 and an impression of the scale of variation is given by the museum skins shown in Fig 4.1. Plumage scores were completely repeatable within and among the observers who contributed data.

4.2.2 Female plumage score and behaviour

4.2.2.1 Multivariate analysis of behaviour.

Focal individual, one-minute interval, one-zero activity budgets (Altmann 1974) were taken for females for 30-minute periods throughout the courtship period. Meteorological, flock and individual plumage score information was recorded for each budget (Chapter 3). Activities recorded were I = no activity, F = feeding, W = walking, A = agonistic, C = courtship. Behavioural data from each budget was summarized as the proportions of fully observed minutes in which each activity occurred, the proportion (L) of times the focal
Table 4.1  Plumage score criteria in dotterel for the three most
important plumage characters.

<table>
<thead>
<tr>
<th>SCORE</th>
<th>MALE</th>
<th></th>
<th></th>
<th></th>
<th>FEMALE</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
</tbody>
</table>

**BELLY**
- *No black* <25% black
- 50%>X>25% black
- >50% black
- 100% black but *not to* extending to wing edge
- >50% pale
- >50% pale
- 50%>X>25%
- <25% white
- <10% white
- streaks on brown cap
- streaks on brown cap
- pale streaks on brown cap
- streaks on brown cap
- Black cap

**CAP**
- *No colour* Incomplete Complete Complete Complete
- *dull colour* *dull colour* bright colour bright colour bright colour

The most important features for field discrimination between adjacent plumage score are italicized.
Figure 4.1 Examples of the six plumage score classes in skin specimens of dotterel: (a) underside, and (b) side view. Birds were sexed on the appearance of their gonads which were drawn on the specimen cards.
individual was at the edge of the flock (i.e., constituted a corner of the convex polygon describing the edge of the flock) at the end of the one-minute intervals and the mean, maximum and variance in the mean of the nearest neighbour distance at the end of the one-minute intervals (mean N-N, max N-N and s N-N respectively) during the budget.

One-zero activity budgets taken in note-books were used to record all behaviours and interactions in preference to battery operated equipment which proved unreliable under the difficult field conditions encountered. One-zero budgets do not generally provide an unbiased estimate of the time spent in any one activity or provide a basis for comparing the allocation of time between activities. Rare events are over-represented and common events under-represented when only short budgets are used. One-zero budgets cannot therefore be used as the basis for energetic models. One-zero data are, however, useful in describing the difference in time allocation between individuals within any one activity because the data are unbiased in this respect. It is a particularly useful method when rare events such as agonistic or courtship encounters are being studied (see also discussion by Bernstein 1991). The effect of non-independence of data arising from observations of, or counts on, the same individual were minimized as described in Chapter 3 but could not be totally eliminated.

The influence of the selection variables - absolute plumage score and rank-within-flock - upon behaviour was studied when the effects of the control variables - date, time, precipitation, wind speed, cloud cover, flock size, flock sex ratio, operational sex ratio, number of males on plateau and number of females on plateau - were kept constant. Meteorological data were recorded as previously described (Chapter 3). Mean 5- or 10-day period values were used for operational sex ratio, site sex ratio, number of males available on plateau and number of females available on plateau (see Chapter 3 for details of these measures). Rank within flock was calculated as the mean rank attributed to each female plumage score within the flock when plumage scores were ranked in ascending order (the same ranking procedure is used in many non-parametric tests; Siegel & Castellan 1988).

The residual values resulting from stepwise multiple regression between each behavioural component (Y variable) and the X variables were significantly skewed. The data for the independent X variables and Y variables V, F, W, L, mean N-N, max N-N and s N-N were therefore rank transformed in order to reduce the skew (M. J. Phillips & B. English personal communication). The data for Y variables A and C were logistically transformed because they were distributed in a Poisson fashion. Stepwise multiple regression analysis was performed with F-to-enter values equivalent to p < 0.10 in simple regression (Sokal & Rohlf 1981; Chapter 3). Relevant control variables (see table 4.2) were forced into the model before any significant selection variables were allowed to enter.
TABLE 4.2  Variation in behavioural components explained by individual variation in female plumage and rank within flock when the effects of control variables are removed using stepwise multiple regression.

<table>
<thead>
<tr>
<th>Behaviour code (Y₁ to Y₇)</th>
<th>L</th>
<th>A</th>
<th>C</th>
<th>I</th>
<th>F</th>
<th>W</th>
<th>mean</th>
<th>max</th>
<th>s</th>
<th>N-N</th>
</tr>
</thead>
<tbody>
<tr>
<td>F(V₂,V₁)</td>
<td>F(30,2)</td>
<td>F(56,5)</td>
<td>F(56,2)</td>
<td>F(56,2)</td>
<td>F(56,6)</td>
<td>F(56,2)</td>
<td>F(56,1)</td>
<td>F(56,3)</td>
<td>F(56,3)</td>
<td></td>
</tr>
</tbody>
</table>

Selection variables (X₁ to X₂)

| Plumeage score | +63.32** | +12.50** | +12.58** | -8.34** | +3.19* | +5.47** | +2.22 | +7.41** | +10.41** |
| Rank within flock | +1.80 | -3.26 | +0.12 | -0.00 | +0.02 | +0.34 | +0.31 | -0.03 | +0.01 |

Control variables (X₃ to X₁₂)

| Date | +0.13 | +10.36** | +0.47 | -17.06** | +3.33* | +16.36** | +1.71 | +7.52** | +11.61** |
| Time | -0.32 | -1.96 | -2.13 | +1.93 | -2.40 | -0.40 | -0.00 | -0.00 | -0.31 |
| Cloud cover | -7.18** | -25.92** | -0.34 | -0.23 | -0.07 | +0.05 | +1.00 | +0.28 | +0.10 |
| Precipitation | +0.56 | -7.56** | -1.10 | -1.03 | +0.61 | +0.79 | +1.06 | +1.51 | +0.25 |
| Wind speed | +0.65 | -0.16 | -0.41 | -0.06 | -0.43 | -0.86 | +0.46 | -0.18 | -0.27 |
| OSR | -2.96 | -0.60 | -1.25 | +1.61 | +5.12** | -0.24 | -0.14 | +0.09 | -0.00 |
| FSR | -2.66 | -3.44 | -1.08 | -0.00 | +2.48# | +0.96 | +8.18** | +0.19 | -0.00 |
| Flock size | -0.35 | +1.56 | +0.60 | -0.02 | +0.24 | +0.00 | -1.36 | -0.35 | +0.13 |
| Number of males | +0.82 | +8.33** | +2.35# | -0.62 | +10.63** | +1.23 | -0.71 | -0.46 | -0.30 |
| Number of females | -0.20 | -0.00 | +2.01 | +0.21 | -7.72** | +0.27 | -0.54 | -4.99** | -4.11* |

Columns show F values and sign of correlation resulting from stepwise multiple regression between each Y variable and the X variables. X variables indicated with a hatch symbol or one or more asterisk were introduced into to the final regression model (# p< 0.10; * p<0.05; ** p<0.01). V₁ = Number of X variable introduced into the final model. V₂ = (Number of observations - 2). Y variables are proportion of time spent at edge of mating arena (L), agonistic encounter (A), courtship (C), inactivity (I), feeding (F), walking (W), mean nearest-neighbour distance (mean N-N), maximum nearest-neighbour distance (max N-N) and variance in nearest-neighbour distance (s N-N). X variables abbreviations include operational sex ratio (OSR), flock sex ratio per observation period (FSR), mean number of males present on study site per day (Number of males) and mean number of females present on study site per day (Number of females).
4.2.2.2 Univariate analysis of agonistic behaviour.

During agonistic events the plumage score of both participants, the initiator of the event and the winner of the event were recorded. The initiator was the individual which first displayed to, or attacked, the other (see Nethersole-Thompson 1973 for detailed descriptions of the form of agonistic behaviour in dotterel). The winner was the individual which did not withdraw from the encounter. The observed proportion of agonistic encounters won by the focal individual of known plumage score against opponents of known plumage score was recorded.

4.2.2.3 Univariate analysis of courtship behaviour.

The plumage score and sex of both individuals involved in courtship events was recorded, as was the sex of the bird initiating the event. The plumage score of all other individuals in the flock at the time was also recorded. The distribution of courtship events between males and females of known plumage score was tested against the distribution predicted from the overall proportion of males of each plumage score in the population within each season using a chi-square test (Siegel & Castellan 1988).

4.2.3 Assortative mating

A population census, covering approximately half the study site each day was carried out as described in Chapter 3. The plumage score of each dotterel encountered was recorded. It was also noted whether the individual was a single, in a pair, or in a flock. The location of pairs was recorded.

The proportion of females of known plumage score paired with males of each plumage score was compared with the null hypothesis that bright and dull females were equally likely to be paired with bright and dull males. Thus, the observed ratio of plumage scores of males paired to bright and dull females was compared with the overall ratio of male plumage scores in pairs by using a chi-square test.

4.2.4 Timing of pairing

Daily observations of the proportion of individuals of each plumage score paired are not independent because the same individuals may be included on successive days. The daily figures were therefore summed over 5-day periods from 5 to 28 May and 10-day periods from the 29 May through to the end of the breeding season (see Chapter 3 for full rationale). A two-tailed, paired Wilcoxon signed rank test (Siegel & Castellan 1988) was used to test for a significant difference between the mean proportion of the appropriate sex paired through the season and the mean proportion of each plumage score paired through the
season. Use of this test minimized pseudoreplication because the ranked scores of the deviation from the mean during each 5- or 10-day period are used as observation points, rather than individual dotterel or the absolute magnitude of the skew from the mean.

4.2.5 Male condition

Males were caught and individually colour-ringed within the last 4 days of incubation or the first 5 days of chick rearing. It was not possible to catch the males at a more standard time because of their liability to desert if caught too early (NCCS unpublished data) and difficulties in finding all the nests on the study site prior to hatching. Measures of male condition should, however, be unbiased with respect to male plumage score and age. Body weight, tarsus length, wing length, head and bill length were recorded. Males were aged using ptilochronological examination of their tail feathers (Michener & Michener 1938; Wood 1950; Grubb 1989). Individuals in which three or more growth bars could be followed continuously through two pairs of tail feathers more than two feathers apart (and those in between) were classed as first-year under the presumption that all these were feathers which had been grown at the same time during the fledging period. Individuals in which less than three growth bars could be followed through feathers which were two or more feathers apart, or individuals in which growth bars appeared unrelated, were classed as adults on the presumption that these tail feathers had grown at different times (Prater et al 1977). Care was taken not to use comparisons between adjacent feathers or correspondingly opposite feathers as informative. In most cases the type of feather growth was very obvious all the way across the tail. Birds which were caught with wet or very heavily abraded tails were not aged.

4.3. RESULTS

4.3.1 Plumage scores

The plumage score criteria in Table 4.1 successfully distinguished between the sexes (when determined by behaviour) in all pairs observed (N = 196). The female was always brighter than the male. Some overlap between the sexes did, however, occur in the plumage score 4 category. From behavioural observations on mating arenas it is estimated that < 4% of 4-score individuals (N = 127) are male. The relative frequency of individuals of each plumage score is shown in Fig 4.2 and Fig 4.3 for females and males respectively. In order to test for any change through the breeding season in the relative frequency of each plumage score within either sex a two-tailed sign test was used (Siegel & Castellan 1988). There was no significant deviation from the null hypothesis of no consistent change and an expectation of an equal number of positive and negative changes in proportion between adjacent periods through the season (p > 0.50 for all scores in both years). Therefore, there
was no significant change through either breeding season in the relative frequency of each plumage score within either sex.

From this point, unless otherwise stated, 'bright' and 'dull' females refer to 6-score and 5-score females respectively and 'bright' and 'dull' males refer to 3-score and 2-score males, respectively. Few 4-score females or 1-score males were included in this part of the analysis.

4.3.2 Female plumage score and behaviour

4.3.2.1 Multivariate analysis of behaviour.

The F values, sign of correlation and associated probabilities resulting from stepwise regression between behavioural components and individual plumage score, individual rank within flock and control variables are shown in Table 4.2. The F-to-remove values are given for those X variables which entered the final model and the F-to-enter values are given for the other variables which did not enter the final model.

3.2.2 Univariate analysis of agonistic behaviour.

The proportion of agonistic encounters won by the focal individual of known plumage score against opponents of known plumage score is shown in Fig 4.4. Data are combined between years.

The observational results were tested against three models of fighting behaviour. The equal resource holding potential (RHP; Parker 1974) hypothesis predicts that the focal individual wins 50% of agonistic encounters. The plumage dominance hypothesis predicts that the focal individual always beats individuals duller than itself, loses to individuals brighter than itself and wins on 50% of occasions against equally bright individuals. The initiator dominance hypothesis predicts that the initiator of an agonistic event wins the event. Comparisons between observed and predicted results were made using two-tailed one sample Kolmogorov-Smirnov tests and Kendall correlation coefficient tests (Siegel & Castellan 1988). Table 4.3 shows the numerical predictions of the three models based on the number of fights observed.

The results predicted by the equal RHP (Kolmogorov-Smirnov one sample test D = -0.153, p < 0.05) and plumage dominance hypotheses (D = 0.209, p < 0.05) are significantly different from the observed results. The results predicted by the initiator dominance hypothesis are significantly more similar to the observed results than would be expected by chance (Kendall correlation coefficient T = 0.943, p < 0.05).
Figure 4.2 Relative frequency of observed female dotterel of each plumage score class: (a) 1989, (b) 1990.
Figure 4.3 Relative frequency of observed male dotterel of each plumage score class: (a) 1989, (b) 1990.
Figure 4.4 Observed outcome of agonistic encounters between a focal female and an opponent female, both of known plumage score. Histogram bars represent the proportion of fights won by the focal female. Heavy horizontal bars represent the expected proportion of wins by the focal female under the 'plumage dominance' hypothesis (compare table 4.3).
Table 4.3 Observed and predicted proportion of wins in agonistic encounters between females of known plumage score using three models of dominance.

<table>
<thead>
<tr>
<th>Plumage score</th>
<th>Observed or predicted number of wins by focal female</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Focal Female</td>
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<tr>
<td>4</td>
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<tr>
<td>6</td>
<td>58</td>
</tr>
<tr>
<td>6</td>
<td>24</td>
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\[
D = -0.152^* \quad D = 0.209^* \quad D = -0.043 \\
T = 0.943^*
\]

N = total number of encounters observed for each pairwise comparison. O = observed results. E (ERHP) = predicted results using the 'equal resource holding potential' model. E (PD) = predicted results using the 'plumage dominance' model. E (ID) = predicted results using the 'initiator dominance' model. D and T values refer to two-tailed Kolmogorov-Smirnov one sample tests and Kendall correlation coefficient values, respectively. An asterisk indicates rejection of the complementary null hypothesis at the p < 0.05 level.
4.3.2.3 Univariate analysis of courtship behaviour.

Females always initiated courtship events \((N = 188)\). The proportions of courtship events between females and males of each plumage score are shown in Fig 4.5. This distribution was tested against the mean proportion of males of each plumage score in the population in each year; the expected results are shown in Fig 4.5. Females show a significant bias towards courting bright males and a significant tendency not to court dull males \(\left( X^2 = 6.726, \text{df} = 2, \ p < 0.05 \right)\).

This analysis was repeated within mating arenas. A two-tailed sign test (Siegel & Castellan 1988) was used to test for a significant bias from the binomial distribution resulting from whether or not a female, upon courting, courted a male of the highest plumage score class present in the flock at the time. Courtship events were observed on 68 independent occasions (different females on the same day or possibly the same female on different days). In 46 of these cases the courting female courted a male of the highest male plumage score on the arena. This confirms a significant bias towards brighter males being courted more (two-tailed sign test, \(z = 2.790, \ N = 68, \ p < 0.01\)).

4.3.3 Assortative mating

90 pairs were observed in 1989 and 97 in 1990. Pairs occupying the same area on subsequent days were not included in this analysis more than once. The comparison between the observed ratio of plumage scores of males paired with bright versus dull females and the predicted ratio from the overall ratio of plumage scores of males in pairs is shown in Fig 4.6. Bright females were significantly more likely to be paired with bright males than expected, dull females were significantly more likely to be paired with dull males than expected \((1989: X^2 = 5.57, \text{df} = 1, \ p < 0.05; \ 1990: X^2 = 12.50, \text{df} = 1, \ p < 0.001\)).

4.3.4 Timing of pairing

The proportions of individuals of each plumage score that were paired and the mean proportion of each sex paired throughout the season are shown in Figs 4.7 and 4.8 for females and males respectively. To minimize pseudoreplication overall figures for 5- and 10-day periods are used for this analysis. Bright females are significantly more likely to be paired (two-tailed paired Wilcoxon signed rank test, \(1989: T+ = 52, \ N = 10, \ p < 0.01; \ 1990: T+ = 45, \ N = 9, \ p < 0.01\)) and dull females significantly less likely to be paired \((1989: T- = 37, \ N = 9, \ p < 0.05; \ 1990: T- = 36.5, \ N = 9, \ p < 0.05)\), than expected from the female mean, throughout the season. Similarly, bright males are significantly more likely to be paired \((1989: T+ = 49, \ N = 10, \ p < 0.05; \ 1990: T+ = 45, \ N = 9, \ p < 0.01)\) and dull males significantly less likely to be paired \((1989: T- = 47, \ N = 10, \ p < 0.05; \ 1990: T- = 45, \ N = 9, \ p < 0.01)\), than expected from the male mean, throughout the season.
Figure 4.5 Female courtship preference. Histogram bars represent the observed proportion of courtship events initiated by a focal female of known plumage score towards males of known plumage score. Heavy horizontal bars represent the expected proportion of courtship events towards males of each plumage score if females simply court males in proportion to the ratio of male plumage scores in the population.
Figure 4.6 Assortative mating. Histogram bars represent the observed proportion of males of each plumage score paired with females of known plumage score. Heavy bars represent the expected proportions if males are paired to females of each plumage score simply in proportion to the ratio of male plumage scores in the population: (a) 1989, (b) 1990.
Figure 4.7 Proportion of females of each plumages score paired through the season compared with the mean proportion of females paired: (a) 1989, (b) 1990.
Figure 4.8 Proportion of males of each plumage score paired throughout the season compared with the mean proportion of males paired: (a) 1989, (b) 1990.
3.5 Male condition

An index of male condition was calculated using linear regression to remove the effects of body size on body weight (Sokal & Rohlf 1981). Body weight (Y variable) was put into a linear regression against wing length (Wi), Wi³, log Wi, tarsus length (Ta), Ta³, log Ta, head and bill length (Hb), Hb³, log Hb and (Wi x Ta x Hb) (X variables). Log Ta was the factor most closely positively correlated with body weight (highest positive r² value) and was therefore the most conservative factor to use in eliminating the effect of body size on body weight. The index of male condition was therefore the residual values resulting from a linear regression of body weight (Y variable) upon log (tarsus length) (X variable). The effects of age upon plumage score were removed using linear regression on rank transformed data and the resulting residual values were used as the index of plumage score. Conversely, the effects of plumage score upon age were removed using linear regression on rank transformed data and the resulting residual values were used as the index of age. Residual variation in age did not explain a significant amount of the variation in the index of body condition (1989: r² = 0.023, N = 23, p > 0.10; 1990: r² = 0.114, N = 13, p > 0.10). The data were rank transformed because they were more likely to satisfy the assumptions of the normal distribution in this form than in the raw state (M. J. Phillips & B. English personal communication). It was not possible to identify rigorously the degree of skew or kurtosis in these data because of the small sample size in both years. Residual variation in plumage score was positively correlated with male body condition (Fig 4.9: 1989: r² = 0.213, N = 23, p < 0.01; 1990: r² = 0.331, N = 13, p < 0.05).

4.4 DISCUSSION

4.4.1 Female plumage variation and behaviour

The most significant difference between females with respect to plumage variation is in the frequency of agonistic and courtship events, the amount of time spent at the edge of the mating arena and fluctuations in the distance to the nearest neighbour (Table 4.2). Bright females fight and court more than do dull females. Bright females also spend more time at the periphery of the mating arena which is where courtship occurs. Additionally, bright females walk more and have a greater mean variance in nearest neighbour distance than dull females. Bright females also tend (p < 0.10 if this variable is forced into the final model) to be further away from their nearest neighbour than dull females and the maximum nearest neighbour distance recorded within a budget is greater.

Bright females are therefore generally more active than duller females. They are particularly more likely to be involved in courtship and fighting and spend more time competing for access to males at the edge of the flock.
Figure 4.9 Male condition, at the end of incubation, correlated with plumage score. Residual variation in male body weight when the effects of body size are kept constant against residual variation in plumage score when the effect of age is kept constant: (a) 1989, (b) 1990.
Bright females also win more fights than do dull females, resulting in the general observation that bright females tend to beat dull females in agonistic encounters (Fig 4.4). However, the predictions of the simple plumage dominance hypothesis were significantly different from the observational data (Table 4.4). The best predictor of the winner of an agonistic encounter was the initiator dominance model. Bright females, therefore, may not win more fights because they have a higher RHP but because they simply start more fights and therefore win more fights. Alternatively, individuals may be using a more direct measure of RHP than can be assessed using the plumage score criteria developed here.

Dull females usually only start fights when they have already separated a male from the mating arena and have been courting him for several minutes. When a dull female in such a situation defends her access to the male against another female she is usually successful, irrespective of the plumage score of the intruding female. This scenario is reminiscent of a set of decision rules for fighting described in game theory models. It is called the 'bourgeois strategy' (Maynard-Smith 1976, 1982; Maynard-Smith and Parker 1976b; Parker 1984a). In animal conflict the participants often indulge in a high degree of ritualized display before physical fighting occurs. Indeed, real fighting is relatively rare. This situation is thought to occur because, in most cases of conflict, the potential costs of a fight are greater than the relative potential benefits. Hence, fighting is not a profitable strategy; behaving as a 'hawk' when the costs are high is not evolutionarily stable (Maynard-Smith & Price 1973). When the opponents are asymmetric with respect to their resource holding potential (Parker 1974), ritualized displays may represent a 'cheap' method by which both parties can access the asymmetry (Maynard-Smith & Parker 1976; Parker 1984a). However, when the asymmetry is negligible a counter-intuitive outcome is stable; the contest is settled according to an arbitrary rule (Maynard-Smith 1977). The bourgeois strategy describes such an arbitrary rule; the owner always wins, or, in game theory terms: play 'hawk' when owner and 'dove' when intruder (Maynard-Smith 1982). Empirical support for the occurrence of the bourgeois strategy in nature has been found in a number of species (e.g., Krebs 1977; Davies 1978; Packer & Pusey 1982; but see also Wickman & Wicklund 1983) and even 'anti-bourgeois' strategies have been reported where the arbitrary rule is that the owner always retreats (Burgess 1976; J. Dawson in Dawkins & Krebs 1978). The important point here is that it is not surprising that dull females can sometimes beat brighter birds. Despite the fact that bright birds are usually more aggressive, the asymmetry between females in true RHP is unlikely to be large and therefore a set of decision rules similar to that postulated by the bourgeois strategy would produce a fighting strategy similar to that observed.
4.4.2 Assortative mating and potential reproductive success

Both bright and dull females prefer to court bright males (Fig 4.5). Females show a tendency to court the brightest male on the mating arena at any one time. Since bright females do more courting than duller females, this results in bright females pairing with bright males (Fig 4.6). Duller females will pair with bright males if possible, but end up with a greater probability of being paired to a dull male (Fig 4.6).

This form of assortative mating which occurs via access dominance leads to bright females obtaining mates earlier in the season than dull females (Fig 4.7). The mates which females obtain earlier in the season are usually bright males, therefore bright males usually obtain mates earlier in the season than dull males (Fig 4.8). As dotterel exhibit sequential polyandry (Nethersole-Thompson 1973; Nethersole-Thompson & Nethersole-Thompson 1986; personal observation of marked females) this suggests that bright females have a higher potential annual reproductive success than duller females.

4.4.3 Female lekking and female choice

Desmond Nethersole-Thompson was the first person to liken the mating system of the dotterel to the leks of polygynous species. He had worked on dotterel in the Grampians, and before moving onto the high tops in the summer, had worked on Scottish crossbills, Loxia scotica, and greenshanks, Tringa nebularia, in the forests of the Spey and Dee valleys. These forests are also the haunt of black grouse, Tetrao tetrix, and capercaille, Tetrao urogallus, both classical examples of lekking species, the display of the former of which he compared to the fighting of female dotterel on the mating arena (Nethersole-Thompson 1973; quoted in Chapter 3). It is not surprising, therefore, that Nethersole-Thompson came to contemplate the similarity between the mating system of the dotterel and the polygynous leks he must have watched only a few weeks earlier.

_The flocks frequently assemble and display at particular locations - often on flats close to burns. Are these locations - at which groups of hen dotterel nest [court] and fight - true leks?_

_A lek is a definite location to which a particular group repeatedly returns to display and wherein each bird dominates a particular part. Judged by this definition, hen dotterel do not establish leks. But group activities in these rather primitive leks presumably have survival value._

Nethersole-Thompson (1973)

These observations form a reliable forerunner of the views expressed by Oring in his influential review of avian mating systems (Oring 1982). Oring preferred that 'the term 'lek' be reserved for situations in which
A group of males defends small closely positioned courts used only for mating, i.e., the courts contain minimal resources other than the males themselves.

Females visit the arena only for the purposes of choosing a mate and mating.

Females subsequently nest off the arena, where they provide parental care.

Oring therefore stressed the importance of the spatial organisation and arrangement of leks. As Nethersole-Thompson observed, the mating arenas of dotterel do not fit this description; the mating arenas are too internally dynamic. I would, however, suggest that Oring's definition places an excessive emphasis on the appearance of the lek. The processes of intra- and inter-sexual selection within the lek are its most important components. In Chapter 3 I listed the similarities between conventional lekking and the mating arenas of dotterel. There are many striking similarities, most of which concern the form of intra-sexual competition.

If the mating system of the dotterel was truly analogous to that of polygynous lekking species except for the role of the sexes, we would predict that male choice, rather than female choice should be in operation (Trivers 1972). This study demonstrates that female choice operates, however. Female dotterel do not defend a specific area; they follow specific males. Males do not select specific females; potential partnerships are broken because of the intervention of other females rather than male rejection. Females select and court males and all females prefer to court bright males.

Mate choice is a phenomenon which has benefitted from a massive amount of theoretical work (reviews in Bateson 1983; Bradbury & Andersson 1987; Pomiankowski 1988; Harvey & Bradbury 1991; Kirkpatrick & Ryan 1991; Maynard-Smith 1991). The potential answers to 'why should females choose bright males?' have been grouped into three categories.

Firstly, brighter male plumage indicates that the male possesses heritable 'good genes' for survival which will be passed on to the female's offspring (Zahavi 1975, 1977; Pomiankowski 1987a, 1988; Grafen 1991a; Heywood 1991; Iwasa et al 1991). Secondly, assuming that females prefer bright males and there is heritable variation in male plumage brightness, female choice will continue to be selected in order to produce 'sexy sons' (Fisher 1930; O'Donald 1962, 1967; Kirkpatrick 1982; Pomiankowski et al 1991). Lastly, irrespective of heritable variation, bright plumage indicates good present condition, therefore females may choose bright males because they are likely to be better parents (Maynard-Smith 1985; Hoelzer 1989).

These theories have been formed around mate choice in species with conventional sex-roles, usually in the context of polygynous mating and frequently applied to polygynous lekking
(reviews in Bradbury & Gibson 1983; Kirkpatrick & Ryan 1991). In the conventional lekking species, males compete to defend an individual-specific area, females approach a male and, if he is suitable, copulate with him. Present evidence suggests that females choose males, on the basis of plumage (Trail 1985a; Petrie et al 1991; Höglund et al 1990) or behavioural cues (Gibson & Bradbury 1985, 1991; Andersson 1989; McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Alatalo et al 1991), which are successful in intra-sexual encounters (Trail 1985b; Alatalo et al 1991), likely to survive (Alatalo et al 1991) or be free of parasites (Boyce 1990; Johnson & Boyce 1991; Pruett-Jones et al 1990; but see also Gibson 1990).

Bright males are in better condition at the end of incubation, when they are trapped for ringing, than are dull males (Fig 4.9). This is most likely the result of bright males also being in better condition than dull males prior to incubation as bright males tended to spend less time off the nest foraging during incubation than dull males (Chapter 5). The energetic demands of the incubation period of the dotterel are likely to be unpredictable. However, the obligate small clutch size (Kålås 1986) of the dotterel and frequent occurrence of periods of prolonged incubation (Nethersole-Thompson 1973; Nethersole-Thompson & Nethersole-Thompson 1986) suggest that, at times, the potential costs may be high (Kålås 1986; Chapter 5). Clutches rarely fail due to desertion except when the weather is unusually bad for a number of successive days (Chapter 3). Males in good condition are better able to withstand these costs of prolonged incubation than males in poorer condition (Kålås & Løfald 1987; Chapter 5). This scenario supports the good parent/direct benefit hypothesis of mate choice and is remarkably similar to the mate choice mechanism previously observed by Petrie (1983a, b) in another sex-role reversed species, the moorhen Gallinula chloropus. Petrie observed that both male and female moorhens may act aggressively, particularly towards individuals of the same sex as themselves. Females are the more aggressive sex but they also appear to be the more choosy sex with respect to mate choice (Petrie 1988). Dominant female moorhens select males which are small but are in good physical condition (1983a, b). Petrie suggested that the adaptive benefit of this form of female choice is that males in good condition are more able to successfully incubate subsequent clutches if the present clutch fails. Moorhens usually exhibit monogamous biparental care and nest failure due to predation is frequent; the male's ability to initiate incubation of a number of clutches is thought to be an important factor in determining annual female reproductive success (Petrie 1983a, 1986).

The fact that plumage brightness predicts female behaviour (and therefore possibly potential reproductive success) as well as male condition could be interpreted that, in dotterel, plumage brightness is an honest signal of condition in both sexes (see Andersson 1982b, 1986a, b; but see also Lande 1987). If this were the case, the plumage-score criteria used in this study would then approximate to a condition-dependent revealing handicap (Hamilton & Zuk 1982; Maynard-Smith 1987; Pomiankowski 1988): all individuals produce the signal
but only those in good condition can produce a 'good' signal. This is the form of signalling favoured in the theoretical treatments of Zahavi (1977, 1987), Grafen (1990b), Pomiankowski et al (1991) and Owens & Hartley (1991; see Appendix). Condition-dependent signals have been identified in the barn swallow, Hirundo rustica, (Møller 1991c) and the pheasant, Phasianus colchicus (von Schantz et al 1989). Through the mechanism of female choice and/or female-female competition, preferred males will acquire females of high phenotypic quality. Field data on both the arctic skua, Stercorarius parasiticus, (O'Donald 1980) and the barn swallow (Møller 1988a) have demonstrated that preferred males do have a reproductive advantage. In the case of the barn swallow, Møller (1991d) has shown that this advantage is due to the higher phenotypic quality of the mates of preferred males, rather than due to the mates of attractive males supplying more parental care simply because they are paired to an attractive male (Burley 1986a, b). However, even in these well studied examples the importance of female-female competition for access to preferred mates is not clear. The potential importance of passive male choice as a result of active female choice/ female-female competition is discussed in Chapter 7.

It must, however, be remembered that this study has only demonstrated that female plumage score is correlated with certain behavioural characteristics (see Mitchell-Olds & Shaw 1987). Without direct experimental manipulations it is impossible to ascertain whether it is plumage characteristics per se which are being used as cues in intra-sexual display or inter-sexual choice. It seems likely that dotterel themselves may use a far more complex set of cues in the assessment of other individuals.

Despite apparent similarities, dotterel do not truly lek. Fundamentally this is because although females compete for males, female choice occurs rather than the predicted male choice. Females compete for access to phenotypically high quality males. An important aspect of lekking is therefore missing; i.e., active choice by the non-competitive sex for non-parental qualities in the competitive sex. The reason for this anomaly is multifold and the subject is given a detailed treatment in Chapter 7. I will summarize here. (1) Although the sex-roles are reversed, access to reproductively viable females still limits male reproductive success, as is the case in conventional sex-role species (Bateman 1948; Trivers 1972); the costs of choice to males therefore remain high (Pomiankowski 1987b, 1988). Males are not selected to become choosy. (2) Because females must leave the mating arena to lay eggs and because polyandrous species tend to breed at low density, polyandrous females encounter fewer alternative reproductive opportunities than lekking males. Therefore the benefits of female choice are higher for polyandrous females than are the benefits of male choice for lekking males (Chapter 7). Females are selected to become choosy. (3) Hatching success is probably largely determined by the condition of the incubating parent (Kålás & Lofaldi 1987; Chapter 5). Males incubate, and variability in the potential parental ability of males is therefore important (Petrie 1983a, b). This increases
the benefits of choice to females (Parker 1983), so females are again selected to become choosy.
CHAPTER 5  Uniparental incubation and variation in male quality

Abstract.- The Eurasian dotterel, *Charadrius morinellus*, exhibits uniparental male care of the clutch and offspring. The effect of incubation schedule upon within-nest temperature was observed over a range of ambient temperatures. Three hypotheses are advanced to explain incubation strategy through the constraints of (a) self maintenance, (b) energetic cost, and (c) developmental requirements. Embryonic developmental and energetic constraints were found to be the most important predictor of male incubation schedule. Self-maintenance behaviour was sacrificed, leading to a possible cost of incubation being reduced body condition in prolonged bad weather. Individual males varied in plumage characteristics known to be correlated with body condition but did not adopt significantly different incubation strategies. Brighter males, whose plumage indicated that they were likely to be in good condition were, however, least likely to desert in bad weather. This may be the primary factor in driving female choice, via the maintenance of high variation in mate quality.

5.1. INTRODUCTION

*Parental care* describes any form of parental behaviour which tends to increase the fitness of the parent's offspring (reviewed in Clutton-Brock 1991; Clutton-Brock & Godfray 1991). For behaviour to constitute *parental investment* a trade-off must exist between the parent's investment behaviour and the parent's residual reproductive value (Trivers 1972; Alexandra & Borgia 1979; Gwynne 1984; Thornhill & Gwynne 1986). The trade-off may become manifest in any component of the parents' fitness (reviewed in Clutton-Brock 1991). Avian incubation is a classic example of parental investment. The incubating parent invests energy in maintaining a suitable environment for the developmental requirements of the offspring. It has been suggested that the critical criterion is that the parent should maintain a sufficiently high and consistent temperature to promote embryonic development (White & Kinney 1974).

The parent is expected to pay immediate costs of incubation through increased energy expenditure incurred in temperature regulation, reduced self-maintenance provisioning and reduced opportunity for alternative simultaneous reproductive opportunities. Longer term costs may also be incurred through lifetime reproductive success trade-offs (reviewed in Clutton-Brock 1988; Newton 1989). Examples of reproductive trade-offs which have been demonstrated in avian studies include observations that: (i) artificial brood enlargement leads to reduced parental survival in pied flycatchers, *Ficedula hypoleuca*, (Askenmo 1977) and blue tits, *Parus caeruleus*, (Nur 1984a), reduced juvenile survival in blue tits (Nur 1984b) and collared flycatchers, *Ficedula albicollis*, (Gustafsson & Sutherland 1988) and reduced parent and offspring fecundity in collared flycatchers (Gustafsson & Sutherland 1988); (ii) in
willow tits, *Parus montanus*, high fledging success leads to reduced parental survival in the subsequent year (Eckman & Askenmo 1986); and (iii) female house martins, *Delichon urbica*, raising two broods are less likely to return than females raising a single brood (Bryant 1979). Parents are therefore expected to adopt a strategy which minimizes the immediate costs of parental care, both in order to maintain residual body condition and also to avoid the possible long term repercussions of parental care.

This study investigates the strategy adopted by incubating male Eurasian dotterel, *Charadrius morinellus*, to resolve the contrasting demands of incubation efficiency and self-maintenance. Usually only the male performs parental care duties in the dotterel (Nethersole-Thompson 1973; Kålås & Byrkjedal 1984; Chapter 3). The parental care system of the dotterel therefore makes this species particularly suitable for an investigation of this type because single-sex incubators not only have to expend energy in maintaining egg temperature but also pay increased costs of reheating the clutch, because the eggs cool whilst the nest is unattended during foraging bouts (Biebach 1979; Vleck 1981; Jones 1987).

Intrasexual plumage variation in the dotterel has been implicated as both a cue used in female choice of males and a predictor of male condition (Chapter 4). Conventional theory predicts that in sex-role reversed systems, males should be selective about with which females to mate in a manner comparable to that of female choice on polygynous leks (Trivers 1972; Petrie 1983a). In dotterel, however, female choice still occurs despite sex-role reversal in competitive behaviour. Females appear to select males which are in good condition (Chapter 4). This mechanism of mate choice has been highlighted as an important feature of avian sex-role reversed mating systems (Petrie 1983a, b; Chapter 7). The benefit to females of being choosy in a sex-role reversed avian system has, however, not yet been empirically demonstrated.

The aims of this study are to (i) establish the relative importance of self-maintenance needs, energetic costs and developmental requirements in influencing the incubation strategy of a uni-parental incubator, and (ii) investigate the effect of male condition upon male incubation strategy and the likelihood of desertion by the male.

### 5.2. METHODS

The study site, a 13km² upland *Racomitrium* heath plateau in the Cairngorm region of Scotland, is described in detail in Chapter 2 where a detailed description of breeding dispersion is given.
5.2.1 Cooling and incubation curves

Seventeen nests, five in 1989 and twelve in 1990, were used to measure within-nest heating and cooling rates. All study nests were incubated by the male bird only and were thus left unattended during foraging bouts (Chapter 3). Most incubating dotterel remain on the nest until very closely approached. It was therefore possible to establish the within-nest cooling curve by flushing the male off the nest and immediately inserting a micro-thermistor connected to a remote Grant Squirrel recorder through the base of the nest into the between-egg-environment. This apparatus does not measure the absolute temperature within the eggs, but the temperature of the between-egg environment has been demonstrated to be linearly correlated with the within-egg temperature in the nests of other species of waders (Bergstrom 1989). The introduction of the thermistor took less than 30 seconds and equilibration occurred within the next 30 seconds. The temperature was recorded each minute for the next 30 minutes, keeping the male off the nest if necessary. After 30 minutes the male was allowed back onto the nest whilst the thermistor was still in position below and between the eggs (the temperature logger was concealed approximately 5 m away from the nest). Observers moved to a position approximately 100 m from the nest and allowed incubation to proceed for a further 30 minutes after the male had returned to the nest. The thermistor and logger were then removed, often without flushing the male, and the final 30 one-minute-interval temperature measurements, which constituted the incubation curve, were noted.

During the process of recording cooling and incubation curves, the ambient surface temperature of the ground was recorded every five minutes using a second probe connected to the Grant recorder. Cooling and heating curves could therefore be grouped according to ambient temperature; ca. 5.00°C (2.50 to 7.49°C), ca. 10.00°C (7.50 to 12.49°C), ca. 15.00°C (12.50 to 17.49°C) and ca. 20.00°C (17.50 to 22.49°C). Recording sessions within which the ambient ground surface temperature fluctuated sufficiently to enter the range of a neighbouring temperature group were discarded. Data from any one nest was only used once within each temperature grouping. Recording sessions were at least two days apart for each nest.

5.2.2 Incubation schedules

Nests were observed from a vehicle or over a distance of at least 100 m using 8x or 10x binoculars or a 30x telescope to determine the incubation schedule of male dotterel at different ambient temperatures. Observations were made between 10.00h and 19.00h GMT, a time during which dotterel are known to regularly leave the nest (Nethersole-Thompson 1973; Wilkie 1981; Kálás 1986). Each nest was observed for long enough to record two complete foraging bouts off the nest by the male and the included incubation bout. During observations, the temperature of the surface of the ground was recorded every 5 minutes using a thermistor connected to a Grant Squirrel recorder. Incubation schedule observations
could therefore be grouped in the same way as the cooling and incubation curves according to ground surface temperature. Similarly, observation periods within which the ground surface temperature fluctuated sufficiently to enter the range of a neighbouring temperature group were discarded. Data from any one nest were only used once within each temperature grouping. The mean foraging bout length, the incubation bout length and the proportion of time in nest attendance (incubation bout length / [incubation bout length + mean foraging bout length]) were noted for each observation period. Confidence intervals were calculated using Student's t-values (Sokal & Rohlf 1981). Data referring to mean proportion attendance were arcsine transformed prior to calculating confidence intervals.

5.2.3 Individual variation

The plumage score criteria described in Chapter 4 were used to grade incubating males according to the brightness of their plumage (2 = dull, 3 = bright; no males of score-1 were included in this part of the analysis). The data collected on incubation curves and incubation schedules were categorized according to the plumage score of the incubating male. Male plumage score is known to be positively correlated with body condition (Chapter 4). It was not possible to use a direct measure of body condition (see Chapter 4) in this part of the analysis because males could only be caught if the incubation was successful. The body condition of those males which deserted could not be measured directly.

5.2.3.1 Incubation curve.

The incubation curves of 2-score and 3-score males were compared using a two-tailed Wilcoxon-Mann-Whitney test (Siegel & Castellan 1988). The analysis was performed within time groups (5-minute intervals) because subsequent points along the time axis of the incubation curves are non-independent since they represent repeated measures on a single nest.

5.2.3.2 Incubation schedule.

The mean foraging bout length, mean incubation bout length and mean proportion attendance of 2-score and 3-score males were compared using a two-tailed students t-test (Siegel & Castellan 1988). The analysis was performed within ambient temperature groups to avoid pseudoreplication resulting from the same nests being used in different temperature-groups. Data referring to mean proportion attendance were arcsine transformed prior to calculating confidence limits. This analysis does not control for temporal variation in incubation schedule with development; however, Kálás (1986) found such variation in dotterel was minimal.
5.2.3.3 Nest desertion.

Dotterel rarely desert their clutches except when weather conditions are exceptionally bad for a number of successive days (Nethersole-Thompson 1973; Chapter 3). It is therefore difficult to relate the probability of desertion to the characteristics of individuals because of confounding factors such as point in the season and stage in incubation. However, in 1990 a large snowfall occurred late in the season and all 18 nests known to be active at the time and which had been laid at approximately the same time were covered with snow (Chapter 3). All the males sat through the first 12 hours of snow-fall and several were subsequently covered to a level over their backs with snow. Over the next 2 days the snow cover was approximately constant and males were unable to forage on the study plateau. During the subsequent 4 days, during which the snow melted on the breeding areas, half the males deserted their clutch (Chapter 3).

The likelihood of desertion during this period was compared between 2-score and 3-score males arranged in a 2 x 2 table using a G-test with Williams' correction for small sample sizes (Sokal & Rohlf 1981). A Wilcoxon-Mann-Whitney Test was used to test for any difference in first egg dates between deserted and non-deserted nests. First egg dates were recorded directly if nests were found during the laying-up stage or back-calculated from successful hatch dates using mean annual incubation period (Chapter 3).

5.3. RESULTS

5.3.1 Cooling and incubation curves

The cooling and incubation curves at each ambient temperature grouping are shown in Fig 5.1. These curves show unexpectedly low within-nest temperatures compared with the known optimum temperature (ca. 28°C; White & Kinney 1974) for avian development. However, these measurements are similar to those recorded in other studies of arctic-breeding waders (J. A. Kállás personal communication).

5.3.2 Incubation schedules

The mean foraging bout length, incubation bout length and mean proportion attendance with respect to ambient temperature are shown in Fig 5.2. Mean foraging bout length was positively correlated with ambient surface temperature, whereas mean incubation bout length and mean proportion nest attendance were negatively correlated with ambient ground temperature.
5.3.3 Individual variation

5.3.3.1 Incubation curve.

No significant difference was found at any point along the time axis of the incubation curve between the temperature in the nests of 2-score males and the temperature in the nests of 3-score males (two-tailed Wilcoxon-Mann-Whitney test; p > 0.20 at all stages through the incubation curves taken when ground surface temperature was ca. 5°C, ca. 10°C, ca. 15°C and ca. 20°C).

5.3.3.2 Incubation schedule.

The variation in mean foraging bout length, mean incubation bout length and mean proportion attendance with respect to ambient ground surface temperature for 2-score and 3-score males is shown in Fig 5.3. No consistent significant (Student's t-test p > 0.05) difference was found between 2-score and 3-score males in mean foraging bout length, incubation bout length or mean proportion attendance within ambient temperature groups. However, there was a strong trend (p < 0.10 within each individual ambient temperature group) for 3-score males to have a higher mean proportion attendance than 2-score males (Fig 5.3c).

5.3.3.1 Nest desertion.

Of the eight 2-score males incubating prior to the snowfall, six deserted. Of the ten 3-score males incubating during the same period, three deserted. Bright (3-score) males were therefore significantly less likely to desert than dull (2-score) males (G with Williams correction = 3.89, p < 0.05). Among a subsample (N = 13 nests) of the same 18 nests no significant difference was found between the first egg dates of clutches which were deserted and clutches which were not deserted (Wilcoxon-Mann-Whitney test m = 5, n = 8, Wx = 33, p = 0.42).

5.4. DISCUSSION

5.4.1 Constraints on incubation

The incubation strategy adopted by a uniparental species such as the dotterel must balance the conflicting demands of the thermal requirements of temperature regulation and the metabolic requirements of self-maintenance (Kálás 1986). In common with other wader species, the dotterel achieves this by relatively frequent, but individually short, foraging bouts (c.f., Parmelee 1970; Norton 1972; Wilkie 1981; Kondrat'ev 1982; Løfaldí 1985; Kálás 1986). This pattern was also observed in this study (Fig 5.2). Three, non-mutually exclusive,
Figure 5.1 (a) Cooling curve (male leaves the nest at Time = 0), and (b) incubation curve (male returns to the nest when Time = 0) over a range of ambient temperatures.
Figure 5.2 Mean foraging bout length (a), mean incubation bout length (b), and proportion of time in nest attendance (c), over a range of ambient temperatures. Error bars are 95% confidence intervals.
Figure 5.3 Mean foraging bout length (a), mean incubation bout length (b), and proportion of time in nest attendance (c), for male dotterel of plumage scores 2 and 3 separately. Error bars are 95% confidence intervals.
explanations have been put forward to explain this pattern: (i) immediate body condition is critical in predicting whether a parent will be able to endure an enforced period of prolonged incubation and parents therefore keep in good condition by feeding frequently (Afton 1980), (ii) short periods off the nest mean that the parent does not have to rewarm the eggs continually (Biebach 1979; Vleck 1981), and (iii) embryonic development requires precise temperature regulation which can only be ensured through almost constant incubation (Drent 1975; Lofaldi 1985). This study provides evidence that the latter two of these hypotheses best describe the constraints on incubation in the dotterel.

If the first of these hypotheses were of primary importance we would predict that the mean proportion attendance should be positively correlated with ambient temperature, more time being spent foraging when the temperature was low. This was not observed. The mean proportion attendance increased as the temperature decreased (Fig 5.2c). Thus, despite the frequently cold weather and snowfall during the incubation period and the fact that dotterel do often sit on the nest for very long periods (Spjøtvoll 1972; Nethersole-Thompson 1973), maintenance of residual body condition does not seem to be the primary determinant of incubation pattern.

The second hypothesis predicts that the incubating parent should minimize the extent of cooling that the eggs suffer during each foraging bout. Figure 5.1 illustrates the cooling flux of the eggs with varying ambient temperature. The third hypothesis predicts that mean incubation bout length and mean proportion attendance are negatively correlated with ambient temperature and that mean foraging bout length is positively correlated with ambient temperature. All three of these predictions are supported by this study (Fig 5.2). Hypotheses two and three, therefore, cannot be differentiated from the results presented here. I suggest that this may be a reflection of hypothesis two explaining the proximate strategy by which the causal function, described by hypothesis three, is achieved.

The developmental requirements of the embryos appear to be of primary importance in predicting the incubation strategy of uniparental male dotterel (see also White & Kinney 1974). In order to maintain a sufficiently high and consistent temperature for successful embryonic development, dotterel sacrifice immediate self-maintenance requirements. Incubation of warm eggs is likely to be a relatively cheap activity in energetic terms (Walsberg & King 1978) and the costs are minimized by allowing minimal cooling at low ambient temperature. The costs of incubation are most considerable in terms of lost foraging time in bad weather and the possibility of depleting body condition below a critical threshold for desertion.
5.4.2 Individual variation

Bright males showed a non-significant tendency to leave the nest less often (Fig 5.3b) and spent a shorter period off the nest each time (Fig 5.3a) than did dull males. However, no consistent significant difference was found in the incubation efficiency or schedule of males of different plumage scores. These observations are not consistent with those of Kålås & Løfaldli (1987) who reported a positive correlation between body weight and mean nest attendance per day (bright males are in significantly better condition than dull males; Chapter 4). However, their study was on only four individual males and their subsequent analysis was statistically invalid due to pseudoreplication resulting from the non-independence of data points originating from a single male. If this non-independence is taken into consideration the correlation is still positive but no longer significant. The fact that within-male correlations were also positive (Fig 5.3 in Kålås & Løfaldli 1987) is, however, perhaps indicative of an underlying relationship. Both this study and that of Kålås & Løfaldli (1987) are therefore inconclusive as to the effect of body condition upon incubation schedule.

Bright males were significantly less likely than dull males to desert their clutch during the 1990 snow fall. This interesting correlation may be confounded if 3-score males are, on average, further into incubation than 2-score males. It has been shown that 3-score males, on average, become paired before 2-score males (Chapter 4). In this case we may expect 3-score males to demonstrate more tenacity since they would have to invest more heavily at any given instance to regain their present state (Dawkins & Carlisle 1976). However, due to variation in the pre-laying period the dichotomy in the pre-laying period is small. The result is that most of the nests laid at the beginning of the season are laid within a few days of each other (Chapter 3) and both 2-score and 3-score males may care for early clutches. It is difficult to analyse the present data in this respect as some first egg dates are back-calculated from hatching dates (Chapter 3) and therefore, inevitably, first egg dates are not available for some deserted nests. Using the available data there was, however, no significant difference between the first egg dates of deserted and non-deserted nests when the data from both 2-score and 3-score males are combined (a two-way analysis could not be performed because of the small sample size). Additionally, the anecdotal observation that all of the first four clutches laid were deserted supports the hypothesis that incubation stage was not an important factor in determining probability of desertion during the 1990 snow fall. These early nests accounted for two of the three desertions by 3-score males.

In conclusion, brighter, more striking males tend to be less likely to desert nests than duller, less striking birds. This is independent of any additional benefit of continued incubation when, for example, development is more advanced. Brighter males do not, however, adopt significantly different incubation schedules. This may be in agreement with the conclusion that incubation itself is a relatively cheap activity (Ricklefs 1974; Walsberg & King 1978; Vleck 1981) or else it may be that the net benefits of remaining on the nest are so high that all
males attempt to do so independent of the costs. All males can successfully incubate a clutch providing they can occasionally leave the nest to forage. It is only during particularly severe weather, when extremely prolonged periods of incubation (at least 2 days, Nethersole-Thompson 1973; unpublished data) are enforced, that incubation becomes expensive in terms of lost foraging time. During such periods only the higher score males, these being those individuals in better condition (Chapter 4), can endure the conditions and avoid desertion. I suggest that this is perhaps the factor which, through the maintenance of high variation in male 'environmental' quality (Parker 1983; Petrie 1983a), drives female choice in this species (Chapter 4). Females may select males which are in good condition because such males are less likely to desert their clutches.
CHAPTER 6 Alternative reproductive strategies

'...jealous Dottrels, who through the bewry of their honest wiues grow suspitious.'
Greene, Quippe for an Upstart Courtier, 1592

Abstract.- Reversed sex roles in birds typically result in paternal rather than maternal care of both the eggs and chicks, this therefore leads to a low potential reproductive rate in males. In such species, theory predicts that males should be under strong selection to ensure that all the young cared for are fathered by themselves. Males may be cuckolded as a result of alternative reproductive strategies such as extra-pair copulation (EPC), rapid mate switching (RMS) and intra-specific brood parasitism (IBP). Individual males in the dotterel, Charadrius morinellus, a sex-role reversed species, were found to guard their mate against EPC attempts by continually following her at a close distance prior to egg laying. The probability of fertilizations resulting from RMS was reduced as a result of a prolonged pre-laying phase during which the pair-male only copulated with the female shortly before egg laying. The male does not copulate earlier despite frequent courtship from the female. In experiments incorporating the introduction of a false egg to a clutch, no evidence was found of behaviour that would indicate a high incidence of IBP. It is concluded that male dotterel protect their paternity of the brood for which they care through a combined strategy of prolonged mate guarding and strategic timing of copulations.

6.1. Introduction

A number of recent empirical studies of wild bird populations have demonstrated that in certain species the notion of a monogamous, or sequentially polygynous, 'pair' of birds may be misleading (e.g., Gowaty & Karlin 1984; Birkhead et al 1985; Møller 1985, 1988b; Frederick 1987; Quinn et al 1987; Westneat 1987a, b, 1990; Wetton et al 1987; Evans 1988; Smith 1988; Lank et al 1989; Birkhead et al 1990; Morton et al 1990; Bollinger & Gavin 1991; Smith et al 1991; Wetton & Parkin 1991; but see also Gyllensten et al 1990; Lifjeld 1991; Hunter et al 1992; unpublished data in Burke et al 1991; Hartley 1991). Furthermore, in species in which behavioural observations suggest that social relationships are more complex than simple monogamy, new techniques for assigning genetic parentage have demonstrated that parentage within a brood may be similarly complex (e.g., Burke et al 1989; Gibbs et al 1990; Rabenold et al 1990; Jones et al 1991). Therefore, although birds are typically monogamous with respect to parental care (Lack 1968; Gowaty 1983, 1985; Mock 1985), this does not always reflect an exclusive mating relationship (Wittenberger & Tilson 1980). Chicks within a brood may be the offspring of a parent other than one, or both, of the pair of adults that raises them through any of three behavioural mechanisms: extra-pair copulation (EPC), rapid mate switching (RMS) and / or

An EPC is defined as a copulation between a female and a male other than her partner. EPCs may be forced, in which case the female attempts to avoid copulation with the non-pair male (e.g., Birkhead et al 1985) or else females may actively solicit EPCs (e.g., Møller 1988b). RMS involves a female becoming paired to a male whilst potentially still retaining viable sperm from a previous mate (Møller 1985). Both EPCs and RMS may result in offspring within a brood which are not the true offspring of the putative father as a result of sperm competition (Parker 1984b; McKinney et al 1984; Birkhead 1987).

IBP results from a female laying an egg in a nest other than her own (reviewed in Yom-Tov 1980; Andersson 1984; Rohwer & Freedman 1989; Petrie & Møller 1991). In such cases the parasitic offspring may be fathered either by the parasitic female's own pair male, the host pair male (known as quasi-parasitism; Emlen & Wrege 1986; Birkhead et al 1990), or a male other than her pair male and the host male. Therefore IBP may result in offspring within a brood which are either not related to either of the putative parents of the brood or else only related to the father via quasi-parasitism.

EPCs, RMS and IBP are all expected to produce selection pressures leading to both intra-sexual and inter-sexual conflict (Trivers 1972; Andersson 1984). For example, males may be selected to gain EPCs with other males' females, but should also take care to guard their own female. Also, males should not care for the offspring of a previous partner of the pair female. Equally, females may attempt to dump eggs in the nests of conspecifics, but both females and males should aim to prevent parasitism of their own nest. The question of whether females will be selected to accept or solicit EPCs and whether males should encourage quasi-parasitism is more complex. The strength of selection promoting the adoption of alternative reproductive strategies will depend upon the fitness differential experienced through (i) producing offspring which are more genetically diverse and which will therefore be able to adapt to a wider diversity of environments and between which competition will not be as strong (Williams 1975; Maynard-Smith 1978; Gladstone 1979), (ii) producing offspring with a genetically more fit partner (Weatherhead & Robertson 1979; Hamilton & Zuk 1982), (iii) reducing the risk of genetic abnormality or reduced fertility through sperm storage (Halliday & Arnold 1988), (iv) insurance against pair-male sterility (Gibson & Jewell 1982; Wetton & Parkin 1991), (v) the increased risk of contracting a sexually transmitted pathogen as a result of having more sexual partners (Hamilton 1990), (vi) increased probability of being cuckolded by another male as a result of allocating more resources towards soliciting EPCs (Westneat et al 1990), (vii) a potential reduction in parental care if the pair partner anticipates parasitism (Zenone et al 1979; Winkler 1987; Møller 1988c, 1991a; Westneat 1988), and (viii) the behavioural benefits of accepting extra-
pair solicitation from another individual (Trivers 1972; Halliday 1980; Davies & Lundberg 1984; Svard & Wiklund 1986; Colwell & Oring 1989).

EPCs have now been documented in a wide variety of avian species and the use of plumage markers, protein electrophoresis and molecular techniques has demonstrated that extra-pair fertilizations may indeed result from such behaviour (reviewed in Burke 1989; Westneat et al 1990). Although the subject of less research, IBP has also been demonstrated in a range of bird species and has been found to be unexpectedly common in a number of cases (reviewed in Yom-Tov 1980; Rohwer & Freeman 1989; Petrie & Möller 1991). The realization that 'mixed reproductive strategies' (Trivers 1972) are more common than once thought has led to research into the mechanisms by which individuals not only attempt to gain reproductive opportunities but also how they attempt to prevent themselves being parasitized. 'Mate guarding' by males in order to prevent EPC attempts with their female mate(s) has been noted in a wide range of avian species (e.g., Birkhead 1979, 1982; Power 1980; Mumme et al 1983; Birkhead et al 1985, 1988; Carlson et al 1985; Björklund & Westman 1986; Alatalo et al 1987; Gowaty & Plissner 1987; Gowaty et al 1989; Hobson & Sealy 1989) and females may prevent IBP attempts by guarding their nests (Møller 1987a, 1989; Gowaty & Wagner 1988; Gowaty et al 1989) or destroy eggs which appear in their nest before their own egg laying begins (e.g., Victoria 1972; Lombardo et al 1989). It is therefore logical to predict that we may expect to observe such anti-cuckoldry behaviour by the males at its most extreme in species in which only the male invests in parental care and, as a result, the potential reproductive rate of males is low (Birkhead et al 1987).

The Eurasian dotterel, Charadrius morinellus, exhibits reversed sex-roles with respect to both competition for mates and parental care; females are the competitive sex and males undertake virtually all parental care (Nethersole-Thompson 1973; Kålås & Byrkjedal 1984; Chapter 3). The potential rate of reproduction is therefore higher for females than for males (Chapter 4) and each individual offspring may represent a greater fraction of potential annual fitness gain for a male than for a female. Male dotterel, therefore, in common with other sex-role reversed species have much to lose from extra-pair paternity within the brood for which they care (Møller 1991b). This means that dotterel are an ideal species in which to investigate the tactics males use to prevent being cuckolded.

The aims of this study are to (i) quantify the existence of EPCs and mate-guarding behaviour in dotterel, (ii) estimate the probability of RMS occurring and identify what tactics males use to avoid it resulting in cuckoldry, and (iii) establish whether IBP occurs in dotterel and what tactics may be used by males and/or females to prevent its occurrence.
6.2. METHODS

The study site, an upland plateau in the central Cairngorm region of Scotland, the breeding chronology and size of the breeding population are described in Chapter 2 and Chapter 3 respectively. This study uses data from 1989 and 1990 in which there were approximately 61 and 45 nesting attempts on the study area, respectively. The effect of non-independence of data from the same, unmarked, individual(s) was minimized as described in Chapter 3 but could not be totally eliminated.

6.2.1 Extra-pair copulations and mate guarding

6.2.1.1 Temporal pattern of copulations.

The temporal patterns of within-pair and extra-pair copulations were studied with respect to the number of days prior to first egg date. A pair was defined as a duo comprising the same male and female throughout an observation period of at least one hour. In many cases pairs thus defined remained in the area and made a nesting attempt. For the purposes of estimating how long a pair had been present in an area, individuals were recognized either by colour-rings from previous years' study or else by their individually recognizable plumage. Pairs which could not be identified in this way were not used in this part of the analysis.

The observed distribution of within-pair copulations with respect to days prior to the first egg date was tested against a model assuming that within-pair copulations are equally frequent throughout the pre-laying period. Expected values were calculated from the distribution of the number of days prior to the first egg date that behavioural budgets were made. The observed and expected distributions of copulations were compared using a two-tailed, one sample Kolmogorov-Smirnov test for small samples (Siegel & Castellan 1988). The Kolmogorov-Smirnov test is particularly suitable here as it is sensitive to variation in both the shape and position of the distribution.

6.2.1.2 Multivariate analysis of mate guarding behaviour

Focal individual, one-minute interval one-zero activity budgets (Altmann 1974) were taken for 30-minute periods throughout the breeding season. Focal individuals were males and females in pairs (for sexing criteria see Kálas 1987; Chapter 4). Meteorological and plumage score information were recorded for each budget (Chapter 3 & Chapter 4) and the number of days that the pair had been present in the immediate area (within 100 m radius) and the number of days before the first egg date were estimated (see section 2.2). Activities recorded were F = feeding, W = walking, A= agonistic, C = courtship, K = within pair copulation, KK = extra-pair copulation. At the end of each minute the distance between the
birds was estimated and recorded. At the end of each fully observed minute the net effect of the focal individual's movements was recorded as $W^+ =$ walking towards partner, or $W^- =$ walking away from partner. Behavioural data from each budget was summarized as the sex of the focal individual ($0 =$ female, $1 =$ male), the proportion of fully observed minutes that each activity occurred in, the proportion of minutes that the focal individual walked towards or away from the other individual, the mean male-female distance (mean M-F), the maximum male-female distance (max M-F) and the variance in male-female distance ($s$ M-F) during the budget.

Mate-guarding behaviour was quantified by using stepwise multiple regression to assess the influence of the selection variables sex and days prior to first egg date upon proportion of agonistic events, proportion of courtship events, proportion of time moving towards partner, proportion of time moving away from partner, mean M-F, max M-F and $s$ M-F when controlling for the control variables meteorological components, date, time of day, plumage score of focal bird and plumage score of partner.

The residual values resulting from stepwise multiple regression between each behavioural component (Y variable) and the X variables were significantly skewed. The data for the independent X variables and Y variables $F$, $W$, $W^+$, $W^-$, mean M-F, max M-F and $s$ M-F were therefore rank transformed (M. J. Phillips & B. English personal communications) in order to comply with the assumptions of the normal distribution ($p < 0.30$, Chapter 3) (Sokal & Rohlf 1981). The data for Y variables A and C were logistically transformed because these data were distributed in a manner similar to the Poisson distribution. The stepwise multiple regression procedure was repeated with F-to-enter values equivalent to $p < 0.10$ for simple regression (Sokal & Rohlf 1981). Relevant control variables (see table 6.1) were forced into the final model before any significant selection variables were allowed to enter.

6.2.1.3 Univariate analysis of mate-guarding behaviour.

The proportions $W^+/W$ and $W^-/W$ were calculated within budgets for males and females and mean values compared across and within the sexes using Student's t-tests (Sokal & Rohlf 1981).

The distribution of mean M-F, max M-F and $s$ M-F from this study were compared with the distribution of, respectively, mean N-N, max N-N and $s$ N-N resulting from the study of flocking behaviour on mating arenas described in Chapter 4 by using the two-tailed two sample Kolmogorov-Smirnov test (Siegel & Castellan 1988). This provides a comparison between flocking and paired birds with respect to nearest-neighbour distance in order to detect mate guarding behaviour.
6.2.2 Rapid mate replacement

A daily census was made during which approximately half the study site was covered each day (see Chapter 3, Chapter 4). Pairs were recorded during the census and the areas which they frequented were revisited approximately every other day. Colour-ringed birds were noted and it was also possible to estimate how long some other pairs had been in a specific area because they had individually recognizable plumage characters such as patches of retained (unmoulted) feathers on their underparts.

During behavioural budgets courtship behaviour was observed simultaneously in both the male and female. The initiator of each courtship event was noted and plotted against days prior to laying to establish any sexual dimorphism in time of receptivity. Courtship events in dotterel are described in detail by Nethersole-Thompson (1973). Data were scored logistically for whether the male and/or female had initiated courtship behaviour during the budget. Observations on any one pair of individuals were at least two days apart. The distribution of male versus female initiated courtship behaviour with respect to first egg date was analyzed using a two-tailed, two sample Kolmogorov-Smirnov test for small sample sizes (Siegel & Castellan 1988).

6.2.3 Intraspecific brood parasitism

False dotterel eggs, were made by filling natural shells (collected from failed nests under NCC licence in 1989) with plaster of Paris. These false eggs were introduced into all nests found during the laying-up stage in 1990. At the same time, the natural egg(s) were each marked individually with waterproof marker pen. The proportion of eggs resulting from IBP has been predicted to be high in dotterel (Thomas et al 1989). This manipulation simulated a dumped egg in an incomplete clutch. If egg dumping occurs, to be consistent with the observation that almost all dotterel clutches consist of three eggs and clutches of four eggs are very rare (Nethersole-Thompson 1973; Kålås & Løfaldli 1987; Thomas et al 1989; IPFO unpublished data), an egg must be removed either by the parasitic female or by the nesting pair. The false eggs were left in the nest for a week after the beginning of incubation and checked every other day to see if they had been removed.

In both 1989 and 1990, all eggs in as yet incomplete clutches found during the laying up stage were marked individually with a waterproof marker pen and revisited to establish the order of laying. When the clutch was complete these eggs were measured and categorized with respect to physiognomy as 'similar' or 'odd' in comparison to another egg in the clutch. Categories were based on background colour and minor markings as recommended in the more complete study of dotterel egg physiognomy by Thomas et al (1989).
6.3. RESULTS

6.3.1 Extra-pair copulations and mate guarding

6.3.1.1 Temporal pattern of copulations.

Copulations and attempted copulations were only ever observed between individuals who were paired to each other. No EPCs or EPC attempts were observed. The observed distribution of within-pair copulations relative to days prior to first egg date is shown in Fig 6.1a. The expected distribution of within-pair copulations, if copulations are equally likely throughout the pre-laying period is shown in Fig 6.1b. The observed and expected distributions are significantly different (one sample Kolmogorov-Smirnov test for small samples n = 25, D = 0.52, p < 0.01).

On seven occasions a pair was seen to interact with other individuals away from the mating arenas. On one of these occasions two pairs met and male-male and female-female aggression was noted before the pairs separated. Twice, a lone male appeared and was attacked by both the male and female of the pair. After the intruder's departure the pair copulated twice and once respectively. Lone females were seen to approach pairs on four occasions, and each time both the male and female of the pair attacked the intruder.

6.3.1.2 Multivariate analysis of mate guarding behaviour.

The F values, sign of correlation and associated probabilities resulting from stepwise regression between behavioural components and sex, days prior to first egg date and control variables are shown in Table 6.1. The F-to-remove values are given for those X variables which finally entered the model. The F-to-enter values are given for the other variables which did not enter the final model.

6.3.1.3 Univariate analysis of mate guarding behaviour.

The mean proportion of W+ and W- movements by males and females are shown in Figs 6.2a and 6.2b respectively. Males walked towards their pair female significantly more often than they walked away (p < 0.01) and significantly more often than females walked towards their pair male (p < 0.01).

Figs 6.3a and 6.3b show the distribution of mean M-F and mean N-N distances respectively. These distributions do not differ significantly (two sample Kolmogorov-Smirnov test m = 41, n = 79, D = 0.143, p > 0.10). Figs 6.4a and 6.4b show the distribution of max M-F and max N-N distances respectively. These distributions do not differ significantly (m = 39, n = 78, D = 0.174, p > 0.10) Figs 6.5a and 6.5b show s M-F...
Figure 6.1 The distribution of (a) within-pair copulations with respect to days prior to the first egg date, and (b) the predicted distribution of within-pair copulations if they are equally likely to occur at any time during the pre-laying phase.
Table 6.1  Variation in behavioural components explained by sexual dimorphism and the number of days prior to the first egg date when the effects of control variables are removed using stepwise multiple regression.

<table>
<thead>
<tr>
<th>Behaviour code(Y₁ to Y₂)</th>
<th>A</th>
<th>C</th>
<th>F</th>
<th>W</th>
<th>W+</th>
<th>W-</th>
<th>mean M-F</th>
<th>s M-F</th>
<th>max M-F</th>
</tr>
</thead>
<tbody>
<tr>
<td>F(V₂,V₁)</td>
<td>F(84,1)</td>
<td>F(84,2)</td>
<td>F(84,2)</td>
<td>F(60,1)</td>
<td>F(60,1)</td>
<td>F(84,2)</td>
<td>F(84,1)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Selection variables (X₁ to X₂)

| Sex         | -0.82  | -0.07  | -5.88* | -2.26  | +62.98*** | -60.53*** | 0.00     | 0.00  | 0.00    |
| Days pre-laying | -0.62  | +2.00  | -0.00  | -0.36  | +0.10     | -0.00     | +0.01    | +0.25 | -0.12   |

Control variables (X₃ to X₁₀)

| Date         | -0.07  | -0.95  | -0.51  | -0.52  | +1.69     | -0.40     | -0.01    | -1.30  | +0.22   |
| Time         | +1.17  | +8.29**| +1.20  | +2.91# | -1.29     | +1.77     | -7.73**  | +1.93  | -0.94   |
| Cloud cover  | +3.17# | +1.23  | -0.14  | -0.19  | -0.74     | +0.22     | +0.23    | +0.13  | -0.23   |
| Precipitation| -0.37  | +0.00  | -15.18*** | -8.02** | -0.30     | -0.11     | -3.14#   | -4.26* | -2.87#  |
| Wind speed   | -1.40  | -3.20  | +0.24  | -0.29  | -1.75     | +0.58     | +0.00    | -0.33  | -0.88   |
| Plumage score| +0.85  | +6.52* | -0.03  | +0.92  | +2.24     | -1.95     | +1.83    | +0.54  | +2.06   |
| Plumage score of partner | -0.01  | -0.01  | +0.41  | -1.14  | -0.02     | +0.10     | +1.83    | +0.54  | +2.06   |

Columns show F values and sign of correlation resulting from stepwise multiple regression between each Y variable and the X variables. X variables indicated with a hatch symbol or one or more asterisk were introduced into the final model (# p<0.10, * p<0.05, ** p<0.01, *** p<0.001). Relevant control variables were introduced into the final model before any selection variables were introduced. V₁ = Number of X variables introduced into the final model. V₂ = (Number of observations - 2). Y variables are proportion of time spent in agonistic encounter (A), courtship (C), feeding (F), walking (W), walking towards partner (W+), walking away from partner (W-), mean male-female distance (mean M-F), variance in male-female distance (s M-F) and maximum male-female distance (max M-F).
Figure 6.2 The proportion of minutes during which the focal individual moved towards (W+) and away (W-) from their partner for: (a) males, and (b) females. Error bars represent 95% confidence intervals.
Figure 6.3 The distribution of mean (a) within-pair male-female distances, and (b) non-pair nearest-neighbour distances.
Figure 6.4 The distribution of the maximum (a) within-pair male-female distances, and (b) non-pair nearest-neighbour distances.
Figure 6.5 The distribution of the variance in (a) within-pair male-female distance, and (b) non-pair nearest-neighbour distance.
and \(s\) N-N distances respectively. These distributions differ significantly; the distribution of \(s\) M-F is shifted towards smaller values than that of the distribution of \(s\) N-N \((m = 41, n = 77, D = 0.304, p < 0.05)\).

6.3.2 Rapid mate switching

The distributions of courtship events initiated by males and females are shown in Figs 6.6a and 6.6b respectively. These distributions are significantly different; the distribution of male courtship is shifted towards the later stages of the pre-laying period \((\text{two sample Kolmogorov-Smirnov test for small samples } m = 13, n = 16, D = 101, p < 0.05)\).

6.3.3 Intra-specific brood parasitism

Six nests were found during the laying up stage with an incomplete clutch during the 1990 season. Two nests were found with only one egg laid, four with two eggs. A false egg was introduced into all these clutches. In all cases the female continued laying to produce 3 eggs resulting in 4-egg clutches including the false egg. The male successfully incubated these clutches without removing or damaging the false egg for 7 days at which point the false egg was removed.

Of 10 clutches in 1989 and six clutches in 1990 in which the order of laying was known and measurements taken, four and two clutches, respectively, were found to include a distinctly odd egg with respect to both background colouration, major blotching and minor markings \((\text{Thomas et al. 1989})\). Of these odd eggs three and two in 1989 and 1990, respectively, were the last egg laid in the clutch. The remaining odd egg in 1989 was very unusual because its background colour was blue \((\text{see Thomas et al. 1989})\) and was the first laid in the clutch.

6.4. DISCUSSION

6.4.1 Extra-pair copulations and mate guarding

No direct EPC attempts were observed either during the activity budgets or incidentally at other times. Nethersole-Thompson (1973; Nethersole-Thompson & Nethersole-Thompson 1986), however, reports that he observed males caring for clutches or young chicks copulating with 'strange hens' (unpaired females on mating arenas). He also noted aggression if one or more other individual approached a pair too closely:

*Sometimes two couples - two hens and two cocks, still only loosely paired - fly high, purring angrily and milling on the ground and in the air. But, at this stage, the dotterels are still fighting for mates rather than territory or living space.*
Figure 6.6 The distribution of courtship initiation behaviour with respect to the number of days prior to the first egg date for: (a) males, and (b) females.
Extra-pair paternity may therefore be a possibility, if not through EPC then a mechanism similar to RMS; a female may retain sperm from a non-pair copulation which took place before she was paired to her present mate. A range of behaviours which may be interpreted as mate-guarding were observed.

Pair males usually copulated with their mates close to the first egg date and did not do so earlier in the pre-laying period (Fig 6.1a). This pattern is significantly different from the random model (Fig 6.1b), demonstrating that males selectively copulate just prior to the female laying. This fits the pattern observed in other species in which such behaviour has been described as adaptive (reviewed in Birkhead 1987). In a simple mate-guarding context, however, this is puzzling because the pair male should copulate with the pair female throughout the pre-laying stage, as has indeed been observed in other species (reviewed in Birkhead 1987; Birkhead et al 1987). Copulation may occur only in the period immediately prior to egg-laying either because (i) females are not receptive before this time, or (ii) males are under strategic selective pressure to only copulate during this phase. The first explanation is unlikely as females are observed to court their pair-male continually throughout the pre-laying period (Fig 6.6b). The male, however, only begins to court the female close to the first egg date (Fig 6.6a). These distributions are significantly different and suggest that the copulation pattern is strategic with respect to male paternity assurance. Nethersole-Thompson also noted this pattern:

In birds with reversed courtship, the adjustments and synchronising of male and female sex-rhythms is a subtle process. At first the hen, whose sex drive is initially stronger, dictates the pattern of early ground-chases and displays, simultaneously isolating, dominating and courting the cock, and attacking other hens......Cocks soon become active partners in the sex-dances, in which they now pursue and dominate the hens.


Pair males walk towards their female significantly more than they walk away (Fig 6.2a) and towards the female significantly more than the female walks towards the male (Table 6.1, Fig 6.2). The female usually walks away from the male (Fig 6.2b). Compared to birds in flocks, individuals in pairs are a similar mean distance apart (Fig 6.3), are a similar mean maximum distance apart (Fig 6.4) but have a significantly smaller mean variance in distance apart (Fig 6.5). Males and females in pairs are therefore consistently closer together than would be expected from typical dotterel behaviour on mating arenas (Chapter 4).

No significant variation was found in any behavioural component connected to mate-guarding which could be attributed to the number of days prior to first egg date (Table 6.1). Other studies have indicated that mate-guarding becomes more intense nearer to the first egg date (reviewed in Birkhead 1987; Westneat et al 1990) but no evidence of this was found in
this study. Male dotterel guard their pair female equally intensely throughout the pre-laying period.

The occurrence of EPCs and mate-guarding has only been studied in one other sex-role reversed avian species, the spotted sandpiper, *Actitis macularia* (Colwell & Oring 1989). Colwell and Oring found that female spotted sandpipers actively sought EPCs. A possible adaptive benefit of this behaviour to the female was that there was, subsequently, a higher probability of her securing the male with whom the EPC was performed as a mate, either in the present, or a future, breeding season.

6.4.2 Rapid mate switching

Most dotterel are paired for between 6 and 10 days (Nethersole-Thompson 1973; Glutz et al 1975; Cramp & Simmons 1983; Kålås & Byrkjedal 1984; Chapter 3) before the first egg is laid. Little information is available on the typical pre-laying period in other plover and lapwing species (Charadriidae). However, though this period is probably longer than required simply for egg production (Sæther et al 1986), anecdotal observations suggest that such a period of 'engagement' is not unusual in wader species (Cramp & Simmons 1983; Nethersole-Thompson & Nethersole-Thompson 1988).

Despite the fact that the male continues to follow the female at a close distance (Table 6.1, Figs 6.3a, 6.4a & 6.5a), the early part of the pre-laying period is notable for the total absence of copulation attempts (Fig 6.1). Males do not respond to female solicitation early in the pre-laying period and only court and copulate closer to egg laying (Fig 6.6). These observations are consistent with the hypothesis that males attempt to reduce the probability of being cuckolded as a result of RMS by guarding the female for a number of days prior to copulating. A similar strategy has also been observed in the ringed turtle dove, *Streptopelia risoria* (Zenone et al 1979; Sims et al 1987). This form of behaviour may have the effect of (i) providing the male with the certainty that any eggs laid during the first few days of pair formation are a consequence of RMS or EPCs and therefore may be abandoned, and/or (ii) reducing the viability of sperm held within the female as a result of previous copulations (Gibson & Jewell 1982). This pattern of copulations is unusual amongst plover and lapwing species in which the almost universal rule is for copulations to begin immediately upon pairing (Glutz et al 1975; Leisler, Makatsch, Flint & Kondratiev referenced in Cramp & Simmons 1983; Nethersole-Thompson & Nethersole-Thompson 1986).

In other sex-role reversed wader species - the painted snipe (*Rostratula benghalensis*), the spotted sandpiper (*Actitis macularia*) and the phalaropes (Phalaropodinae) - observations suggest that copulations occur throughout the pre-laying period (Oring & Knudson 1972; Ridley 1980; Cairns, Höhn, Miller & Miller referenced in Cramp & Simmons 1983). In one of these species, the red-necked phalarope, *Phalaropus lobatus*, male mate choice
operates and males prefer to pair with females which have not been previously paired within that season (Whitfield 1990). This preference has been interpreted as avoidance of sperm competition arising through RMS. In the dotterel, however, contrary to conventional theory on sex-role reversed species (Trivers 1972), female choice is exhibited and males presumably do not get the opportunity to select females using such criteria (Chapter 4). Thus, even amongst sex-role reversed species the paternity defence strategy of the dotterel may be unusual.

6.4.3 Intra-specific brood parasitism

Females continue to lay second and third eggs in nests to which a false egg had been added, thus resulting in a 4-egg clutch. Neither the male nor female parent removed the false egg or any of the natural eggs. Males continued to incubate the 4-egg clutches. Contrary to the 'odd-egg' suggestion put forward by Thomas et al (1989), these observations provide evidence against the frequent occurrence of egg dumping in dotterel. To be consistent with the rarity of 4-egg clutches the parasitic female would need to simultaneously remove a host egg. Consider the selective pressures likely to cause removal behaviour by the parasitic female: (i) incubating four eggs is maladaptive in the uniparental dotterel so to ensure optimal conditions for the parasitic offspring the parasitic female removes a host egg, or (ii) the host will remove an egg if dumping has obviously occurred. The first selective pressure is parsimonious with the observations of Kâlâs & Lofaldi (1987) who noted unusual weight loss in male dotterel incubating experimentally enlarged clutches. However, this potential factor should exert a greater force upon hosts than upon the parasitic female. The observation that hosts do not expel fourth eggs therefore invalidates this argument. The second selective pressure may also be dismissed since dotterel hosts do not in fact expel dumped eggs. The only potential argument left then is that of 'selective history'; parasites remove host eggs because the host species previously (in evolutionary time) used to remove parasitic eggs. This case of special pleading is in contrast to the scenario described by Davies & Brooke (1989a, b) in the interspecific brood parasite the European cuckoo, Cuculus canorus, where it appears that species that were once common, but now rare, hosts still reject parasitic eggs. Additionally, observations of removal of host eggs by intraspecific brood parasites in other avian species are generally scarce (reviewed in Petrie & Moller 1991), thus complementing the conclusion that the phenomenon is unlikely in dotterel. The only point to note in favour of egg-removal by the parasite rather than by the host is that the parasite may remove an egg before laying their own, whereas the host must discriminate between the parasite's egg and its own and therefore runs the risk of making a costly mistake. This process, in theory, may reduce the probability of egg-rejection by the host. However, the whole thrust of the previous claim that IBP is common in dotterel (Thomas et al 1989) relied on the fact that intra-clutch variation in physignomy was low compared with inter-clutch variation. This pattern of variation, it was suggested, is adaptive and has arisen in order that hosts can recognise dumped eggs and subsequently reject them.
But dotterel do not reject dumped eggs (present study). In the light of this experimental evidence, the fact that intra-clutch variation is low does not demonstrate that IBP occurs in dotterel.

Previous hypotheses predicting that occasional exceptions to the general rule in dotterel that intra-clutch physiognomic variation is low are due to IBP (Thomas et al. 1989) may therefore be better explained under the 'final egg' hypothesis, which states that the final egg of a clutch is often different in appearance from the other eggs in the clutch (Baerands & Hogan-Warburg 1982). This may arise because, either (i) the female sometimes cannot fully pigment all her eggs due to physiological constraints, or (ii) the 'odd' third egg is an adaptation to increase the probability of this being the egg to be taken if an egg is predated; the third egg is perhaps less valuable because it is smaller or less well developed. Under this hypothesis the observation that intra-clutch variation in physiognomy is low may be explained if egg pattern is primarily determined by the physiological state of the female (S. McCrae personal communication). In this case, the pattern of variation observed would not be described as adaptive.

In summary, the prediction that in sex-role reversed species, in which male care is high but potential male reproductive rate low, active male protection of paternity should be intense is upheld. A prolonged pre-laying period, combined with sustained mate-guarding whilst withholding copulations until just prior to egg laying, together minimize the probability of cuckoldry as a result of either RMS or EPCs. IBP, the remaining potential cause of mixed paternity, also appears unlikely in this species.
PART TWO

Sexual selection in sex-role reversed species
CHAPTER 7  Mate choice and sexual selection in sex-role reversed species: can females lek?

Abstract.—Sex-role reversed species represent an opportunity to test the theoretical framework of mate choice and sexual selection. A satisfactory model of mate choice must analyze the influence of sexual dichotomies in potential reproductive rate (PRR) and parental investment in concert with genotypic and environmental variation in mate quality. In this study, a model of this form is introduced and used to discuss the direction and strength of selection for mate choice in mating systems when parental investment and PRR are uncoupled. The simplest interpretation of this model is that if, for example, the PRR of males is N times greater than that for females then females will be the choosy sex unless the net benefit of being choosy to males is more than N times as great as the net benefit of being choosy to females. The predictions of this model agree with the observations of the direction of mate choice, indicating that the underlying framework of the model is robust.

The question of why female choice is the convention in many species despite the apparent importance of female quality in parental care is addressed. In non-territorial species exhibiting conventional sex-roles female choice, is more common than male choice primarily because males usually have a higher PRR, rather than because of the direct net benefits of choice being greater to females. A special case of the model is then put forward and the new predictions are compared with the observations of the direction of mate choice in documented cases of sex-role reversal. Lastly, mating systems displaying sex-role reversal in combination with mate-access polyandry are compared with the analogous case of lekking in polygynous species. Constraints on the PRR of females in non-territorial sex-role reversed species determine that the direction of mate choice will only rarely be reversed; an important component of lekking is therefore missing; female vertebrates are unlikely to truly lek.

7.1. INTRODUCTION

According to Halliday (1983) mate choice occurs only when there is (i) a non-random pattern of mating, (ii) active mate choice rather than the passive acceptance of the result of intra-sexual contests, and (iii) the adaptive benefit of choice to the chooser. Mate choice represents an example of interactions among natural selection, intra-sexual selection and inter-sexual selection (Bradbury & Davies 1987). The signals used as cues for mate choice and the possible adaptive reasons for its occurrence may, therefore, give valuable insights into the critical components of reproductive success within a species.

The classical scenario for the study of mate choice is a polygynous species with conventional sex-roles. Usually it is assumed that females are the limiting sex; males become the competitive sex and females become choosy (Williams 1975; Trivers 1985).
Females may choose males on the basis of phenotypic cues which may be either morphological (e.g., O'Donald 1980b; Andersson 1982a; Trail 1985a; Grant & Grant 1987; Heisler et al 1988; Möller 1988a,b; Norris 1990a; Höglund et al 1990; Petrie et al 1990) or behavioural (e.g., Gibson & Bradbury 1985, 1991; Andersson 1989; McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Alatalo et al 1991). Females may gain an adaptive benefit from being choosy through (i) selecting a male which is likely to be a good parent (Maynard-Smith 1985; Hoelzer 1989), (ii) settling upon a good territory (Wittenberger 1976), (iii) gaining a direct benefit in some other respect from the male such as high fertility (Kirkpatrick & Ryan 1991), (iv) producing offspring of high genetic quality (Zahavi 1977; Hamilton & Zuk 1982; Pomiankowski 1988b; Grafen 1990a; Iwasa et al 1991), (v) producing sexy sons (Fisher 1958; Weatherhead & Robertson 1979; Heywood 1991; Pomiankowski et al 1991), or (vi) avoiding sexually transmitted pathogens (Freeland 1976; Hamilton 1990). All of these advantages are potentially important in species with biparental care and in such cases the first two factors may often be of primary importance (Davies 1991). In species exhibiting uniparental female care and lekking by males, however, the first two factors cannot apply and if a benefit is received by the female it must be in the currency of one of the other hypotheses (but see Kirkpatrick & Ryan 1991 for an alternative view). Because, primarily, of the interest in the evolution of extravagant epigamic characters and mate choice for genotypic characters, the special case of lekking species has received a disproportionate amount of interest relative to its frequency of occurrence across species (reviewed in Bradbury & Gibson 1983; Bradbury & Andersson 1987; Kirkpatrick & Ryan 1991). Lekking is thought to be the extreme polygynous mating system and is the classic arena in which to observe mate choice.

How do sex-role reversed species fit into this framework? If the theoretical basis of mate choice is robust we would expect a reversal of the sex-roles to simply lead to a reversal in the direction of mate choice (Trivers 1972). Males should become choosy and potentially benefit from being choosy for exactly the same reasons as females may benefit in species with conventional sex-roles [(i) to (vi) above] (Chapter 4). Sex-role reversed species should show an equally diverse range of mating systems and choice mechanisms from monogamy to polyandry, culminating presumably in female lekking (Chapter 3).

A number of studies of sex-role reversed species have, indeed, demonstrated male choice. For example, sex-role reversal in mate choice has been demonstrated in pipefish, Sygnathidae (Gronell 1984; Berglund et al 1986, Svensson 1988; Rosenqvist 1990), spotted sandpipers, Actitis macularia, (Oring et al 1991b) and red-necked phalaropes, Phalaropus lobatus, (Whitfield 1990).

Several studies have, however, indicated that a reversal in the direction of mate choice is not an obligate manifestation of sex-role reversal. Sex-role reversal in parental care occurs in three-spined sticklebacks, Gasterosteus aculeatus, (Li & Owings 1978a, b) moorhens,
Gallinula chloropus, (Petrie 1983a, b) and Eurasian dotterel, Charadrius morinellus, (Chapter 3; Chapter 4; Chapter 5) but these studies have also demonstrated that females are the choosy sex. This situation is not altogether unexpected. The original reason for the evolution of 'conventional' sex-roles in most higher forms is probably anisogamy (Parker et al 1972; Williams 1975; Maynard-Smith 1978). As this is also the state in sex-role reversed species, male gametes are unlikely to ever truly limit female reproductive rate (Petrie 1983b). Males become a scarce resource to females when (i) there is an absolute shortage of males and the male contribution to parental care is vital, or (ii) there is a large variation in quality between males with respect to their ability to increase offspring fitness (Parker 1983; Petrie 1983b). Thus, the generalization that the form of the sex-roles determines the direction of the dichotomy in PRR which in turn predicts the direction of mate choice is not satisfactory. Both the relative potential rates of reproduction of both sexes and the potential benefits and costs of choice to either sex must be considered in concert.

The aims of this study are to (i) develop a model which predicts the direction of mate choice under all combinations of sex-role and dichotomy in PRR, (ii) use this model to identify the primary factors in determining the direction of mate choice in species with conventional sex-roles, (iii) apply this model to sex-role reversed species with male choice and to sex-role reversed species with female choice, and (iv) discuss the implications of this model to sexual selection in sex-role reversed species.

7.2. MODELS OF MATE CHOICE

7.2.1 Components of mate choice

7.2.1.1 Potential reproductive rate.
Trivers (1972) understood that 'the sex whose parental investment is greater than that of the opposite sex will become the limiting resource for that sex.' This may lead to the sex which has the lower parental investment competing for access to the other sex and the sex which has the greater parental investment exerting mate choice. Although it is true that one must be careful in the way one thinks of parental investment past and present (Dawkins & Carlisle 1976) and that it is not always the sex with the lower parental investment that achieves the higher PRR (Clutton-Brock & Vincent 1991), the basis of Trivers' argument remains valid. The critical measure, however, is not relative parental investment but relative PRR. All other things being equal, the sex with the higher PRR will be the competitive sex and the sex with the lower PRR will be more choosy. This relationship is shown in Fig 7.1a.

7.2.1.2 Mate quality.
The importance of the relative variance in mate quality between the sexes as an influence on active mate choice was emphasized by Parker (1983), who summarized that 'the greater the
variance in mate quality of the opposite sex, the greater the relative benefits of mate choice'. Petrie (1983) independently applied this principle to sex-role reversed species and discussed the potential importance of male parental quality in such species. These arguments are summarized in Fig 7.1b.

7.2.1.3 Genotypic versus environmental mate quality.

Parker (1983) continued his argument to sub-partition the potential components of mate quality into 'genotypic' and 'environmental' attributes; 'because genetic variance may be small, the main contribution to variance in mate quality is likely to be environmental variance in the ability to supply parental investment'. However, at this stage he ran into difficulties in making general predictions because 'as one sex increases its parental investment, it becomes more costly for individuals of the other sex to be choosy'. Therefore both the costs and the benefits of choice increase with increasing parental investment by the opposite sex (Parker 1983; Pomiankowski 1987b). Additionally, this form of model cannot be extended to all combinations of sex-role and sexual dimorphism in PRR. Specifically, this model cannot be applied to species exhibiting 'pseudo-sex-role reversal' in which the sex which has the highest parental investment also has the highest short-term PRR. The American greater rhea, *Rhea americana*, is an example of a pseudo-sex-role reversed species (Bruning 1974a, b); in this species the male provides all parental care but retains a high PRR because one male can care for more eggs than a single female can lay within a single reproductive period (see Clutton-Brock & Vincent 1991 for other examples of pseudo-sex-role reversal).

7.2.2 A general model

7.2.2.1 The direction of mate choice.

In order for a model of mate choice to be applicable to all combinations of sex-role and sexual dimorphism in PRR, four variables must be simultaneously taken into account; (i) the relative PRRs of the sexes, (ii) genetic versus environmental variation in mate quality, (iii) the costs of mate choice, and (iv) relative parental investment. What is more, if this model is also to be valid for pseudo-sex-role reversed species, this must be achieved without mentioning sex!

The initial framework for such a model can be constructed by substituting 'primary parent' and 'secondary parent' for the sexes in Fig 7.1. The primary parent is the sex which supplies the majority or all of the parental investment, the secondary parent is the sex which supplies the minority or none of the parental investment. This has two effects; (i) it removes the problem of species in which the sex which has the highest parental investment also has the highest short-term PRR (see Fig 7.1a), and (ii) it partitions the variation in mate quality with respect to cause rather than sex (see Fig 7.1b).
Figure 7.1 The net direction of mate choice with respect to a sexual dichotomy in (a) the potential rate of reproduction, and (b) mate quality.
Let us now define the important variables:

- $r_1$: Potential reproductive rate of the primary parent in the absence of mate choice (absolute potential increase in inclusive fitness per unit time as a result of producing direct progeny).
- $r_2$: Potential reproductive rate of the secondary parent in the absence of mate choice.
- $v_1$: Potential effect of variation in the quality of the primary parent upon the fitness gained by the secondary parent per reproductive opportunity (multiplying factor increase in inclusive fitness as a result of the cumulative potential fitness of offspring produced per unit time). The effect of variation in the quality of the primary parent may be represented through variation in (i) the ability to supply parental investment (Parker 1983; Maynard-Smith 1985; Hoelzer 1989), (ii) fertility or likelihood of gametes being retained from previous mates (Zenone et al 1979; Gibson & Jewell 1982), or (iii) genetic quality (Trivers 1972). In species with uniparental care, variation in the quality of the primary parent therefore approximates to the 'environmental quality' used by Parker (1983).
- $v_2$: Potential effect of variation in the quality of the secondary parent upon the fitness gained by the primary parent per reproductive opportunity. The effect of variation in the quality of the secondary parent may be represented through (i) territory quality in territory holding species (Wittenberger 1976; Searcy 1979), (ii) the ability to supply parental investment, (iii) fertility or likelihood of gametes retained from previous mates, or (iv) genetic quality. In non-territorial species with uniparental care variation in the quality of the secondary parent therefore approximates to what has been termed 'good genes' in many discussions concerning the adaptive benefits of female choice (reviewed in Pomiankowski 1988) and the 'genotypic quality' used by Parker (1983).
- $c_1$: The cost of mate choice per reproductive opportunity to the primary parent (multiplying factor decrease in inclusive fitness as a result of the reduced cumulative potential fitness of offspring produced per unit time)(see Pomiankowski 1987b for a review of the potential sources of the costs of mate choice).
- $c_2$: The cost of mate choice per reproductive opportunity to the secondary parent.

Using these variables it is possible to construct a model which predicts the direction of mate choice for all combinations of sexual dichotomy in PRR and variation in mate quality. The direction of increasing strength of selection for mate choice by the primary and secondary parent is shown in Figs 7.2a and 7.2b respectively. These figures illustrate the absolute gradation in the strength of selection for mate choice in either direction. However, given that at many points of the framework illustrated in Fig 7.2 there is positive selection for mate choice by both sexes, it is important to understand the realized effect of potential
selection for mate choice in both sexes. I suggest that in such cases (and assuming that the selective forces are temporally constant) mate choice will occur in one direction only. This is because the sex which is under the strongest selective pressure to become choosy should be the most selective when mating. Therefore, despite the potential advantages of mate choice, the other sex should be selected to maximize the rate of encounter with mates (Sutherland 1985a). Thus, even when there is a net benefit to choice for both sexes, one sex should become choosy and the other should become competitive. It is therefore the net direction of mate choice which is important here.

For example,

when \( r_2^* > r_1^* \)

1° parent choice occurs when

\[
\frac{v_{1}^* - c_{2}^*}{v_{2}^*} < \frac{r_2^*}{r_1^*}
\]

Here, \( (v_{1}^* - c_{2}^*) \) approximates to the net benefit of choice to a secondary parent per reproductive opportunity based on the potential benefits gained through variation in the quality of primary parents versus the costs of choice to the secondary parent. Similarly \( (v_{2}^* - c_{1}^*) \) approximates to the net benefit of choice to a primary parent per reproductive opportunity.

Similarly,

when \( r_1^* > r_2^* \)

2° parent choice occurs when

\[
\frac{v_{2}^* - c_{1}^*}{v_{1}^*} < \frac{r_1^*}{r_2^*}
\]

Hence, 1° parent choice occurs when

\[
\frac{v_{1}^* - c_{2}^*}{v_{2}^*} < \frac{r_2^*}{r_1^*}
\]

The model is therefore symmetrical about the point where \( r_2^* = r_1^* \).

These results are illustrated graphically in Fig 7.3. The most important points to notice are that (i) the direction of mate choice is a function of the inequality between two ratios and therefore absolute measures of PRR or variation in mate quality cannot, in isolation, predict the net direction of mate choice, and (ii) even when, for example, the relative net benefit from choice per reproductive opportunity is greater for the secondary parent, primary parents may be selected to become the more choosy if the relative PRR of the primary parent
Figure 7.2 The direction of the gradient of the strength of selection for mate choice by (a) the primary parent, and (b) the secondary parent. The direction of the arrows indicates the direction of increasing strength of selection for mate choice behaviour.
Figure 7.3. The net direction of, and potential strength of selection for, mate choice with respect to se
dichotomy in potential reproductive rate and the relative net benefits of choice. Increasing
circle size represents increasing strength of selection for mate choice in the direction
indicated.
is even lower than the relative net benefit which the primary parent receives from mate choice.

Decreasing relative PRR of either parent causes increasing selective pressure for mate choice in that parent. Increasing relative net benefits of mate choice for the primary parent causes either (i) an increase in selection for mate choice in the secondary parent when the relative PRR of the secondary parent is low, or (ii) an increase in selection for mate choice in the primary parent when the relative PRR of the secondary parent is high. Vice versa, increasing relative net benefit of mate choice for the secondary parent causes either (i) an increase in selection for mate choice in the secondary parent when the relative PRR of the primary parent is low, or (ii) an increase in selection for mate choice in the secondary parent when the relative PRR of the primary parent is high. The directions of the selective forces causing the distribution of mate choice are also shown in Fig 7.3. Increasing circle size represents increasing power of selection for mate choice in the direction indicated by the shading of the circles.

7.2.3 A special case

The graphical representation of the model in Fig 7.3 may be made intuitively more pleasing by allowing the indulgence of referring to sex again. If it is assumed that, for the species in question, the sex with the higher PRR is also the sex which has the lower parental investment (secondary parent) the model in Fig 7.2 may be simplified to that in Fig 7.4. This simplification may be widely applied as only pseudo-sex-role reversed species are excluded (see Clutton-Brock & Vincent 1991). However, before any application of the model it is important to validate the implicit assumption and to remember that this is simply a special case of the true mechanism.

The abscissa now describes the relative PRRs of males and females. In species with conventional sex-roles the male PRR is usually greater, and in species with reversed sex-roles the female PRR is usually greater. The ordinate describes the relative potential net benefits of choice to secondary parents relative to primary parents. The sex with the lower PRR is the primary parent under the assumptions of this special case. Thus, the ordinate approximates to the relative importance of environmental variation between primary parents versus genetic or territorial variation between secondary parents upon the fitness of the secondary and primary parent respectively.

It is important to note the abrupt reverse in the direction of the gradient of the strength of selection which occurs about the point at which \((r_2/r_1) = 0\) in Fig 7.3. This occurs because of the assumption made in this special case. This reversal leads to an important result when the model describing the net direction of mate choice is constructed (Fig 7.5). The conclusions of this model are exactly complementary to those of the general case. The most
Figure 7.4 The direction of the gradient of the strength of selection for mate choice by (a) females, and (b) males. The direction of the arrows indicates the direction of increasing strength of selection for mate choice behaviour. PRR refers to potential reproductive rate. The primary parent is the parent which supplies most or all of the parental care and the secondary parent is the parent which supplies the minority or none of the parental care. It is assumed that when male PRR > female PRR the female is the primary parent, and when female PRR > male PRR the male is the primary parent.
Figure 7.5 The net direction of, and potential strength of selection for, mate choice with respect to sexual dichotomy in potential reproductive rate and the relative net benefits of choice. Increasing circle size represents increasing strength of selection for mate choice in the direction indicated. PRR refers to potential reproductive rate. The primary parent is the parent which supplies most or all of the parental care and the secondary parent is the parent which supplies the minority or none of the parental care. It is assumed that when male PRR > female PRR the female is the primary parent, and when female PRR > male PRR the male is the primary parent.
important conclusion being that if, for example, the male PRR is N times greater than the female PRR, then females will be the choosy sex unless the net benefit to choice to the male is more than N times the net benefit of choice to the female. This argument applies in reverse to sex-role reversed species, where the female PRR is usually higher than the male PRR. This result appears remarkably obvious. However, this relationship between relative variation in mate quality and relative PRR with respect to the benefit of mate choice has not been made use of in empirical studies.

7.4. MATE CHOICE IN SEX-ROLE REVERSED SPECIES

How does this model help to understand the data concerning mate choice in sex-role reversed species?

First, consider those species in which the assumption that the sex supplying the majority of the parental investment has the lower PRR is valid. Here, reversed sex-roles indicate that the male is the primary parent and that the female has the higher PRR and is the competitive sex. Reversal in the direction of mate choice is expected when variation in the quality of the female, or resources held by the female, has a greater effect upon the potential fitness gained by the male than variation in the quality of the male has on the potential fitness gain to the female when the cost of mate choice with respect to the sexual dichotomy in PRR is taken into account (Fig 7.5). This prediction is upheld. Examples of reversed (male) mate choice are observed in (i) several species of pipefish in which female body size is correlated with egg number which, in turn, is the most important component of annual male reproductive success (Gronell 1984; Berglund et al 1986, Svensson 1988; Rosenqvist 1990), (ii) the territorially polyandrous spotted sandpiper (Oring et al 1991b) in which female territory quality is an important component of male annual reproductive success (Oring et al 1991a), and (iii) the red-necked phalarope in which previously mated females are discriminated against by males in order to prevent cuckoldry through rapid mate switching (Whitfield 1990). Conventional (female) mate choice is predicted in those species in which variation in the quality of the male has a greater effect upon the potential fitness gained by the female than has variation in the quality of the female upon the potential fitness gain of the male when the cost of mate choice with respect to the sexual dichotomy in PRR is taken into account (Fig 7.5). Again, this prediction is upheld. Female choice is observed in both the moorhen and Eurasian dotterel where male quality has a significant effect upon the parental capability of the male and may thus represent a major component of annual female reproductive success (Petrie 1983a, b, 1986; Chapter 4; Chapter 5).

Parallel examples of conventional and reversed mate choice can be observed in species with conventional sex-roles. Conventional mate choice is expected when the variation in the quality of the male or resources held by the male has a greater effect upon the potential fitness gained by the female than variation in the quality of the female has on the potential
fitness gain to the male when the cost of mate choice with respect to the sexual dichotomy in PRR is taken into account (Fig 7.5).

Despite female choice in species with conventional sex-roles being the most researched form of mate choice, there is little direct evidence linking female choice for male traits to increased viability of offspring (reviewed in Partridge 1983; Harvey & Bradbury 1991). Experiments on Drosophila melanogaster (Partridge 1980; Taylor et al 1987; but see also Schaeffer et al 1984) and Gryllus bimaculatus (Simmons 1987) have demonstrated that females, given a choice of mates, produce offspring of higher viability than females which were not given a choice of mates. However, a number of problems remain with these results, for example the relative importance of intrasexual selection between males is not addressed, and the direct benefit to females of multiple matings was not investigated. It is, therefore, not clear whether female choice is the convention in species with conventional sex-roles because (i) there is a large amount of variation in the quality of males, or (ii) male PRR is so much higher than female PRR that male choice is rarely profitable.

In species displaying conventional sex-roles and in which males defend breeding territories, or contribute greatly to the provisioning of the offspring, it has been demonstrated that females may increase the number of young reaching independence from their present reproductive attempt by choosing males with a good quality territory (e.g., Searcy 1979; Garson 1980; Askenmo 1984; Alatalo et al 1986; Slagsvold 1986) or which are likely to be good parents (e.g., Davies 1986; Norris 1990b). In territorial species inter-male variation in territory quality may therefore be the primary force driving female choice. Further work is, however, required to demonstrate why inter-male variation in provisioning ability is more important than inter-female variation in provisioning ability; it is possible that such variation simply powers a system whose direction is already defined by the large male bias in the sexual dichotomy in PRR.

Charlesworth (1987) reviewed the concept of the true genetic heritability of fitness. Fisher (1930, 1941) predicted that a population at equilibrium under selection exhibits no genic variance in fitness (Fisher's Fundamental Theorem of Natural Selection, see also Kimura 1958). This hypothesis is, however, theoretically unstable if there are sex differences in genotypic fitness; a situation of interest when studying sexual selection for stability. However, Nagylaki (1979) demonstrated that the effects of sex differences must be of the order of the fourth power of the intensity of the maximum range of natural selection. Fisher's theorem is therefore probably a good approximation to what we may expect to find in a population at equilibrium. In his review of data for Drosophila, Charlesworth (1987) found little empirical evidence of additive genetic variance in natural populations beyond that which would be expected to be maintained by biased-mutation pressure (Mukai et al 1974). Genetic variation may, however, be maintained in a population experiencing a continuously deteriorating environment, such as that produced by parasite-host coevolution (Hamilton
1982; Hamilton & Zuk 1982). Such mechanisms would not, however, produce a sexual dichotomy in additive genic variation and it is still unclear whether females would have the ability to select males with 'good genes' if the influence of environmental sources of variation, relative to genic sources, is large (Mukai et al 1972; Kirkpatrick 1987). Therefore, in the absence of male territories, female mate choice is likely to be primarily driven by the high relative PRR of males.

Reversed mate choice is predicted to occur in species with conventional sex-roles when variation in the quality of females has a greater effect upon the potential fitness gained by the male than has variation in the quality of the male, or resources held by the male, upon the potential gain in fitness by the female (Fig 7.5). Empirical support of this prediction has been found in invertebrates (e.g., Manning 1975; Gwynne 1981; Johnson 1982; Gwynne & Simmons 1990; Pitafi et al 1990; Pitafi 1991), amphibians (e.g., Bervin 1981; Verrel 1982) and fish (e.g., Downhower & Brown 1980; Loiselle 1982; Côte & Hunte 1989). In all these examples female fecundity is greatly influenced by female size and it is adaptive for males to pay the costs of choosing larger females because female size is also the primary predictor of male reproductive success (e.g., Dewsbury 1982; Nakatsura & Kramer 1982; Sargent et al 1986). Reversed mate choice has also been reported in species in which the time / energy investment expended by males during mating varies markedly between females (e.g., Hunte et al 1985; Hunte & Myers 1988; Loiselle 1982); this is simply another mechanism by which females may differ in quality from the point of view of the male.

Second, consider the pseudo sex-role reversed species; those species in which the male adopts the role of primary parent but the PRR of males remains higher than that of females. Here, the male remains the competitive sex (Clutton-Brock & Vincent 1991). Reversal in the direction of mate choice is expected when variation in the quality of females has a greater effect upon the potential fitness gained by the male than has variation in the quality of the male, or resources held by the male, upon the potential gain in fitness by the female (Fig 7.3). Evidence of this form of mate choice has not been published. The only species in which males are the primary parent but retain the higher PRR and for which mate choice information is available is the three-spined stickleback, in which male condition is important for the survival of the eggs (Li & Owings 1978a, b; Milinski & Bakker 1990). In this example, where the quality of the primary parent is of greater importance than the quality of the secondary parent and when the primary parent apparently has a higher relative PRR the direction of mate choice is, as predicted, not reversed.

This last example illustrates the difficulty in isolating the net benefits of choice for either sex; both male and female mate choice has been demonstrated in the three-spined stickleback (Rowland 1982; Milinski & Bakker 1990). The most widely studied aspect of mate choice is that individuals of the non-selective sex (usually males), which are of a morph preferred by the selective sex (usually females), have a higher potential reproductive success than
members of the same sex which are of a morph which is not preferred. In species where the sexual dichotomy in PRR is large this may be the most important effect of intersexual mate choice. However, when (i) the parental investment pattern of the sexes is not too asymmetric, and (ii) both sexes are ranked in quality, assortative mating for quality will result from mate choice by one sex (Parker 1983). Hence, 'active' mate choice by one sex may lead to 'passive' mate choice in the other sex in many monogamous species (Parker 1983). Empirical data for Arctic skuas, Stercorarius parasiticus, (O'Donald 1980), swallows, Hirundo rustica, (Møller 1988) and zebra finches, Taeniopygia guttata, (Burley 1985, 1986a,b,c) demonstrates that preferred males do indeed have a reproductive advantage. This advantage may arise through preferred males (i) acquiring mates earlier in the season and thus breeding at a better time in the season or producing more broods (Darwin 1871), (ii) attracting mates of phenotypically higher quality (e.g., Møller 1991), and / or (iii) gaining a reproductive advantage if their mate supplies a larger proportion of the parental care (e.g., Burley 1986a). The relative net benefits of active mate choice in such circumstances are very different from those usually considered in lekking species. Species in which the PRRs of the sexes are near to parity are the ideal arena in which to study the largely unexplored importance of passive mate choice (Chapter 4).

7.5. SEXUAL SELECTION IN SEX-ROLE REVERSED SPECIES

Sex-role reversed species provide a useful natural experiment which may be used to test existing models of sexual selection. One of the most obvious respects in which sex-role reversal can be used is in the explanation of sexual dimorphism. Briefly, epigamic characters may be used as a cue in either (i) intrasexual competition, (ii) intersexual mate choice, or (iii) a combination of these forces (Chapter 4). Usually the independent effects of these forces are difficult to separate because the competitive sex is also the sex which is likely to be less selective, hence the competitive sex is expected to be more 'showy' according to all the above hypotheses. However, in the case of species such as the dotterel where the sex-roles are reversed but mate choice is conventional, mutually exclusive hypotheses are produced. If inter-sexual mate choice is of primary importance then males are expected to be more showy, if intra-sexual competition is of primary importance then females are expected to be more showy. In common with most sex-role reversed species, the female is the larger and more showy sex in the dotterel (Nethersole-Thompson 1973; Kálás 1988; Chapter 4). This evidence supports the hypothesis that intrasexual competition between females is the most important factor in the evolution of secondary sexual characters in this species.

Returning to the title of this chapter, the question is: can females lek? Polygynous lekking is typified by (i) intense inter-male competition for access to females at a spatially predictable, non-resource based site, (ii) female breeding attempts being non-synchronous
and males remaining reproductively active throughout the female breeding season, (iii) the male reproductive time unit is much shorter than that of the female, (iv) the operational sex ratio becomes highly male-biased as the breeding season progresses, and (v) the potential variation in male reproductive success is far greater than the potential variation in potential female reproductive success. Conventional lekking occurs in species in which the PRR of males is very high compared with that of females. This is a result of (i) the extremely short individual reproductive time unit for males, and (ii) the plethora of alternative reproductive opportunities for males (Chapter 4). When the PRR of males is very high compared with that of females (position $X_m$ in Fig 7.6) the selective force on females to become choosy is strong, and even when the net benefit of choice is greater for males than females (position $Y_v$ in Fig 7.6) selection occurs for female choice. In some sex-role reversed species, such as the Eurasian dotterel, the mating system is very similar to that expected of a female lek (Chapter 3; Chapter 4). The five characteristics of lekking listed above have all been noted within sex-role reversed species (Chapter 3). In these species, however, females will rarely achieve such a relatively high PRR because the constraints of egg-laying determine that the individual reproductive time unit is longer for females. Under these circumstances (position $X_f$ in Fig 7.6), a reciprocally greater net benefit of choice for females than males (again, position $Y_v$ in Fig 7.6) may not be sufficient to cause a reversal of the direction of mate choice; and so female choice occurs.

The constraints upon female PRR noted in the dotterel, which preclude reversed mate choice, are likely to be valid for most sex-role reversed vertebrates. Therefore, in the absence of female territories, active male choice is predicted to be unusual in sex-role reversed vertebrates. However, the PRR of female invertebrates may not be so limited as 'many, small eggs' are often produced (Lessels 1991). Gwynne (1991) reviewed the occurrence of reversed courtship roles across taxonomic groups. He found a number of species in which females actively competed for males (Table 1 in Gwynne 1991) but reversed mate choice was not demonstrated in any of these species. Male choice has been recorded in the dance fly, *Empis borealis*, and females are known to aggregate in 'lek swarms' (Svensson & Peterson 1987, 1988; Svensson et al 1989; see also Sivinski 1989 for another possible example of lek swarms in the phorid fly *Megaselia aurea*). In this species, males select large and/or young females according to the time post-emergence (Svensson et al 1989). However, the females do not directly compete for access to males (Svensson & Peterson 1988). Therefore, no sex-role reversed case of lekking has yet been documented; the mating arenas of dotterel incorporate the aspects of intra-sexual conflict typical of leks, and the lek swarms of the dance fly encompass the form of inter-sexual mate choice expected in sex-role reversed leks, but neither system incorporates both aspects simultaneously.

In summary, the word *lek* probably comes from the Old English word *lécan* meaning to fight or frolic, or the Swedish word *leka* meaning play. The behaviour associated with
Figure 7.6 Net direction of mate choice with respect to sexual dichotomy in potential reproductive rate and the relative net benefits of choice to either parent per reproductive opportunity. In a mating system such as that observed in polygynous lekking species, where male PRR is much higher than female PRR (Xm), even when the net benefits of choice per reproductive opportunity are greater for males than females (Yv), female choice may still operate. However, in many sex-role reversed species female PRR is only slightly higher than male PRR (Xf), thus when the net benefits of choice per reproductive opportunity are greater for females than males the direction of mate choice is not reversed and female choice still operates.
intrasexual competition on the mating arenas of dotterel is astonishingly similar to the 'frolicking' on conventional leks (Chapter 3; Chapter 4). This example probably represents the closest female equivalent to a male lek yet found in vertebrates. The direction of mate choice is, however, not reversed; an essential component of true lekking is therefore absent. Female mating arenas initially appear as male leks but the selective forces at work are different and yet informative.
APPENDIX
"TROJAN SPARROWS": EVOLUTIONARY CONSEQUENCES OF DISHONEST INVASION FOR THE BADGES-OF-STATUS MODEL

IAN P. F. OWENS AND IAN R. HARTLEY*

Department of Zoology, University of Leicester, Leicester LE1 7RH, United Kingdom

Submitted May 15, 1990; Revised December 5, 1990; Accepted December 12, 1990

Abstract.—An adapted game-theory model for the "badges of status" hypothesis is introduced, and factors influencing the formation of "honest" stable population states are investigated. The stability of these states is then studied when two "dishonest" mutant strategies, "cheat" and "Trojan sparrow," are evoked. The honest population states are stable against invasion by the cheat strategy if social control of deception, in the form of punishment from aggressive individuals, is sufficiently severe. The Trojan-sparrow strategy is found to be successful for invading honest population states under all conditions, which indicates that the conventional badges-of-status model is fundamentally evolutionarily unstable in the absence of constraints limiting phenotypes to honesty. Without honest phenotypic limitation we predict that mixed fighting strategies will evolve but that individuals will not display accurate information regarding their aggressive intent and that dominance hierarchies will be based on true measures of resource-holding potential and not badge size. Hence, the conventional badges-of-status theory can be reduced to the conventional hawk-dove model and cannot be used to explain the evolution of mixed fighting strategies without honest phenotype limitation. We identify the reproductive trade-off, honest "handicap," and/or genetic and/or pleiotropic constraints under which badges of status may prove evolutionarily stable by the limitation of the strategy set to honesty.

Many avian species show a considerable degree of intraspecific plumage variability that is not readily attributed to cryptis, physiological efficiency, species recognition, or sexual selection, but that a plethora of empirical evidence suggests has a significant effect on fitness. A number of theories have been put forward to explain this observation, both within and between age and sex classes (reviews in Balph et al. 1979; Lyon and Montgomery 1986; Roper 1986; Watt 1986a; Whitfield 1987; Rohwer and Butcher 1988).

Adaptive hypotheses for plumage variability between (but not necessarily within) age classes center around the delayed acquisition of full adult plumage by males in their first potential breeding season (second-calendar-year males), as found in a number of passerine species (Rohwer et al. 1980; Lyon and Montgomery 1986). Selander (1965, 1972) proposed the sexual selection/cryptic hypothesis, which suggests that second-year males cannot successfully compete with the older males' superior display, mate-attraction, and territory-acquiring abilities...
and thus do not receive the benefits of showy plumage. By retaining dull, female-like plumage, young males avoid any increased risk of mortality through increased predation, physiological cost, or male aggression associated with bright plumage. Rohwer et al. (1980) proposed the female mimicry/deception hypothesis, by which the retention of female-type plumage allows young males to avoid the aggressive attentions of older males and thus investigate and take over a portion of an older male's attractive, high-quality territory.

Plumage variability both within and between age and sex classes is explored by the controversial individual recognition hypothesis (IRH; Collias 1943; Shields 1977; Whitfield 1986) and status-signaling/badges-of-status hypothesis (for the status-signaling hypothesis [SSH] see Rohwer 1975, 1977; for badges of status see Dawkins and Krebs 1978). These two explanations may operate with equal force in both the breeding and nonbreeding seasons. The IRH argues that it is not the size of the badge, or overall brightness of plumage, that is important but rather the inherent variation, for it is this that allows the recognition of individuals. In a population with repeated pairwise interactions such as a foraging flock or neighboring territorial individuals, individual recognition may bestow increased group stability and fewer escalated contests through the establishment of a linear hierarchy.

In this article we concentrate on the theoretical basis of the SSH (Rohwer 1975, 1977, 1978, 1985; Shields 1977; Rohwer and Rohwer 1978; Balph and Balph 1979; Ketterson 1979; Parsons and Baptista 1980; Rohwer and Ewald 1981; Rohwer et al. 1981; Fugle et al. 1984; Järvi and Bakken 1984; Watt 1984, 1986b; Eckert and Weatherhead 1987; Möller 1987a, 1987b, 1988, 1989; Maynard Smith and Harper 1988; Norris 1990; Norris and Bradbury, in press), although, as we discuss, our conclusions may be usefully extended to the investigation of the other hypotheses. Indeed, the results presented here allow a more realistic appraisal and integration of the above approaches.

The SSH suggests that individuals with "large" badges are more aggressive than, and dominant over, individuals with "small" badges. This relationship may be independent of age class. Following Maynard Smith and Harper (1988) we refer to aggressive dominants as having large badges, although in some studies the observed variation may be of a form other than size (Balph and Balph 1979). Similarly, the badges of subdominants are termed small.

Initially it seems that the dominance-signaling phenomenon may come about simply because individuals of higher fitness (higher resource-holding potential [RHP]; Parker 1974) are able to produce a larger, more "expensive" plumage form, and it thus pays weaker individuals (with lower RHP) to respect the honest advertisement (Rohwer 1975; but see also Jackson et al. 1988). By this mechanism, escalated fighting may often be avoided.

The conventional SSH argues that a mixed evolutionarily stable strategy (ESS; Maynard Smith 1974, 1982) may occur in such situations as winter foraging flocks. Individuals with large badges win many contests over food items but suffer a reduced net payoff owing to the cost of escalated aggressive interactions with other high-ranking individuals and aggressive threats to subordinates. Although apparently at a disadvantage, individuals with small badges do not incur fight
costs and may receive an equal payoff (fight costs vs. value of food items secured) while foraging (Rohwer and Ewald 1981; Rohwer et al. 1981; Maynard Smith 1982; Järvi and Bakken 1986).

If such a mixed ESS evolves and, as seems likely, badges are physiologically relatively inexpensive (Rohwer 1975, 1977), one has to ask why the system is not open to deception. In particular, a dishonest "cheat" mutant that has a large badge but is not aggressive would gain the benefits of dominance while avoiding fight costs and may be viable if the cost of repeated attack from aggressive individuals (punishment costs) is relatively low (Rohwer 1975; Watt 1984; Maynard Smith and Harper 1988). In this article, we quantify, in terms of the model's parameters, the level of punishment required for honest strategies to be evolutionarily stable in the presence of such a cheat.

Additionally, we introduce a new, dishonest "Trojan sparrow" strategy: individuals with small badges that incur no fight costs when food is plentiful but become aggressive as food becomes intermediately scarce hence become dominant over honest subordinates, which are compelled to be aggressive only when food is very scarce and the risk of starvation high. This form of strategy proves invasive against honest strategies whenever food availability is variable, the most profitable strategy being to fight when resources are scarce without advertising aggressive intent. We therefore conclude that "badge honesty" is a vital prerequisite for the establishment of status-signaling systems and discuss how, under the influence of social, genetic, and biochemical constraints, such strategy limitation may occur.

THE MODEL

The Strategy Set

We developed a game-theory model based on the "badges of dominance" game described by Maynard Smith and Harper (1988) and used it to examine the outcome of interactions between four phenotypes of fighting/foraging behavior. These four phenotypes are a large badge with an aggressive fighting/foraging strategy (LA), a small badge with a submissive fighting/foraging strategy (SS), a large badge with a submissive fighting/foraging strategy (LS), and a small badge with a variably aggressive fighting/foraging strategy (SA). Individuals come into conflict over food items that may vary in availability with time and thus in relative value to the individuals (table 1). In addition, it is assumed that the fights can escalate to varying intensities (table 1). During three conditions of food availability, aggression between strategists can be ranked as follows: LA > LS > SS = SA when food is abundant (food value = B), LA = SA > LS > SS when food is intermediate (Bn), and LA = LS = SS = SA when food is scarce. Thus, an individual that pursues the LS strategy is termed a cheat mutant, and one that pursues the SA strategy, because of its misleading appearance at intermediate food availability, is termed a Trojan-sparrow mutant. The relationships between the phenotypes, food availabilities, and fighting/foraging strategies are detailed in the outline of the model in table 2.
TABLE I

DESCRIPTION OF COST AND BENEFIT VARIABLES USED IN THE MODIFIED BADGES-OF-STATUS MODEL

<table>
<thead>
<tr>
<th>Variable</th>
<th>Use in Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Food value:*</td>
<td>Value of food items when food is abundant</td>
</tr>
<tr>
<td>( B )</td>
<td>Value of food items when food is intermittently scarce (set in units relative to ( B ))</td>
</tr>
<tr>
<td>( h )</td>
<td>Value of nonsecured food items (set at zero)</td>
</tr>
<tr>
<td>Fight costs:†</td>
<td>Cost of escalated fight (set comparatively to ( af ) and in units relative to ( B ))</td>
</tr>
<tr>
<td>( AF )</td>
<td>Cost of threat only (set comparatively to ( af ) and in units relative to ( B ))</td>
</tr>
<tr>
<td>( af )</td>
<td>Cost of retreating when threatened (set at zero)</td>
</tr>
<tr>
<td>( aF )</td>
<td>Punishment cost from dominant individuals to nonaggressive with large badge (set comparatively to ( af ) and in units relative to ( B ))</td>
</tr>
</tbody>
</table>

* As the food supply varies in reliability and abundance the relative value of a food item will fluctuate. This inequality is described by the variables \( B \) and \( Bn \). If \( Bn \approx B \) is large, then food availability is highly variable. A high value of \( Bn + B \) indicates low food availability.

† Individuals come into conflict when foraging. Aggression levels are variable and dependent on the fighting/foraging strategy employed and the present level of food abundance. All fight costs are measured in terms of the increase in cost experienced by fighting in comparison to simply withdrawing from the contest.

These strategies may be discrete with respect to individuals, or individuals may vary their tactics with time—in either case, freely or under phenotypic limitation (Maynard Smith and Parker 1976; Parker 1982).

Nomencature and Payoff Matrix

It is assumed that individuals interact in an infinite population and have fitness before contests \((W_0)\) of zero. Ecologically, in winter-flocking birds, the first assumption is validated by the large operational gene pool from which the small flocks are formed, which, in the absence of group selectionist arguments, gives freedom from the influences of drift and premature fixation in small populations, and the second assumption is valid because here we are interested in the effects of flocking behavior and thus hold preflocking fitness constant to allow a relative measure of fitness gains.

In generation \( n \), let \( p, q, r, \) and \( s \) be the frequencies of LA, SS, LS, and SA strategists, respectively, such that \( p + q + r + s = 1 \); let \( W(LA) \) be the fitness of LA strategists (with similar notation for other strategies); and let \( E(LA,SS) \) be the payoff to an individual adopting the LA strategy against an SS opponent (with similar notation for other pairwise interactions). Then

\[
W(LA) = pE(LA,LA) + qE(LA,SS) + rE(LA,LS) + sE(LA,SA)
\]

(with similar expressions for other strategists' fitnesses).

Individuals reproduce asexually in numbers proportional to their fitness. For example, the frequency, \( p' \), of LA strategists in generation \( n + 1 \) is

\[
p' = pW(LA)/W_T,
\]
TABLE 2

THE FOUR FIGHTING/FORAGING STRATEGIES USED IN THE MODIFIED BADGES-OF-STATUS MODEL

<table>
<thead>
<tr>
<th>Strategy</th>
<th>Description</th>
<th>Food Abundant (Value = B)</th>
<th>Food Intermediate (Value = Bn)</th>
</tr>
</thead>
<tbody>
<tr>
<td>LA</td>
<td>Aggressive to all individuals; if opponent does not retreat escalated fighting occurs (cost = AF); individuals with small badges that retreat are only threatened (cost = AF)</td>
<td>Wins 50% of fights (benefit = B/2) and all contests from which the opponent retreats (benefit = B)</td>
<td>Wins 50% of fights (benefit = Bn/2) and all contests from which the opponent retreats (benefit = Bn)</td>
</tr>
<tr>
<td>SS</td>
<td>Nonaggressive and retreats immediately if threatened or on encountering an individual with a large badge (cost = af)</td>
<td>Loses on retreat (benefit = 0) and wins 50% of contests against nonaggressive opponents (benefit = B/2)</td>
<td>Loses on retreat (benefit = 0) and wins 50% of contests against nonaggressive opponents (benefit = Bn/2)</td>
</tr>
<tr>
<td>SA</td>
<td>Variable fighting/foraging strategy with food abundance; submissive when food is abundant but becomes aggressive at intermediate food value</td>
<td>Nonaggressive and retreats if threatened or from any individual with a large badge (cost = af); loses on retreat (benefit = 0) and wins 50% of contests against nonaggressive opponents (benefit = B/2)</td>
<td>Aggressive toward all individuals, fighting with those that do not retreat (BA and SA) (cost = AF); wins 50% of fights (benefit = Bn/2) and all contests from which opponent retreats (benefit = Bn)</td>
</tr>
<tr>
<td>LS</td>
<td>Nonaggressive and retreats if threatened (cost = af); aggression from LA strategists persistent owing to LS's large badge (cost = af)</td>
<td>Loses on retreat (cost = af); wins all contests (benefit = B/2) from which opponent retreats owing to LS's large badge (SS and SA)</td>
<td>Loses on retreat (cost = af); wins all contests (benefit = Bn/2) from which opponent retreats owing to LS's large badge (SS)</td>
</tr>
</tbody>
</table>

Note.—When food is scarce all individuals act aggressively and escalated fighting occurs (cost = AF). Fighting ability is assumed to be equal, so all individuals win 50% of fights entered into. Thus the fitness payoffs for all four strategies are equal when food is scarce.

\[ W_t = pW(\text{LA}) + qW(\text{SS}) + rW(\text{LS}) + sW(\text{SA}) \]

(with similar expressions for the frequencies of other strategies in generation \( n + 1 \)).

From the model outlined in table 2 we can see that the relative fitness accrued by an individual's adoption of a strategy is dependent on the costs of fighting (table 1), the extent of variation in food abundance (table 1), and the relative frequency of other strategies encountered.

For comparison between strategies,

\[ \text{total } W(\text{LA}) = W(\text{LA}) \text{ when food is abundant} \]

\[ + W(\text{LA}) \text{ when food is intermediate} . \]
**TABLE 3**  
**Player’s Payoff Matrix for Modified Badges-of-Status Model**

<table>
<thead>
<tr>
<th>Payoff</th>
<th>Opponent Strategy</th>
<th>Food Abundant</th>
<th>Food Intermediate</th>
</tr>
</thead>
<tbody>
<tr>
<td>W(LA)</td>
<td>(AF + B/2)</td>
<td>(Af + B)</td>
<td>(AF + Bn/2)</td>
</tr>
<tr>
<td></td>
<td>1/2 win</td>
<td>Win</td>
<td>1/2 win</td>
</tr>
<tr>
<td>W(SS)</td>
<td>(af + b)</td>
<td>(af + B/2)</td>
<td>(Af + Bn)</td>
</tr>
<tr>
<td></td>
<td>Lose</td>
<td>1/2 win</td>
<td>(af + b)</td>
</tr>
<tr>
<td>W(SA)</td>
<td>(af + B/2)</td>
<td>(af + B/2)</td>
<td>(AF + Bn/2)</td>
</tr>
<tr>
<td></td>
<td>Lose</td>
<td>1/2 win</td>
<td>Lose</td>
</tr>
<tr>
<td>W(LS)</td>
<td>(af + B)</td>
<td>(af + B)</td>
<td>(af + Bn)</td>
</tr>
<tr>
<td></td>
<td>Lose</td>
<td>Win</td>
<td>Lose</td>
</tr>
</tbody>
</table>

**Note.**—No matrix is given for conditions when food is scarce, when all strategists are aggressive and their payoffs equal.
CHEATING AND THE BADGES-OF-STATUS MODEL

with similar expressions for other strategies, since \( W(LA) = W(SS) = W(LS) = W(SA) \) when food is scarce. Thus, a payoff matrix may be constructed (table 3).

**Observations on the Model**

*Establishment of an Honest, Stable Population State*

If only honest strategies (LA and SS; table 1) are introduced \( (p + q = 1, r = 0, s = 0) \), a stable population state (Maynard Smith 1982) is achieved \( (LA : SS = p : q) \), dependent on the ratio of fight costs to food values (table 1).

At equilibrium, that is, when \( W(LA) = W(SS) \),

\[
pE(LA,LA) + qE(LA,SS) = pE(SS,LA) + qE(SS,SS).
\]

The conditions required to satisfy this equation, by substituting payoff values from table 3, are calculated in Appendix A.

As predicted (Rohwer and Ewald 1981; Rohwer et al. 1981; Maynard Smith 1982; Järvi and Bakken 1984), in the absence of dishonest strategies, an honest, stable population state may occur, in which both aggressive and nonaggressive individuals gain equal payoffs \( (W(LA) = W(SS)) \).

The honest, stable state of a population is described by

\[
\frac{LA}{SS} = -1 \times \frac{4Af + (B + Bn)}{4AF + (B + Bn)}, \tag{1}
\]

where \( Af \) is the cost of displaying a threat only, and \( AF \) is the cost of an escalated fight.

If fighting is very costly with respect to the value of food items, subordinate individuals with small badges will predominate in the population because they do not waste resources fighting over abundant food. Alternatively, if food is valuable and fighting costs are relatively low, the aggressive strategy will become more abundant, since food items are worth fighting for. Hence the exact form of the population state achieved \( (LA : SS) \) is dependent on the relationship between the value of food \( (Bn; \text{fig. 1, top}) \) and the cost of fighting \( (AF; \text{fig. 1, bottom}) \).

*Invasion by a Cheat Mutant with a Dishonestly Large Badge (LS)*

If LS is to prove invasive, then \( W(LS) \geq W(LA) \) and/or \( W(LS) \geq W(SS) \). But at honest equilibrium, \( W(LA) = W(SS) \). For invasion by an LS strategist to succeed against an LA strategist, that is, if \( W(LS) \geq W(LA) \), it must be true that

\[
\]

Similarly, for invasion to succeed against an SS strategist, that is, if \( W(LS) \geq W(SS) \), it must be true that

\[
pE(LS,LA) + qE(LS,SS) + rE(LS,LS) \geq pE(SS,LA) + qE(SS,SS) + rE(SS,LS).
\]
Fig. 1.—Dependence of the ratio of LA to SS strategies in the population on food value and fight costs. Top, strategies as functions of the relative values of food items, $Bn$. Constants are $AF = -5$ and $Af = -1$. Bottom, strategies as functions of the cost of fighting, $AF$. Constants are $Bn = 7$ and $Af = -1.$
The conditions required to satisfy these inequalities, by substituting payoff values from table 3, are calculated in Appendix B.

Invasion by a large-badged, nonaggressive mutant (LS) occurs if punishment costs are low with respect to the benefits from winning contests against subordinates (fig. 2). Invasion by LS occurs when

\[-4AF \leq \frac{-(B + Bn) - (B + Bn)^2}{(B + Bn) + 4Af},\]

where $aF$ is the punishment cost to an LS mutant from dominant individuals.

Honest, stable population states may prove stable against the cheat mutant that forges a dishonestly large badge if the unit punishment costs ($aF$) are very high and/or the proportion of large-badged, aggressive strategists (LA) is high ($Bn$ is large and/or $AF$ is small), so that cumulative punishment costs during a feeding bout are prohibitively high.

Invasion by a Trojan-sparrow Mutant with a Dishonestly Small Badge (SA)

If SA is to prove invasive, then $W(SA) \geq W(LA)$ and/or $W(SA) \geq W(SS)$. But at honest equilibrium, $W(LA) = W(SS)$. For invasion by an SA strategist to succeed against an LA strategist, that is, if $W(SA) \geq W(LA)$, it must be true that

\[pE(SA,LA) + qE(SA,SS) + sE(SA,SA) \geq pE(LA,LA) + qE(LA,SS) + sE(LA,SA).\]

Similarly, for invasion to succeed against an SS strategist, that is, if $W(SA) \geq W(SS)$, it must be true that

\[pE(SA,LA) + qE(SA,SS) + rE(SA,SA) \geq pE(SS,LA) + qE(SS,SS) + rE(SS,SA).\]

The conditions required to satisfy these inequalities, by substituting payoff values from table 3, are calculated in Appendix C.

The most effective invasive mutant strategy tested is a small badge with aggression when food abundance is reduced. This Trojan-sparrow mutant always proves invasive when food value is variable ($Bn > B$).

Invasion by SA occurs when $Bn > 1$ (from eqqs. [C1], [C2]). When food is abundant ($Bn$ is low), the Trojan-sparrow strategy (SA) completely replaces the large-badged, aggressive strategy (LA) in the population and forms a new stable ratio with the small-badged, subordinate strategy (SS), which survives owing to the low incidence of aggression under such conditions (fig. 3, top). When food is scarcer ($Bn$ is high), the nonaggressive, subordinate strategy (SS) also declines to extinction owing to aggressive interference from the mutant, and the Trojan sparrow becomes a monostable strategy (fig. 3, bottom).

ECOLOGICAL CONSEQUENCES OF THE MODEL

The model indicates the stringent ecological conditions required for an honest, stable population state to be established. Food availability must be unpredictable.
Fig. 2.—Stability of honest population states (LA:SS) against invasion by the dishonest, cheat (LS) mutant when punishment costs are high (af is large) and/or ecological conditions cause LA:SS to be high (Bn is large and/or AF is small). Top. Bn = 14, AF = -7, AF = -1, af = -5 (high af, high percentage of LA). Bottom. Bn = 16, AF = -7, AF = -1, af = -4 (low af, high percentage of LA).
Fig. 3.—Instability of honest population states (LA : SS) against invasion by the dishonest, Trojan-sparrow (SA) mutant. Top, Bn = 9, AF = −5, Af = −1, unstable (stable SA : SS ratio achieved); bottom, Bn = 15, AF = −5, Af = −1, unstable (monostable SA ratio achieved).
and fight costs low. Potential for aggressive interactions is high, but the conflicts
are not of long-term detriment with respect to either time or physical damage.

From these predictions, a likely scenario emerges of individuals foraging in
a mixed flock (with respect to intraspecific plumage variation) for aggregated,
low-value, ephemerally distributed food items. Also, we may expect that aggres­sive individuals that advertise the trait do so with an easily recognized, unambigu­ous signal, thus reducing the cost of prolonged threat or misinterpretation.

Furthermore, given these ecological conditions, the conventional badges-of-
status model will not be evolutionarily stable, since it does not consider the full
strategy set (Grafen 1984). Honest population states may be stable against inva­sion by the otherwise invasive dishonest cheat strategy through social control of
deception via high cumulative punishment. However, unless badges are honest
and uncheatable, invasion by a dishonest Trojan-sparrow mutant is inevitable on
the introduction of such a strategy.

In the absence of honest constraints we have demonstrated that $W(LS) > W(LA)$ under all conditions, $W(LS) > W(SS)$ when resources are limiting, and
$W(LS) \geq W(SS)$ at all other times. Thus, when observing such a system at equilib­rium, we expect mixed fighting/foraging strategies, but strategy adoption will be
related to resource availability and not badge size. Dominance hierarchies will
therefore be correlated with true measures of RHP, individual recognition, or
higher aggression of Trojan sparrows relative to true subordinates. This form of
system is based on the conventional hawk-dove model (Maynard Smith and Price
1973; Maynard Smith 1982; but see also Maynard Smith and Harper 1988) and
does not require the assumptions regarding plumage form intrinsic to the SSH (J.
Maynard Smith, personal communication).

Evolutionary stability of status signaling can therefore be achieved only by
invoking one or more of the following conditions:

1. High cumulative punishment costs ($aF$) endow resistance against invasion
by a large-badged, nonaggressive mutant (LS). Social control of deception has
been demonstrated by Möller (1987a,b) in winter foraging flocks of the house spar­row Passer domesticus, although in Harris's sparrow, Zonotrichia querula,
(Rohwer and Rohwer 1978; Rohwer 1985) and the white-crowned sparrow, Zono­trichia leucophrys gambelii (Fugle and Rothstein 1987), experimental studies
have indicated that deception is possible and cheats prosper. This form of control
would not, however, confer resistance against the Trojan-sparrow strategy.

2. More complex social interactions than considered in this model cause it to
be advantageous for subordinates to display their dominance rank honestly.
Rohwer and Ewald (1981) described the "shepherd's hypothesis" in Harris's
sparrow, under which dominants guard a flock of subordinates against other domi­nant individuals in order to exploit the subordinates' food-finding abilities. Thus
the honest subordinates gain by reduced interference. In this situation, however,
and in a similar "producers and scroungers" effect described in the house spar­row (Barndard and Sibly 1981), dominants frequently displace subordinates from
food items and thus costs are also incurred through honesty, potentially making
dishonesty advantageous. Again, this mechanism provides no resistance against
the Trojan-sparrow mutant, which receives a high net benefit resulting from low
aggressive interference and high foraging efficiency.
3. Dominance and subordination represent alternative, but potentially equally successful lifetime strategies. High net benefits gained by dominants during one phase are balanced by net costs during another phase, which results in equal lifetime reproductive success of dominants and subordinates (Lyon and Montgomery 1986; Rohwer and Butcher 1988; Møller 1989). In the house sparrow, Møller found that males with large badges gained by holding better nest sites, by being preferred by females in mate-choice experiments, by apparently rearing more offspring (Møller 1988), by being more efficient mate guards (Møller 1987c), and by being more effective foragers in winter flocks (Møller 1987a, 1987b), but suffered increased autumn mortality due to predation (Møller 1989).

4. Røskåft et al. (1986) and Høgestad (1987) suggest that if the cost of dominance is in terms of raised metabolic rate, leading to greater nutritional requirements and/or shorter average life, the system may be resistant to cheats because poorer-quality birds cannot afford to raise their metabolic rate in order to become dominant. Trojan-sparrow strategists may, however, avoid some metabolic costs because of a reduced aggression level and therefore prove invasive if the costs of reduced aggression do not outweigh the benefits of dominance when the food supply is partially reduced.

Parasite resistance may form an alternative form of trade-off. Androgens associated with aggressive behavior and dominance are costly in terms of suppressed immune defense (Cohn 1979a, 1979b; Grossman 1985; Grossman and Roselle 1986; Alexander and Stimson 1988; Zuk 1990; I. Folstad and A. J. Karter, unpublished data). This relationship between hormones and immune defense may lead to both lifetime and within-season trade-offs. Individuals with inherently high testosterone levels may be susceptible to parasites per se, or testosterone level expressed within any phase may have to be balanced against present infestation level (I. Folstad and A. J. Karter, unpublished data). This argument and that of Røskåft et al. (1986), described above, form primary examples of the “handicap route” to honesty initially advocated by Zahavi (1975, 1977, 1987) and recently supported via ESS modeling by Grafen (1990).

5. A gene that contributes to the variable plumage character is in linkage disequilibrium with a gene that contributes to aggressive/dominant behavior. This might then bias the strategy set toward honest strategies. Such disequilibrium would, however, be expected to occur only as a consequence of genetic linkage between the traits, combined with natural selection (see conditions 1–3) against the recombinant dishonest phenotypes (Turner 1972; Hendrick et al. 1978; Manly 1985). As yet, there is no direct evidence for a genetic mechanism of linkage between dominance and plumage type in birds, although it has been well documented that testosterone and dark coloration are positively correlated (Keeler et al. 1968, 1970; Lofts et al. 1973; Møller 1988). A large body of data on the heritable basis of dominance and aggression also exists (Craik et al. 1965; Boag and Alway 1981; Boag 1982; Moss et al. 1982; Dewsbury 1990; Westman 1990), and again testosterone is indicated as a causal or proximate factor (Møller and Erritzøe 1988). Watt (1984), studying white-throated sparrows, Zonotrichia albicollis, found that spring plumage was more often correlated with fall dominance than was fall plumage, which suggests a genetic or causal relationship between dominance and plumage rather than a proximate (status-signaling) function.
6. Badge size and dominance behavior are pleiotropic effects of alleles at a single polymorphic locus. This could theoretically occur if the biochemical pathway determining the level of aggression were, at some stage, in quantitative series with the pathway controlling plumage form. The same gene product might, for example, be a precursor both for a plumage pigment and for a hormone involved in aggressive behavior. For example, a positive correlation has been found between dark pigmentation, aggressive behavior, and testosterone (Dorfman 1948; Zeller 1971; Moss et al. 1979; Stokkan 1979; Møller and Erritzøe 1988). Strategies might then be limited to the honest advertisement of aggression.

Only conditions 3, 4, 5, and 6 are therefore useful in supporting the evolutionary stability of the SSH. If badges of status are used as an assessment cue in aggressive pairwise encounters during foraging, these signals must be limited to honesty with respect to an individual's RHP. Honesty may arise either through trade-offs in lifetime reproductive success (condition 3), honest limitation through signals acting as "handicaps" (4), or genetic (5) or pleiotropic (6) phenotypic limitation. In the absence of such constraints the most successful strategy is for an individual to become aggressive only when resources are limited and avoid providing accurate information regarding aggressive intent to opponents prior to contests (see Enquist 1985). The work of Watt (1984, 1986b) may provide an interesting example of just such a Trojan-sparrow strategist, in which female white-throated sparrows have a small badge and low aggression until food becomes scarcer, when they become much more aggressive (D. Watt, personal communication).

ACKNOWLEDGMENTS

We thank T. A. Burke and I. G. Henderson for constructive discussion and comments throughout the work, D. B. A. Thompson, A. P. Møller, J. Maynard Smith, D. Watt, R. Sibly, W. Shields, D. G. C. Harper, and S. L. C. O'Malley for comments on an earlier draft of the manuscript, I. Folstad, K. Norris, and M. Zuk for discussion and access to unpublished manuscripts, and G. Parker for initial guiding comments. I. P. F. O. and I. R. H. are supported by studentships from the Natural Environmental Research Council/Nature Conservancy Council and the Science and Engineering Research Council, respectively.

APPENDIX A

Establishment of an Honest, Stable Population State

At equilibrium, that is, when \( W(LA) = W(SS) \),

\[
pE(LA,LA) + qE(LA,SS) = pE(SS,LA) + qE(SS,SS).
\]

Therefore (from table 3),

\[
p(AF + B/2 + AF + Bn/2) + q(AF + B + Af + Bn)
\]

\[= p(AF + B + Af + h) + q(AF + B/2 + Af + Bn/2).\]

But \( af = 0 \) and \( h = 0 \) (table 1). Therefore,

\[
p[2AF + (B + Bn)/2] = q[[(B + Bn)/2] - [2AF + (B + Bn)]]
\]

\[= -q[2AF + (B + Bn)/2].\]
Therefore,

\[
\frac{p}{q} = -1 \times \frac{2AF + (B + Bn)/2}{2AF + (B + Bn)/2}.
\]  

(A1)

Thus LA goes to fixation when \( AF \leq (B + Bn)/4 \), and SS goes to fixation when \( AF \geq (B + Bn)/4 \).

**APPENDIX B**

**INVASION BY A CHEAT MUTANT WITH A DISHONESTLY LARGE BADGE (LS)**

For invasion by an LS strategist to succeed against an LA strategist, that is, if \( W(\text{LS}) \geq W(\text{LA}) \), it must be true that

\[
pE(\text{LS, LA}) + qE(\text{LS, SS}) + rE(\text{LS, LS}) \geq pE(\text{LA, LA}) + qE(\text{LA, SS}) + rE(\text{LA, LS}).
\]

But at honest population-state equilibrium, \( r = 0 \). Therefore (from table 3),

\[
p(2AF) + q(B + Bn) \geq p[2AF + (B + Bn)/2] + q[2AF + (B + Bn)],
\]

which yields

\[
p[2AF - 2AF - (B + Bn)/2] \geq q(2AF).
\]

Thus, in an honest, stable population state (eq. (A1)),

\[
\frac{-2AF - (B + Bn/2)}{2(2AF - AF)} \geq \frac{2AF - (B + Bn)/2}{2AF + (B + Bn)/2}.
\]

which yields

\[
aF[(B + Bn) + 4AF] \geq \frac{(B + Bn)^2}{4} + AF(B + Bn).
\]

and finally

\[
-4AF \leq \frac{-4AF(B + Bn) - (B + Bn)^2}{(B + Bn) + 4AF}.
\]

Similarly, for invasion by an LS strategist to succeed against an SS strategist, that is, if \( W(\text{LS}) \geq W(\text{SS}) \), it must be true that

\[
pE(\text{LS, LA}) + qE(\text{LS, SS}) + rE(\text{LS, LS}) \geq pE(\text{SS, LA}) + qE(\text{SS, SS}) + rE(\text{SS, LS}).
\]

But at honest population-state equilibrium, \( r = 0 \). Therefore (from table 3),

\[
p(2AF) + q(B + Bn) \geq p[(B + Bn)/2].
\]

Thus, in an honest, stable population state (eq. (A1)),

\[
\frac{-2AF - (B + Bn)/2}{2(2AF - AF)} + \frac{2AF + (B + Bn)/2}{2(2AF - AF)} \geq 0,
\]

which yields

\[
aF[(B + Bn) + 4AF] \geq \frac{(B + Bn)^2}{4} + AF(B + Bn).
\]
This is a condition identical to that met when LS versus LA was considered.

Thus, when

$$-4aF \leq \frac{-4AF(B + Bn) - (B + Bn)^2}{(B + Bn) + 4Af}.$$  \hspace{1cm} (B1)

the dishonest, cheat strategy (LS) will prove invasive.

APPENDIX C

Invasion by a Trojan-Sparrow Mutant with a Dishonestly Small Badge (SA)

If SA is to prove invasive, then $W(SA) \geq W(LA)$ and/or $W(SA) \geq W(SS)$. But at honest equilibrium, $W(LA) = W(SS)$. For invasion by an SA strategist to succeed against an LA strategist, that is, if $W(SA) \geq W(LA)$, it must be true that

$$pE(SA,LA) + qE(SA,SS) + sE(SS,SA) \geq pE(LA,LA) + qE(LA,SS) + sE(LA,SA).$$

But at honest population-state equilibrium, $s = 0$. Therefore (from table 3),

$$p(AF + Bn/2) + q(AF + (B + Bn)/2) \geq p[2AF + (B + Bn)] + q[2AF + (B + Bn)].$$

Thus, in an honest, stable population state (eq. [A1]),

$$\frac{[AF - (B + Bn)/2](-AF - Bn/2)}{2(AF - Af)} \geq \frac{[AF + (B + Bn)/2](AF + Bn/2)}{2(AF - Af)},$$

or,

$$\frac{(AF - Af)(B + Bn)}{2B} \geq B(AF - Af).$$

If $B = 1$, then for invasion to succeed it must be true that

$$\frac{(B + Bn)}{2} \geq \frac{AF - Af}{AF - Af}.$$ \hspace{1cm} (C1)

This is true when $Bn \geq 1$.

Similarly, for invasion by an SA strategist to succeed against an SS strategist, that is, if $W(SA) \geq W(SS)$, it must be true that

$$pE(SA,LA) + qE(SA,SS) + rE(SS,SA) \geq pE(SS,LA) + qE(SS,SS) + rE(SS,SA).$$

But at honest population-state equilibrium, $s = 0$. Therefore (from table 3),

$$p(AF + Bn/2) + q(AF + (B + Bn) + Bn) \geq q[(B + Bn)/2].$$

Thus, in an honest, stable population state (eq. [A1]),

$$\frac{[-2AF - (B + Bn)/2](AF + Bn/2)}{2(AF - Af)} \geq \frac{[2AF + (B + Bn)/2](-AF - Bn/2)}{2(AF - Af)},$$

or,

$$Bn(AF - Af) \geq (AF - Af)[(B + Bn)/2].$$

For invasion to succeed it must be true that

$$Bn \geq \frac{(B + Bn)}{2}.$$ \hspace{1cm} (C2)

This condition is always met when $Bn \geq 1$.

Hence, the dishonest, Trojan-sparrow strategy (SA) will prove invasive when $Bn > 1$ ($B$ is unitary); this is true by definition when food availability is variable.
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